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CHAPTER 4

COMPARATIVE MORPHOMETRIC STUDY OF *A. planci* FROM THE WESTERN PACIFIC

4.1. **Introduction**

In marine zoological studies, morphometry is used to compare size in various body components and in individual development within populations and therefore, can show how individuals grow through the larval, juvenile and adult stages, achieve size, and body components develop in relation to each other over a range of habitats. Application of the SPBC method of age determination to *A. planci* is of primary interest in these analyses, for comparisons are made among individuals or populations in similar chronological and size-related stages of their life-cycle, assuming the SPBC method is widely applicable.

The failure to obtain consensus on the characteristics of *A. planci* has particularly limited our progress in understanding how outbreaks develop and what information modelling studies require to explain and predict fluctuations in populations in the GBR region (see Bradbury et al., 1985; Antonelli et al., 1990). Scandol (unpublished) concluded that more biological detail might enhance model credibility in the scientific community and introduced size-structuring to his population dynamics modelling work based on the age determination studies of Stump and Lucas (1990) and Stump (1993). Evidence for the validity of a novel method of determining age in *A. planci* from a population on Davies Reef, Central GBR (Stump, 1992; Chapter 2) and recognition of similar banding patterns in spine collections made from a number of populations from the Indo-Pacific region has led to more detailed comparative population studies than has been previously attempted. Novel studies on structured models of populations have the potential to gain useful insights into life history strategies of *A. planci* (Scandol, unpublished). Therefore, prior to implementation of large scale and time consuming validation studies, application of the age determination method to samples from populations in other regions is warranted if only as an exploratory tool.

Morphometric data obtained from five populations from Guam, Fiji and the GBR are discussed in this chapter while Chapter 5 has been devoted to a comparison of the reproductive characteristics among these populations with the underlying assumption of a trade-off between lifespan and reproductive patterns. Those life history aspects involved with age-specific fecundity will be dealt with in Chapter 5.

4.2. **Methods**

A study of morphometric relationships of estimated age and size, and their consequences in five *A. planci* populations was undertaken. The five populations were selected from three areas of the Pacific Region, Guam (North Western Pacific; 3 sites), Suva Reef (Central West Pacific), and Davies Reef (GBR, South Western Pacific). Primarily, the three areas were selected because they have a well documented history of repeated outbreak populations over at least the past 25 years. The most recent populations have developed under high coral cover (Davies Reef), and low coral cover (Suva Reef, Guam).

Linear regression analyses of populations using the relationships among morphometric variables, growth and lifespan were undertaken to assess variation in the life-history characteristics. The investigation used similar data to the variables used in the Davies Reef study (see Chapters 2 and 3), including skeletal ossicle morphometry, with the addition of madreporite ossicles and the third major ossicle from the oral group, the interbrachial. Both skeletal ossicle variables and measures of whole body size; whole wet weight, underwater weight, and whole body diameter, and estimated age were used to obtain comparative growth information in each population.

4.2.1. Description of regions and population histories

Locations of the 5 sampling sites and their locations in the Indo-Pacific Region are presented in Figure 4.1. Detail of the position of sites where collections were made are described by inset maps on Figure 4.1.

4.2.1.1. Davies Reef, Central GBR

See **Methods** section, Chapter 3.

4.2.1.2. Guam, USA

A rapid decline in hard corals was first reported along the north-west coast of Guam in 1967 by Chesher (1969b), where 90% of hard corals were killed along 38km of coastline by aggregations of *A. planci*. Since then, variable numbers of *A. planci* have been observed on these reefs and, apart from exposed shallow and lower intertidal areas, live coral cover has remained relatively low (C. Birkeland, personal communication). Therefore, recovery of coral communities on the north-western coast of Guam has not occurred since the 1960s.

4.2.1.3. Suva Reef, Fiji

Suva Reef is a part of a barrier chain of elongate coral reefs just off the windward south-eastern coast of the main island of Fiji, Viti Levu. It is an emergent reef where large areas behind the crest are exposed at low tides leaving much of the coral growth restricted to shallow pools. Back reef areas have been infilled with sandy sediment due to the proximity of the reef to large river discharges and seagrass beds merge with the reef approximately 300-500m behind the crest. A history of *A. planci* outbreaks in the Suva area was reconstructed by Zann et al. (1990). They estimated growth rates, mortality and longevity from two large cohorts which settled in 1984 and 1987. A mass recruitment was discovered in July, 1984 and was sampled monthly until major mortality occurred around December 1987. The second cohort settled in 1987 and was monitored until November 1989.

Between 1979 and 1989 the distribution and abundances of *A. planci* were quantified by Zann et al. (1990) using counts from walk transects at low tides along the reef crest and a permanent cross reef transect (ca. 100x900m) through an aggregation. Longevity in the population was estimated to be about 7-8 years from the pre-1984 outbreak population where the majority of *A. planci* were assumed to have recruited in 1977 (Zann et al. 1990).

4.2.2. Collection methods for each location

Methods of collection, holding and processing *A. planci* were adapted to suit the conditions and facilities for each location.

4.2.2.1. Davies Reef

As per Chapter 3.

4.2.2.2. Guam

Collections were made from 3 sites on the north-western fringing reefs of Guam between 30th June and 14th July, 1992. These were: Hospital Point, South Tumon Bay and Double Reef adjacent to Bare Ass Bay. Starfish were collected by snorkel and SCUBA, and held in bins aboard the University of Guam (UOG) dive tender. Outdoor concrete aquaria with continuous fresh running seawater at the UOG Marine Laboratory were used to maintain the starfish prior to dissection.

4.2.2.3. Suva Reef

Juveniles and adults were collected during walk/wade transects at daytime low tides between 19th and 26th October 1992. Juveniles were typically located on the reef crest-rubble zone in small pools or under coral rubble associated with feeding scars on small loose pieces of *Acropora sp.*. At low tide the crest was identified as a well defined narrow strip between the reef crest and the wide ponded area of the combined reef flat and back reef areas. The low density of *A. planci* was reflected by the small numbers obtained during each of the collecting trips lasting three to four hours each time.

A. planci collected in the field were transported by dinghy back to the Institute of Marine Research - University of the South Pacific (IMR/USP) and maintained in glass aerated aquaria.

4.2.3. Sample preparation

A representative collection of the six major skeletal ossicles and associated soft tissues were dissected from each starfish, labelled and immersed in formalin seawater for fixation to prevent decay during transportation. Walbran (1987) described the skeletal ossicles in *A. planci* and a similar terminology for ossicle types was used in this study. Selected ossicle variables for the morphometric study are: the oral ossicle group (primary orals, secondary orals and interbrachials), spine ossicles, whole spine (spine plus pedicel ossicle lengths) and madreporite ossicles.

Starfish from Guam and Fiji were air transported damp in sealed plastic "camper-cans" after tipping off the excess formalin and seawater mixture. The samples were placed in 1.0L pots and sodium hypochlorite solution (35%) was added to dissolve the soft tissues from the ossicles. The ossicles were then rinsed in tap water thoroughly and dried in an oven cabinet for 2-3 days at approximately 50°C. Ossicle collections were sorted and undamaged ossicles selected for the morphometric exercise. Mean lengths and weights of the ossicles were then recorded for each starfish.

4.2.4. Age determination and morphometry

Age of each starfish was determined from pigment band counts on spine ossicles under the assumption that the validity of the ageing method of Stump and Lucas (1990) was applicable to the Suva Reef and Guam populations.

Length of spine and pedicel ossicles were measured using vernier callipers (accurate to 0.1mm). All other ossicles were weighed using a Sartorius micro balance (accurate to 0.0001g). Mean lengths or weights were calculated from ca. 10 of each ossicle type for individual starfish. Mean primary and secondary oral, interbrachial and madreporite weights were adjusted according to the number of arms or number of madreporites which vary according to individual starfish. Ages were calculated to number of months by assuming larval settlement occurred in late December or early

January, and assuming the same length of time taken for the appearance of the first band in both Suva Reef and Davies Reef populations (reported for Central Section populations (Kettle, 1990). Both populations occur at a similar latitude. Guam spawning times are probably more variable. A narrow range in annual seawater temperature (Amesbury and Babin, 1990) may cause a protracted spawning season (see **Discussion** section on work by Cheney (1972b; 1974)) but is assumed to have occurred in April or May of each year.

4.2.5. Morphometric analyses

Although significant differences have been demonstrated between the pre-outbreak and post-outbreak groups on Davies Reef (Chapter 3), the analyses of morphometric variables used the combined data to compare whole populations. The pre- and post-outbreak groups from Davies Reef were separated in the final sections dealing with their life-history characteristics, where the groups were assumed to be separate populations on the basis that the cohorts in each group developed under different population densities and resource availability.

All tests are conducted with a significance level of $\alpha = 0.01$ unless otherwise stated. A summary of the steps involved in the statistical analyses procedure is:

1. Plots of percentage frequency distributions were compared for all variables between 5 populations from Guam (Hospital Point, South Tumon Bay and Double Reef); Suva and Davies Reef populations. Population frequency distributions of variables were checked for violation of the assumptions of parametric ANOVA. If so they were then grouped using the results of Kruskal-Wallis non-parametric ANOVA and the non-parametric "Tukey-type" test for multiple comparison of mean ranks.

2. An investigation of the extent of sexual dimorphism in morphometric variables other than gonad weight (see Chapter 5 for gonad morphometry). The analyses used to test for differences between sexes were: (a) tests for the significance of

differences between individual variables due to sex (using the two sample t-test and results were compared with results from the Mann-Whitney U test when violations of assumptions were found and; (b) regression analyses to determine the significance of differences due to sex, where the dependent variables were adjusted for body size (whole body diameter, underwater weight and whole wet weight).

3. Plots of allometric relationships of all variables and whole body size relationships in populations were tested for significance and comparison of values of the exponent in the power equation. Replication tests-of-fit were used to assess for linearity and minimal linear regression models were constructed using backward elimination to test for the significance of differences between populations.

4. Analyses of the relationships between morphometric variables and estimated age grouped by adult (omitting all sub-adult starfish i.e. < 3 years) to assess growth rates of all morphometric variables following maturity. The standard error of estimate (standardised to compare populations) was used as an index of predictive accuracy between populations (Dapson, 1980) under the assumption that the SPBC is valid in all populations.

5. Analyses of factors involved in determining size in all skeletal morphometric variables by developing parsimonious models using multiple linear regression analyses. Models were selected by parsimony where no significant difference in the relationships were determined from the $\mathbf{F_{(ratio)}}$ statistic calculated from the full model containing all possible variables compared with the final minimal model.

$$\mathbf{F_{(ratio)}} = \frac{\dfrac{\mathbf{RSS_{(h)} - RSS_{(l)}}}{\mathbf{k_{(h)} - k_{(l)}}}}{\mathbf{MSE_{(h)}}} \qquad (4.1)$$

where RSS = residual sums of squares ((h) higher model; (l) lower model)
k = number of variables
MSE = mean squared error

Models are built by selecting from a range of possible explanatory variables, testing their significance and contribution to trends in standardised residual plot analyses (when $P < 0.01$ the variables are retained in final minimal model).

4.3. **Results**

4.3.1. Populations and habitats

4.3.1.1. Davies Reef

Davies Reef had the highest starfish density and population size for all populations sampled in this study. Large *A. planci* aggregations were observed in the north and south-eastern areas along the perimeter of the reef during the field collections. Collecting efficiencies (CE) were estimated to range from aggregations yielding 50 starfish.person^{-1}.hr^{-1} in 1988-89 to less than five starfish.person.hr^{-1} in late 1991 (Chapter 3) where the population was generally dispersed and cryptic. Visually estimated, coral cover decreased dramatically in 1988-89 (see Chapter 3); however, pockets of unexploited coral cover remained throughout the study, particularly in the lagoon areas.

4.3.1.2. Guam

Coral cover in the three areas in which specimens of *A. planci* were collected around Guam in July 1992 was generally poor. This was particularly noted in the Hospital Point and South Tumon Bay areas where *A. planci* feeding scars were observed on *Porites* sp. which, according to Keesing (1990) is not a preferred food species of *A. planci*.

Hospital Point: A shallow, narrow-margin fringing reef dropping off to ~ 20m depth. Collecting was undertaken by manta tow snorkelling and SCUBA. The lowest density of starfish found in the Guam study, CE was estimated at < five starfish.person^{-1}.hr^{-1}. Coral cover was very low in a habitat dominated by rubble and sand. Starfish were generally dispersed but not cryptic, due to the lack of reef structure and nooks to hide.

South Tumon Bay: A shallow broad-margin fringing reef, located close to Hospital Point. Collecting was undertaken by manta tow snorkelling and with SCUBA. CE was estimated at ~ five starfish.person^{-1}.hr^{-1}. Live coral was dominated by *Porites* sp. and numerous small (< 0.5m) diameter colonies with associated common coral communities. Similar starfish habitat to Hospital Point.

Double Reef: A small barrier reef (approximately 500m in length) sheltering a narrow lagoon and shoreward fringing reef on the north side of a narrow bay (Bare Ass Bay). Collecting took place over both reefs including the bay by snorkelling and with SCUBA. CE was estimated at ~ 10 starfish.person^{-1}.hr^{-1}. Habitat was structurally more complex than Hospital Point or South Tumon Bay. Generally corals were more abundant including several acroporid species and were supporting a higher density of *A. planci* than the other Guam sites.

4.3.1.3. Suva Reef

A large elongate barrier reef with dispersed *A. planci* located at the base of shrubby acroporid corals and around the edges of small pools. Collections were undertaken on foot at low tide from the reef front. CE was estimated at ~ five starfish.person^{-1}.hr^{-1} and higher for juveniles from specific areas just behind the reef crest. Most starfish were dispersed but generally cryptic due to the emergence of the reef at low tide. The highest densities of *A. planci* were juveniles (< 0.01m^{-2}) using counts found in the rubble zone behind the reef crest in the central area of the reef off the Nasese district. Densities of juveniles in the areas where they were found were estimated to be < 0.2m^{-2}. Counts of scars were ca. 2 - 5 times the number of starfish located in each area and therefore densities may have been underestimated to some extent. Densities of this order were categorised as small recruitment events according to Zann et al. (1990: Table 2) and as these juveniles grow and become more mobile the densities will decrease further. Most adults obtained in the population subsampling exercise were obtained in the north-western area and in the ponded back-reef areas at varying distances from the reef crest.

4.3.2. Frequency distribution analyses

Three of the five population samples contained both juvenile and adult *A. planci*: Davies Reef (GBR), Double Reef (Guam) and Suva Reef (Fiji) and therefore the ranges of body size in these populations extended in the smaller size range (approximately < 15cm). Histograms describing the size frequency distributions of morphometric characteristics are presented in Figures (4.2 to 4.12).

(4.2) whole body diameter (BD)
(4.3) underwater weight (UW)
(4.4) whole wet weight (WET)
(4.5) spine ossicle length (S)
(4.6) whole spine appendage length (WS)
(4.7) spine pigment band count (SPB)
(4.8) estimated age classes (AGE)
(4.9) primary oral ossicle weight (adjusted for number of arms) (POA)
(4.10) secondary oral ossicle weight (adjusted for number of arms) (SOA)
(4.11) inter-brachial ossicle weight (adjusted for number of arms) (IBA)
(4.12) madreporite weight (adjusted for number of madreporites) (MA).

The internal ossicles from the oral group (primary oral, secondary oral and interbrachial) were adjusted for the number of arms in each individual (where there are two primary oral and secondary oral ossicles per arm and one interbrachial ossicle per arm) following preliminary ANOVA tests which showed significant differences in arm number among the populations. Starfish in the Davies Reef pre-outbreak population had significantly greater numbers of arms than individuals in the Hospital Point and Suva Reef populations (ANOVA: $F = 7.90$; $P < 0.01$; $n = 412$; $P_B = 0.001$

for Bartlett's test of equal variances; Tukey (HSD) DA (PRE) > HP and SU; DA (PRE) ≈ DA (PST) ≈ ST ≈ DO; and SU ≈ HP ≈ DA (PST) ≈ DO ≈ ST). Similarly the madreporite ossicle weight was also adjusted for the total number of madreporites on each individual following the preliminary analyses demonstrated significant differences among the populations. Davies Reef outbreak population starfish (mean = 8.2 madreporites) had significantly greater numbers of madreporites than individuals from Hospital Point (mean = 6.8 madreporites) (ANOVA: $F = 2.89$; $P = 0.01$; $n = 253$; $P_B = 0.01$; Tukey (HSD) DA (PST) > HP; DA (PST) ≈ ST ≈ DA (PRE) ≈ SU ≈ DO; and HP ≈ DO ≈ SU ≈ DA (PRE) ≈ ST).

Frequency distribution of morphometric variables for individuals with estimated age ≥ 3 years were reanalysed in order to compare size frequency distributions from adult populations (Appendix 1). The Davies Reef population contained much larger adult individuals with greater body weights compared with the other populations in the study (Table 4.2). At comparable body size determined by whole body diameter (BD), individuals from the Davies Reef population were much heavier than those from Guam, i.e., there was less overlap in the size frequency distributions for whole wet weight (WET) than for whole body diameter (BD).

Table 4.1. Ranked *A. planci* population characteristics according to mean adult body diameter (MA(BD)) in five populations from the Western Pacific region.

Reef	(BD)	(UW)	(WET)	EL (years)	(n)	*A. planci* density	Coral cover
DA	39.5	106	2167	9+	211	high	high
DO	29.2	54	1078	6+	36	low	low
SU	27.1	41	725	6+	56	low	low
ST	26.8	45	746	5+	40	low	low
HP	23.5	28	484	5+	40	low	low

where units = (BD) cm; (UW) g; (WET) g

EL = estimated longevity (determined from highest SPBC in each population sample)

DA = Davies Reef, GBR

HP = Hospital Point, Guam

ST = South Tumon Bay, Guam
DO = Double Reef, Guam
SU = Suva Reef, Fiji

There were significant differences in variances among the variables (where $P_B < 0.01$ for Bartlett's test of equal variances). Standardised residual plots for the analyses of the five populations show the relatively large variances in the Davies Reef population samples (Figures 13a-i), and the sample sizes are correlated with the size of variances. Therefore, under these conditions the probability of a Type I (α) error (rejection of a null hypothesis when it is true) is $\alpha < 0.01$ and results with small levels of significance are not dependable (Zar, 1984). Therefore, the Kruskal-Wallis non-parametric analysis of variance was used to determine the significance of differences between distributions of variables among populations. Significant results were then further investigated using non-parametric Tukey-type multiple comparisons for unequal sample sizes (Zar, 1984). Full results of Bartlett's tests, Kruskal-Wallis AOV and Tukey-type multiple comparisons of variables in the five populations are presented in Appendix 4.1 and summarised in Table 4.2.

Table 4.2. Summary of non parametric size frequency analyses (Appendix 4.1) to group five *A. planci* populations from the Western Pacific region using ANOVA where no significant differences were found among the frequency distributions in each of the morphometric variables.

Region	Grouped Populations	Variables grouped
Guam	HP, ST	(BD) (UW) (WET) (POA) (SOA) (MA)
Guam	HP, ST, DO	(BD)
Fiji	SU	nil.
GBR	DA	(BD) (UW) (WET) (S) (WS) (POA) (SOA) (IBA)
Guam/Fiji	HP, ST, DO, SU	S, WS
Fiji/GBR	SU, DA	MA
Guam/GBR	nil.	nil.

Size frequency distributions for Guam and Suva Reef populations using all morphometric variables except adjusted madreporite weight (MA) were significantly different to the Davies Reef population distributions. The South Tumon Bay and Hospital Point populations had similar distributions in all variables except for inter-brachial ossicles (IBA). Size frequency distributions were similar in the Guam and Suva Reef populations for spine ossicle and whole spine appendage length. Overall the populations in Guam and Fiji developed similar size frequency distributions of morphometric variables and these were lower in range than those developed from the Davies Reef samples.

4.3.3. Sexual dimorphism

The analyses of whole wet weight between sexes in the Davies Reef population was the only variable to show significant sexual dimorphism (where females were larger than males) in the five populations (t-test; $t = 0.94$, $P < 0.01$; Appendix 4.3A). Whole body variables (whole body diameter (BD), underwater weight (UW) and whole wet weight (WET)) were regressed against all skeletal ossicle variables using log-normal transformations after standardised residual plots (standardised for the standard error of the residual) demonstrated heteroscedasticity in the plotted distributions indicating that a log transform function should be used for initial analyses (see section on multiple regression models for detailed analyses of potential dependent variables used to determine skeletal ossicle size).

The significance of differences in slope and elevation of regressions for each sex are presented in Appendix 4.3B. There were weakly non significant differences in all the morphometric variables. Sexual dimorphism in the regression analyses for all variables was found to be non-significant. The regression equations and statistics pertaining to estimation of sex differences are presented in Appendix 4.3B.

4.3.4. Allometry of body size and skeletal ossicles

To compare morphological variability the relationships between skeletal variables and whole body size were determined using the general allometric equation (4.2). Exploratory analyses of the dependence of variations in skeletal morphometric variables on body size ((BD), (UW) and (WET)) were undertaken by comparing the relationships using the allometric power equation in the form;

$$y = b \,.\, X^{a} \qquad (4.2)$$

A summary of the exponent **a**, coefficient of determination (**r^2**) and sample size for allometric relationships between skeletal variables and whole body size ((BD), (UW) and (WET)) is presented in Table 4.3. The allometric relationships between the six skeletal ossicle variables and whole body size for male and female starfish in each population are presented in Figures 4.14 (BD), 4.15 (UW), and 4.16 (WET). A summary of allometric exponents for whole body size relationships ((BD), (UW) (WET)) for 5 populations is presented in Table 4.4. The replication test-of-fit analyses were summarised for all age groups (summary in Table 4.6a from results presented in Appendix 4.4a) and for all starfish where sex was determined, i.e. omitting all starfish which had not reached full sexual maturity or where sex had not been determined (Table 4.6b from results in Appendix 4.4b)

Table 4.3a, b, c. Allometric power coefficients for five *A. planci* populations from the Western Pacific region derived from analyses between skeletal ossicle variables and whole body size variables (BD, WET, UW).

Reef	Davies Reef	Hospital Pt.	Sth. Tumon	Double Reef	Suva Reef
(a) Independent (BD)					
Dependent	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n
(UW)	1.87;0.58;92	2.57;0.72;40	2.56;0.67;40	2.73;0.91;40	2.27;0.84;56
(WET)	2.43;0.79;211	2.50;0.72;40	2.95;0.66;40	2.22;0.73;40	2.90;0.92;56
(S)	0.25;0.05;194	NS;n=40	NS;n=40	NS; n=40	1.00;0.75;56
(WS)	0.34;0.07;168	NS;n=40	NS;n=40	NS; n=40	1.18;0.77;56
(POA)	1.42;0.42;60	1.54;0.38;40	1.63;0.47;40	2.35;0.76;40	2.47;0.85;56
(SOA)	1.44;0.42;64	1.61;0.35;40	1.67;0.38;40	2.37;0.76;40	2.37;0.86;56
(IBA)	1.41;0.34;59	1.65;0.39;40	1.72;0.37;40	2.26;0.72;40	2.42;0.90;54
(MA)	2.03;0.20;35	1.33;0.09;40	2.31;0.34;40	2.12;0.43;40	2.28;0.63;54
(b) Independent = (UW)					
Dependent;	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n	**a; r^2**; n
(BD)	0.31;0.58;92	0.28;0.72;40	0.26;0.67;40	0.33;0.91;40	0.37;0.84;56
(WET)	0.94;0.67;92	0.92;0.90;40	1.07;0.85;40	1.09;0.93;40	1.14;0.87;56
(S)	0.19;0.13;91	NS;n=40	NS;n=40	0.26;0.37;40	0.39;0.72;56
(WS)	0.21;0.12;90	NS;n=40	NS;n=40	0.31;0.40;40	0.46;0.72;56
(POA)	0.62;0.63;36	0.67;0.66;40	0.70;0.83;40	0.92;0.93;40	1.01;0.88;56
(SOA)	1.03;0.77;36	0.65;0.52;40	0.78;0.72;40	0.93;0.94;40	0.97;0.87;56
(IBA)	0.72;0.62;36	0.65;0.57;40	0.76;0.69;40	0.84;0.80;40	0.98;0.88;56
(MA)	0.91;0.32;36	0.76;0.25;40	0.85;0.45;40	0.89;0.64;40	0.94;0.65;56

(c) Independent = (WET)

Dependent;	a; r^2; n	a; r^2; n	a; r^2; n	a; r^2; n	a; r^2; n
(BD)	0.32;0.78;211	0.29;0.72;40	0.22;0.66;40	0.29;0.87;40	0.32;0.92;56
(UW)	0.71;0.67;92	0.98;0.90;40	0.79;0.85;40	0.85;0.93;40	0.77;0.87;56
(S)	0.08;0.04;194	NS;n=40	NS;n=40	0.25;0.59;40	0.33;0.77;56
(WS)	0.10;0.04;168	NS;n=40	NS;n=40	0.30;0.49;40	0.40;0.77;56
(POA)	0.55;0.44;60	0.68;0.64;40	0.54;0.68;40	0.77;0.86;40	0.84;0.89;56
(SOA)	0.45;0.30;64	0.67;0.52;40	0.58;0.60;40	0.77;0.85;40	0.80;0.88;56
(IBA)	0.45;0.30;59	0.63;0.50;40	0.61;0.62;40	0.74;0.80;40	0.87;0.91;54
(MA)	0.79;0.21;35	0.84;0.29;40	0.70;0.41;40	0.66;0.44;40	0.77;0.63;54

where **a** > 1 demonstrates an exponential accelerating increase in y, i.e. there are relative growth increases in the dependent variable compared with the independent variable

a ≈ 1 demonstrates an isometric relationship between x and y, i.e. similar relative growth between the dependent and independent variables

a < 1 demonstrates a decelerating increase in y, i.e. relative growth increases in the independent variable compared with the dependent variables.

There were significant positive relationships with the three whole body size variables for all variables except spine ossicle length (S) and whole spine length (WS) in all populations.

Table 4.4. Five *A. planci* populations from the Western Pacific region ranked using the size of exponents from the power equation ($\mathbf{y} = \mathbf{b} \cdot \mathbf{X}^{\mathbf{a}}$) for three variables measuring whole body size (UW, WET and BD).

Rank	(UW) v. (BD)		(WET) v. (BD)		(WET) v. (UW)	
1	Guam	DO; 2.73	Guam	ST; 2.95	Guam	HP; 0.98
2	Guam	HP; 2.57	Fiji	SU; 2.89	Guam	DO; 0.85
3	Guam	ST; 2.56	Guam	HP; 2.50	Guam	ST; 0.79
4	Fiji	SU; 2.27	GBR	DA; 2.43	Fiji	SU; 0.77
5	GBR	DA; 1.87	Guam	DO; 2.22	GBR	DA; 0.71

Guam populations generally had greater exponent values for whole body size analyses using underwater weight (UW) (Figures 4.14 and 4.15). Generally, underwater weight increased at a faster rate in the Guam populations than either whole wet weight or whole body diameter compared with the rates obtained from individuals from Suva Reef or Davies Reef (see also Section 4.6, linear regression analyses).

4.3.5. Influence of estimated age on population morphometry

The analyses of variables with estimated age were first tested for linearity using the Replication Test-Of-Fit (RTOF) for all morphometric relationships by comparing the performance of least squares linear regression analysis with ANOVA tests (Appendix 4.4A, all cases; and Appendix 4.4B, omitting starfish where sex was not determined). The test was conducted to determine the suitability of the use of linear regression analyses. The test for linearity hypothesis is stated as $\boldsymbol{H_0}$ for the RTOF: where there is a linear trend in the regression analysis of the dependent variable and estimated age.

Tables 4.5a and 4.5b summarise the results from tests of assumptions for parametric analyses used Bartlett's test for equal variances between age groups; where; H_0 = the variances of the dependent variable is not significantly different between age groups. Full results of analyses are presented in Appendix 4.4.

Table 4.5a. Summary of Bartlett's test of equal variances between estimated age classes in five *A. planci* populations from the Western Pacific region (including all age classes); where H_0 = there is no significant difference in variances of the variable between estimated age groups.

Variable	Davies Reef	Hospital Pt.	Sth. Tumon	Double Reef	Suva Reef
(BD)	0.99 acptH_0	NA	0.76 acptH_0	0.94 acptH_0	0.96 acptH_0
(UW)	0.68 acptH_0	0.31 acptH_0	0.41 acptH_0	0.17 acptH_0	< 0.01; No
(WET)	0.78 acptH_0	0.47 acptH_0	0.31 acptH_0	0.23 acptH_0	< 0.01; No
(S)	0.92 acptH_0	0.43 acptH_0	0.89 acptH_0	0.08 acptH_0	0.09 acptH_0
(WS)	0.86 acptH_0	0.04 acptH_0	0.21 acptH_0	0.13 acptH_0	0.24 acptH_0
(POA)	0.66 acptH_0	0.91 acptH_0	0.70 acptH_0	0.56 acptH_0	< 0.01; No
(SOA)	0.06 acptH_0	0.97 acptH_0	0.72 acptH_0	0.53 acptH_0	< 0.01; No
(IBA)	0.67 acptH_0	0.84 acptH_0	0.22 acptH_0	0.58 acptH_0	< 0.01; No
(MA)	< 0.01; No	0.26 acptH_0	0.49 acptH_0	0.37 acptH_0	0.27 acptH_0

where NA = not tested due to at least one sample size in the estimated age class being too small to obtain variance estimates.

acptH_0 = accept the hypothesis of H_0

Table 4.5b. Summary of Bartlett's test of equal variances between estimated age classes in five *A. planci* populations from the Western Pacific region, omitting starfish which were not sexed; H_0 = there was no significant difference in variances of the variable between estimated age groups (i.e. $P > 0.01$). Where: NA = not tested due to single value for one age class.

Variable	Davies Reef	Hospital Pt.	Sth. Tumon	Double Reef	Suva Reef
(BD)	0.82 acptH_0	NA	0.76 acptH_0	0.88 acptH_0	0.96 acptH_0
(UW)	0.99 acptH_0	0.31 acptH_0	0.41 acptH_0	0.36 acptH_0	0.15 acptH_0
(WET)	0.50 acptH_0	0.47 acptH_0	0.31 acptH_0	0.77 acptH_0	0.01 acptH_0
(S)	0.83 acptH_0	0.43 acptH_0	0.89 acptH_0	0.12 acptH_0	0.12 acptH_0
(WS)	0.79 acptH_0	0.04 acptH_0	0.21 acptH_0	0.18 acptH_0	0.23 acptH_0
(POA)	0.20 acptH_0	0.91 acptH_0	0.70 acptH_0	0.99 acptH_0	0.24 acptH_0
(SOA)	0.06 acptH_0	0.97 acptH_0	0.72 acptH_0	0.97 acptH_0	0.24 acptH_0
(IBA)	0.67 acptH_0	0.84 acptH_0	0.22 acptH_0	0.91 acptH_0	0.29 acptH_0
(MA)	0.56 acptH_0	0.26 acptH_0	0.49 acptH_0	0.56 acptH_0	0.16 acptH_0

Table 4.6a. Summary of results of the replication tests-of-fit analyses (P_{RTOF}) for all age groups in five *A. planci* populations from the Western Pacific region. Full results are presented in Appendix 4.3A. H_0 = there was a linear trend with estimated age.

	Davies Reef	Hospital Pt.	Sth. Tumon	Double Reef	Suva Reef
	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$
(BD)	>0.25 acptH_0	>0.05 acptH_0	=0.25 acptH_0	< 0.01 No	< 0.01 No
(UW)	>0.10 acptH_0	>0.05 acptH_0	>0.25 acptH_0	< 0.01 No	>0.01 acptH_0
(WET)	>0.25 acptH_0	>0.10 acptH_0	>0.25 acptH_0	< 0.01 No	>0.10 acptH_0
(S)	< 0.01 No	>0.25 acptH_0	>0.25 acptH_0	< 0.01 No	< 0.01 No
(WS)	>0.01 acptH_0	>0.25 acptH_0	>0.25 acptH_0	< 0.01 No	< 0.01 No
(POA)	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	< 0.01 No	< 0.01 No
(SOA)	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	< 0.01 No	< 0.01 No
(IBA)	>0.25 acptH_0	>0.10 acptH_0	>0.25 acptH_0	< 0.01 No	< 0.01 No
(MA)	>0.25 No	>0.25 acptH_0	>0.25 acptH_0	>0.10 acptH_0	>0.05 acptH_0

Table 4.6b. Summary of results of the replication tests-of-fit analyses (P_{RTOF}) in five *A. planci* populations from the Western Pacific region, omitting starfish which were not sexed. Full results are presented in Appendix 4.4B. H_0 = there was a linear trend with estimated age.

	Davies Reef	Hospital Pt.	Sth. Tumon	Double Reef	Suva Reef
	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$	$P_{(RTOF)}$
(BD)	>0.25 acptH_0	>0.05 acptH_0	=0.25 acptH_0	>0.25 acptH_0	>0.01 acptH_0
(UW)	>0.25 acptH_0	>0.05 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0
(WET)	>0.25 acptH_0	>0.10 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.10 acptH_0
(S)	< 0.01 No*	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	< 0.01 acptH_0*
(WS)	>0.02 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.02 acptH_0
(POA)	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.01 acptH_0
(SOA)	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.10 acptH_0	≈0.01 acptH_0
(IBA)	>0.25 acptH_0	>0.10 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.02 acptH_0
(MA)	< 0.01 No	>0.25 acptH_0	>0.25 acptH_0	>0.25 acptH_0	>0.05 acptH_0

test rerun using 2nd order polynomial regression, where; $S_{(poly.)}$= >0.25 0 acptH_0

Many of the relationships between the variables and estimated age were found to be not linear for samples using all age groups (Table 4.6a; Figure 17). By omitting starfish < 3 years, i.e., individuals which had not achieved full sexual maturity, the RTOF tests showed that the hypothesis of linearity was accepted in all the variables except madreporite weight and spine ossicle length. Further analysis of spine ossicle length in the Davies Reef population involved using a 2nd order polynomial equation into the analysis (Table 4.6b). This showed there was an attenuation in spine growth over the range of adult age classes. While pigment bands continue to develop with age, a pattern of attenuating growth of spine ossicles in the population samples showed there is a maximum estimated longevity in those starfish (see Chapter 3). Further transformations of the madreporite weight data from the Davies Reef sample proved unsuccessful and there was no linear trend with estimated age (Table 4.5b; Figure 4.18).

The relationships between estimated age and morphometric variables with standard errors (SE) for combined sexes are plotted in Figures 4.17a. to h. In all variables there was a rapid growth phase up to 3+ years and variable tapering of rates thereafter. Figures 18a. to h. present the changes in morphometric variables with SE for age > 3 years. Of all the variables tested, only spine ossicle length and whole spine length were consistent with significant changes in size at estimated age after full sexual maturity. Appendix 4.5 shows the comparison of significance in the rates of change between the variables and estimated age using the standardised standard error of estimate (SSEE) to compare population samples. In accord with the prior distinction made between adult and juvenile growth phases, tests were conducted on population samples divided into 2 groups; the juvenile/young adult phase (< 4 years) and the adult phase (> 3 years), the overlap allowing for more data points to be analysed within both groups. By ranking mean values of the standard error of estimate for the five populations, the variable which consistently best described changes in estimated age is spine ossicle length (Appendix 4.4).

Table 4.7. Ranked mean standard error of estimates for each morphometric variable for five *A. planci* populations from the Western Pacific region.

Combined $(S_{Y.X}/Y_{(mean)})$ = **(S) > (WS) > (BD) > (PO) > (UW) > (SO) > (IB) > (WET) > (MA)**

where $S_{Y.X}/Y_{(mean)}$ = (standard error of estimate) / ($Y_{(mean)}$) used to compare the accuracy with which the regression can predict the dependence of Y on X).

4.3.6. Adult population morphometric relationships

Population morphometric analyses were carried out using whole body size and skeletal ossicle variables from the five populations. For population analyses the data included all fully mature individuals (> 3 years estimated age) to compare differences among adult individuals. Models were developed by backward elimination of variables using least squares linear regression analyses.

4.3.6.1. Underwater weight and whole body diameter

An heteroscedastic trend found in preliminary standardised residuals suggested the data be transformed by natural logs for the regression analyses of underwater weight and whole body diameter. The residual plot for the final model selected from the analyses of underwater weight and whole body diameter demonstrated no apparent trend (Figure 19a). Thus the model is a reasonable description of the data (Figure 19b).

minimal model

Dependent Variable = ln (UW)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-3.5079	0.1958	-17.92	< 0.01
ln (BD)	2.2200	0.0552	40.21	< 0.01
$(HP)_{elev.}$	-0.1645	0.0362	-4.55	< 0.01

AOV of regression model

	SS	df	MS	$F_{(ratio)}$	**P**
model	82.1204	2	41.0602	1406.2	< 0.01
error	7.6208	261	0.0292		
total	89.7413	263			

model $\ln(UW) = \ln(BD) - (HP)_{elev.}$

$r^2 = 0.92$; $n = 264$; $P < 0.01$; $MSE = 0.0292$

$F_{(ratio)} = 1.27 < F_{(\alpha 1;0.01;7,257)} \approx 2.70$; $0.25<P<0.10$

Therefore, analyses formed two significantly different groups from the five populations. In all the populations except for Hospital Point there was a similar relationship for underwater weight over the ranges of whole body diameter assessed.

Group	Regression equation	Regression analvses
HP	$\ln(UW) = (2.5727 \times \ln(BD)) - 4.7860$	$r^2 = 0.72$; $n = 40$; $P < 0.01$; MSE = 0.0263
ST DO SU DA	$\ln(UW) = (2.2051 \times \ln(BD)) - 3.4553$	$r^2 = 0.87$; $n = 224$; $P < 0.01$; MSE = 0.0296

The differences in slope coefficients were determined using the students t test to assess if relationships were different from the hypothetical isometric relationship where underwater weight decreases relative to (whole body diameter)^3. The hypothesis tested by the t test is H_0 = the slope of the regression was not different from isometry.

Guam (HP)	$t_{statistic} = 1.64 > t_{(0.01(1)222)} \approx 2.341$	$P < 0.01$
Guam (ST, DO), SU and DA	$t_{statistic} = 14.01 < t_{(0.01(1)38)} = 2.429$	$0.1 > P > 0.05$

Therefore, there was a significant difference between the allometric coefficients for the combined relationship between underwater weight and whole body diameter for ST, DO, SU and DA (exponent = 2.205) and the hypothetical relationship using the isometric coefficient (3). The coefficient of the relationship for HP (2.573) was not significantly different from isometry, although the range of values was relatively low.

4.3.6.2. Whole wet weight and whole body diameter

An heteroscedastic trend found in preliminary standardised residuals suggested that data be transformed by natural logs for the regression analyses of whole wet weight and whole body diameter. The residual plot for the final model selected showed no apparent trend (Figure 20a) and therefore, is a reasonable description of the data (Figure 20b).

Dependent Variable = ln (WET)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-1.4721	0.2334	-6.31	< 0.01
ln (BD)	2.4238	0.0735	32.96	< 0.01
$(SU)_{elev.}$	0.1463	0.0430	3.40	< 0.01
$(ST)_{slope}$	0.0358	0.0113	3.18	< 0.01
$(DA)_{elev.}$	0.2376	0.0476	4.99	< 0.01
$(DO)_{elev.}$	0.3055	0.0408	3.18	< 0.01

AOV of regression model

	SS	df	MS	$\mathbf{F}_{(ratio)}$	**P**
model	139.448	5	27.890	1097.18	< 0.01
error	9.583	377	0.0254		
total	149.03	382			

minimal model

$$\ln (WET) = \ln (BD) + (SU)_{elev.} + (ST)_{slope} + (DA)_{elev.} + (DO)_{elev.}$$

$r^2 = 0.94$; $n = 383$; $P < 0.01$; $MSE = 0.0254$

$\mathbf{F}_{(ratio)} = 1.07 < \mathbf{F}_{(\alpha 1;0.01;4,379)} \approx 3.36$; $P > 0.025$

Therefore the regression analyses formed five significantly different groups from the five populations.

Population	Regression equation	Regression analyses
HP	$\ln (WET) = (2.5030 \times \ln (BD)) - 1.7207$	$r^2 = 0.72$; $n = 40$; $P < 0.01$; $MSE = 0.0243$
SU	$\ln (WET) = (2.4306 \times \ln (BD)) - 1.3491$	$r^2 = 0.70$; $n = 31$; $P < 0.01$; $MSE = 0.0344$
ST	$\ln (WET) = (2.9513 \times \ln (BD)) - 3.0903$	$r^2 = 0.66$; $n = 40$; $P < 0.01$; $MSE = 0.0429$
DA	$\ln (WET) = (2.3820 \times \ln (BD)) - 1.0802$	$r^2 = 0.78$; $n = 236$; $P < 0.01$; $MSE = 0.0229$
DO	$\ln (WET) = (2.2192 \times \ln (BD)) - 0.4710$	$r^2 = 0.73$; $n = 36$; $P < 0.01$; $MSE = 0.0170$

where (BD) = whole body diameter (cm); (WET) = whole wet weight (g)

The differences in slope coefficients were determined using the students t test to determine if the relationships were different from the hypothetical isometric relationship; where whole wet weight decreases relative to (whole body diameter)^3. Where the hypothesis for the t test is H_0 = the slope of the regression was not different from isometry.

Guam (Hospital Point HP)	$t_{statistic} = 1.98 > t_{(0.01(1)38)} = 2.43$	$P < 0.05$
Fiji (Suva Reef SU)	$t_{statistic} = 1.91 < t_{(0.01(1)36)} = 2.43$	$P < 0.05$
Guam (South Tumon Bay ST)	$t_{statistic} = 0.14 > t_{(0.01(1)38)} = 2.43$	$P > 0.25$
GBR (Davies Reef DA)	$t_{statistic} = 7.40 > t_{(0.01(1)234)} = 2.34$	$P < 0.01$
Guam (Double Reef DO)	$t_{statistic} = 3.38 > t_{(0.01(1)34)} = 2.44$	$P < 0.01$

The allometric coefficients for all populations except South Tumon Bay were significantly lower than the hypothetical relationship developed using the isometric coefficient (3) (where the relationships for populations HP and SU were weakly significant). The coefficient for the relationship for ST was not significantly different from isometry (coefficient = 2.951). Overall the populations with higher whole body diameter ranges had relationships for whole wet weight and whole body diameter which were significantly different from isometry.

4.3.6.3. Underwater weight and whole wet weight

An heteroscedastic trend found in preliminary standardised residuals suggested data transformation by natural logs for the regression analyses of whole wet weight and whole body diameter. The residual plot for the final model selected showed no apparent residual trend (Figure 21a) and therefore, the model is a reasonable description of the data (Figure 21b).

Dependent Variable = ln (UW)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-1.7873	0.1493	-11.97	< 0.01
ln (WET)	0.8306	0.0221	37.51	< 0.01
$(ST)_{elev.}$	0.0937	0.0269	3.48	< 0.01
$(DA)_{elev.}$	0.0892	0.0294	3.03	< 0.01

AOV of regression model

	SS	df	MS	$\mathbf{F_{(ratio)}}$	**P**
model	84.293	3	28.098	1340.8	< 0.01
error	5.4485	260	0.0210		
total	89.741	263			

minimal model

$$\ln (UW) = \ln (WET) + (ST_{elev.}) + (DA_{elev.})$$

$r^2 = 0.94$; $n = 264$; $P < 0.01$; MSE = 0.0210

$\mathbf{F_{(ratio)}} = 1.39 < F_{(\alpha 1;0.01;6,258)} \approx 2.86$; $0.10 < P < 0.25$

The analyses formed three significantly different regression groups out of the five populations for analysis of underwater weight (g) and whole wet weight (g);

Population	Regression equation	Regression analysis
DO, SU, HP	$\ln (UW) = (0.8814 \times \ln (WET)) - 1.9939$	$r^2 = 0.93$; $n = 107$; $P < 0.01$; MSE = 0.0146
ST	$\ln (UW) = (0.7893 \times \ln (WET)) - 1.4201$	$r^2 = 0.85$; $n = 40$; $P < 0.01$; MSE = 0.0142
DA	$\ln (UW) = (0.7743 \times \ln (WET)) - 1.2633$	$r^2 = 0.67$; $n = 117$; $P < 0.01$; MSE = 0.0287

where (UW) = underwater weight
(WET) = whole wet weight

The difference in slope coefficients was determined using the students t test to assess the significance of the difference of the transformed regression slope from the hypothetical isometric relationship of 1 for whole wet weight and underwater weight. Where the hypothesis for the t test is H_0 = the slope of the regression is not different from isometry.

Guam/Fiji (HP, DO, SU)	$t_{statistic} = 11.182 > t_{(0.01(1)152)} \approx 2.350$	$P < 0.01$
South Tumon Bay	$t_{statistic} = 3.850 > t_{(0.01(1)38)} = 2.429$	$P < 0.01$
Davies Reef	$t_{statistic} = 5.011 > t_{(0.01(1)120)} = 2.358$	$P < 0.01$

There was a significant difference between the allometric coefficients of the relationship between underwater weight and whole wet weight for HP, DO, SU = 0.856; ST = 0.789 and DA = 0.767 and the hypothetical relationship determined using the isometric coefficient (1).

4.3.6.4. Spine ossicle length and estimated age

Data for estimated age < 3 years in all populations were omitted to remove the juvenile exponential growth phase so that all populations were compared in the adult phase following full sexual maturity. Data for regression analyses of spine ossicle length were transformed by natural logs following inspection of the preliminary standardised residuals. There was no apparent trend in the residual plot for the final model selected (Figure 22a) and therefore, the model is a reasonable description of the data. Linear regressions of log transformed spine ossicle length (S) and estimated age (AGE) (with SE for each estimated age class) in the five populations are presented in Figure 4.22b.

Dependent Variable = ln (S)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	2.6275	0.0191	137.6	< 0.01
(AGE)	0.0068	0.0003	19.78	< 0.01
$(SU)_{elev.}$	0.0859	0.0150	5.72	< 0.01
$(DO)_{elev.}$	0.0634	0.0158	4.00	< 0.01
$(DA)_{elev.}$	0.3890	0.0119	32.61	< 0.01

AOV of regression model

	SS	df	MS	**$F_{(ratio)}$**	**P**
model	22.0265	4	5.5066	1035.7	< 0.01
error	1.9141	360	0.0053		
total	23.9407	364			

minimal model

$$\ln S = AGE + (DO_{elev.}) + (SU_{elev.}) + (DA_{elev.})$$

$r^2 = 0.92$; $n = 365$; $P < 0.01$; $MSE = 0.0053$

$$\mathbf{F}_{(ratio)} = 2.90 < F_{(\alpha 1;0.01;5,360)} \approx 3.05;\ 0.025 < P < 0.01$$

The population analysis forms four parallel regression groups.

Population	Regression equation	Regression analysis
(a) HP, ST	$\ln (S) = (0.1192 \times (AGE)) + 2.3672$	$r^2 = 0.42$; $n = 80$; $P < 0.01$; $MSE = 0.0046$
(b) DO	$\ln (S) = (0.0076 \times (AGE)) + 2.6623$	$r^2 = 0.72$; $n = 35$; $P < 0.01$; $MSE = 0.0031$
(c) SU	$\ln (S) = (0.0048 \times (AGE)) + 2.8089$	$r^2 = 0.25$; $n = 31$; $P < 0.01$; $MSE = 0.0085$
(d) DA	$\ln (S) = (0.0066 \times (AGE)) + 3.0303$	$r^2 = 0.57$; $n = 219$; $P < 0.01$; $MSE = 0.0053$

where (AGE) = estimated age (month)
(S) = spine ossicle length (mm)

There is a significant difference in elevation but not slope for spine ossicle length versus estimated age between the 4 regressions for combined Hospital Point and South Tumon Bay (HP + ST), Double Reef (DO), Suva Reef (SU), and Davies Reef (DA). Therefore, the rates of spine ossicle growth in adult individuals is similar in all populations, however the spine ossicle length at maturity (determining the elevation of the regressions) was significantly greater in the Davies Reef population than the populations from the other two regions.

4.3.7. Adult body growth in populations

There was an initial diminution in growth rates after approximately 30 months of age in overall growth of whole body size variables ((BD), (UW) and (WET)) using estimated age (AGE) (Figure 4.23). Davies Reef and Double Reef growth curves have similar trajectories however, the influence of estimated age class (3+) in the Double Reef population strongly affected growth analyses in that population. The Suva population showed less rapid growth, achieving maximum body size later than Davies Reef and Double Reef populations (Figure 4.23a). The significance of these differences was not strong due to relatively high standard errors of mean whole body diameter at age in the Suva Reef and Double Reef populations.

Adult body growth in populations was determined by omitting data for individuals not sexed. Linear regressions were fitted for each population over the range of adult age classes found in each population. The significance of these regressions was used to indicate the extent of continued growth past maturity and the derived regression coefficients were then used as estimates of growth rates.

Table 4.8. Summary of linear regression analyses of adult growth (where (AGE) > 3 years) in five *A. planci* populations from the Western Pacific region, using log normal transformed dependent variables; whole body diameter, underwater weight and whole wet weight.

Dependent variable: ln (BD)

Population	Regression equation	Regression analysis
HP	NS	$r^2 = 0.01$; $P = 0.50$; $n = 40$; MSE = 0.010
ST	NS	$r^2 = 0.09$; $P = 0.06$; $n = 40$; MSE = 0.009
DO	NS	$r^2 = 0.06$; $P = 0.17$; $n = 35$; MSE = 0.009
SU	$\ln(BD) = 7.35\times10^{-3}(AGE) + 2.953$	$r^2 = 0.40$; $P < 0.01$; $n = 54$; MSE = 0.021
DA	$\ln(BD) = 2.18\times10^{-3}(AGE) + 3.533$	$r^2 = 0.07$; $P < 0.01$; $n = 224$; MSE = 0.012

Dependent variable: ln (UW)

Reef	Regression Analysis	Regression equation
HP	NS	$r^2 < 0.01$; $P = 0.99$; $n = 40$; $MSE = 0.094$
ST	NS	$r^2 = 0.05$; $P = 0.17$; $n = 40$; $MSE = 0.088$
DO	NS	$r^2 = 0.03$; $P = 0.35$; $n = 35$; $MSE = 0.060$
SU	$\ln (UW) = 2.18\times10^{-2} (AGE) + 2.663$	$r^2 = 0.48$; $P < 0.01$; $n = 54$; $MSE = 0.128$
DA	$\ln (UW) = 7.22\times10^{-3} (AGE) + 4.189$	$r^2 = 0.13$; $P < 0.01$; $n = 121$; $MSE = 0.081$

Dependent Variable: ln (WET)

Reef	Regression Analyses	Regression Equation
HP	NS	$r^2 < 0.01$; $P = 0.97$; $n = 40$; $MSE = 0.090$
ST	NS	$r^2 = 0.06$; $P = 0.14$; $n = 40$; $MSE = 0.118$
DO	NS	$r^2 < 0.01$; $P = 0.79$; $n = 35$; $MSE = 0.065$
SU	$\ln (WET) = 2.52\times10^{-2} + 5.380$	$r^2 = 0.48$; $P < 0.01$; $n = 54$; $MSE = 0.174$
DA	NS	$r^2 = 0.03$; $P = 0.01$; $n = 224$; $MSE = 0.099$

where (BD) = whole body diameter (cm)
(UW) = underwater weight (g)
(WET) = whole wet weight (g)
(AGE) = estimated age (month)

The Suva Reef population showed a significant increase in all 3 whole body size variables with age in adult individuals (Figure 4.8), while the regressions for the Davies Reef population had relatively low coefficients of determination.

4.3.8. Multiple regression models for skeletal ossicle variables.

Multiple regression models were constructed to form a minimal equation of independent variables and used to establish potential cause and effect relations in the five populations. The independent variables used to develop the models were three whole body size variables and individual age for the populations. Standardised error plots (Figures 4.24a-f) and the Durbin-Watson statistic were used to assess error trends to select appropriate transformation functions and requirements for additional variables. A value close to 2.0 for the Durbin-Watson statistic relating to the final model indicates that random errors are independent and there is no significant autocorrelation in the residual errors.

4.3.8.1. Minimal model analyses for spine ossicle length

The dependent variables used in the analyses of spine ossicle length are; whole body diameter, estimated age and a variable representing the Davies Reef population.

Dependent variable = ln (S)

Ind. V	Coefficient	Std. Error	t-stat.	P
Constant	0.16345	0.11207	1.4585	0.1455
(BD)	0.17977	0.01293	13.9037	< 0.01
$(BD)^2$	-0.00489	0.00043	-11.3068	< 0.01
$(BD)^3$	0.000044	4.555×10^{-6}	9.5794	< 0.01
AGE	0.20871	0.01784	11.7026	< 0.01
$(AGE)^2$	-0.01025	0.00158	-6.4915	< 0.01
POP. = DA	0.30027	0.01630	18.4224	< 0.01

AOV of regression model

$r^2 = 0.952$

Durbin-Watson statistic = 1.898

	SS	df	MS	$\mathbf{F_{(ratio)}}$	**P**
model	53.1512	6	8.8585	1362.01	< 0.01
error	2.65365	408	0.00650		
total	55.8049	414			

The independent variables used to determine spine ossicle length were whole body diameter represented as a 3rd order polynomial, estimated age and a parameter separating the Davies Reef population (POP. = DA) from the other populations. The standardised residuals plot from the model showed no trend (Figure 4.24a).

4.3.8.2. Minimal model analyses for whole spine appendage length

Dependent Variable = ln (WS)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	0.38693	0.12483	3.0998	< 0.01
(BD)	0.18009	0.01442	12.4871	< 0.01
$(BD)^2$	-0.0047	0.00048	-9.6429	< 0.01
$(BD)^3$	0.00004	5.107×10^{-6}	7.8359	< 0.01
AGE	0.20963	0.01987	10.4999	< 0.01
POP. = DA	0.34453	0.01822	18.9144	< 0.01

AOV of regression model
$r^2 = 0.958$

Durbin-Watson statistic = 1.899

	SS	df	MS	**$F_{(ratio)}$**	**P**
model	70.0309	6	11.6718	1463.92	< 0.01
error	3.05365	383	7.973×10^{-3}		
total	73.0846	389			

The independent variables used to determine whole spine length were similar to those for spine ossicle length; whole body diameter represented by a 3rd order polynomial, estimated age and a parameter separating the Davies Reef population (POP. = DA) from the other populations. The standardised residuals plot from the model showed no trend (Figure 4.24b).

4.3.8.3. Minimal model analyses for adjusted primary oral ossicle weight

Dependent Variable = ln (POA)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-4.31966	0.14650	-29.4862	< 0.01
ln (UW)	0.66698	0.01942	34.3528	< 0.01
(AGE)	1.12366	0.11167	10.0628	< 0.01
$(AGE)^2$	-0.17873	0.02365	-7.5564	< 0.01
$(AGE)^3$	0.009346	0.00158	5.9157	< 0.01

AOV of regression model

$r^2 = 0.963$

Durbin-Watson statistic = 1.965

	SS	df	MS	$F_{(ratio)}$	P
model	111.434	4	27.8586	1454.43	< 0.01
error	4.25225	222	0.01915		
total	115.687	226			

The independent variables used to determine adjusted primary oral ossicle weight were underwater weight and estimated age represented by a 2nd order polynomial. The standardised residuals plot from the model showed no trend (Figure 4.24c).

4.3.8.4. Minimal model analyses for adjusted secondary oral ossicle weight

Dependent Variable = ln (SOA)

Ind. V.	Coefficient	Std. Error	t-statistic	P
Constant	-3.77211	0.13064	-28.8736	< 0.01
(UW)	0.17378	0.01442	12.0498	< 0.01
$(UW)^2$	-0.00506	0.00060	-8.3972	< 0.01
$(UW)^3$	$7.50\text{x}10^{-5}$	0.00001	6.7617	< 0.01
$(UW)^4$	$-5.23\text{x}10^{-7}$	$8.97\text{x}10^{-8}$	-5.8324	< 0.01
$(UW)^5$	$1.37\text{x}10^{-9}$	$2.60\text{x}10^{-10}$	5.2589	< 0.01
(AGE)	0.51272	0.07611	6.7363	< 0.01
$(AGE)^2$	-0.04786	0.00864	-5.5406	< 0.01

AOV of regression model

$r^2 = 0.939$

Durbin-Watson statistic = 1.948

	SS	df	MS	$F_{(ratio)}$	**P**
model	84.972	7	12.1389	430.463	< 0.01
error	5.3297	189	0.02820		
total	90.3017	196			

The independent variables used to determine adjusted secondary oral ossicle weight were underwater weight represented by a 5th order polynomial and estimated age represented by a 2nd order polynomial. The standardised residuals plot from the model showed no trend (Figure 4.24d).

4.3.8.5. Minimal model analyses for adjusted interbrachial ossicle weight

Dependent Variable = (IBA)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-0.03054	0.01290	-2.3673	0.019
(UW)	0.008919	0.000833	10.7128	< 0.01
$(UW)^2$	-0.00010	0.000016	-6.1321	< 0.01
$(UW)^3$	7.19×10^{-7}	1.15×10^{-7}	6.2297	< 0.01
$(UW)^4$	-1.74×10^{-9}	2.59×10^{-10}	-6.7076	< 0.01
(POP.= DA)	4.65×10^{-2}	1.37×10^{-2}	-3.3865	< 0.01

AOV of regression model

$r^2 = 0.899$

Durbin-Watson statistic = 1.932

	SS	df	MS	$F_{(ratio)}$	P
model	3.23421	5	0.64684	398.598	< 0.01
error	0.35539	219	0.00162		
total	3.58960	224			

The independent variables used to determine adjusted secondary oral ossicle weight was underwater weight represented by a 4th order polynomial and a parameter separating the Davies Reef population (POP. = DA) from the other populations. The standardised residuals plot from the model showed no trend (Figure 4.24e).

4.3.8.6. Minimal model analyses for adjusted madreporite ossicle weight

Dependent Variable = ln (MA)

Ind. V.	Coefficient	Std. Error	t-stat.	P
Constant	-8.48682	0.25500	-33.2815	< 0.01
ln (WET)	0.79241	0.04815	16.4563	< 0.01
(AGE)	-0.28315	0.09672	-2.9275	< 0.01
$(AGE)^2$	0.03388	0.00916	3.7007	< 0.01

AOV of regression model

$r^2 = 0.750$

Durbin-Watson statistic = 1.877

	SS	df	MS	$F_{(ratio)}$	P
model	117.153	3	39.0509	250.983	< 0.01
error	38.4312	247	0.15559		
total	155.584	250			

The independent variables used to determine adjusted madreporite weight were log transformed whole wet weight and estimated age represented by a 2nd order polynomial. There was no obvious trend in the residuals plot for the final model (Figure 4.24f). However, there was a relatively low coefficient of determination (r^2 = 0.75) compared with the other analyses, which resulted in a relatively low Durbin-Watson statistic (D-W = 1.877). Therefore, there appeared to be at least one significant morphometric variable missing from the MA model which is involved in determining adjusted madreporite weight that was not considered in this study.

4.3.8.7. Summary of principal dependent variables used in the multiple regression modelling analyses of the skeletal ossicle variables.

Table 4.9. Summary of principal dependent variables used to explain ossicle length (S) or (WS), or weight (POA), (SOA), (IBA) and (MA) among five *A. planci* populations of the Western Pacific region.

Type	Principal dependent variables	Multiple regression analyses
(S)	(BD), (AGE), (Davies Reef)	$r^2 = 0.95$; $P < 0.01$; $n = 415$; MSE = 0.0065
(WS)	(BD), (AGE), (Davies Reef)	$r^2 = 0.96$; $P < 0.01$; $n = 390$; MSE = 0.0080
(POA)	(UW), (AGE)	$r^2 = 0.96$; $P < 0.01$; $n = 227$; MSE = 0.0192
(SOA)	(UW), (AGE)	$r^2 = 0.94$; $P < 0.01$; $n = 197$; MSE = 0.0282
(IBA)	(UW), (Davies Reef)	$r^2 = 0.90$; $P < 0.01$; $n = 225$; MSE = 0.0016
(MA)	(WET), (AGE)	$r^2 = 0.75$; $P < 0.01$; $n = 251$; MSE = 0.1560

Overall the modelling exercise demonstrated the strong relationship between ossicle size and different measurements of whole body size: ((BD) for (S) and (WS); (UW) for (POA), (SOA) and (IBA); and (WET) for (MA). Estimated age (AGE) was also a significant determinant of size in ossicles (S), (WS), (POA) and (SOA) but was not a significant determinant of interbrachial ossicle weight (IBA) or adjusted madreporite weight (MA). The Davies Reef population differed significantly from other populations in the relationships derived for spine ossicle length, whole spine appendage length, and interbrachial ossicle weight. There were no differences in the relationships of these variables between the Suva Reef and Guam populations.

4.3.9. Life-history characteristics among populations

The growth parameters of four variables (whole body diameter, spine ossicle length, whole wet weight, and underwater weight) were obtained using the von Bertalanffy growth equation. A summary of the analyses predicting the three principal life history characters (asymptotic size ($\mathbf{L}_\infty$), size at maturity ($\mathbf{L}_\alpha$), and the growth constant $\boldsymbol{K}$) for the five populations are presented in Table 4.10.

Table 4.10. Summary of life-history characteristics in five *A. planci* populations from the Western Pacific region predicted from analyses using the von Bertalanffy growth equation (where coefficients significance is $P < 0.01$).

Variable	Population	L_∞	L_α	K (mo^{-1})
(BD) (cm)				
	DA (PRE)	44.4	28.7	0.0415
	DA (PST)	42.2	30.4	0.0510
	HP	23.7	NS	NS
	ST	29.4	23.4	0.0632
	DO	31.1	25.6	0.0690
	SU	34.2	23.9	0.0483
(S) (mm)				
	DA (PRE)	45.2	19.5	0.0225
	DA (PST)	39.9	20.9	0.0296
	HP	29.0	14.4	0.0275
	ST	25.1	15.5	0.0382
	DO	28.6	16.1	0.0330
	SU	26.4	16.2	0.0380
(WET) (g)				
	DA (PRE)	2601	NS	NS
	DA (PST)	2358	1823	0.0593
	HP	512	NS	NS
	ST	NS	NS	NS
	DO	NS	NS	NS
	SU	NS	NS	NS
(UW) (g)				
	DA (PRE)	NS	NS	NS
	DA (PST)	116	NS	NS
	HP	31	NS	NS
	ST	55	NS	NS
	DO	66	NS	NS
	SU	NS	NS	NS

Spine ossicle length is the variable which is best described by the von Bertalanffy growth equation over all five populations, with a range of r^2 estimates between 0.35 (ST) and 0.88 (SU) (Appendix 4.6B). Von Bertalanffy type growth (VBG) was also evident from the analyses using whole body diameter (range of r^2 was 0.10 (ST) to 0.77 (SU), while HP was not significant). The variables whole wet weight and underwater weight were not adequately described by von Bertalanffy type growth. There were generally higher $\boldsymbol{K}$ values but lower maximum size and size at maturity in the populations from Guam and Fiji.

The relationship between $\boldsymbol{K}_{(BD)}$ and $\boldsymbol{K}_{(S)}$ among the populations was investigated using the Pearson correlation coefficient, where $\boldsymbol{r} = 0.628$; $_{(ratio)} = 4.37 < \mathbf{F}_{(\alpha1;0.05;3,3)} = 9.28$; $0.10 < P < 0.25$. The relationship between $\boldsymbol{K}_{(BD)}$ and $\boldsymbol{K}_{(S)}$ was not significant. The coefficients from Table 4.9 are estimates of the growth constants $\boldsymbol{K}$, asymptotic size and size at maturity used to determine the life-history constants among the five populations (Table 4.10).

Table 4.11. Life-history constants and mortality rates calculated for five *A. planci* populations from the Western Pacific region.

Population	$(S)_\alpha/(S)_\infty$	$(BD)_\alpha/(BD)_\infty$	M (mo^{-1})	$K_{(S)}/M$	$K_{(BD)}/M$	$M.\alpha$
DA (PRE)	0.431	0.646	0.049	0.459	0.847	1.72
DA (PST)	0.524	0.720	0.120	0.247	0.425	4.20
HP	0.497	NS	0.111	0.248	NS	3.89
ST	0.615	0.794	0.111	0.344	0.569	3.89
DO	0.562	0.822	0.077	0.430	0.896	2.70
SU	0.613	0.701	0.086	0.444	0.562	3.01

where $M.\alpha$ = (adult mortality rate) x (age at full sexual maturity)

M = adult mortality rate, estimated using the method employed in Chapter 3; assuming total mortality of 95% of the cohort over a period equalling the highest adult longevity (lifespan after age at maturity i.e. > 35 mo.) estimated from the population sample.

The values for the constants calculated in each population assumed that the age at full sexual maturity is 3 years (35 months). The assumption remains largely untested in this study because juvenile starfish were obtained only from the Suva Reef and Double Reef populations. However, if the assumptions of valid age determination, age at maturity and the mortality rate estimates are true then there are consistent differences between the life-history constants for Davies Reef outbreak and the remaining non outbreaking populations in those constants related to mortality.

The relationship between the life-history constants $\mathbf{(S)_{\alpha}/(S)_{\infty}}$ and $\mathbf{(BD)_{\alpha}/(BD)_{\infty}}$ among the populations was; $r = 0.676$; $\mathbf{F}_{(ratio)} = 5.16 < \mathbf{F}_{(\alpha 1;0.05;3,3)} = 9.28$; $0.10 < P < 0.25$. The differences in the ratio of body size at maturity to asymptotic body size were not reflected in the same life-history constant analyses using spine ossicle data among the five populations.

The mortality estimates rely principally on the accuracy of the estimated persistence of individuals which was assumed to be equivalent to the oldest estimated age obtained from each population sample. These estimates were less sensitive to the error in estimation of cohort size than estimated longevity and differed little when tested with large variances in the estimates of population size. Over a range of at least ± 50% of the estimated size of the cohort at maturity the mortality estimates remained relatively constant. Therefore, the mortality rate estimates rely principally on the accurate estimates of age. By assuming that 95% of each cohort died between the age at maturity and the beginning of the ultimate age class, since the population samples were relatively small, consistent estimates of the adult mortality rate were able to be calculated for each population.

The relationships between the growth constant, mortality rate and maximum size in both spine ossicle length and whole body diameter were estimated from correlation coefficient analyses (Table 4.12).

Table 4.12. Pearson correlation coefficient analyses for life-history constants: the growth constant using ($\boldsymbol{K}_{(S)}$, $\boldsymbol{K}_{(BD)}$) and mortality rate $\boldsymbol{M}$ and, estimated maximum size using (BD) and (S) for the five *A. planci* populations from the Western Pacific region.

Variable	Correlation analyses (H_0: $\rho \leq 0$) where $\boldsymbol{r}$ estimates ρ.
(BD_∞); M	$r = -0.493$; $\mathbf{F}_{(ratio)} = 2.94 < \mathbf{F}_{(\alpha 1;0.05;3,3)} = 9.28$; $0.10 < P < 0.25$; $M \approx (\mathbf{BD})_\infty^{-0.69}$
$(\mathbf{S}_\infty)$; M	$r = -0.481$; $\mathbf{F}_{(ratio)} = 2.85 < \mathbf{F}_{(\alpha 1;0.05;4,4)} = 6.39$; $0.10 < P < 0.25$; $M \approx (\mathbf{S})_{\infty\text{-}0.70}$
	Correlation analyses (H_0: $\rho \leq 0$) where $\boldsymbol{r}$ estimates ρ.
$\mathbf{K}_{(BD)}$; M	$r = 0.485$; $\mathbf{F}_{(ratio)} = 2.88 < \mathbf{F}_{(\alpha 1;0.05;3,3)} = 9.28$; $0.10 < P < 0.25$; $M \approx K_{(BD)}^{0.84}$
$K_{(S)}$; M	$r = 0.481$; $\mathbf{F}_{(ratio)} = 3.24 < \mathbf{F}_{(\alpha 1;0.05;4,4)} = 6.39$; $0.10 < P < 0.25$; $M \approx K_{(S)}^{0.70}$
	Correlation analyses (H_0: $\rho \geq 0$) where $\boldsymbol{r}$ estimates ρ.
$K_{(BD)}$; $(\mathbf{BD}_\infty)$	$r = -0.839$; $\mathbf{F}_{(ratio)} = 11.38 > \mathbf{F}_{(\alpha 1;0.05;3,3)} = 9.28$; $0.02 < P < 0.05$; $K_{(BD)} \approx (\mathbf{BD}_\infty)^{-1.22}$
$K_{(S)}$; $(\mathbf{S}_\infty)$	$r = -0.846$; $\mathbf{F}_{(ratio)} = 11.99 > \mathbf{F}_{(\alpha 1;0.05;4,4)} = 6.39$; $0.01 < P < 0.02$; $K_{(S)} \approx (\mathbf{S}_\infty)^{-0.99}$

There was a positive correlation between mortality rate and asymptotic size, and mortality rate and the growth constants, in both whole body diameter and spine ossicle length, although the significance was poor. However, there was a significant negative relationship between the growth constant and asymptotic size ($\boldsymbol{K}_{(BD)}$) $\approx$ $(\mathbf{BD}_\infty)^{-1.22}$ and $\boldsymbol{K}_{(S)} \approx (\mathbf{S}_\infty)^{-0.99}$, the spine ossicle relationship is proportional (i.e. the exponent ≈ 1), demonstrating a trade-off between these two life-history characteristics among the five populations.

4.4. **Discussion**

4.4.1. Morphometric characteristics of populations

4.4.1.1. Morphometric characteristics in the low density populations

The morphometric analyses revealed a number of differences among the populations, in particular between the high density population (Davies Reef) and the low density populations (Suva Reef and the Guam reefs). The four low density populations were grouped by:

(a) distributions and morphometric analyses of (S) and (WS)
(b) relationship between (UW) and (WET)
(c) skeletal ossicle regressions for (S) and (AGE)
(d) similar maximum body size and estimated longevity (maximum estimated (AGE) was 6+ years in SU and DO; 5+ years in HP and ST).

The five populations ranked according to mean adult body size (Table 4.1) showed a general negative trend between mean body size and the visually estimated availability of coral resources among regions. Differences among regional reef habitats and the potential for genetic differences between populations (see Chapter 2) can confound the correlation of morphometric variables and habitat types. However, there was also a correlation between mean adult body size and observed live coral cover among the three Guam populations (see site descriptions 4.3.1.), where these confounding factors are less likely to apply. This relationship is similar to that found by Cheney (1974) who reported a positive relationship between coral abundance and body size from a survey of three *A. planci* populations around Guam.

The morphometric analyses were used to group or separate populations where consistent trends among the variables had been established. The South Tumon Bay and Hospital Point population samples were grouped together by a number of the analyses suggesting they may be from a single population. The analyses were;

(a) size frequency distributions (D), (UW), (WET), (POA), (SOA), and (MA).
(b) skeletal ossicle morphometric regressions, (S) and (AGE).
(c) similar patterns in the relative size of cohorts from size frequency distributions of estimated age and the same estimated longevity (5+ years).

Although the South Tumon Bay starfish were generally larger than those from Hospital Point, the extent of similarity in the analyses using estimated age, together with their habitat proximity (Figure 4.1), showed they were probably from the same population or, at least were derived temporally from the same larval pulses. Cheney (1974) concluded that a southward current flow along the western side of Guam developed eddy systems off points of coastline where larvae can be concentrated. Reefs off Tumon Bay were among the first to develop outbreaks in 1967 (Chesher, 1969a). Therefore, eddy systems which developed under favourable conditions near Hospital Point appear to be linked to ongoing larval settlement.

The primary difference between the Hospital Point and South Tumon Bay populations was in their estimates of mean body size which developed from; (a) resource differences between habitats with settlement occurring widely over both areas or, (b) size-selective migration as cohorts approached maturity. If the majority of larval settlement occurred out of an eddy system off Hospital Point then larger maturing individuals (being more mobile) would move into the bay area from the Point as their energy requirements became greater than the available supply (i.e. due to the poor coral cover around Hospital Point. Longer term observations of *A. planci* movement around Hospital Point may be used to test this hypothesis. A similar response to resource conditions was identified by Paine (1976a) from his field studies on the temperate asteroid, *Pisaster* (see Chapter 1).

4.4.1.2. Morphometric characteristics of a high density population

The lower ranges in sizes of morphometric variables in this study were a characteristic of populations outside the GBR (see Chapter 2). The elevation of the relationship between underwater weight and whole wet weight was significantly lower in the Guam and Suva reef populations because the shape of *A. planci* in high density populations from the GBR becomes progressively thinner with increasing body size (see Kettle, 1990). Therefore, a thinner dimension in the oral aboral axis results in a relatively higher contribution by the skeleton to total body weight (Figure 4.21).

The attributes which distinguish the Davies Reef population from the other four populations were:

(a) the population sample is predominantly comprised of individuals involved in a recent large scale recruitment event.
(b) size, distributions and variance ranges were higher in all variables.
(c) sexual dimorphism in whole wet weight.
(d) significant differences in three morphometric regressions:
    (WET) and (BD)
    (UW) and (WET)
    (S) and (AGE)
(e) lower exponents (decelerating) in a number of allometric relationships.
(f) estimated longevity was greater in the pre-outbreak group (where maximum (AGE) = 9+ years).

Sexual dimorphism was found to be significant only in the Davies Reef population under conditions which included high population density (see also Chapter 5). *A. planci* has previously been shown to exhibit differences in body size distributions between sexes (where females are larger) in outbreak populations from the Ryukyus, Japan, by Sakai (1985) and Nakamura (1986). Therefore, the consistently higher ranges of size in the morphometric variables from the Davies Reef population reflected, at least in part, differences in sex, habitat and available coral resources.

4.4.2. Allometric relationships with body size

Allocation of energy to reproduction in *A. planci* increases at an accelerating rate with increasing body size (Kettle, 1990; Chapter 5). The concomitant variation in energetic requirements can be satisfied either by variation in morphology of feeding structures to accommodate higher resource intake or, by changes in behavioural characteristics in foraging and movement to meet the energetic demands that increase with body size. *A. planci* feeds externally through stomach eversion which is placed in close contact with the coral tissue during the digestion process (Goreau, 1964). Therefore, an increase in nutrient intake can only be achieved by feeding for longer periods or, by increasing the surface area of the absorptive organ to increase the rate of digestion. Although the stomach does appear to be simply convoluted when everted, its size is related to the size of the central disc area (Lawrence and Moran, 1992) and is physically limited by the requirement for close contact with the coral surface for digestion. Therefore the size of the stomach is governed by body size relationships, being isometric with whole body diameter ($(BD)^1$) and allometric with whole wet weight ($(WET)^{0.67}$). Lawrence (1990b) suggested that the evolution of body shape in *A. planci* has involved fusion of the proximate parts of the arm to the disc and a reduction in the free portion of the arms in order to increase stomach size because the size of the stomach is related to disc size. Fusion of the proximal arms would increase the protected area of the stomach while feeding and protect the origin of the gonads and pyoric caeca and may have been the basis for the multiarmed condition in this species (Lawrence, 1990b).

Lucas (1984) discussed evidence for the development of a determinate growth pattern in *A. planci* including the limitation of rates of assimilation in relation to body mass. The amount of coral tissue obtained per meal is proportional to $(BD)^2$ due to the limited surface area of the digestive tissues in the stomach. However, the mass of starfish tissue is proportional to $(BD)^3$, if the animal maintains the same relative dimensions at all sizes. As a consequence of these allometric relationships, Kettle (1990) found that larger *A. planci* from high density populations were thinner in the oral/aboral axis, a mechanism where the increase in volume of somatic tissues is slowed, relative to changes in body diameter, from intrinsic limitation as well as the influence of diminishing food resources. Therefore, the exponent in the relationship between whole wet weight and whole body diameter was determined by;

(a) resource availability.

(b) demand for energy from gametogenesis, over the body wall and somatic growth (i.e. reproductive effort).

A number of studies have estimated the body diameter to wet weight relationship for *A. planci* populations, these were: BD$^{2.32}$ by Yamagichi, 1974; BD$^{2.87}$ by Nishihira and Yamazato, 1972; BD$^{2.64}$ by Conand, 1984; BD$^{2.93}$ by Kettle, 1990 for early outbreak conditions ((BD) range 20 - 46cm) and BD$^{2.45}$ under late outbreak conditions ((BD range 14 - 32cm) on Helix Reef. In the present study this relationship was also found to vary among populations: BD$^{3.11}$ for Double Reef, Guam (not significantly different from isometry); BD$^{2.69}$ for grouped populations Hospital Point, South Tumon Bay and Suva Reef; BD$^{2.41}$ for Davies Reef (Chapter 4). The pattern from the relationships for the GBR populations suggests that where coral resources are high the exponent is not significantly different from 3 (isometry) i.e.; BD$^{2.93}$ for Helix Reef, early outbreak (Kettle, 1990) and BD$^{2.74}$ for the Davies Reef pre-outbreak group. In those populations where resources were limited, the exponent was significantly lower, BD$^{2.45}$ for Helix Reef, late outbreak (Kettle, 1990) and BD$^{2.51}$, Davies Reef post-outbreak group. However, the habitat characteristics and the relationship found in the Double Reef population from Guam do not conform to those predicted from the GBR pattern.

A. planci from Double Reef maintained isometric growth (and developed a relatively thicker body wall) throughout the observed body size range in conditions of relatively low resources (i.e. smaller adult body size, mean = 31cm). If body size relationships generally hold for all populations then there must be another body compartment variable which is restricted in its growth to sustain isometric body dimensions under extrinsic resource limitation. The most likely body compartment which could support this type of growth without limiting their lifespan is the gonads. Therefore, it is predicted that the level of reproduction must be significantly lower in the Double Reef population (and in all Guam *A. planci* where the thicker body wall characteristic was determined), compared with the GBR outbreak populations. Unlike the GBR outbreak populations, the Guam starfish developed from metamorphosis on reefs with poor coral cover, so that lowered feeding rates throughout the developmental phase resulted in a reduced body size at maturity. A slower growth rate from the restricted access to coral resources is predicted to lead to an reduction in reproductive effort to sustain their iteroparous life history interpreted from the SPBC analyses. This hypothesis will be examined in Chapter 5.

4.4.3. Morphometry and estimated longevity

There is an important difference in the way the data were collected in the Davies Reef population compared with the other regions. The Davies Reef data base was built up over 38 months and, therefore, individuals from the same cohort were sampled in different years. These combined data caused a blending of the cohorts into different age classes which has reduced the influence from the differences in life-history characteristics among the cohorts, determined from the SPBC analyses. Evidence for this effect was found in the significant differences in maximum size between the pre-outbreak and post-outbreak groups, once separated, for in the combined analyses the smaller individuals from later samples were included in the same age classes with larger individuals from earlier samples (see Chapter 3).

The Guam and Fiji data were obtained in single sample collections. Therefore, if their cohorts had developed under a range of environmental conditions, i.e. if the assumption of stable habitat conditions throughout their lifespan is not valid, then the growth analyses derived from these data would not be reliable. However, the habitats in both the Guam and Suva Reef areas were in stages of post-outbreak recovery with relatively low coral resources, indicating there were no significant changes in habitat which might have influenced their development (given that the impact on habitats from any cyclone or typhoon damage over the lifespan of these populations was minimal). The outbreaks which heavily impacted the coral cover on these reefs occurred prior to the settlement of the majority of the estimated cohorts sampled in this study (i.e. outbreaks occurred in 1967 in Guam, and in 1984 and 1987 on Suva Reef).

The variables representing the oral ossicle group (POA, SOA and IBA) formed significant allometric relationships with body size in all populations, where the r^2 values ranged from 0.30 (Davies Reef, IBA and WET) to 0.94 (Double Reef, SOA and WET) (Appendix 4.3A, B). The relative size relationships among these internal ossicles remained stable throughout life and therefore, ultimate ossicle size (POA, SOA and IBA) depended primarily on relative body growth. The allometric relationships developed using the oral ossicle group and estimated age were found to be weakly significant in the Davies Reef, Hospital Point and South Tumon Bay populations (Appendix 4.4A, B). External appendage ossicles (S and WS) showed weak relationships with whole body size (BD, UW and WET) in the Davies Reef, Hospital Point and South Tumon Bay populations (where $r^2 < 0.22$). Therefore, the external ossicles do not conform to the same body size constraints that apply to internal ossicle growth and the relationship between body size and the size of the oral ossicle group variables can vary throughout life (i.e. the relatively stable adult body size with increasing sizes in the oral ossicle group through the course of the Davies Reef study.

The poor significance or low coefficients of determination in the relationships between whole body size (BD, UW and WET) and estimated age of adult starfish in the Davies Reef, Hospital Point, South Tumon Bay and Double Reef populations reflected a relatively determinate mode of growth in these populations. The results differ from those in the Suva Reef population where whole body size and internal ossicle variables significantly increased in size throughout the range of estimated adult age classes. This apparent continued growth throughout adult life reflects a more indeterminate mode of growth in this population. The results support the theoretical growth pattern developed by Sebens (1987), where there is a continuum between habitat dependent asymptotic growth (determinate) and plastic asymptotic growth (indeterminate) in certain species. Asymptotic growth occurs when life-history characteristics, including the growth constant and final body size, are determined by food availability and factors affecting physiological cost (Sebens, 1987). The factors implicated in this growth pattern are similar to those invoked by Paine (1976a) to describe the growth of *Pisaster ochraceus*. He showed that the average local size of starfish reflected a complex interdependence between size-related metabolic needs, starfish density, and character of the food resource.

The strong relationship between the external ossicles (S, WS) and estimated age (AGE) in all population samples (HP, ST, DO, SU and DA) albeit not surprising (as pigment band counts were made along the length of the shaft in spine ossicles) is an important result. It demonstrates that bands develop consistently on growing spines in various types of populations and their growth is relatively independent of adult body size (see Chapters 2 and 3). These factors are important attributes for a reliable method of age determination in *A. planci*.

The estimated longevity of pre-outbreak individuals was at least 1.7 times greater than those which developed under outbreak conditions (Chapter 3). Recruitment of massive numbers of *A. planci* responsible for the outbreak population on Davies Reef was estimated to have occurred in 1985 and 1986 (Chapter 3). The population subsequently decreased in size, as indicated by the estimated collection efficiencies and estimated mortality rates during 1989-90 (Chapter 3). Therefore, the results reflect the influence of high density aggregation and food limitation on longevity. Kettle (1990) also found these factors influenced mortality processes and suggested that survival was probably only 3+ years in a very high density outbreak, using evidence that four successive cohorts experienced low food availability while their reproductive effort remained high over two consecutive spawning seasons on Helix Reef (Central GBR; 1985-87).

Longevity estimates in the other populations made from single sample analyses may not be as reliable as those from the Davies Reef population. Estimates of longevity are best obtained by following individuals through their life cycle, particularly in a species which is highly mobile and where there is little *a priori* information on their population dynamics. However, the presence of *A. planci* populations in Guam and on Suva Reef had been relatively consistent for at least a decade prior to the present studies suggesting that the estimates made from the maximum pigment band counts may be a fair indication of their lifespan. Maximum longevity in the Suva Reef population was estimated to be 6+ years therefore, there were *A. planci* surviving on this reef which may have settled as early as 1986. Larger body size in the older starfish in this population supports the view that those starfish may not have experienced the severity of environmental influences and competition for food which affected the majority of the 1987 outbreak population. To have avoided the factors limiting growth, the surviving individuals may have moved away from the isolated aggregations described by Zann et al. (1987; 1990) and therefore, maintained a dispersed mode of life as had been found on Davies Reef towards the end of the field study.

4.4.4. Multiple regression models

The modelling exercise focussed on determining the potentially important independent variables in multiple regression analyses for each of the ossicle types by examining the nature and extent of the association between the dependent and independent variables in the regression analyses. The results from the multiple regression modelling exercise for spine ossicle length showed that the addition of a term identifying the Davies Reef population was retained in the final equation, and this represented a significant elevation of the Davies Reef regression. *A. planci* from Davies Reef have relatively longer spines than Guam or Suva Reef populations which cannot be accounted for by body size differences alone. This difference can be illustrated by extrapolation of the power equation derived from the Suva Reef population for (S) and (WET), i.e. a starfish with similar maximum spine length obtained from the GBR (~45mm) would need to be approximately 10kg whole wet weight, or greater than two times the approximate maximum size observed in this species. Aboral spine ossicles are assumed to have developed as a defence strategy in *A. planci*, therefore, a relationship between spine length and body size was expected. However, the results showed that spine length does not always develop in relation to body size among populations of the Western Pacific. The potential reasons for this are:

(a) Race allomorphosis (Gould, 1966). The GBR *A. planci* are more genetically isolated than Guam and Fiji populations and have evolved as a long spined variety. Significant mean genetic variation among populations across the Pacific was found to be small (7%) but significant ($F_{ST} = 0.072$; $P < 0.01$) by Nishida and Lucas (1988). The review by Benzie (1992) also concluded there are low levels of genetic differentiation among populations over the Pacific region supporting this argument.

(b) The rapid growth phase occurred at a greater rate in *A. planci* during which time a longer spine ossicle apex developed (see Stump and Lucas, 1990; Table 4.9) resulting in significantly longer spines at maturity (i.e. higher levels of resource availability). A longer juvenile growth period would also produce the same result, however maturity appears to occur at the same age in populations across the Pacific (see Chapters 3 and 5).

One way to test these hypotheses would be to compare data from large-sized specimens collected from low density populations in different regions. In the Micronesian region, Chesher (1969b) reported *A. planci* up to 60cm diameter had been collected outside the areas of outbreak aggregations from Guam and, Zann (personal communication) found *A. planci* ca. 50cm diameter in low densities on reefs off the northern side of Viti Levu, Fiji. Minimum sizes at full sexual maturity in *A. planci* (minimum ($\mathbf{BD}_\alpha$)) observed from this study were considerably smaller in the Guam populations (Double Reef, minimum ($\mathbf{BD}_\alpha$) = 18cm) and Suva Reef (minimum ($\mathbf{BD}_\alpha$) = 13cm) than from the Davies Reef population (minimum ($\mathbf{BD}_\alpha$) = 27cm) (see Chapter 5). Therefore, the second hypothesis (b) must be the preferred option until further population studies are undertaken. Ultimately, the assessment of the method of age determination and subsequent analyses of individual growth constants must be carried out on a wide range of populations to more accurately determine the sources of variation in spine length at maturity.

Whole body size had a primary influence on the growth of the oral ossicle group. The oral ossicle group (adjusted for arm number; POA, SOA) showed a significant relationship with underwater weight and estimated age. The third internal ossicle (interbrachial ossicle weight, adjusted for arm number) developed a weakly significant relationship with estimated age and therefore, the optimum model employed a 4th order polynomial for underwater weight and included an additional variable representing the Davies Reef population. The model for adjusted madreporite weight did not form a satisfactory final residual plot with a low coefficient of determination and a reasonably distinct trend in the results after the range of variables had been considered. Therefore, this model required an additional unknown variable to explain variation in madreporite size other than whole body size measurements, age or location.

4.4.5. Life-history characteristics

4.4.5.1. Variation in life-history constants

The life history analyses described the variation in the Beverton-Holt constants using spine ossicle length more reliably than those using whole body diameter (i.e. the coefficient of determination was generally higher in the analyses using spine ossicle length). Therefore, the relationship between the growth constant for spines and whole body growth is estimated to compare life-history characteristics among populations derived from both variables. Unfortunately, the correlation between these two growth estimates was not significant, although the derived exponents were similar to the relationship between the two growth constants for the Davies Reef cohorts = 0.73 (when forced through the origin). While body growth may cease soon after maturity, spine growth continues throughout the range of estimated age classes in each population. Therefore, the VBG curve analysis is better suited to describing the continued growth of spine ossicles through adult life.

There were variations in all the life-history constants ($(\mathbf{S})_{\alpha}/(\mathbf{S})_{\infty}$, $(\mathbf{BD})_{\alpha}/(\mathbf{BD})_{\infty}$, $\boldsymbol{K}_{(\mathrm{S})}/\boldsymbol{M}$, $\boldsymbol{K}_{(\mathrm{BD})}/\boldsymbol{M}$, and $\boldsymbol{M}.\alpha$) among the populations. The ratio of size at maturity to asymptotic size ranged from 0.701 (Suva Reef) to 0.822 (Double Reef). By comparison, the ratio for the Suva Reef population calculated from the data of Zann et al. (1987; 1990) showed that initial gametogenesis occurred at 23 months (approximate (BD) = 15cm) but when subsequent growth to full sexual maturity at 35 months was taken into account the calculation of the life-history constant for the ratio between estimated size at maturity and maximum body size was $\mathbf{(BD)_{\alpha}/(BD)_{\infty}} = 0.921$. This value was within the range obtained from the individual analyses of the outbreak cohorts from Davies Reef (1985 = 0.911; 1986 = 0.967). Charnov (1993) suggested that indeterminate growth occurs where size at maturity is between 50 to 80% of maximum size, and therefore, indicated that *A. planci* can develop in either determinate or indeterminate-type growth modes depending on the habitat characteristics. The differences between the analyses from this study and the results of Zann et al. (1987; 1990) also indicated that the different modes of growth were also determined by processes involving post-settlement population density.

The ratio of $\mathbf{(S)_{\alpha}/(S)_{\infty}}$ relied on the range of estimated age classes in each population, since there was a positive linear relationship between asymptotic spine length and estimated age. The lower range of the ratios found among the populations (0.431 for the Davies Reef pre-outbreak group to 0.615 for the South Tumon Bay population) compared with the $\mathbf{(BD)_{\alpha}/(BD)_{\infty}}$ ratios reflected the continuation of spine growth past maturity in all populations i.e., an indeterminate growth mode in spine ossicles, where the ratio $\mathbf{(S)_{\alpha}/(S)_{\infty}} < 0.8$ in all five populations. As a result, the differences in growth characteristics produced a low level of correlation between $\mathbf{(BD)_{\alpha}/(BD)_{\infty}}$ and $\mathbf{(S)_{\alpha}/(S)_{\infty}}$ ($r^2 = 0.46$; $P > 0.10$) and therefore, the variable nature of these ratios among the populations was the single most dominant influence on the variances determined for the Beverton-Holt life-history constants. This variation showed that the processes involved in the determination of principal life-history characteristics were influenced by the mode of growth in *A. planci.*

Pauly (1991) described the growth constant $\boldsymbol{K}$ as the VBG curvature parameter that was determined by levels of environmental *stress*, as defined by Seyle (1980), which included influences from temperature, population density and resource availability. What the various forms of *stress* have in common is that they can cause an elevated metabolism in the short-term but lead eventually to decreased production. Although this may not be so straightforward since not even siblings react the same way to *stress* factors (Pauly, 1991) and metabolic rates are limited primarily by water temperature in aquatic poikilotherms. In addition, any changes in oxygen consumption related to metabolic activity are limited by the strong correlation with relative body size as found in *A. planci* by Kettle and Lucas (1987); also see Chapter 1. However, differences in metabolic rates leading to variation in rates of energy conversion may be achieved through behavioural differences peculiar to populations or cohorts, including levels and duration of activity such as feeding and reproductive effort (see Chapter 5).

The results of the VBG curve fitting exercise showed that $\boldsymbol{K}$, particularly in the spine ossicle length variable, was higher in those populations where; (a) population density increased significantly (i.e. Davies Reef: $\boldsymbol{K}_{(S)}$ PRE = 0.023 to PST = 0.030; and $\boldsymbol{K}_{(BD)}$ PRE = 0.042 to PST = 0.051) or, (b) coral cover in the population's habitat was very low (i.e. Suva Reef: $\boldsymbol{K}_{(S)}$ = 0.038; and South Tumon Bay $\boldsymbol{K}_{(S)}$ = 0.038). These results generally concur with those predictions made from Pauly's definition of $\boldsymbol{K}$ (see above). Therefore, the non-significance of the correlations determined between mortality and growth constants with asymptotic sizes may have been due to the variety of different influences on $\boldsymbol{K}$, peculiar to each population.

Kettle and Lucas' (1987) physiological studies did not find any metabolic differences between starfish from high and low density populations, i.e. to differences in resources, apart from those related to body size. They demonstrated an overall decrease in oxygen consumption over a large range of body sizes from juveniles collected from outbreak populations to giant individuals from Lady Musgrave Reef (see Chapter 2). There was no suggestion of any differences in metabolic rate (corrected for temperature differences) between smaller (high density, high *stress*) and very large individuals (low density and high level of resources, low *stress*) since they appeared to belong to the same general metabolic rate and body mass relationship (Kettle, 1990). Therefore, while this study showed there were differences in morphometric relationships between high and low density populations (as indicated by variation in growth constants) reflecting differences in metabolic rate, Kettle's results imply that any differences were not significant. Further investigations are needed to investigate the disparate conclusions from these different approaches in describing metabolic rates, possibly by attempting to directly quantify metabolic rates of individuals *in situ* from a large range of populations.

4.4.5.2. Life-history characteristics of populations.

The most striking difference in macroscopic appearance among all five populations (apart from size) was that under outbreaking conditions the Davies Reef starfish, being large individuals were relatively thin body walled and often very fragile. Kettle (1990) described the body wall as a food reserve compartment which always contained more energy than any other compartment and these reserves were available to metabolic demand under certain conditions. This strategy differs from the general pattern in asteroids described by Lawrence (1990) who interpreted data on starfish species which occurred in low density populations as showing they partition more energy to body wall reserves (maintenance) and somatic maintenance resulting in a more competitive life strategy (i.e. promoting a longer-lived iteroparous life).

A strategy to partition high levels of food storage into the body wall, and therefore promoting continued growth throughout life can result from selective pressure caused by high mortality and competition in adult as well as the juvenile stages. In high density populations, *A. planci* "trades strength and structural integrity in their later years for rapid growth, the feeding advantages of a pliable body form and enhanced reproductive potential in their earlier years" (Kettle, 1990). Therefore, the evidence supports the development of a dichotomy in *A. planci* life-history characteristics between high and low density populations.

Variation in the results of the morphometric analyses among populations can be interpreted as a result of phenotypic responses to environmental conditions with or without an underlying intraspecific genetic variation (i.e. from geographic separation). A summary of the results where there was significant variation in morphometric variables is used to estimate the overall variability in the characteristics of this species. The Davies Reef population was divided into the pre-outbreak and post-outbreak groups to distinguish the differences in estimated longevities. Generally, all other variables are similar between the groups.

Table 4.13. Summary of population and morphometric characteristics of *A. planci* from five populations in the Western Pacific region.

Population	R; M(WET)	Longevity	Body GC	(AGE) GC (WET)	$(S)_{maturity}$
HP	low; 503	5+ years	(a) 2.57 (*I*) (b) 2.50 (*I*) (c) 0.98 (*I*)	NS	16.1
ST	low; 786	5+ years	(a) 2.56 (*I*) (b) 2.95 (*I*) (c) 0.79	NS	16.6
DO	low; 1108	6+ years	(a) 2.28 (b) 2.22 (c) 0.87 (*I*)	NS	18.8
SU	low; 676	6+ years	(a) 2.27 (b) 2.43 (*I*) (c) 0.82 (*I*)	0.0252 $r^2 = 0.48$ MSE = 0.174	19.7
DA (PRE)	high; 2527	9+ years	(a) 1.89 (b) 2.50 (c) 0.78	NS	NA
DA (PST)	high; 2253	5+ years	(a) 1.86 (b) 2.47 (c) 0.68	NS	24.6

where R = coral resource availability

M(BD) = mean body diameter of the population

GC = growth exponent

(a) = exponent of relationship between (UW) and (BD)

(b) = exponent of relationship between (WET) and (BD)
(c) = exponent of relationship between (UW) and (WET)
(*I*) = not significantly different from isometry
$(S)_m$ = spine ossicle length (mm) at maturity
NA = estimate not available; NS = not significant

The most obvious differences among the populations are shown by the Davies Reef population which are characterised by:

(a) location, GBR region.
(b) most of the starfish developed in phase with regional population outbreaks.
(c) access to a high level of coral resources, becoming limited during the outbreak phase.
(d) allometric body growth.

In the conditions experienced by the starfish in the Davies Reef outbreak, juveniles apparently grew at a relatively high rate promoting allometry in body dimensions. This was determined from the comparative population results of size at maturity in both mean whole body diameter and mean length of spine ossicle at maturity. Allometric growth in adult starfish occurs from the development of a relatively thinner aboral/oral axis and a thin, fragile body wall (Kettle, 1990) which supports a pattern of resource allocation that switches from somatic growth and maintenance in the juvenile phase to higher levels of partitioning to reproduction after maturity. This is the paradigm of *A. planci* life history in outbreak populations from the GBR.

The characteristics shared by the Guam and Suva Reef populations include:

(a) low densities of starfish and relatively low coral resources.
(b) isometric body growth where resource acquisition and allocation permitted (see also Chapter 5).

Similar longevities were estimated from the Davies Reef outbreak population and the low density populations from the other two regions. This showed that the relative allocation to maintenance or the energy in body reserves used to maintain somatic functions were similar in both types of populations. However, there were large differences in levels of resource acquisition between these population types, and as a consequence there also must have been differences in resource allocation to growth and reproduction. As previously assumed, the differences in growth rates were manifested as significant differences in adult body size at maturity and, since the potential for reproductive output changed according to body size, the Davies Reef starfish were expected to have a significantly greater capacity for fecundity, demonstrated by gonad mass morphometry. The body size at maturity and the differences in allocation to reproduction (determined fom gonad mass relationships) with estimated age among the five populations are among the subjects of Chapter 5.

Figures

Figure 4.1. Regional map of the Indo-Pacific with inset detail of the 5 study areas: Davies Reef (GBR), Suva Reef (Fiji) (IMR = Institute of Marine Resources laboratoies) and the north western side of Guam with the positions of Hospital Point, South Tumon Bay and Double Reef.

Figure 4.2. Size frequency distributions of whole body diameter (cm) for *A. planci* in five populations.

Figure 4.3. Size frequency distributions of underwater weight (g) for *A. planci* in five populations.

Figure 4.4. Size frequency distributions of whole wet weight (g) for *A. planci* in 5 populations.

Figure 4.5. Size frequency distributions of spine ossicle length (mm) for *A. planci* in five populations.

Figure 4.6. Size frequency distributions of whole spine length (mm) for *A. planci* in five populations.

Figure 4.7. Size frequency distributions of spine pigment band counts for *A. planci* in five populations.

Figure 4.8. Size frequency distributions of estimated age (year) determined by spine pigment band counts for *A. planci* in five populations.

Figure 4.9. Size frequency distributions of primary oral ossicle weight (g) (adjusted for number of arms per individual) for *A. planci* in five populations.

Figure 4.10. Size frequency distributions of secondary oral ossicle weight (g) (adjusted for number of arms per individual) for *A. planci* in five populations.

Figure 4.11. Size frequency distributions of inter brachial ossicle weight (g) (adjusted for number of arms per individual) for *A. planci* in five populations.

Figure 4.12. Size frequency distributions of madreporite ossicle weight (g) (adjusted for number of madreporites per individual) for *A. planci* in five populations.

Figure 4.13a-i. Plots of standardised residuals derived from ANOVA for nine variables in five populations of *A. planci*.

Figure 4.14. Allometric relationships between whole body diameter (cm) and eight morphometric variables (two whole body and six skeletal ossicle variables) for *A. planci* in five populations.

Figure 4.15. Allometric relationships between underwater weight (g) and eight morphometric variables (two whole body and six skeletal ossicle variables) for *A. planci* in five populations.

Figure 4.16. Allometric relationships between whole wet weight (g) and eight morphometric variables (two whole body and six skeletal ossicle variables) for *A. planci* in five populations.

Figure 4.17. Relationships between all estimated age groups using spine pigment band counts (year) and nine morphometric variables (three whole body and six skeletal ossicle variables) for *A. planci* in five populations.

Figure 4.18. Relationships between estimated age groups > three years using spine pigment band counts and nine morphometric variables (three whole body and six skeletal ossicle variables) for *A. planci* in five populations.

Figure 4.19a. Plot of standardised residuals of underwater weight (g) and whole body diameter (cm) for *A. planci* in five populations. 4.19b. Linear regressions of ln (underwater weight) (g) and ln (whole body diameter) (cm) for *A. planci* in five populations omitting estimated age < three years.

Figure 4.20a. Plot of standardised residuals of whole wet weight (g) and whole body diameter (cm) for *A. planci* in five populations. 4.20b. Linear regressions of ln (whole wet weight) (g) and ln (whole body diameter) (cm) for *A. planci* in five populations omitting estimated age < three years.

Figure 4.21a. Plot of standardised residuals of whole wet weight (g) and underwater weight (cm) for *A. planci* in five populations. 4.21b. Linear regressions of ln (whole wet weight) (g) and ln (whole body diameter) (cm) for 5 populations omitting estimated age < three years.

Figure 4.22. Linear regressions of ln (spine ossicle length) (mm) and age (month) estimated by spine ossicle pigment band counts for *A. planci* in five populations omitting estimated age < three years.

Figure 4.23a-d. Growth curves derived from; (a) whole body diameter (cm) and estimated age (month), (b) spine ossicle length (mm) and estimated age, (c) whole wet weight (g) and estimated age (month), and (d) underwater weight and estimated age (month) using spine ossicle pigment band counts in three Western Pacific *A. planci* populations; Davies Reef (GBR), Double Reef (Guam) and Suva Reef (Fiji) populations.

Figure 4.24a-f. Standardised residual plots for final models estimated for six skeletal ossicle types for *A. planci* in five populations

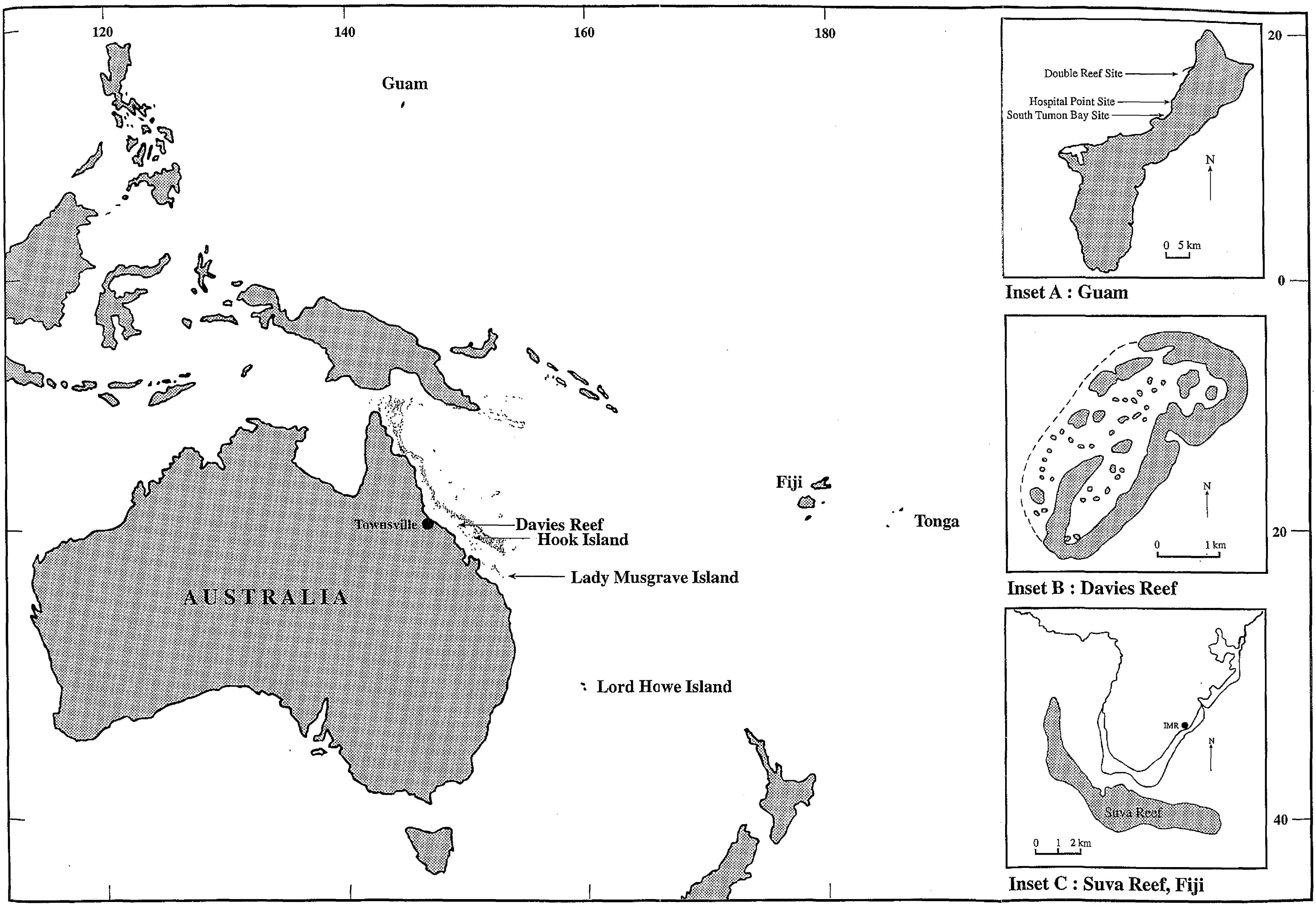

120
140
160
180
Guam
Fiji
Tonga
Townsville
Davies Reef
Hook Island
Lady Musgrave Island
AUSTRALIA
Lord Howe Island
20
0
20
40
Double Reef Site
Hospital Point Site
South Tumon Bay Site
N
0 5 km
Inset A : Guam
N
0 1 km
Inset B : Davies Reef
IMR
N
Suva Reef
0 1 2 km
Inset C : Suva Reef, Fiji

FIGURE 4.2

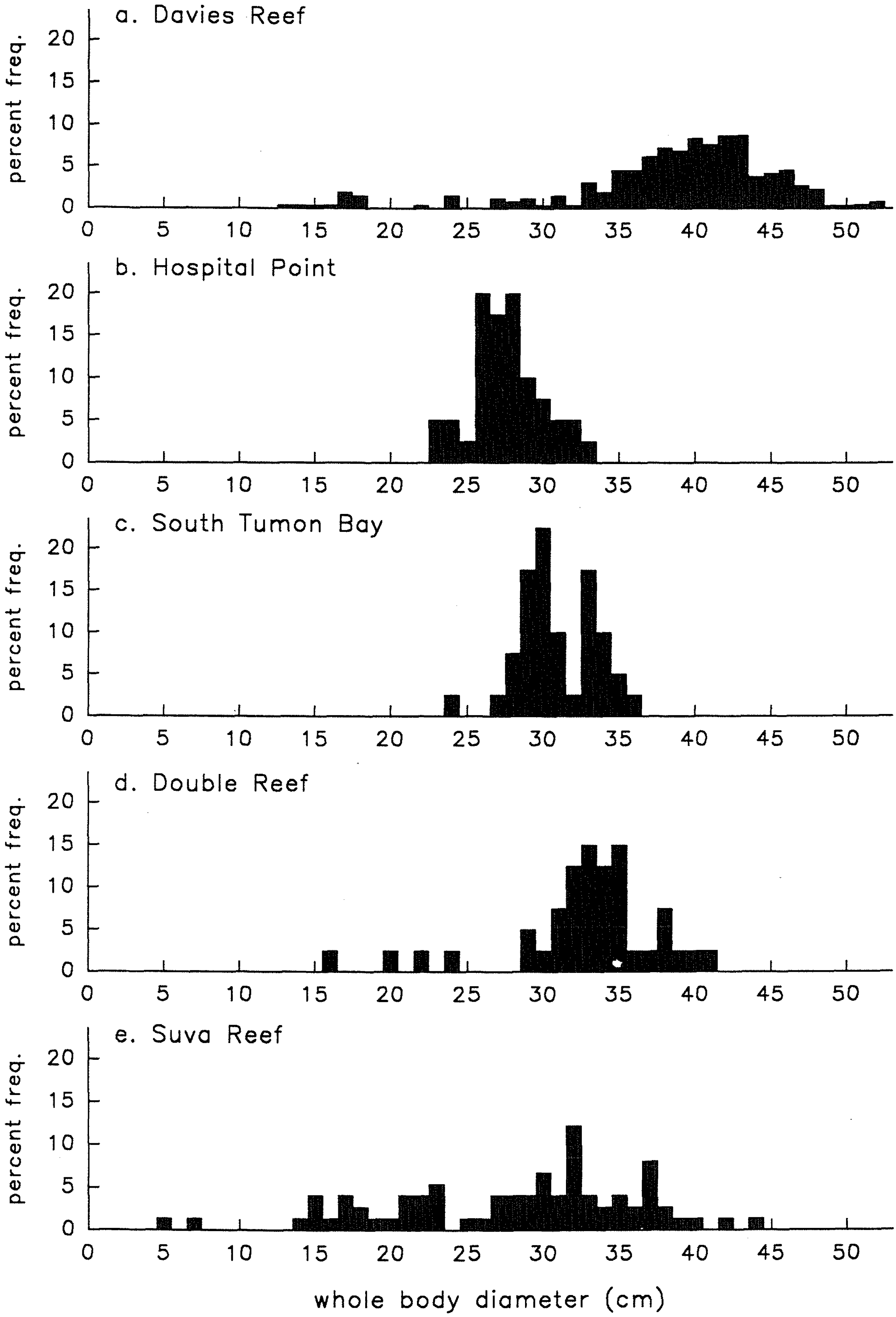

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
0 5 10 15 20 25 30 35 40 45 50
whole body diameter (cm)

FIGURE 4.3

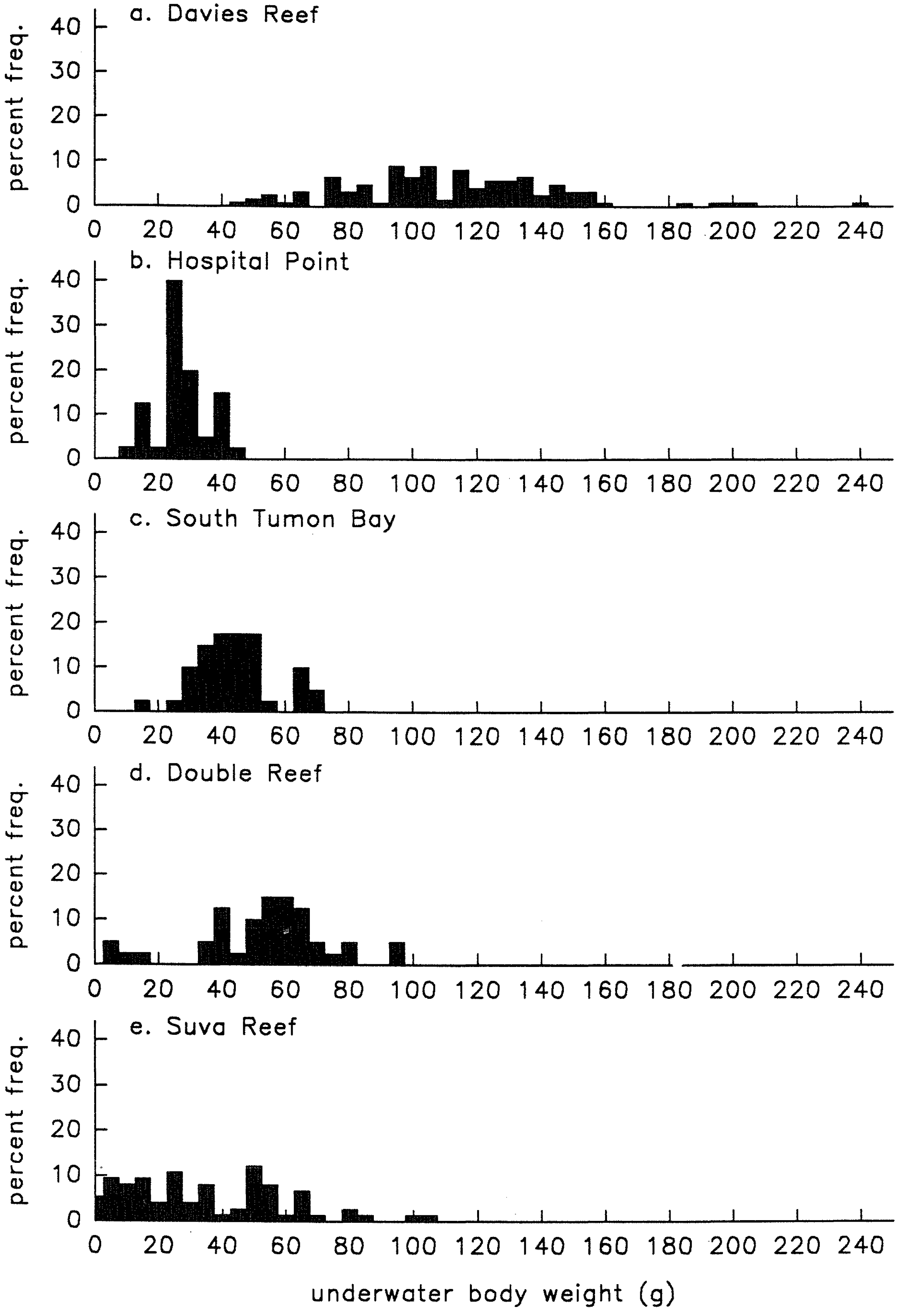

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
10
20
30
40
0
20
40
60
80
100
120
140
160
180
200
220
240
underwater body weight (g)

FIGURE 4.4

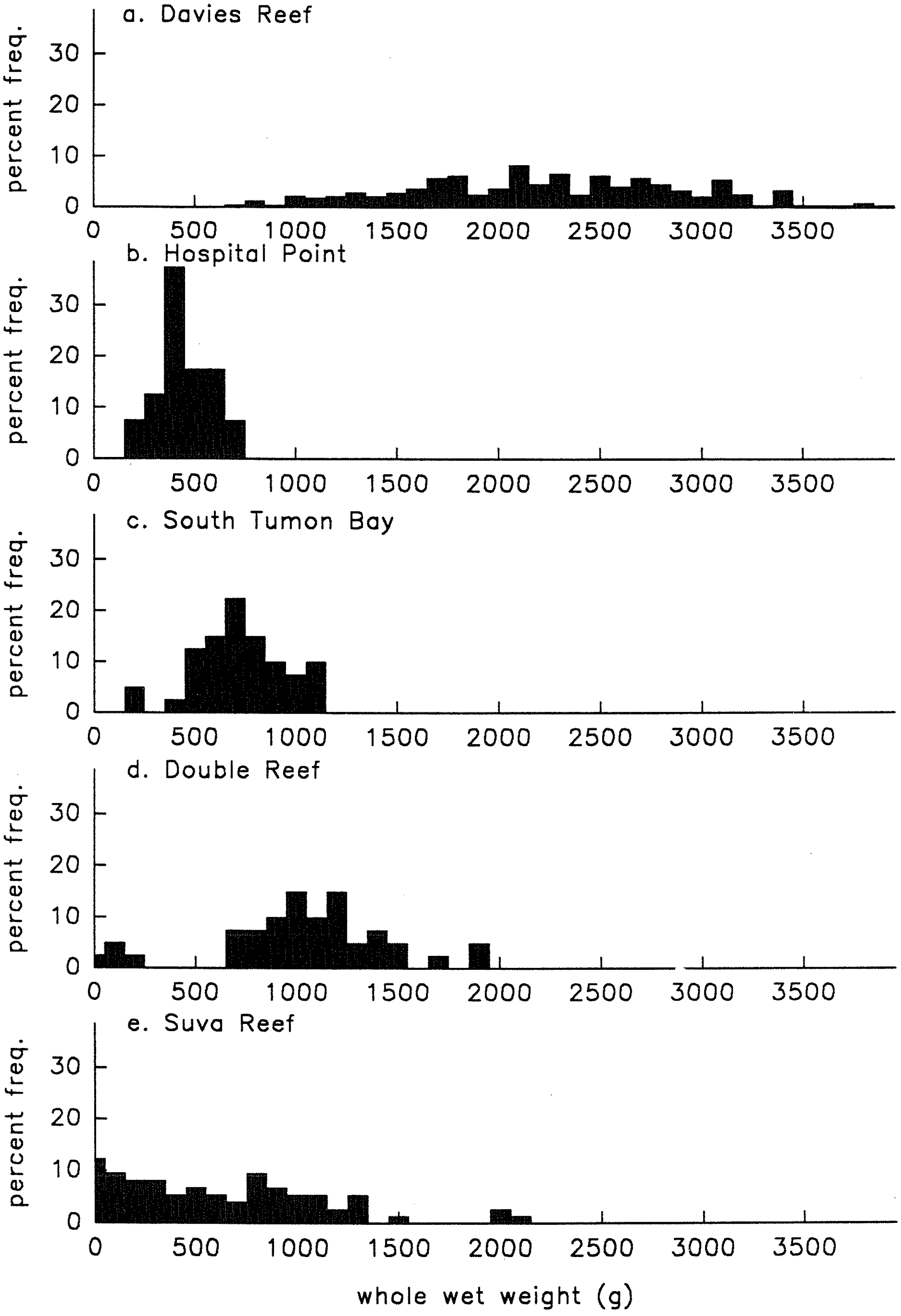

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
10
20
30
0
500
1000
1500
2000
2500
3000
3500
whole wet weight (g)

FIGURE 4.5

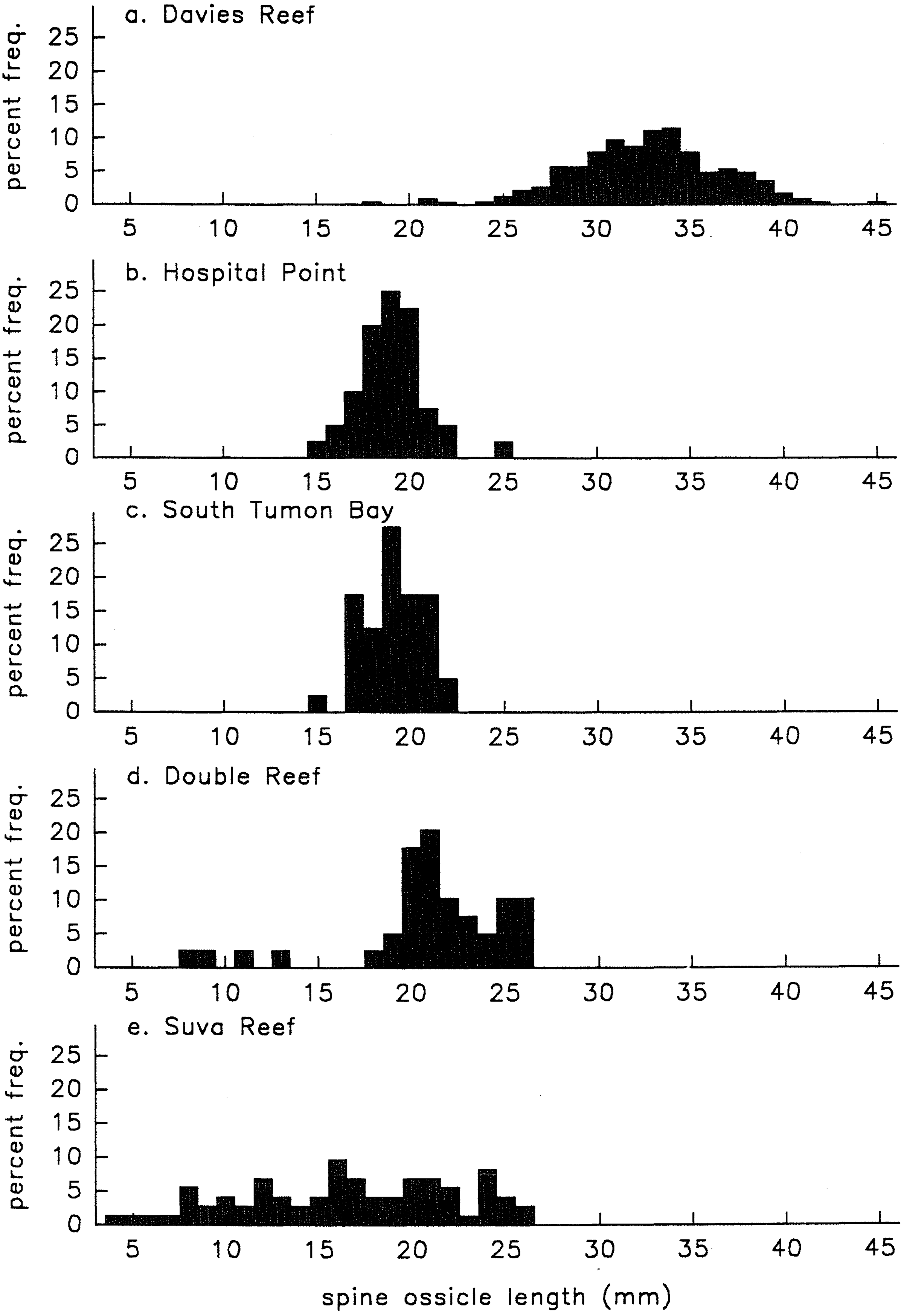

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
25
5
10
15
20
25
30
35
40
45
spine ossicle length (mm)

FIGURE 4.6

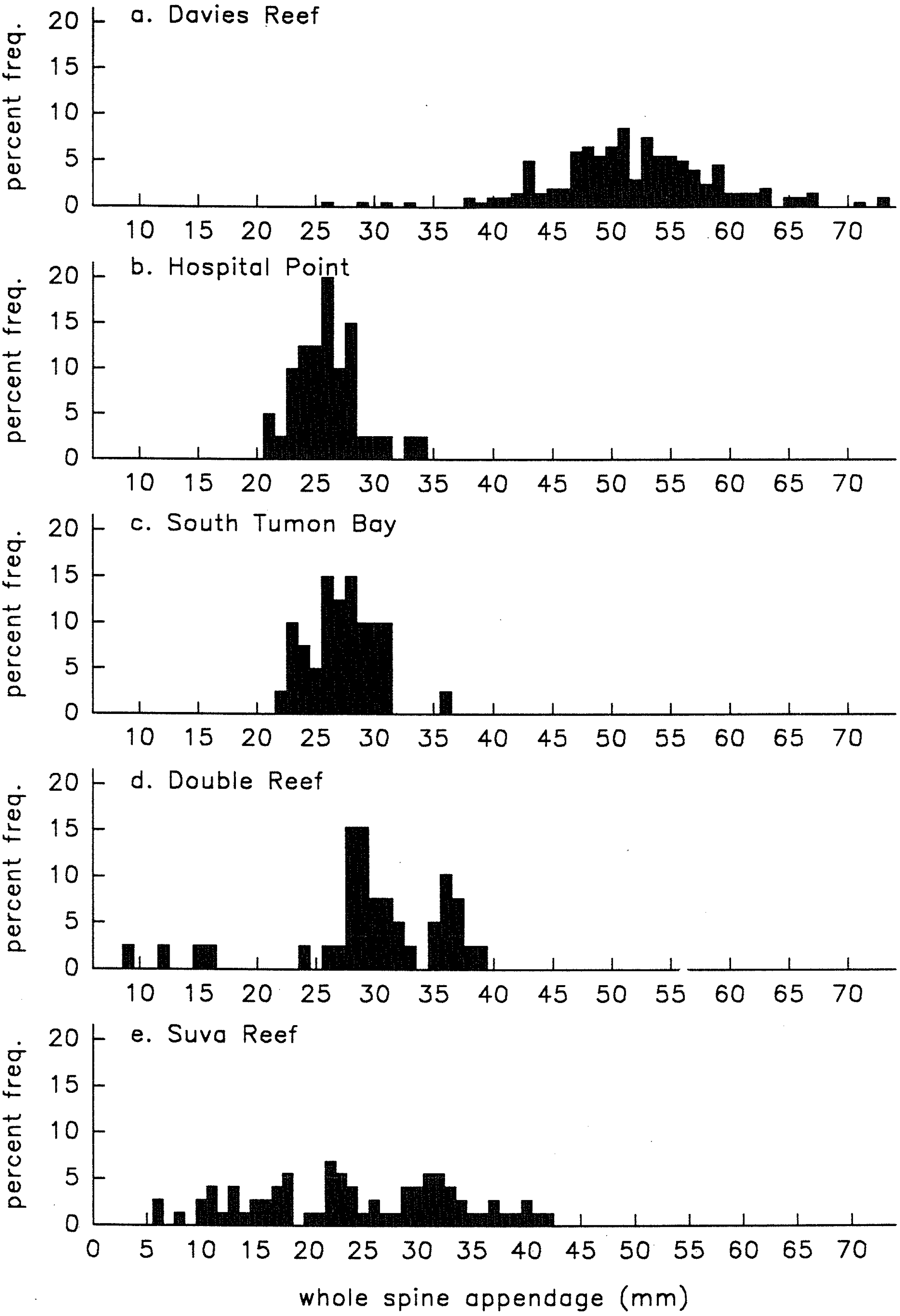
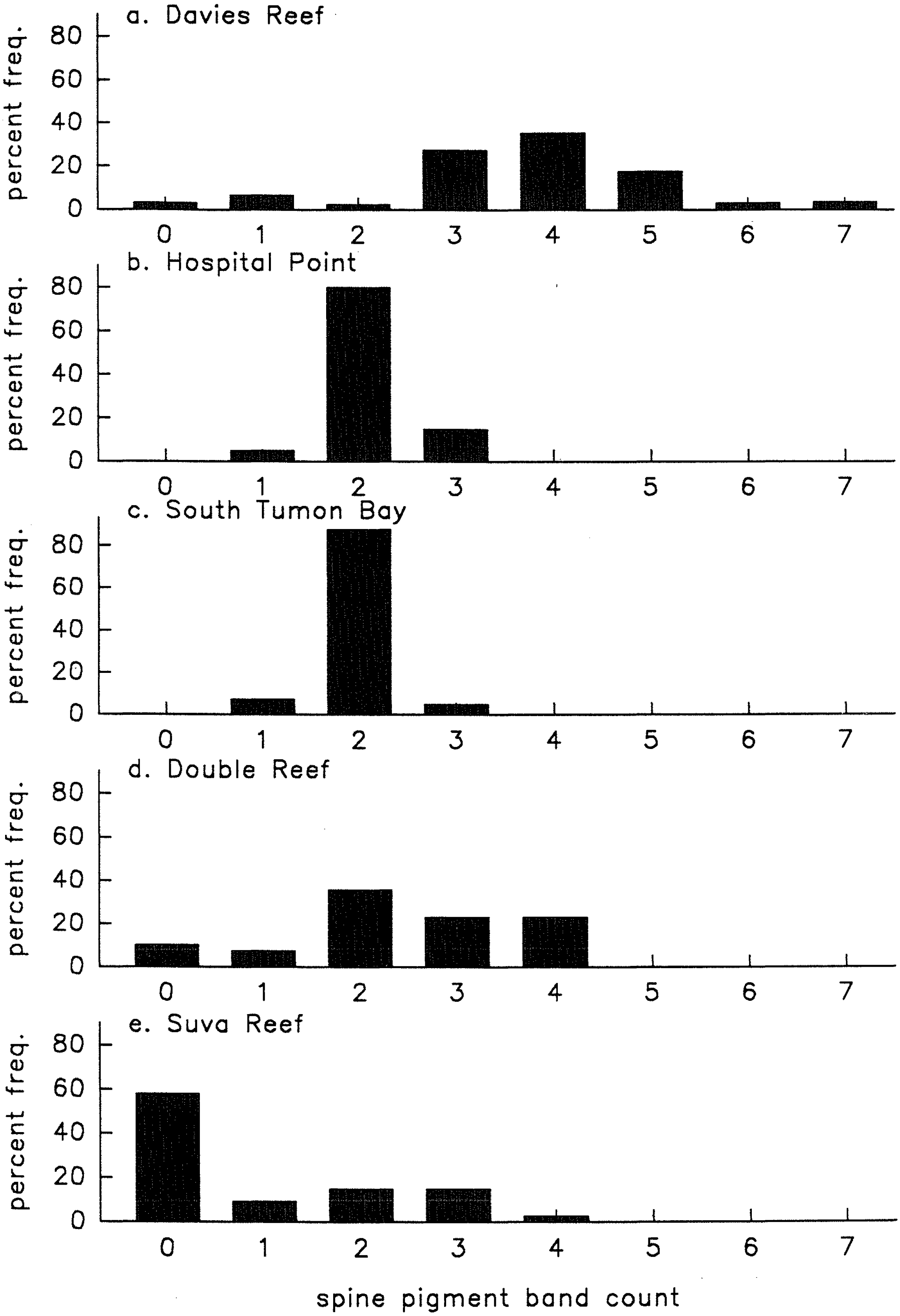

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
whole spine appendage (mm)

FIGURE 4.7



a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
20
40
60
80
0
1
2
3
4
5
6
7
spine pigment band count

FIGURE 4.8

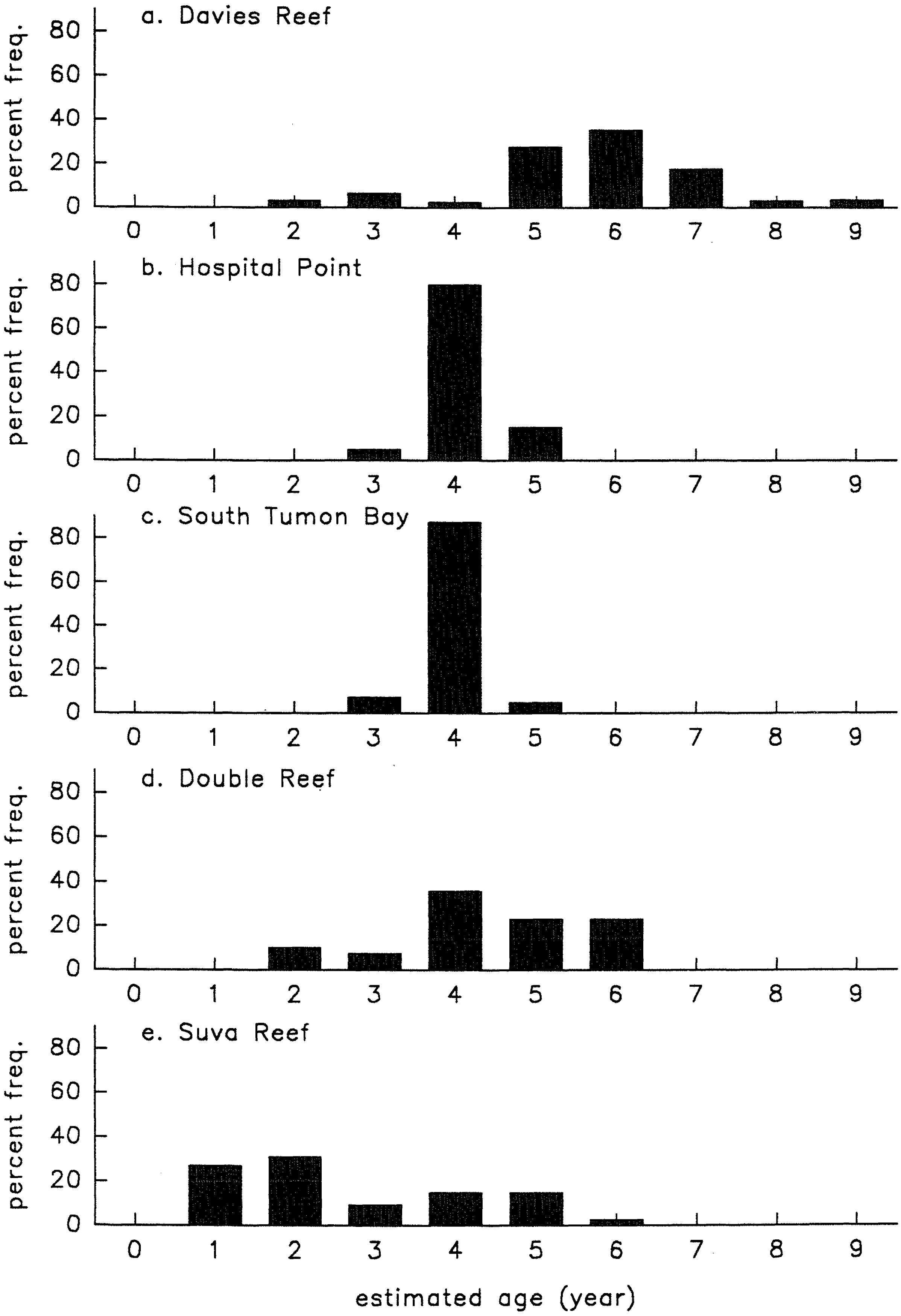
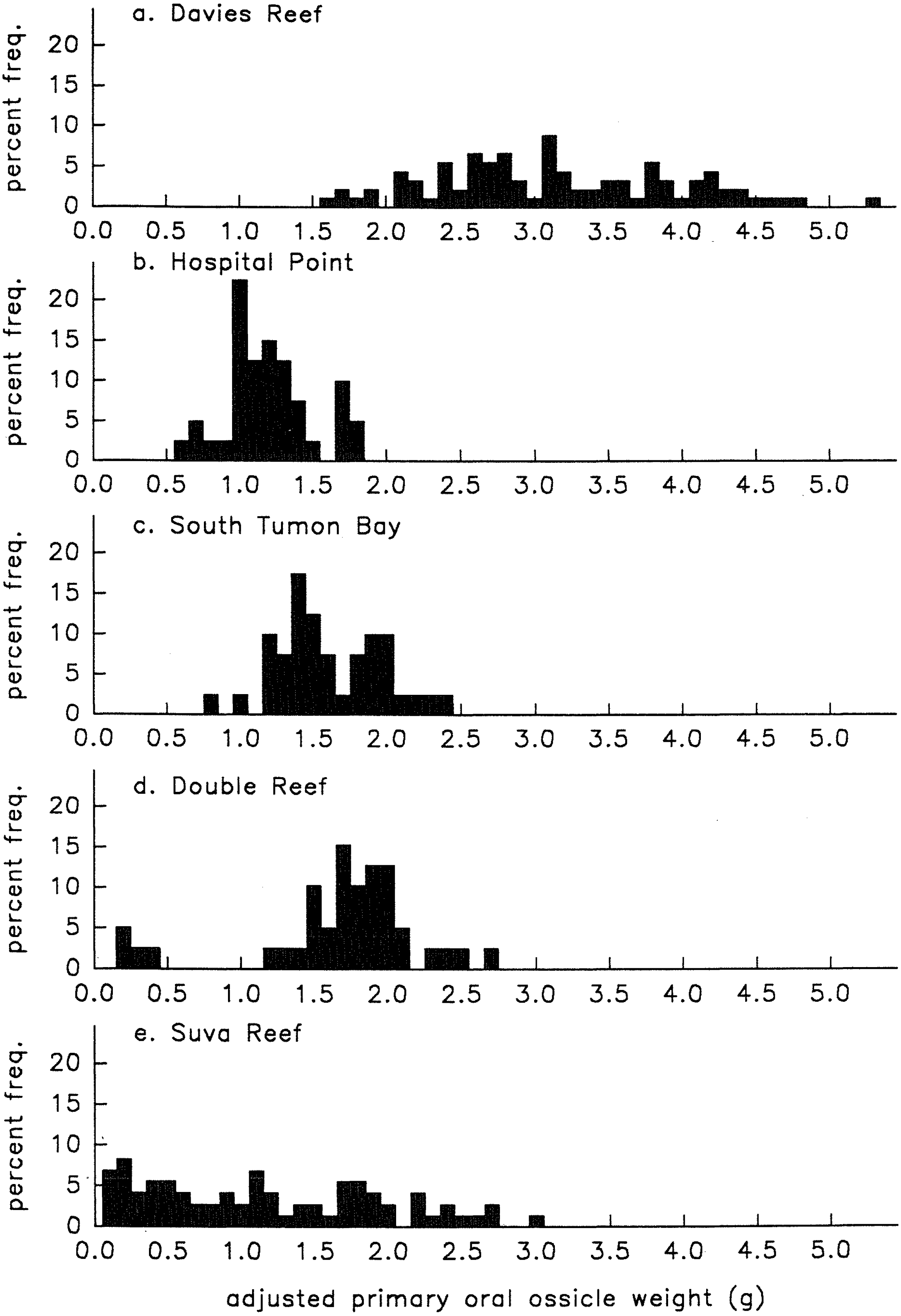

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
20
40
60
80
0
1
2
3
4
5
6
7
8
9
estimated age (year)

FIGURE 4.9



a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
adjusted primary oral ossicle weight (g)

FIGURE 4.10

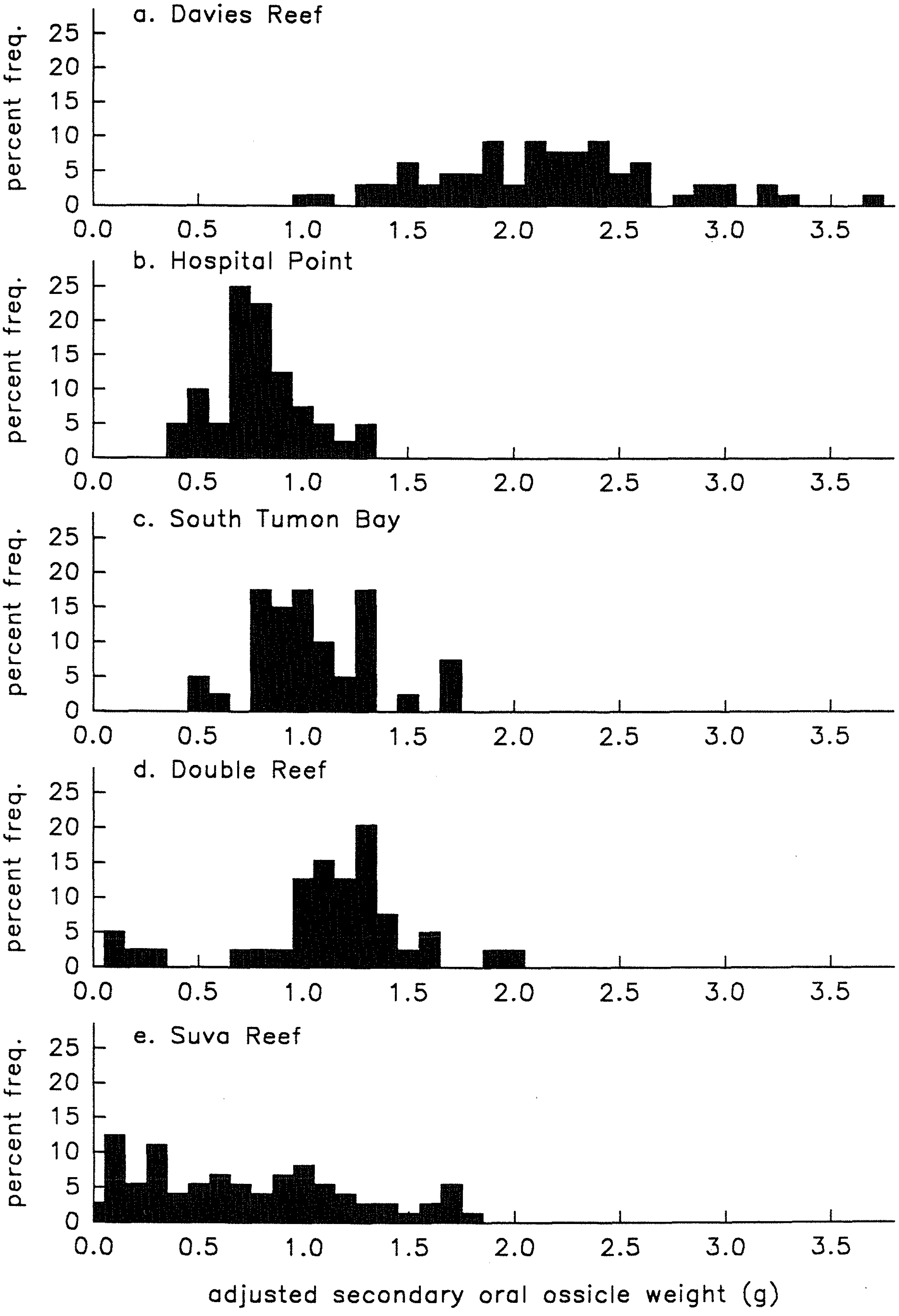

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
25
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
adjusted secondary oral ossicle weight (g)

FIGURE 4.11

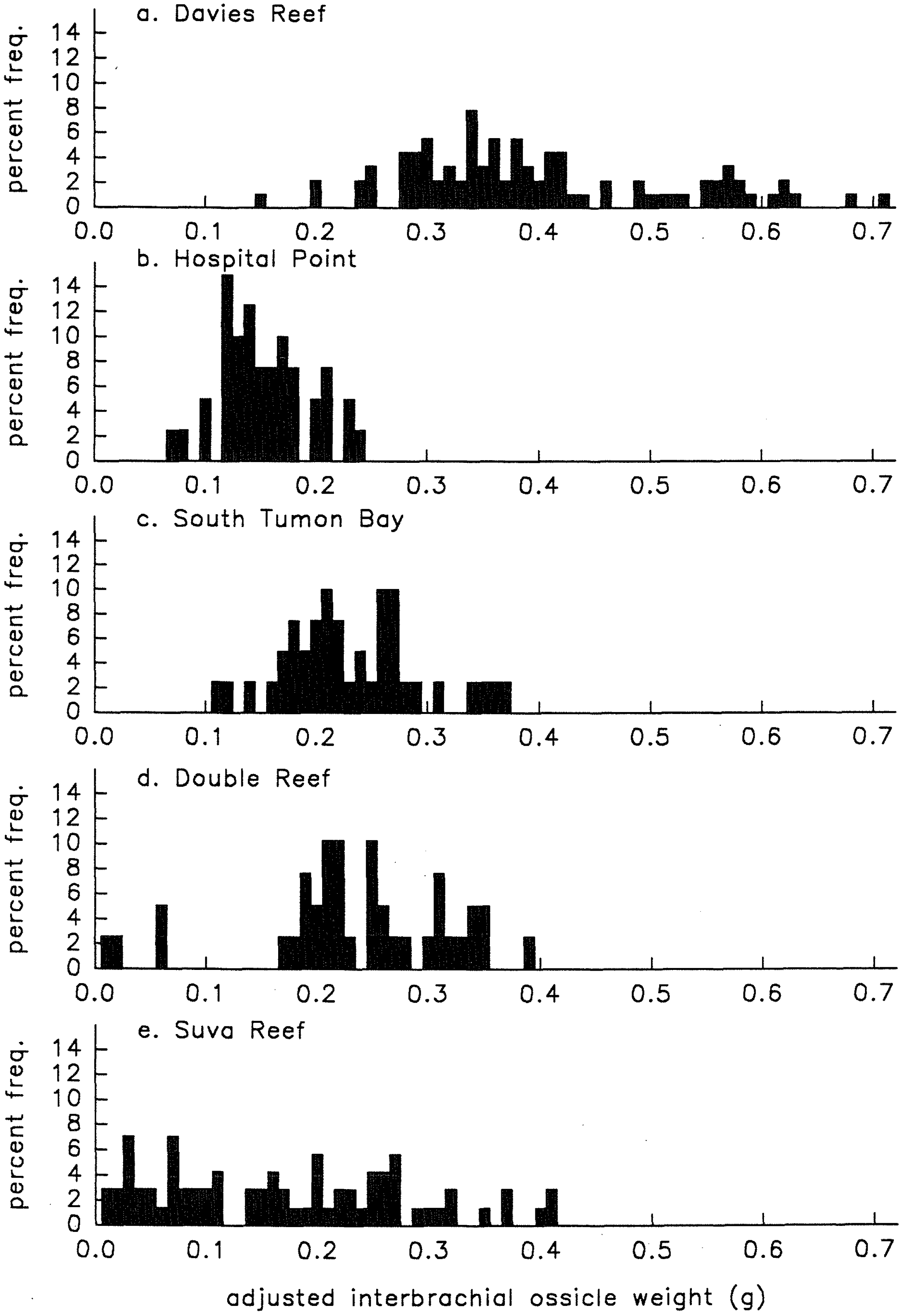

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
2
4
6
8
10
12
14
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
adjusted interbrachial ossicle weight (g)

FIGURE 4.12

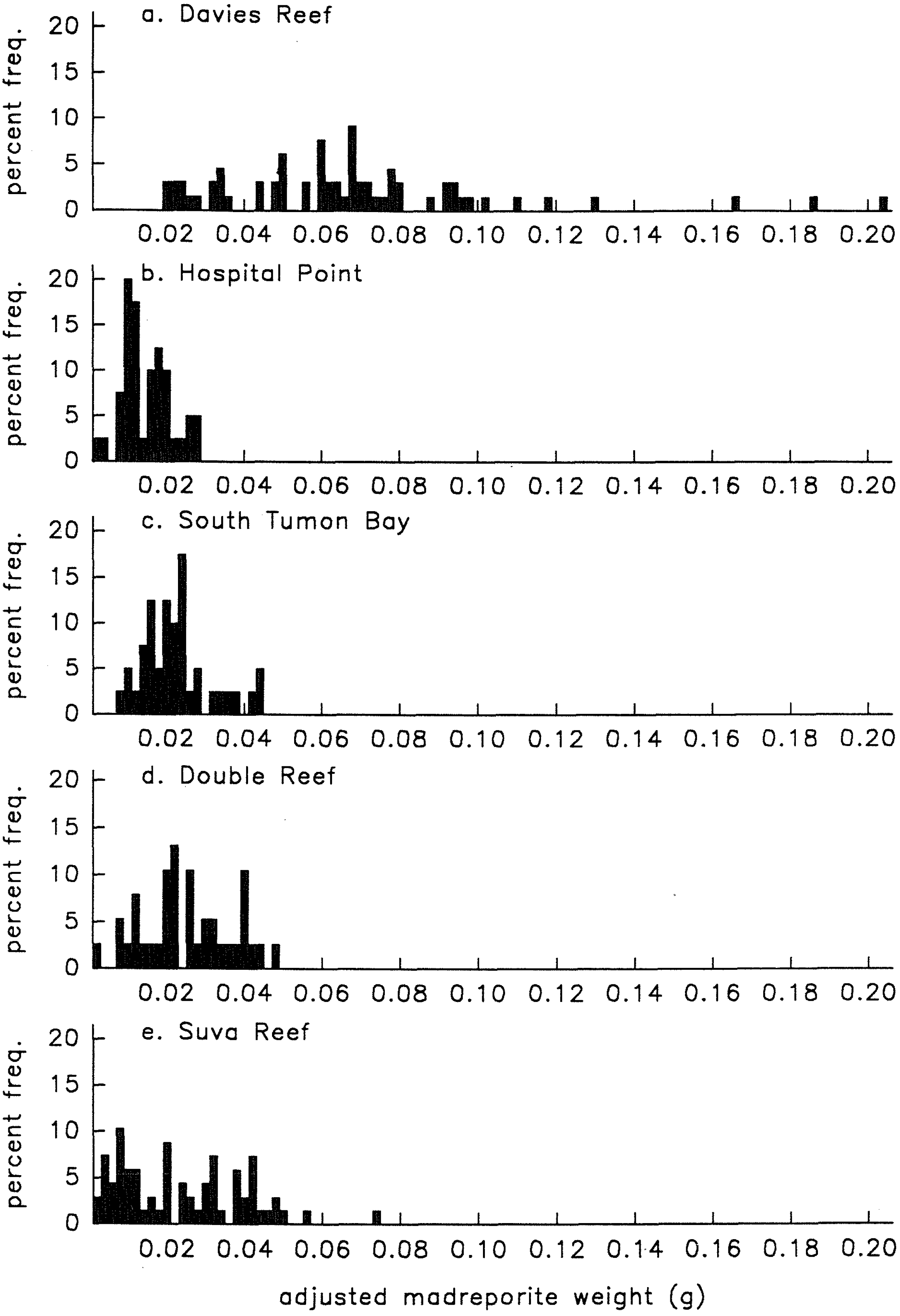

a. Davies Reef
b. Hospital Point
c. South Tumon Bay
d. Double Reef
e. Suva Reef
percent freq.
0
5
10
15
20
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0.18
0.20
adjusted madreporite weight (g)

FIGURE 4.13

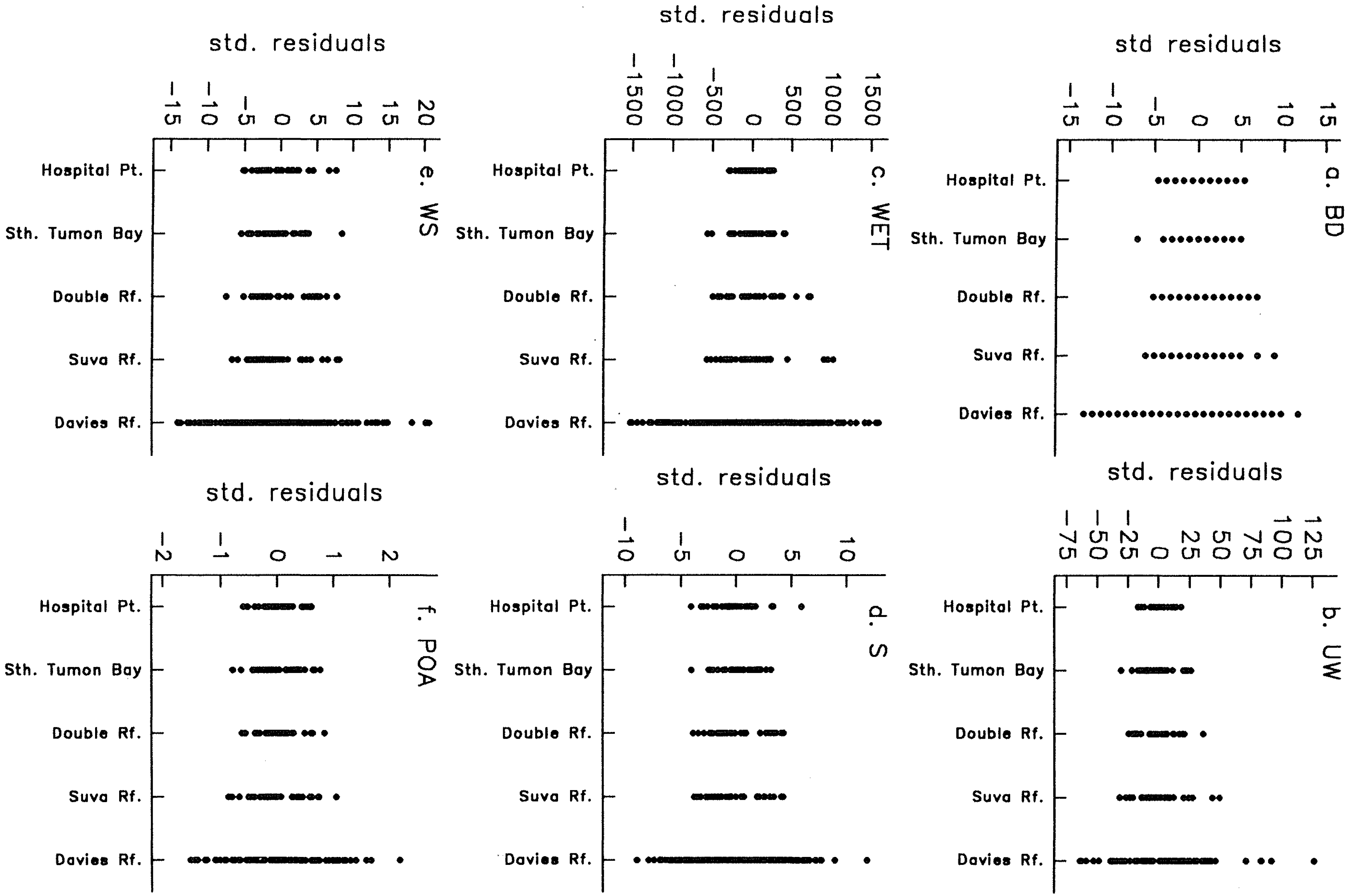

a. BD
std residuals
-15
-10
-5
0
5
10
15
b. UW
std. residuals
-75
-50
-25
0
25
50
75
100
125
c. WET
std. residuals
-1500
-1000
-500
0
500
1000
1500
d. S
std. residuals
-10
-5
0
5
10
e. WS
std. residuals
-15
-10
-5
0
5
10
15
20
f. POA
std. residuals
-2
-1
0
1
2
Hospital Pt.
Sth. Tumon Bay
Double Rf.
Suva Rf.
Davies Rf.

FIGURE 4.13

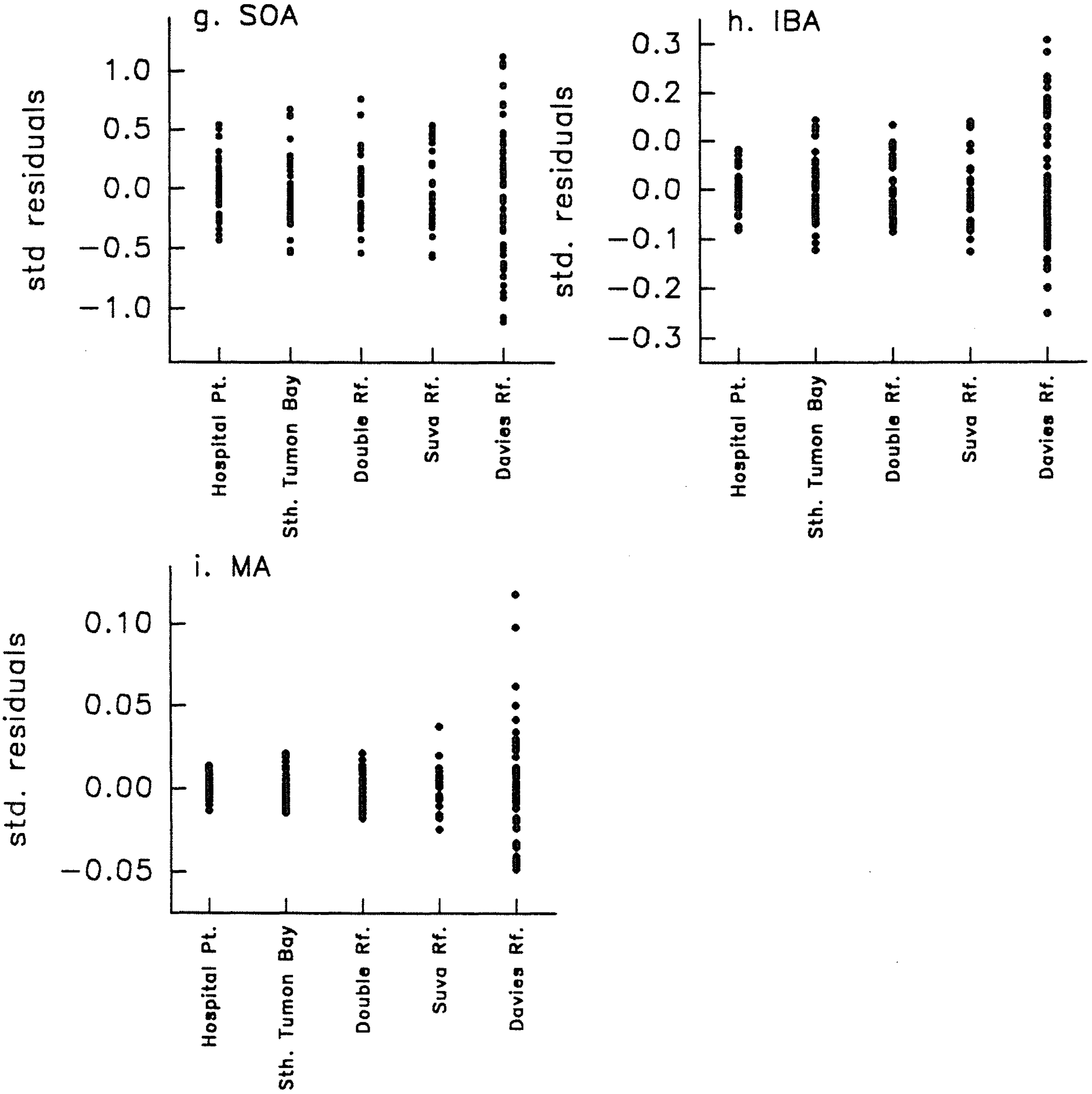
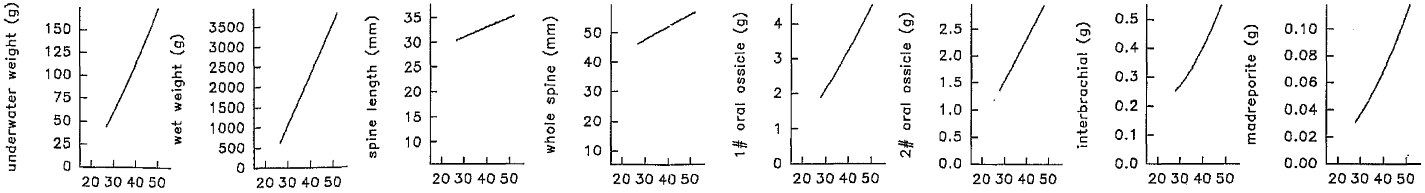
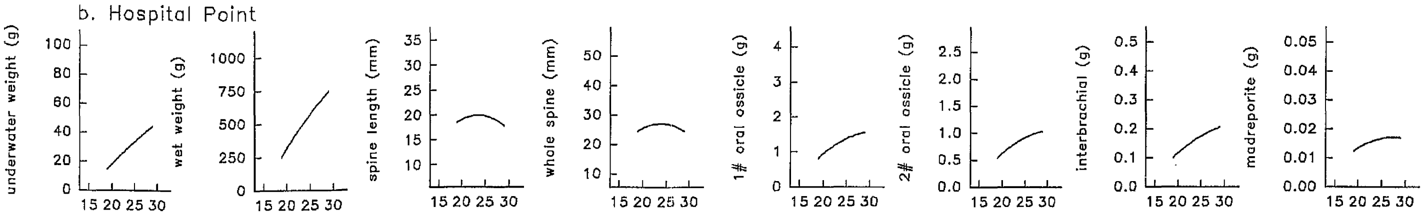

g. SOA
std residuals
1.0
0.5
0.0
−0.5
−1.0
Hospital Pt.
Sth. Tumon Bay
Double Rf.
Suva Rf.
Davies Rf.
h. IBA
std. residuals
0.3
0.2
0.0
0.0
−0.1
−0.2
−0.3
Hospital Pt.
Sth. Tumon Bay
Double Rf.
Suva Rf.
Davies Rf.
i. MA
std. residuals
0.10
0.05
0.00
−0.05
Hospital Pt.
Sth. Tumon Bay
Double Rf.
Suva Rf.
Davies Rf.

FIGURE 4.14

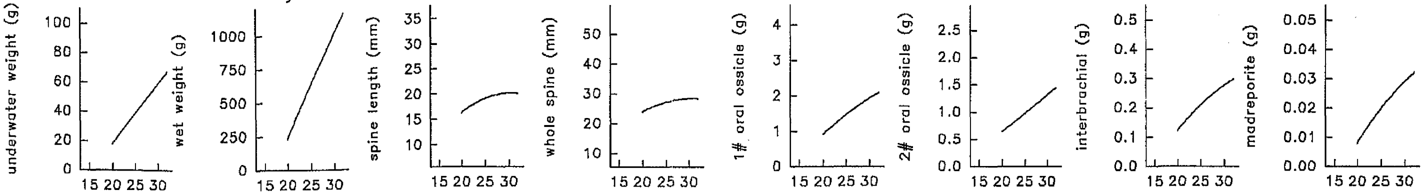
a. Davies Reef



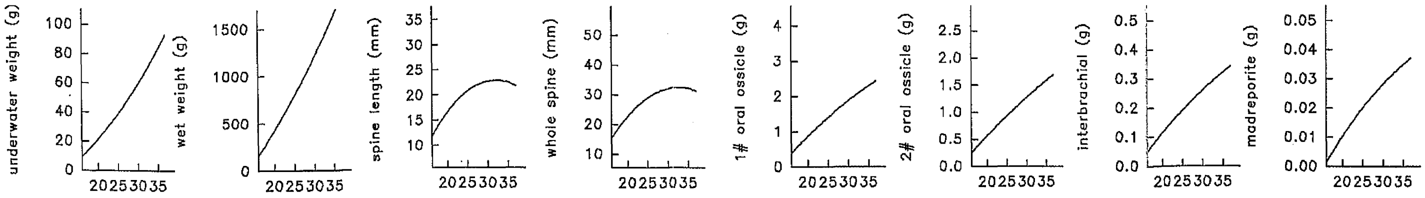
b. Hospital Point



c. South Tumon Bay



d. Double Reef



e. Suva Reef

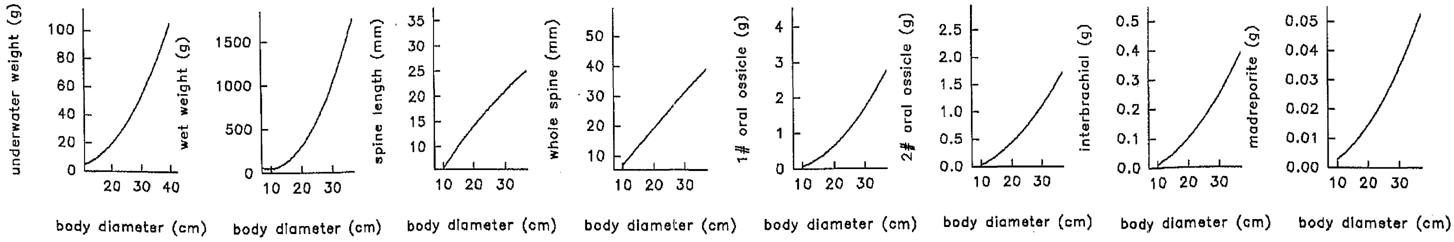
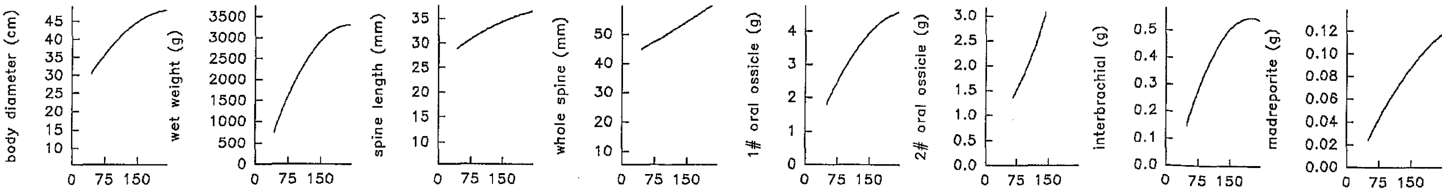
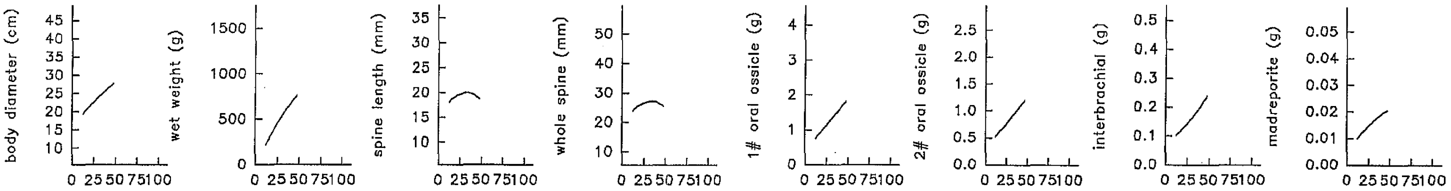


FIGURE 4.15

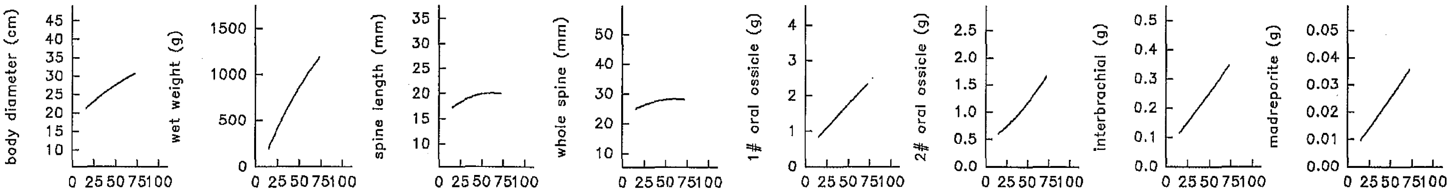
a. Davies Reef



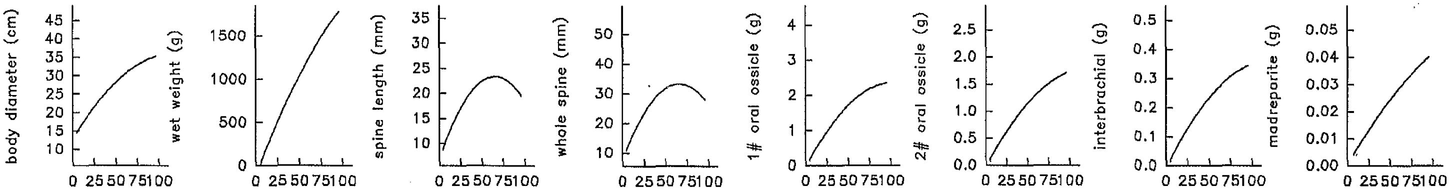
b. Hospital Point



c. South Tumon Bay



d. Double Reef



e. Suva Reef

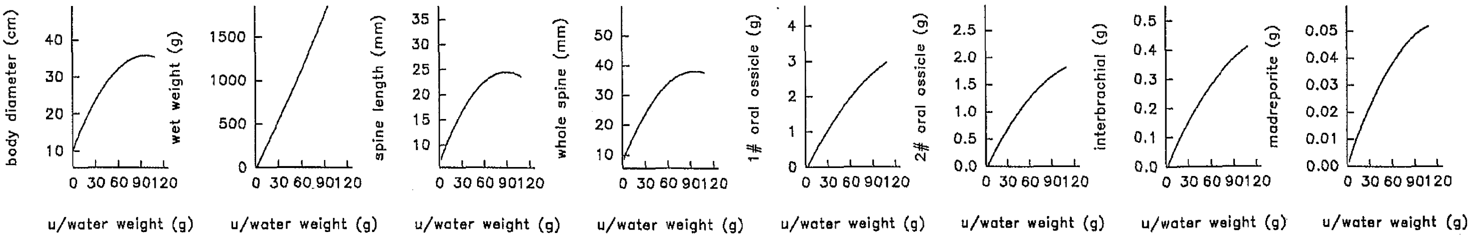
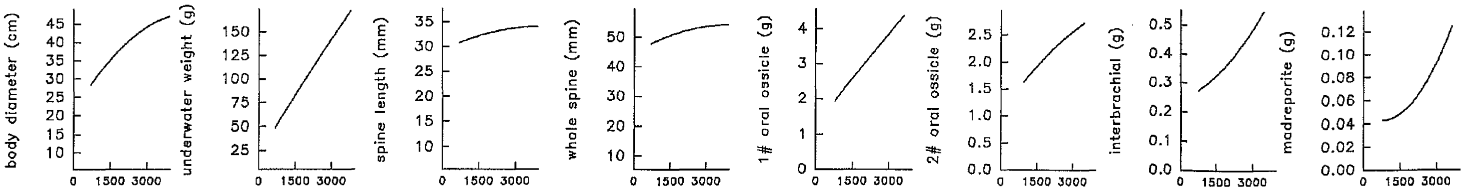
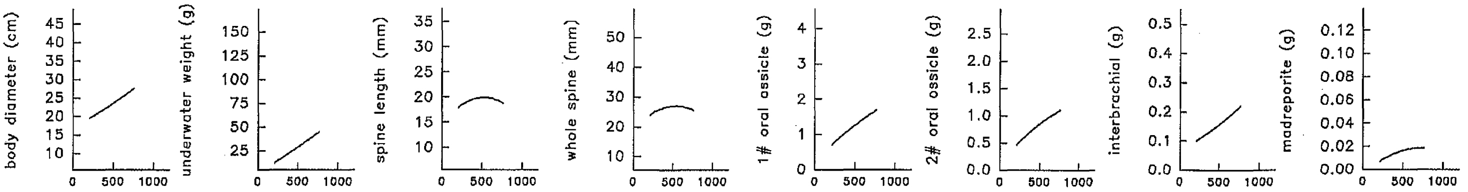


FIGURE 4.16

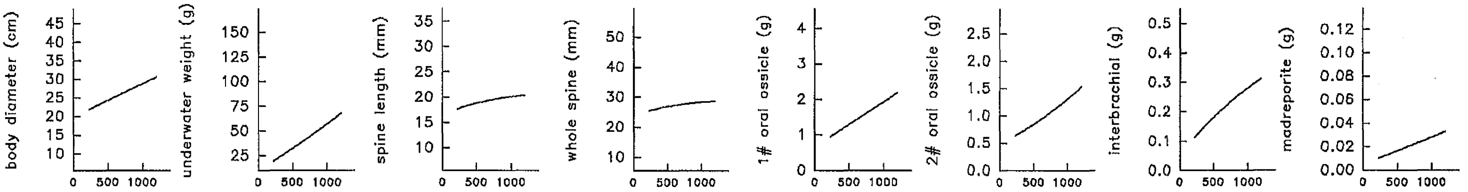
a. Davies Reef



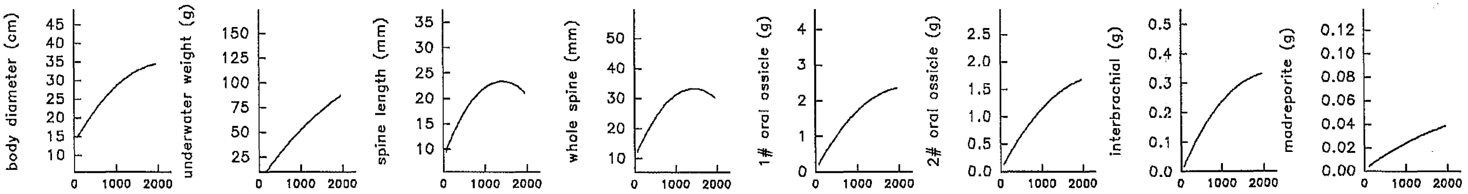
b. Hospital Point



c. South Tumon Bay



d. Double Reef



e. Suva Reef

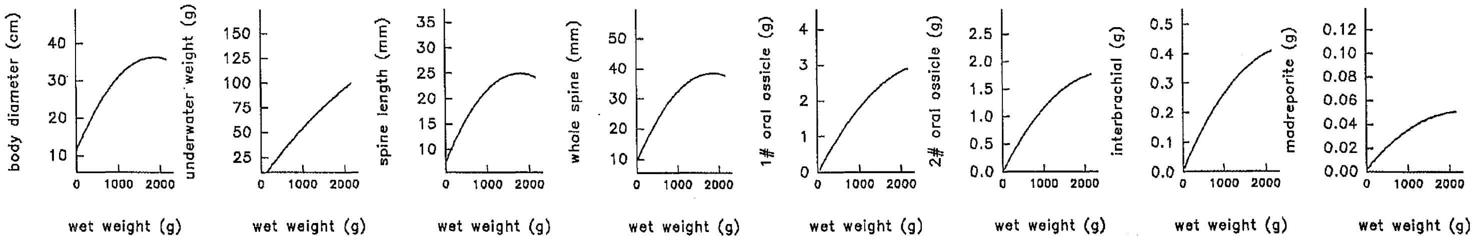
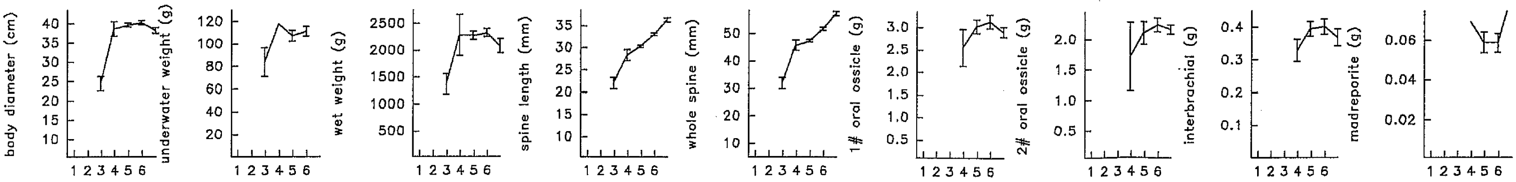
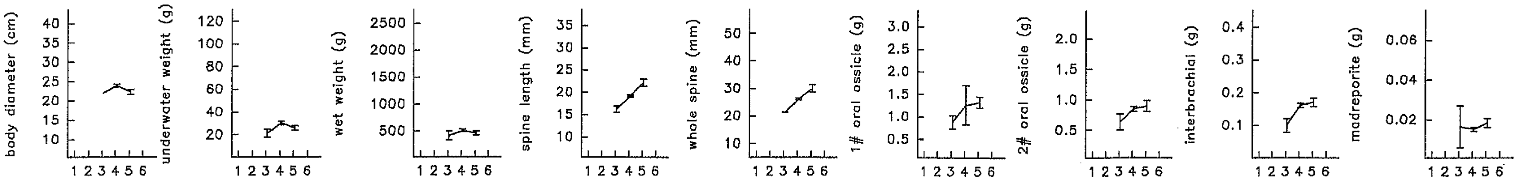


FIGURE 4.17

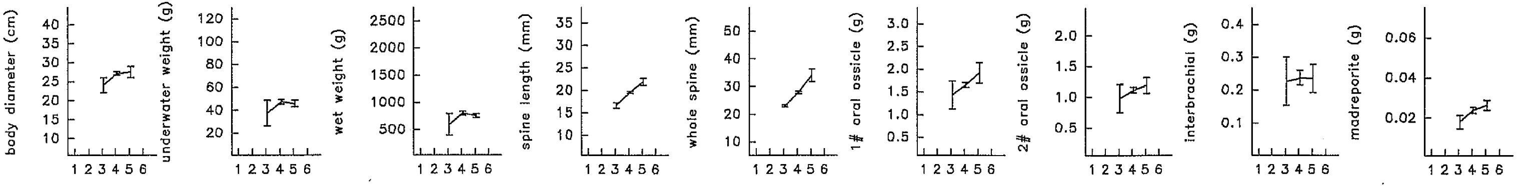
a. Davies Reef



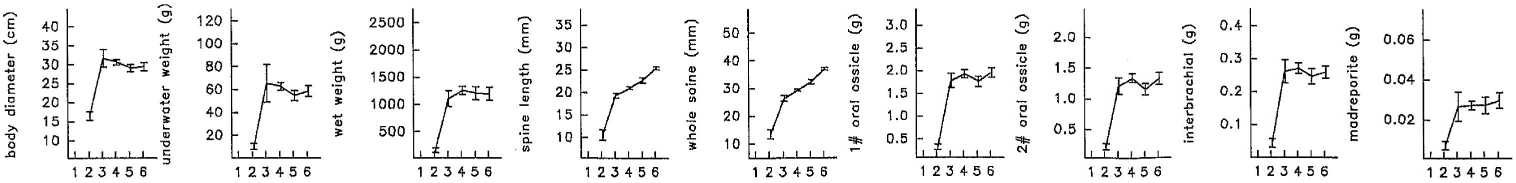
b. Hospital Point



c. South Tumon Bay



d. Double Reef



e. Suva Reef

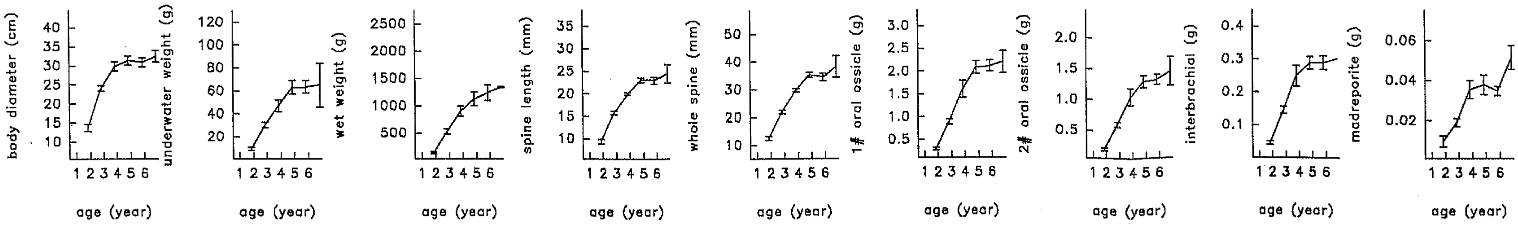
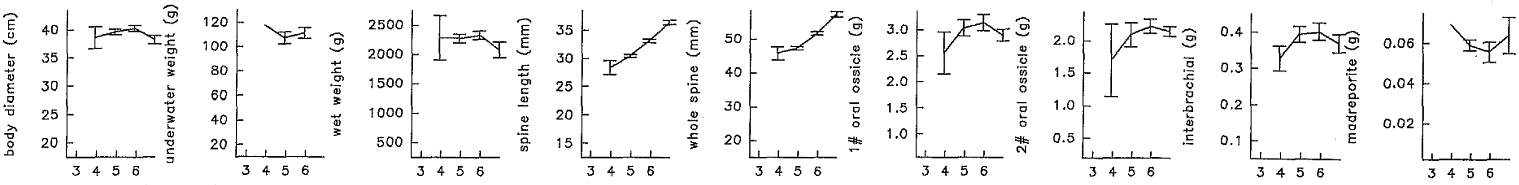
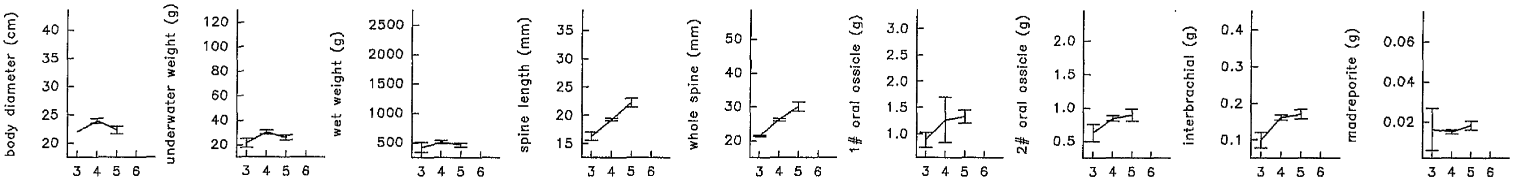


FIGURE 4.18

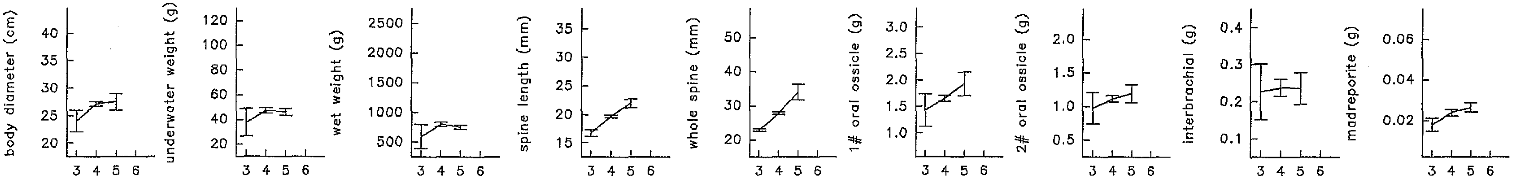
a. Davies Reef



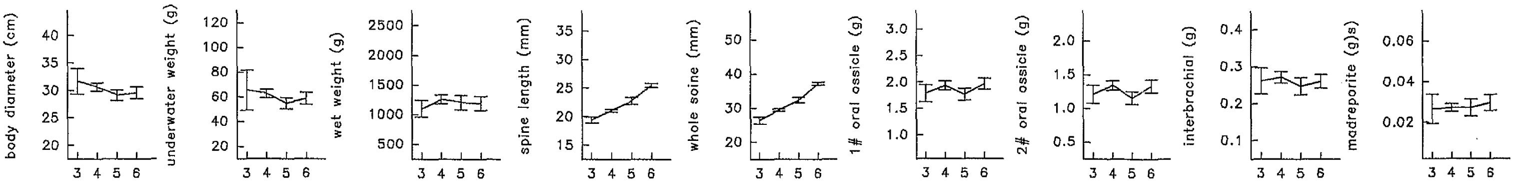
b. Hospital Point



c. South Tumon Bay



d. Double Reef



e. Suva Reef

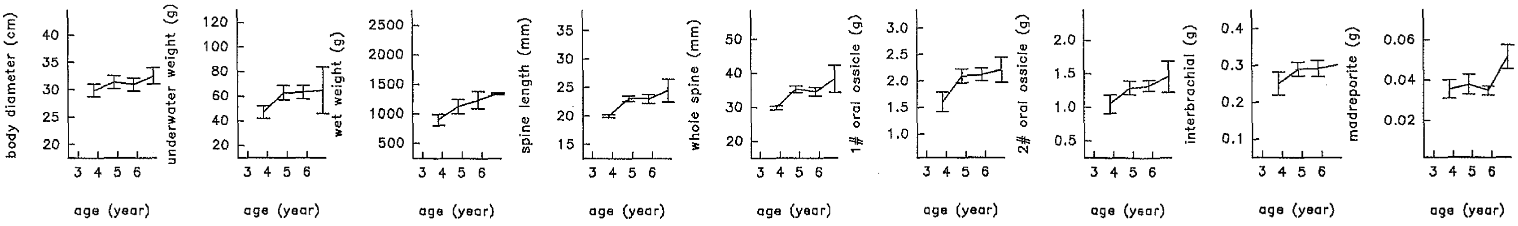


FIGURE 4.19

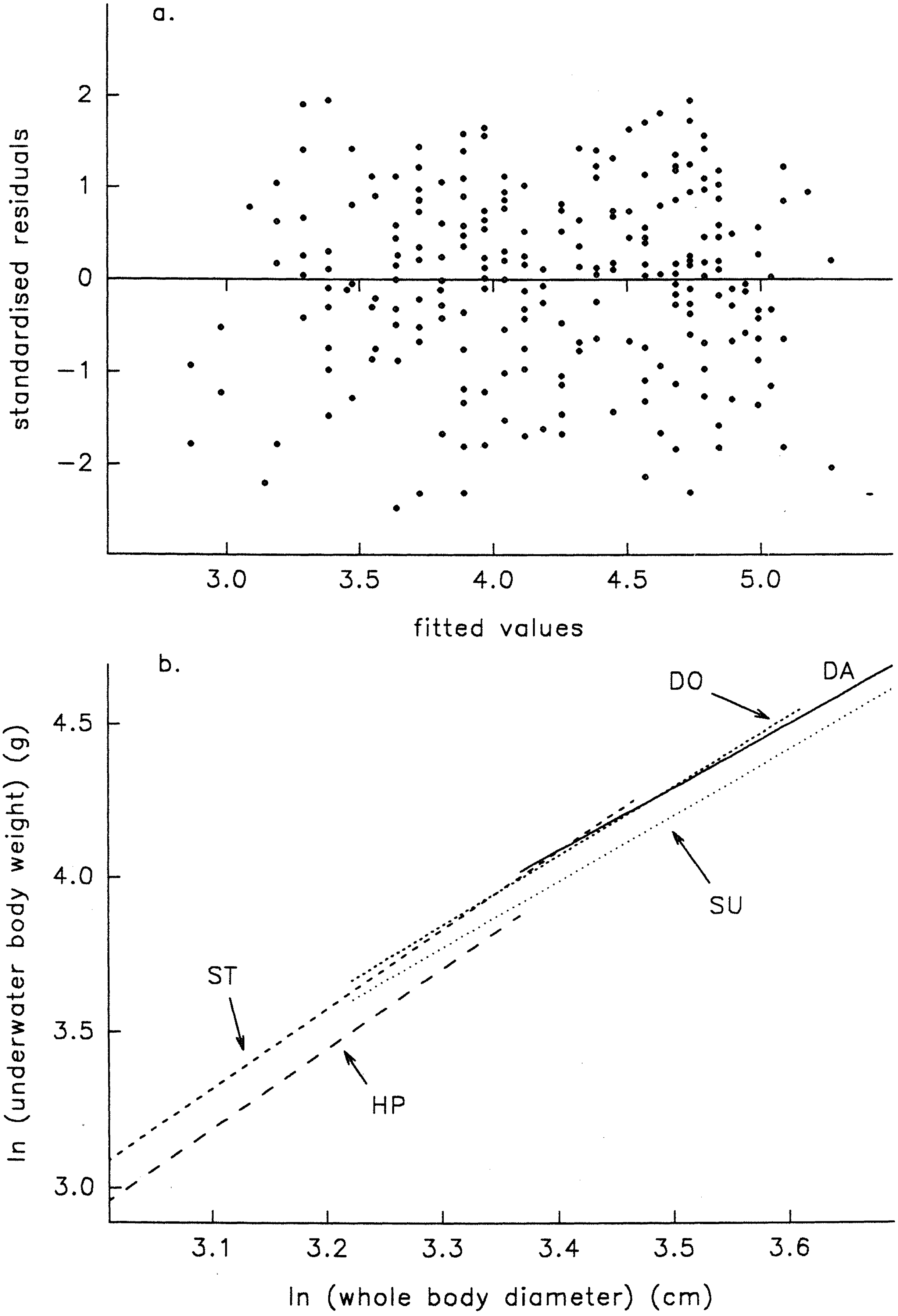
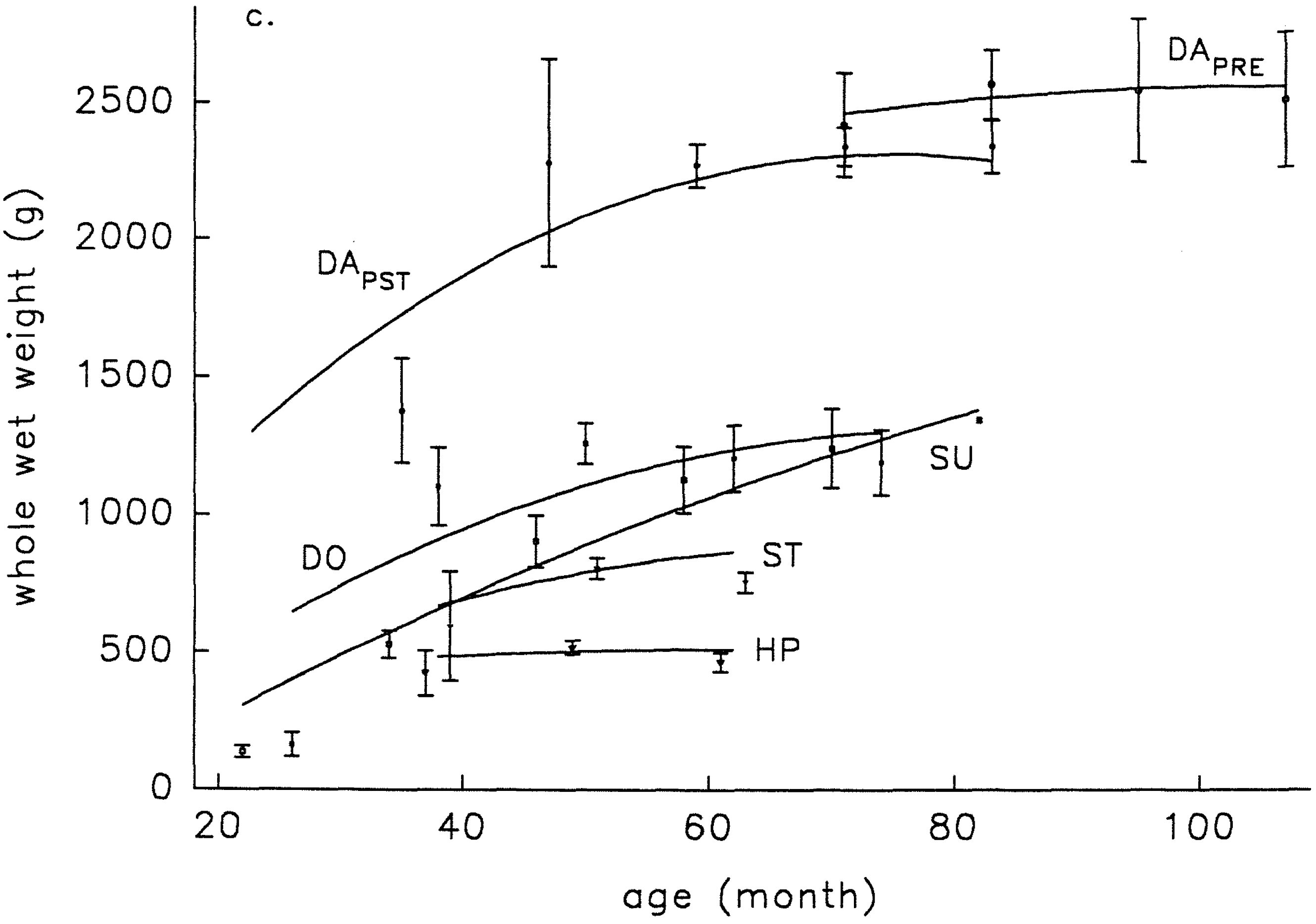
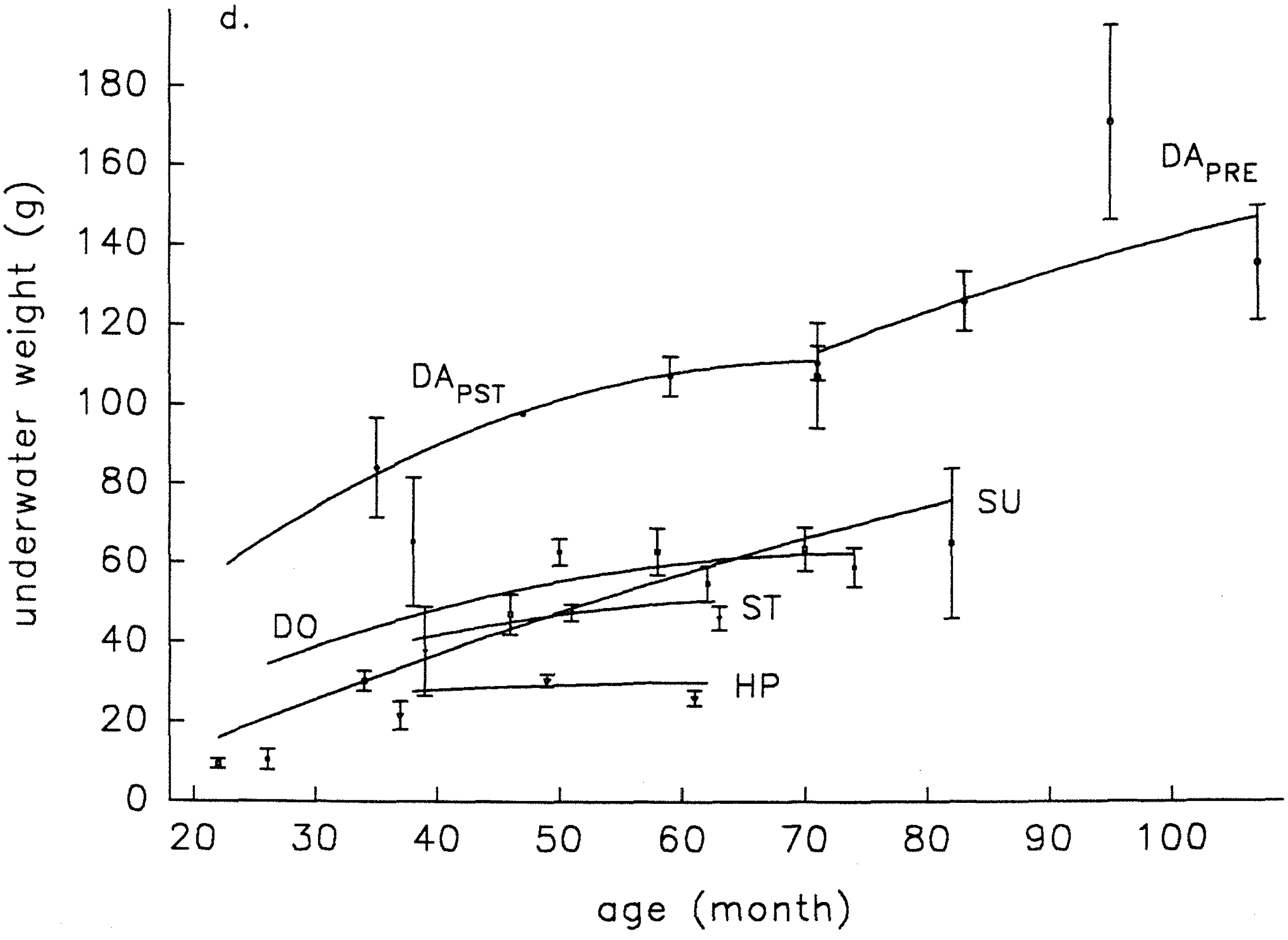

a.
standardised residuals
2
1
0
−1
−2
3.0
3.5
4.0
4.5
5.0
fitted values
b.
ln (underwater body weight) (g)
4.5
4.0
3.5
3.0
3.1
3.2
3.3
3.4
3.5
3.6
ln (whole body diameter) (cm)
DO
DA
SU
ST
HP

FIGURE 4.23

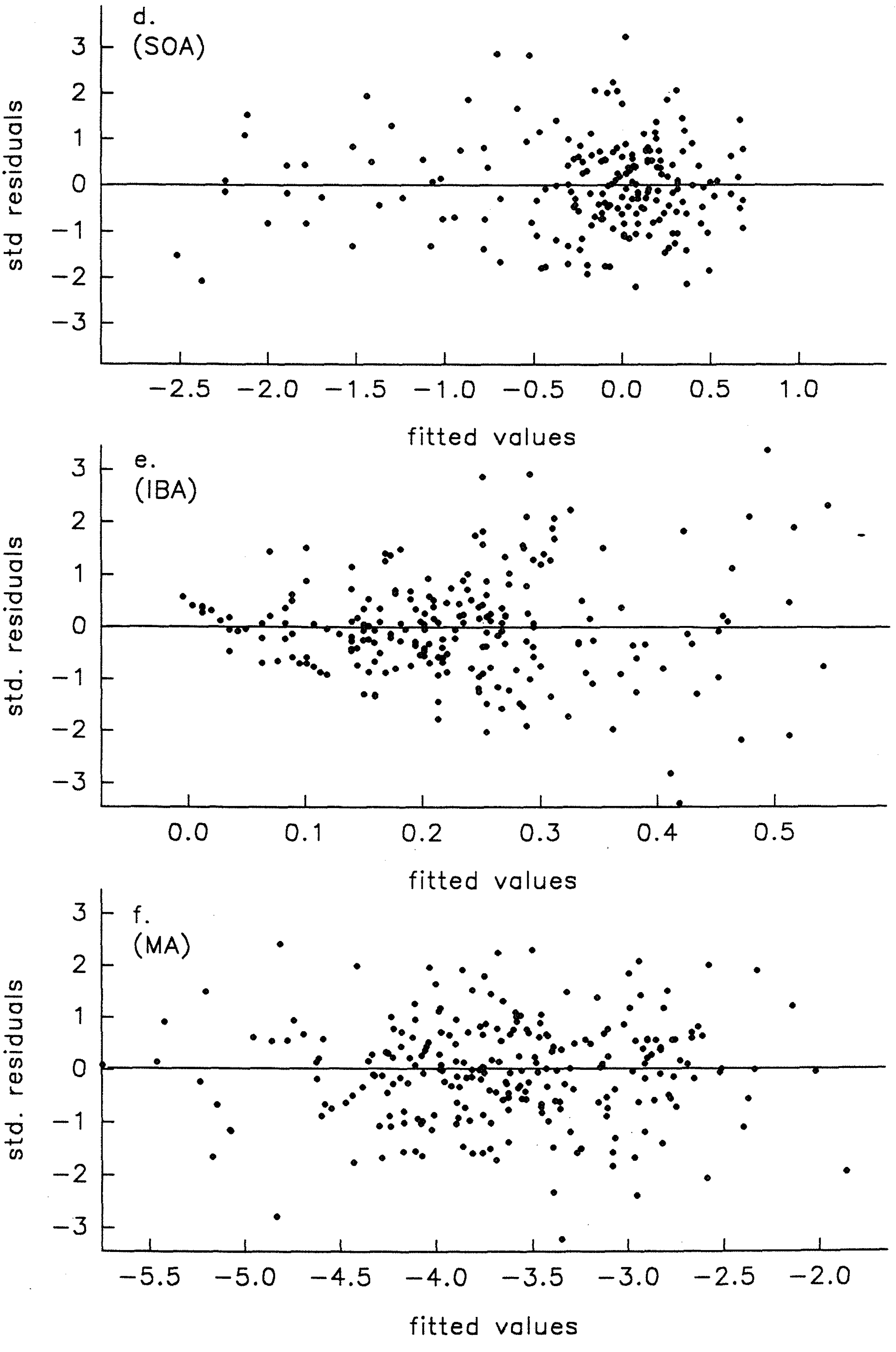


c.
whole wet weight (g)
0
500
1000
1500
2000
2500
20
40
60
80
100
age (month)
DA_PST
DA_PRE
DO
SU
ST
HP



d.
underwater weight (g)
0
20
40
60
80
100
120
140
160
180
20
30
40
50
60
70
80
90
100
age (month)
DA_PST
DA_PRE
DO
SU
ST
HP

FIGURE 4.24


d.
(SOA)
std residuals
3
2
1
0
−1
−2
−3
−2.5
−2.0
−1.5
−1.0
−0.5
0.0
0.5
1.0
fitted values
e.
(IBA)
std. residuals
3
2
1
0
−1
−2
−3
0.0
0.1
0.2
0.3
0.4
0.5
fitted values
f.
(MA)
std. residuals
3
2
1
0
−1
−2
−3
−5.5
−5.0
−4.5
−4.0
−3.5
−3.0
−2.5
−2.0
fitted values