Stump, Richard J. W. (1994) ***Age determination and life-history characteristics of Acanthaster planci(L.)(Echinodermata:Asteroidea)*****. PhD thesis, James Cook University.**

CHAPTER 3

THE DAVIES REEF POPULATION STUDY OF *A. planci.*

3.1. **Introduction**

3.1.1. *A. planci* population studies

Appropriate field data to describe *A. planci* population dynamics are lacking primarily because individuals have not been able to be monitored in the wild for any length of time (Moran, 1986). The paucity of information on population dynamics also stems from the often transient nature of populations as well as the physical and economic limitations incurred by longer term field studies on coral reefs. These circumstances have compelled researchers to search for indirect methods to gain an understanding of population characteristics involving their life history; i.e. extrapolation of results from laboratory rearing experiments and mathematical modelling studies. Much information on recruitment, age distribution, growth, mortality and longevity remains to be determined and is essential for an understanding of their population dynamics (Moran, 1986).

The objectives of this study were to obtain data for morphometric analyses to:

(a) obtain support for the results of the mark/recapture study.

(b) describe the dynamics of cohorts within the population.

(c) identify characteristics of the life history among cohorts, attempt to determine how they relate to population dynamics and habitats, and discuss how the predicted life history has influenced the regional history of outbreaking events.

3.1.2. Recent history of populations in the Central GBR

The Central GBR has experienced two outbreak episodes in the past 25 years (Reichelt et al., 1990). The first occurred between 1969 and 1973 in the Central Section and included Davies Reef. Small numbers of adult *A. planci* were commonly sighted on many reefs in this Section of the GBR during the 10 years leading up to the second episode. Observations over the past decade have shown there were only small numbers in the population on Davies Reef up to 1986. In 1982 seven individuals were sighted (J. Oliver, personal observation). In 1984 six individuals were sighted (R. Olsen, personal observation), and during the AIMS COT-CCEP survey in 1985, five individuals were sighted in 100 two-minute manta tows of the reef perimeter (Moran et al., 1988).

The most recent outbreak on Davies Reef was first reported by Johnson et al. (1988) on 28 June 1987 when 73 *A. planci* were sighted in 55 two-minute manta tows covering the area of the reef circumference. Large-scale recruitment, approximately 2+ years after their settlement, appeared first on the fore reef slope areas and then began to move around the reef following the less mobile, early juvenile phase. This timing of the outbreak was not observed within the lagoonal study site by Keesing and Lucas (1992), where *A. planci* densities were reported as 0.17 - 0.26 ha^{-1} in October 1987, increasing to 0.53 - 0.88 ha^{-1} in October 1988. Strip transects along the perimeter of Davies Reef were used by Ayling and Ayling (1992) and these areas contained higher densities being 34 - 64 ha^{-1} by June 1989. Therefore, at the time the present study commenced (October 1988) the outbreak starfish densities were moderate to high along the fore-reef slope with relatively abundant coral resources in most areas of the reef.

Initial hard coral cover on Davies Reef was high, ranging from 28% on back reef to 47% on the reef front slope in 1984 (Ayling and Ayling, 1992). They demonstrated a correlation between a substantial decrease in corallivorous chaetodontid species by approximately 0.5 and a significant decline in live corals during the *A. planci* outbreak on Davies Reef, between 1986 and 1989. Therefore, the outbreak population caused a significant impact on the live coral cover in many areas of Davies Reef over a period of approximately two to three years.

3.1.3. Life-history characteristics of *A. planci*.

3.1.3.1. Life history information from experimental *A. planci*

The life cycle of *A. planci* has been reported from laboratory studies by Lucas (1973; 1984) and Yamaguchi (1973; 1974). Lucas (1984) described the post-settlement life history phases in relation to age and reproductive status where: phase 1 involved the post-settlement and juvenile stages; phase 2 was identified by initial gametogenesis with gonads remaining small during the second year; phase 3 was sexual maturity where individuals "swell" with mature gonads in the third year and older; and phase 4, declining gametogenesis and body shrinkage after the fourth year. Lucas (1984) maintained several starfish in aquaria for up to 8 years and used this as an estimate of their longevity. However, the complete life-cycle as described by Lucas (1984) has yet to be confirmed from field population studies. Zann et al. (1987, 1990) showed that individuals in high density populations on Suva Reef had poorly developed gonads at 23 months of age and were unlikely to spawn large quantities of gametes that year. This field evidence supports the timetable up to phase 3 of the life history proposed by Lucas (1984) as Zann found starfish in high densities on Suva Reef with well developed gonads at the end of their third year (2+ years) and very large gonads at age 3+ years when they approached their asymptotic sizes.

3.1.3.2. The mode of growth in *A. planci*

The potential for large ranges in the body size of *A. planci* occurs in coral reef habitats because there is a wide variety of extrinsic factors which can affect development in these heterogenous environments (see section 1.3. on growth in Asteroidea). This is particularly applicable to *A. planci* which has been shown to experience food limitation (Kettle and Lucas, 1987) interpreted as *stress*, and survive significant levels of partial predation (Glynn, 1982b; McCallum, Endean and Cameron, 1989; Lawrence, 1991) interpreted as *disturbance*. These influences on development are particularly important when *A. planci* occurs in large aggregations and consumes large proportions of its coral food resources on reefs in relatively short periods of time.

A. planci growth was first described from laboratory rearing experiments (see Yamaguchi, 1973; Lucas, 1984). Several different growth functions have been applied to the results of laboratory experiments using *A. planci*. Yamaguchi (1975) reared individuals to sexual maturity, describing the size and age relationship with the logistic growth function, allowing for the exponential growth phase in the first year;

$$\mathbf{L}_t + {}_t = \mathbf{L}_\infty \, (\mathbf{1} - \boldsymbol{b} \, . \, \boldsymbol{e}^{(-K.L\,(t+\;t))})^{-1}$$

where:
$\mathbf{L}_\infty$ = 245mm
$\boldsymbol{b}$ = 188mm
K = 0.402
$_t$ = time span taken to measure growth

Birkeland and Lucas (1990) also concluded that the shape of the growth curve is sigmoidal where initial growth is exponential, tapering off after sexual maturity. This pattern is best represented by logistic or Gompertz equations (Birkeland and Lucas, 1990), however, Lawrence (1987) concluded that, under normal conditions the von Bertalanffy equation was appropriate for echinoderms that had passed through the initial exponential phase of growth. While there is an ongoing dispute and speculation concerning the mode of body growth in adult populations, the extent of variation in the mode of growth in *A. planci* is also not resolved because of the lack of appropriate data from field populations (Birkeland and Lucas, 1990).

In outbreak populations on the GBR the adult size of *A. planci* is generally less than 40cm (Lucas, 1984) under extrinsic resource limitation and therefore, there is significant overlap in size ranges of age classes in the adult population when cohorts reach their size maximum soon after maturity. However, field measurements from low density, high coral cover areas show *A. planci* can commonly grow to over 50cm in this region (Davies Reef; this study), 68cm (Lady Musgrave Reef; personal observation), 73cm (Kenchington; in Lucas, 1984) and approximately 100cm (Flinders Reef; GBRMPA COT database). Lucas (1984) proposed that the existence of these large animals was due to a greater availability of food in low density populations and possibly gamete resorption in the absence of conspecific stimulation to spawn. He suggested that large starfish found in low density populations develop by either;

(a) indeterminate growth under certain field conditions or,

(b) determinate growth, as found in laboratory studies but variability in genotype and/or phenotype results in a large potential size range.

Lucas (1984) argued that since the determinate mode of growth was also supported with field data, interpreted as characterising determinate growth in a population study from Hawaii (see Branham et al., 1971), his second hypothesis (b) was the preferred explanation. In the Hawaiian habitat, coral cover was very high but dominated by *Porites compressa* which is not a preferred food species. Instead, the starfish were selecting the acroporid *Montipora verrucosa* which comprised about 5% of the coral community, indicating that food-limitation may well have influenced starfish growth in that population and growth under conditions of unlimited food supply has yet to be described.

Moran (1986) reviewed the debate concerning the mode of growth in the field, stating it was unresolved because no growth studies of individual starfish under controlled conditions for extended periods had been possible. Since then, growth studies with accurate age determination have only been achieved in populations by Zann et al. (1987; 1990) and Habe et al. (1989) which were dominated by single, juvenile cohorts in relatively high densities and therefore, enabled age estimation from body size up to the age of maturity. Unfortunately, there is virtually no information on growth in low density populations. The growth pattern observed by Zann et al. (1990) allowed reasonably accurate age estimation in the first and second years during the period of exponential growth, however, it was not possible to age older year classes as the overlap in size ranges was too great. The large population on Suva Reef, comprising a single cohort, was monitored over three years and the rate of body growth was found to slow considerably as individuals approached sexual maturity, although an asymptote in growth was not apparent in their Figure (3) before the study concluded. The predicted mean maximum body size of the Suva Reef cohort was relatively small ($(\mathbf{BD})_\infty$ = 24cm) showing these starfish had probably experienced a shortage of food resources.

Although Kettle (1990) found no suggestion of genotypic differences in the metabolic rate between the rare "giant" *A. planci* (i.e. > 50cm) of the GBR and the smaller individuals from outbreak populations, the results from his study concerning their growth were inconclusive. Kettle and Lucas (1987) had previously suggested there was little variation in the mode of growth in *A. planci* in different densities after finding no difference in the relationship between metabolic rate and wet weight of the "giant" southern GBR animals and smaller adult specimens collected from reefs off Townsville (Central Section, GBR). Kettle (1990) favoured the idea that the cause of large variation in adult size in the field was probably the variability in their environment, for larger starfish were generally found in habitat conditions of unlimited resources within a relatively small habitat range. Paine (1976) compared *Pisaster ochraceus* populations in subtidal habitats characterized by mean body size differences of approximately one order of magnitude. While speculating on the causes of local density and body size variations he suggested that larger body sizes developed in near optimal habitat conditions of continual submergence with an abundance of suitable prey. Differences in densities of populations appeared to be correlated with

Keesing (1990) also contributed to this debate by predicting that very large *A. planci* probably do not develop in the northern areas of the GBR because they would have difficulty consuming sufficient food to meet their metabolic demands at summer water temperatures (where Q_{10} values for 0_2 consumption double between 25 and 30°C (see Birkeland and Lucas, 1990)). However, a report of very large *A. planci* from Lizard Island, Northern GBR (see, Lucas, 1984), either invalidates this argument or supports the notion that metabolic demand may vary with individual histories of population density and food resources experienced. The feeding rates used by Keesing to support his argument were derived with data collected from outbreak populations on Davies Reef and Wheeler Reef, Central GBR, and therefore his argument assumes that several critical life-history characteristics, including growth rates are similar in all types of populations.

It follows that under conditions of extrinsic limitation of food, *A. planci* exhibits low growth rates in its adult phase and is restricted in size at maturity and asymptotic body size (generally below 40cm whole body diameter on the GBR), while the potential to achieve body sizes up to 100cm (see above) occurs in habitats with unrestricted resources.. To resolve the mode of growth debate, individuals from low density populations in habitats with high coral cover must be followed for a number of years. Alternatively, individuals may be reared under controlled conditions with unlimited food for a similar period requiring large aquaria with access to very large quantities of coral (an experiment that is obviously difficult to achieve). However, data from populations describing the variation in growth among individuals over shorter periods, as in this study, may also contribute useful information without undertaking expensive, longer term studies.

3.1.4. The principle of symmetry in life histories

Analyses of life-history characteristics within taxa have shown that there are trade-offs between the rates and stages in life processes (e.g. growth rate, mortality rate, maximum size and size at maturity) among individuals, cohorts or populations such that variation in one produces a relative change in the other resulting in a taxon specific symmetry. The dimensionless ratio or product of the rates and stages remains fixed or invariant (a life-history constant), in a statistical sense, under the range of conditions in which the species is found, which has been confirmed in a wide variety of taxa (Charnov, 1993). Therefore, these dimensionless numbers are used to determine the significance of hypothesised relationships between life-history characteristics of taxa at various levels of classification. However, Vøllestad et al. (1993) found the life-history constants did vary in analyses of 29 brown trout populations in Norway, apparently showing differences in trade-off functions among the populations. They suggested that the unexpected variation was due to the complexity of the life history or the variability of habitat types occupied by the animal in question. These factors may be less important in trout species compared with *A. planci* whose larvae can travel long distances and populations can alter habitat conditions.

A review by Ebert (1975) involving studies on 16 echinoid species showed that the ratio of the growth constant ***K*** and the instantaneous mortality rate ***M*** remained constant with a positive correlation between the two parameters. Ebert suggested that differences in the allocation of limited resources to growth, reproduction, and maintenance result in different sets of adaptations in echinoids where fitness is maximised by the predictability of recruitment success. Therefore, faster growing species allocate relatively more energy to growth and reproduction and have fewer mechanisms to promote individual survival, i.e. for maintenance and protection (higher mortality rates). The adaptations that evolve depend on the phenotypic variability and the unpredictability or harshness of the environment relative to those adaptations (Ebert, 1975):

(a) An unpredictable environment with respect to recruitment promotes species with fugitive characteristics which exploit habitats rapidly or individuals which survive over long periods of unfavourable conditions, expending more resources on maintenance.

(b) A predictable environment in relation to recruitment success promotes adaptations to maximise fitness from high fecundity, early maturation by sacrificing allocation to somatic maintenance resulting in a shortened lifespan.

Application of life-history theory to populations using the Beverton-Holt constants relies on three assumptions (Charnov, 1993):

(a) Fitness is maximised through the net reproductive rate $\boldsymbol{R_0}$ (where $\boldsymbol{R_0} = 1$, assuming a stable population size), and implied through the density dependence of juvenile mortality. Individual growth and adult mortality rates are independent of population size.

(b) The average number of offspring born over a reproductive lifespan is a function of body size at maturity (which is more accurate for a determinate mode of growth).

(c) There is a predicted trade-off between growth rate and asymptotic body size, described by the von Bertalanffy growth function:

$$\mathbf{L}_\infty \propto K^{-h} \quad \text{where } 0 < h < 1$$

further, h is related to $\mathbf{L}_\infty$ through $(\mathbf{L}_\alpha/\mathbf{L}_\infty)$

By applying these assumptions, an assessment of this theory was undertaken using results obtained from the Davies Reef *A. planci* population study. If the patterns derived from life-history constant analyses from such diverse taxa also apply to echinoderm species, then the application of life-history constant analyses may provide useful insights into the evolution of life-history traits of *A. planci* as well as echinoderm species, in general.

3.2. **Methods**

The field study was divided into two parts involving:

(a) searches for recaptured marked starfish for SPBC method validation (Chapter 2).

(b) population subsampling exercises for time-series analyses of morphometric variables over 38 months.

The morphometric study used data collected from eight sampling occasions over 38 months between October, 1988 and December, 1991. The intervals of sampling were at approximately six month intervals, and dependent on available shared ship time.

3.2.1. Davies Reef collections

A. planci collections from Davies Reef were made during daylight hours, generally limiting sampling to the adult population. Collections were undertaken at random points around the reef, although they were focussed on areas of highest densities to reduce the time spent diving under limited allocation of field time. Sampling for the skeletochronometric study on Davies Reef, Central GBR, occurred in: October 1988 (n = 142); April 1989 (n = 142); October 1989 (n = 300); March 1990 (n = 400); October 1990 (n = 200); December 1990 (n = 102), May 1991 (n = 202) and December, 1991 (n = 198). Those starfish not involved in the mark and release exercise were sampled for the morphometric study, including the oral ossicle group to compare with spine ossicle and spine appendage growth analyses. Oral ossicle group collections involved dissection of the entire body so that larger samples of spines and pedicels were also obtained than from the mark/recapture samples. Sample preparation and processing are outlined in Chapter 2.

3.2.2. Other populations from the GBR region

Spine samples from adult *A. planci* were obtained from two other populations from the GBR region. Collections were made from a moderately sized population centred around Butterfly Bay, Hook Island, Whitsunday Group and sampled in October 1989 (n = 16) and November 1990 (n = 52). A low density population had occurred in the area for a number of years, since a number of sightings had been made around Hook Island between 1982 and 1987 (GBRMPA database), and 5 *A. planci* sighted in 31 2-minute manta tows (AIMS survey, 7/11/88). The second population sampled was in very low density from around Lady Musgrave Island, Southern Section. Samples were collected in April, 1986 (n = 9) and September, 1991 (n = 2). Few *A. planci* have been sighted on this reef in the past 12 years: in 1979, six *A. planci* sighted (GBRMPA database; L. Zell, personal communication); in 1982, 12 *A. planci* sighted (no source); in 1984, 8 *A. planci* sighted (GBRMPA database; A. Phipps, personal communication).

Population sizes for Butterfly Bay, Hook Island and Lady Musgrave Reef are estimated from the numbers of starfish obtained after conducting searches over large areas of these locations. The equation for whole population density (PD) is:

$$(\mathrm{PD}) = \frac{(\text{estimated population size})}{(\text{area of reef})} \qquad (3.1)$$

3.2.3. Population morphometric analyses

3.2.3.1. Analyses for seasonal variation and asymptotic growth.

Time series cohort analyses of five morphometric variables (whole body diameter (BD), spine ossicle length (S), whole spine appendage, primary oral ossicle weight (PO), secondary oral ossicle weight (SO) involved three levels of analysis:

(a) ANOVA and serial Tukey (HSD) tests for significant differences between cohorts using all data (i), and omitting all juvenile/sub adult individuals (AGE < 3+ years) (ii). Where; 1982 = 82; 1983 = 83; 1984 = 84; etc..

(b) Replication test of fit for linearity within each cohort over the eight sample dates. Where; 1982 = 82, 1983 = 83, 1984 = 84, etc..

(c) Curve fitting analyses for (a) whole sample and (b) omitting months where apparent asymptotes have developed in cohorts during the study. Comparison of curve fit with regression analyses.

Curve equations were selected to test for seasonal variation and asymptotic growth and both factors combined into one equation. The equations were:

(i) seasonal: $y = a + (b \,.\, \cos((x - c) \,.\, 0.524)) + (d \,.\, x)$ (3.3)

(ii) asymptotic: $y = l \,.\, (1 - (m \,.e^{(-k \,.\, x)}))$ (3.4)

(iii) (a) & (b): $y = b \,.\, (\cos(x - c) \,.\, 0.524)) + (l \,.(1 - (m.\, e^{(-k \,.\, x)}))$ (3.5)

where: a = deseasonalised mean value of the morphometric variable.

b = amplitude of the seasonal variation (2 x b = seasonal range), i.e. negative values mean that c describes a seasonal minimum.

c = offset of the seasonal maxima from t_0.

d = overall slope coefficient throughout study period.

l = asymptotic size maximum of the morphometric variable.

m = correction factor for size of variable when first sampled, i.e. when individuals were first recruited into the adult population.
k = asymptotic growth constant.

3.2.3.2. Mortality rate

Post-maturation mortality rates for the Davies Reef cohorts were calculated using the methods of Ebert (1975), assuming that the total mortality includes physiological mortality and mortality from predation, and is constant through adult life for individuals which have developed and persist under a similar set of environmental conditions, using:

$$N_t = N_o \,.\, e^{-\boldsymbol{M}.(t-to)} \qquad (3.6)$$

where N_t = number of individuals in cohort after time t (years)
N_o = number of individuals in the cohort at maturity (2 years)
$\boldsymbol{M}$ = mortality (year^{-1})
t_0 = age at full sexual maturity (i.e. 35 months)

Mortality rates were obtained from estimates of survival for cohorts calculated from fitted growth curves showing attenuated spine ossicle growth during the study period. The number of individuals in each cohort at maturity was calculated from the mean percentage size of each cohort calculated using samples prior to the large decrease in population size, i.e. the first four samples, and the whole population size estimate.

3.2.3.3. Curve fitting

The SigmaPlot Curve Fit program was used to fit curves. MSE of the curve analyses were compared with the MSE from linear regression analyses to assess the significance of fitting a curve over a straight line. The seasonal equation (i) was selected for its simplicity as a general periodic model (see Kettle, 1990). More sophisticated models were available, such as the seasonally oscillating version of the von Bertalanffy growth function (Somers, 1988; FISAT program) but were considered to be unjustified with the small number of samples obtained within each year (i.e. approximately twice yearly).

3.3. **Results**

3.3.1. Population dynamics

Time series plots of outbreak *A. planci* populations adapted from the AIMS COT survey data show the previously reported pattern of southward movement of *A. planci* population activity during the period 1983 (a) to 1988 (f) in relation to Davies Reef (Figure 3.1). The Davies Reef outbreak occurred later than many of the reefs in the Central Section and the size of the population from the resulting recruitment was lower than many other reefs, reflecting a lower number of massive settlement events.

3.3.1.1. Changes in population density

The estimated collection rates during each sampling occasion reflect the overall decrease in aggregation densities and population size during the field study (Table 3.1).

Table 3.1. Estimates of collection rates (CR, person^{-1}.hr^{-1}) on Davies Reef between October 1988 and December 1991.

Trip	CR	Aggregations	Searches
October 1988	20 to 40	Yes, large	f
April 1989	10 to 20	Yes, small	b
October 1989	20 to 40	Yes, large	f and b
March 1990	10 to 20	Yes, small	all*
October 1990	5 to 10	No, patchy	all*
December 1990	5 to 10	No	all*
May 1991	<5	No	all*
December 1991	<<5	No	all*

where f = front areas of reef

b = back areas of reef (searches restricted due to bad weather conditions).

* = population was considered to be disturbed by collections for other *A. planci* studies and several small scale control programs involving other studies.

3.3.1.2. Timing of settlement of the outbreak cohorts

The timing of settlement of the first outbreak cohort was counted back from the estimated age of the cohort with the consistently largest number of individuals in the first few samples. Using the SPBC method the cohort was estimated to be 3+ years in 1988 and therefore, settlement of the first outbreak cohort occurred during the summer season during 1984/1985. A second large recruitment event occurred during the summer season 1985/1986. Subsequent recruitment was much lower and declined over the latter part of the study period.

3.3.2. Population morphometric analyses

3.3.2.1. Analyses of size frequency distributions

Size frequency distributions of whole body diameter (BD) for each sample are presented in Figure 3.2. The distributions were generally unimodal and relatively stationary over the 38 month period. However, the size frequency distributions of spine ossicle length (S) (Figure 3.3) and whole spine appendage length (WS) (Figure 3.4) show a consistent shift to the right in the modes of the distributions over the study period.

Size frequency distributions of spine pigment band counts (SPBC) (Figure 3.5) include seven band classes (estimated age 2+ - 8+ years) showing an annual incremental shift in the two band classes comprising the majority of the outbreak population. Using the size frequency distributions for estimated age (AGE) (Figure 3.6), the cohorts with the greatest percentage frequency of band counts can be followed serially through successive size frequency distributions for the study period, with a simple annual modal progression of one SPBC increment. There was an apparent decrease in relative size of these cohorts after they reached an estimated age of approximately five years. The Figures 3.5 and 3.6 show that the outbreak was composed predominantly of two consecutive cohorts, responsible for the outbreak population, and estimated to have settled on Davies Reef in January, 1985 and 1986. The size frequency distributions of primary oral ossicle weight (PO) (Figure 3.7) and secondary oral ossicle weight (SO) (Figure 3.8) showed an overall trend of growth throughout the study period, although there was no clear modal progression apparent in their distributions.

3.3.2.2. Analyses of growth in morphometric variables

Linear regression analyses, using all samples over the study period (Table 3.2) were used to test the significance of the apparent modal progressions observed in the size frequency distributions for all variables. To separate the two growth phases between juvenile and adult *A. planci*, those individuals with estimated ages less than three years were omitted from the analyses allowing assessment of changes in morphometric variables from individuals after full sexual maturity (i.e. 36 months).

Table 3.2. Linear regression analyses of five variables using whole samples (* except for the relationship between (S) and (BD) where individuals < 3 years were omitted) from Davies Reef, between October 1988 to December 1991.

Variable	Regression equation	Regression analyses
(BD)	NS	$r^2 < 0.01$; $P = 0.02$; $n = 1676$; $MSE = 18.31$
(S)	$27.042 + 0.1921 \times (T)$	$r^2 = 0.22$; $P < 0.01$; $n = 1513$; $MSE = 12.03$
*(S)	$22.3307 + 0.2090 \times (BD)$	$r^2 = 0.05$; $P < 0.01$; $n = 1516$; $MSE = 14.70$
(WS)	$40.3512 + 0.3513 \times (T)$	$r^2 = 0.24$; $P < 0.01$; $n = 1506$; $MSE = 36.79$
(PO)	$0.0758 + 6.12\times10^{-4} \times (T)$	$r^2 = 0.12$; $P < 0.01$; $n = 552$; $MSE = 3.51 \times 10^{-4}$
(SO)	$0.0535 + 4.21\times10^{-4} \times (T)$	$r^2 = 0.10$; $P < 0.01$; $n = 561$; $MSE = 2.03 \times 10^{-4}$

where (BD) = whole body diameter (cm)
(S) = spine ossicle length (mm)
(WS) = whole spine appendage length (mm)

(PO) = primary oral ossicle weight (g)
(SO) = secondary oral ossicle weight (g)
(T) = time (month) from the commencement of the study (October, 1988)

There was no significant linear relationship for mean whole body diameter from each sample and time (age) over the duration of the study. The relationships for spine ossicle length and whole spine appendage length with time showed similar responses over the study period (Table 3.2). This shows that the relationship between the length of spine ossicles and pedicel ossicles is maintained throughout life. Similarly, size frequency distributions of primary oral ossicle weight (PO) and secondary oral ossicle weight (SO) show significant positive relationships with time over the study period and the two oral group ossicles also maintain a similar size relationship relative to each other throughout life. The slopes and coefficients of determination for the relationships using (S) and (WS) (r^2; (S) = 0.22 and (WS) = 0.24) were significantly greater than those of (PO) and (SO) (r^2; (PO) = 0.11 and (SO) = 0.13). This means that the use of spine ossicle length for the estimation of age (through SPBC) is better than using growth (as determined by ossicle weight) in either primary or secondary oral ossicles.

Analyses of morphometric variables and (AGE) were obtained, with no data omitted, to determine the overall significance in relation to estimated age (Table 3.3).

Table 3.3 Linear regression analyses of five morphometric variables and estimated age (AGE) using all data from the Davies Reef *A. planci* population.

Variable	Regression equation	Regression analyses
(BD)	33.6627 + 0.0904 x (AGE)	$r^2 = 0.08$; $P < 0.01$; n = 1548; MSE = 18.45
(S)	14.8822 + 0.2534 x (AGE)	$r^2 = 0.68$; $P < 0.01$; n = 1549; MSE = 5.51
(WS)	18.1363 + 0.4606 x (AGE)	$r^2 = 0.72$; $P < 0.01$; n = 1542; MSE = 14.81
(PO)	0.0357 + (8.29×10^{-4}) x (AGE)	$r^2 = 0.33$; $P < 0.01$; n = 566; MSE = 2.90×10^{-4}
(SO)	0.0257 + (5.72×10^{-4}) x (AGE)	$r^2 = 0.28$; $P < 0.01$; n = 575; MSE = 1.72×10^{-4}

where (BD) = whole body diameter (cm)

(S) = spine ossicle length (mm)

(WS) = whole spine appendage length (mm)

(PO) = primary oral ossicle weight (g)

(SO) = secondary oral ossicle weight (g)

(AGE) = estimated age using the SPBC method (month)

The analysis between whole body diameter and estimated age although significant, shows a low slope coefficient and a relatively weak coefficient of determination ($r^2 = 0.08$) reflecting limited body growth in the adult phase. Both spine ossicle and whole spine appendage length increased significantly with estimated age throughout the adult phase. Similarly, primary and secondary oral ossicle weight increased significantly throughout the adult phase, although the coefficients of determination were lower ((PO) $r^2 = 0.33$ and (SO) $r^2 = 0.28$) than those of spine ossicle and whole spine appendage ((S) $r^2 = 0.68$ and (WS) $r^2 = 0.72$).

3.3.3. Allometry in pre- and post- outbreak groups

The Davies Reef population was split into two groups containing the cohorts which settled on the reef prior to the initial outbreak cohort in 1985/1986 summer (pre-outbreak group) and those that settled in that season or in later seasons and developed under higher densities and food limitation (post-outbreak group). The two population groups were compared using multiple linear regression analyses with the four ossicle variables (S, WS, PO and SO).

Table 3.4. Multiple regression analyses for the dependent variable spine ossicle length (mm).

Multiple regression model

Dependent variable = ln (S)

I.V.	Coefficient	SE	t-stat.	P
Constant	2.4513	0.0640	38.30	< 0.01
(AGE)	0.0085	0.00019	45.90	< 0.01
ln (BD)	0.1178	0.0182	6.47	< 0.01
$(\mathrm{BD} \times \mathrm{PRE})_{\mathrm{slope}}$	0.0660	0.0166	3.97	< 0.01
$(\mathrm{AGE} \times \mathrm{PRE})_{\mathrm{slope}}$	-0.0033	0.0007	-4.64	< 0.01

AOV of multiple regression model

$r^2 = 0.67$

	SS	df	MS	$F_{(\mathrm{ratio})}$	'P
model	19.7403	4	4.9351	784.27	< 0.01
error	9.7094	1543	0.0063		
total	29.4498	1547			

The independent variables selected to describe spine ossicle length are estimated age and whole body diameter (Table 3.4). There are significant differences in slope of the variables between the pre and post-outbreak groups and these represent slower spine ossicle growth in the pre-outbreak group (older starfish) and a smaller change in spine ossicle length over the range of whole body diameters in starfish from the outbreak cohorts.

Table 3.5. Multiple regression analyses for the dependent variable whole spine appendage length (spine + pedicel ossicle length) (mm).

Multiple regression model

Dependent variable = ln (WS)

I.V.	Coefficient	SE	t-stat.	P
Constant	2.6478	0.0683	38.76	< 0.01
(AGE)	0.0102	0.00020	51.26	< 0.01
ln (BD)	0.1520	0.0191	7.96	< 0.01
$(\mathrm{PRE})_{\mathrm{elev.}}$	0.3000	0.0679	4.42	< 0.01
$(\mathrm{AGE} \times \mathrm{PRE})_{\mathrm{slope}}$	-0.0040	0.0008	-5.25	< 0.01

AOV of multiple regression model

$r^2 = 0.72$

	SS	df	MS	$\mathbf{F_{(ratio)}}$	**P**
model	27.9032	4	6.9758	970.71	< 0.01
error	11.0453	1537	0.0072		
total	38.9486	1541			

The multiple regression analysis of whole spine appendage length gave a different result to the analysis for spine ossicle length (Table 3.5). The pre-outbreak group had significantly longer whole spine appendages than the outbreak cohorts which could not be accounted for by differences in whole body diameter or estimated age. The lower slope coefficient in the pre-outbreak group shows there is a slowing of spine appendage growth in the pre-outbreak group as a size asymptote (maximum length) is approached (i.e. in older starfish).

Table 3.6. Multiple regression analyses of the dependent variable primary oral ossicle weight (g).

Multiple regression model

Dependent variable = ln (PO)

I.V.	Coefficient	SE	t-stat.	P
Constant	-6.9430	0.2188	-31.73	< 0.01
(AGE)	0.0093	0.00059	15.83	< 0.01
ln (BD)	1.0623	0.0598	17.76	< 0.01
$(\text{AGE x PRE})_{\text{slope}}$	-0.0011	0.00037	-2.87	< 0.01

AOV of multiple regression model
$r^2 = 0.56$

	SS	df	MS	$\mathbf{F_{(ratio)}}$	**P**
model	20.9428	3	6.9809	242.10	< 0.01
error	16.1763	561	0.0288		
total	37.1191	564			

The selected variables for primary oral ossicle growth were body size (whole body diameter) and estimated age (Table 3.6). The significantly lower slope coefficient in the pre-outbreak group shows there is a reduction in primary oral ossicle growth in the pre-outbreak group (i.e. in older starfish).

Table 3.7. Multiple regression analyses of the dependent variable secondary oral ossicle weight (g).

Multiple regression model

Dependent variable = ln (SO)

I.V.	Coefficient	SE	t-stat.	P
Constant	-7.6565	0.2647	-28.93	< 0.01
(AGE)	0.0094	0.0007	13.53	< 0.01
ln (BD)	1.1560	0.0721	16.03	< 0.01
$(\text{AGE x PRE})_{\text{slope}}$	-0.0012	0.00044	-2.67	< 0.01

AOV of multiple regression model
$r^2 = 0.49$

	SS	df	MS	$F_{(\text{ratio})}$	P
model	23.0733	3	7.6911	182.34	< 0.01
error	24.0851	571	0.0422		
total	47.1584	574			

The variables involved in secondary oral ossicle growth are similar to those found in the primary oral ossicle analysis.

There is no indication that there are differences in the mode of skeletal ossicle growth for spine ossicle length, primary oral ossicle and secondary oral ossicle weights between those starfish which developed prior to the outbreak and those which developed under outbreak conditions. However, the analyses show that whole spine appendage growth was significantly greater in the pre-outbreak group (significant elevation) than for those in post-outbreak cohorts after the influence of body size and estimated age had been removed. This means there was more rapid growth of pedicels in the pre-outbreak cohorts compared with the post-outbreak group. Further investigation of all variables, through the breakdown of data into analyses for individual estimated age classes, would be required to reveal the differences between the two groups in the Davies Reef population.

3.3.4. Cohort morphometric analyses

3.3.4.1. Whole body diameter growth in cohorts

There was significant variation in mean whole body diameter among all samples (winter minima and summer maxima) oscillating between approximately 38 and 41cm (Figure 3.9). Fitted cubic spline curves (where the sample means (with SE) were fitted with a solid line and dotted lines were used to describe each of the four principle cohorts) show the seasonal nature of fluctuations in whole body diameter. Furthermore, there was a general non-significant decline in body diameter in the population over the study period (approximately 1cm/year). This is in accord with the results from the recaptured starfish (Chapter 2).

The rapid growth phase of young adults up to the estimated age of 3+ years (cohorts 1986 and 1987, Figure 3.12; cf. Figure 2.5b) is followed by a phase of no discernible growth (i.e. post full sexual maturity). Seasonal oscillation is apparent in the data from the 1984 - 1986 cohorts, with maxima in early summer and minima in winter. The 1987 cohort did not exhibit a seasonal pattern, which may have been due to the relatively low numbers obtained from that cohort. Overall linear regression analyses of whole body diameter in each cohort over the study period were not significant (Table 3.2). However, linear regression analyses of samples divided into winter and summer groups, omitting the first sample (October, 1988) which was dominated by starfish not fully grown, show there is a significant negative relationship with time (age) over the study period, although poor coefficients of determination were derived because of the limited groups of samples (3) in each analysis);

Summer samples $(BD) = 41.81 - 0.068 \times (T)$

$r^2 = 0.03$; $P < 0.01$; $n = 709$; $MSE = 18.77$; 3 samples

Winter samples $(BD) = 39.04 - 0.048 \times (T)$

$r^2 = 0.01$; $P = 0.01$; $n = 754$; $MSE = 16.89$; 3 samples

Combined sample analyses between cohorts for all samples (Appendix 3.1A) showed significant differences between successive cohorts from 1984 to 1988. The interpretation of this result becomes clear when all individuals < 3 years are omitted from the samples, i.e. after full body size has been attained (Appendix 3.1B). The serial Tukey (HSD) analyses of the cohorts show there are two groups: one before 1985 and one after, with the earlier cohorts having significantly greater mean whole body diameter than the cohorts responsible for the outbreak (post-outbreak).

There are no significant linear relationships for whole body diameter within cohorts over the study period, as determined by the replication test of fit for linearity (Appendix 3.2A). The relationships between the mean and standard errors of whole body diameter for each cohort in successive samples are presented in Figure 3.10. Curve analyses of whole body diameter for each cohort through the study period are described in Appendix 3.2B. The 1983 cohort shows no significant changes in whole body diameter during the study. Seasonal oscillation and no apparent longer term trend in whole body diameter occurred in the 1984 and 1985 cohorts. With the inclusion of young adult individuals in the 1986 cohort, the curve analyses showed a seasonal oscillation with a longer term trend of asymptotic growth ($\boldsymbol{K} = -0.23$). There were no significant seasonal or longer term trends in the 1987 and 1988 cohorts over the study period.

The preceding results can be used to separate growth responses in each cohort (see Figure 3.10). Under the same habitat conditions both pre and post-outbreak cohorts demonstrated asymptotic growth, at different estimated ages. The differences between the groups, although small, reflected significant differences in growth curves described by each cohort under finite resource conditions. The 1984 and 1985 cohorts showed an oscillation in body size in phase with the gametogenic cycle (i.e. mid-winter to early summer gametogenesis). There was no such oscillation apparent in the data from the young adult cohort which settled in 1987, however they achieved a body size asymptote which was significantly smaller than the previous cohort.

3.3.4.2. Growth of spine ossicle and whole spine appendage length in cohorts.

Mean spine ossicle length and whole spine appendage length for all samples was significantly greater in each successive age class between the 1983 and 1987 cohorts, but not between those that were estimated to have settled in 1982 and 1983 (Appendix 3.1A; Table 3.8; Table 3.9). By omitting all individuals where (AGE) < 3 years from the analyses, the differences between the 1986 and 1987 cohorts also became non-significant (Appendix 3.1B). The linear nature of spine ossicle and whole spine appendage growth in each cohort is apparent in Figures 3.11 and 3.13. Linear regressions of the four principal cohorts (1984 to 1987) depicted by the dotted lines are more or less parallel with similar differences in elevation between each successive cohort. A spline curve (dashed line) is used to join the means and standard errors for each sample and shows the extent of variation among the means from the overall regression (solid line) which is due to the relative contributions of each cohort within each sample. The largest deviation from the overall regression line occurred in the second sample (at six months) and this shows there was a higher contribution of individuals from the pre-outbreak cohorts (1982 to 1984) in this sample compared with other samples during the study.

Table 3.8. Summary of curve analyses of spine ossicle length (S) for *A. planci* cohorts from Davies Reef which settled between 1982 and 1987 (Figure 3.11; Appendix 3.1).

Year	Curve analysis	T; $(\mathbf{S})_\infty$	Longevity	Nα	*M*(year^{-1})
1982	NS; use linear regression analyses				
1983	r^2=0.52; *K*=0.060; P<0.02; MSE=4.85	~39; 40.7	8.5 years	3133	0.839
1984	r^2=0.61; *K*=0.042; P< 0.01; MSE=5.75	>39; 40.8	8.5 years	7281	0.837
1985	r^2=0.30; *K*=0.173; P< 0.01; MSE=4.90	~18; 30.0	5.0 years	27135	0.998
1986	r^2=0.39; *K*=0.140; P< 0.01; MSE=3.71	~24; 29.1	4.8 years	17301	1.070
1987	NS; use linear regression analyses				

where (AGE) at $\mathbf{L}_\infty$ is determined from the relationship for (S) and (AGE) (Table 3.2)

M = mortality rate calculated from estimated longevity in each cohort past full sexual maturity (assumed to be 3 years, or 35 months).

Nα = estimated number of individuals in each cohort at full sexual maturity (35 months). Estimates were calculated from the proportion of each cohort represented in the early population samples, obtained prior to the population decline, multiplied by the population size estimate calculated from the proportion of recaptures to total numbers marked and released.

Curve analyses of spine ossicle length within cohorts showed asymptotic growth in the four principal cohorts (1983 to 1987) (Figure 3.12), with lower growth constants occurring in the pre-outbreak cohorts (1983 and 1984) compared with the post-outbreak cohorts (1985 and 1986). The timing of a decrease in growth approaching an asymptote in spine ossicle length in the post-outbreak cohorts coincided with a marked decline in the population size during the second year of the study. Therefore, the observed spine ossicle growth over the study period reflected a mode best described by an asymptotic growth function. If spine ossicles continue to grow with decreasing increments throughout life then the maxima in growth curve analyses represent the average maximum spine ossicle length achieved during their lifespans. Maximum ages were calculated from the overall relationship between spine ossicle length and estimated age. The results in Appendix 3.3B are summarised in Table 3.9

and show the difference in estimated lifespan (survival) between pre-outbreak cohorts (8.5 years) and post-outbreak cohorts (5 and 4.8 years).

Mortality rates in the pre-outbreak cohorts (1983 - 84) were estimated to include 99% of the cohort, arbitrarily, from the longevity estimates given by spine ossicle asymptotes determined from the curve analyses of spine growth (see Figure 3.12). This calculation was justified because the maximum ages determined from the asymptotes coincided with the maximum ages determined from the SPBC method (8+ years). This means the proportion of individuals remaining in the cohort at the time they reached their estimated longevity (i.e. at 96 months) was estimated to be 1% subject to the method of age determination. Since there were a only few individuals collected in the 8+ years estimated age class, and none in the next. However, the subjective assessment of survival was not justified in the post-outbreak cohorts, where the calculated asymptotes in spine ossicle length for each cohort did not coincide with the disappearance of those age classes from the subsequent collections. Therefore, in the post-outbreak cohorts (1985-86) mortality rates included somewhat less than 99% of the cohorts, since small numbers of non-aggregated (dispersed) individuals from these cohorts survived past their estimated longevity.

The results from the SPBC analyses showed that small numbers of starfish representing the post-outbreak cohorts continued to be collected in the third year of sampling after the curve analyses in spine ossicle growth revealed asymptotic growth during the second year of the study. The proportion of starfish remaining after the observed decline in spine ossicle growth was therefore, arbitrarily assumed to be 5%. The estimated survival rates and the size of each cohort (as a proportion of the total estimated population size) were then used to calculate the mortality rate (see **Methods** section).

Table 3.9. Summary of curve analyses of whole spine appendage length (WS) for *A. planci* cohorts from Davies Reef which settled between 1982 and 1987 (Figure 3.17; Appendix 3.3).

Year	Curve analysis	(T) month	**(WS)$_\infty$** (mm)
1982	NS; use linear regression analyses		
1983	r^2=0.52; K=0.096; P< 0.01; MSE=15.92	~ 39	63.3
1984	r^2=0.61; K=0.031; P< 0.01; MSE=14.28	> 39	70.2
1985	r^2=0.33; K=0.149; P< 0.01; MSE=12.74	~ 18	45.8
1986	r^2=0.45; K=0.123; P< 0.01; MSE=10.11	~ 24	44.4
1987	NS; use linear regression analyses		

Analyses of whole spine appendage length within cohorts also found asymptotic growth during the study period in the four principal cohorts (1983 to 1987) (Figure 3.14). Significant growth constants in the pre-outbreak cohorts (1983 and 1984) are lower than those in the post-outbreak cohorts (1985 and 1986) being composed of older age classes which show that whole spine appendage growth is described by an asymptotic growth function in the same cohorts as found in the spine ossicle analyses.

In theory, the mean spine appendage length at maturity should reflect a selected optimum size of spines for protection from predation at the time of first spawning (Table 3.10). Mean spine appendage length at the age of presumed first spawning (AGE = 2+ years) was 30.4mm in the Davies Reef population and increased at a decreasing rate in subsequent age classes.

Table 3.10. Mean whole spine appendage length and SE of *A. planci* from samples collected during the early summer season (using combined samples from 3 consecutive years) at (AGE) 2+, 3+ and 4+ years from Davies Reef.

(AGE)	Mean (WS) (mm)	SE	n
2+	30.4	0.62	25
3+	39.8	0.26	192
4+	44.3	0.22	304

3.3.4.3. Primary and secondary oral ossicle growth in cohorts

The pattern of oral ossicle growth within cohorts is similar for both the primary and secondary oral ossicles and are presented together in this section. Oral ossicle growth in cohorts was estimated by fitting linear regressions (Figure 3.15 and 3.17) which clearly show the relatively large size of the oral ossicles in the pre-outbreak cohort (1984). Overall regression analysis (with SE) using data from the combined cohorts are shown by a fitted solid line and means are joined by a spline curve (dashed line). The results of secondary oral ossicle weight analyses in the 1987 cohort were omitted from Figure 3.17 due to the small sample size and poor regression fit.

The limited growth in the post-outbreak cohorts (1985, 1986 and 1987) is apparent by the convergence of the fitted regressions compared with those representing the pre-outbreak cohorts. Overall regressions were fitted with a significant positive coefficient indicating a general increase in oral ossicle weights over both the juvenile and adult growth phases. The overall regressions (solid lines; Figure 3.15 and 3.17) were tested for curvature by linear regression analyses using a quadratic polynomial and were found to be not significant using both the primary and secondary oral ossicle variables (PO) ($F = 4.41 < \mathbf{F}_{(\alpha 1;0.01;1,563)} \approx 6.64$; $P < 0.05$) and (SO) ($F = 2.33 < \mathbf{F}_{(\alpha 1;0.01;1,572)} \approx 6.64$; $P > 0.10$). Therefore, the regression analyses for straight lines were retained for discussion.

A preliminary inspection of the straight line fitted data in Figures 3.16 and 3.18 showed that a seasonal oscillating curve as well as the asymptotic growth function should be assessed. The analyses of the cohorts found significant linear trends in the 1984, 1985 and 1986 cohorts for both ossicle types (see Replication Test Of Fit RTOF analyses for linearity; Appendices 3.4A and 3.5A). A summary of curve fitting analyses for primary and secondary oral ossicle weights is presented in Table 3.11.

Table 3.11. Summary of curve analyses of primary and secondary oral ossicle weight for *A. planci* cohorts which settled between 1982 and 1987 from Davies Reef ((PO); Figure 3.16; Appendix 3.4) and ((SO); Figure 3.18; Appendix 3.5).

(a) (PO)

Year	Curve analysis; equations (a), (b) or (c).	(T) month	**(PO)**$_\infty$ (g)
1982	NS		
1983	NS		
1984	NS		
1985	using (b), for asymptotic growth data		
	r^2=0.32; K=0.050; P< 0.01; MSE=1.75x10^{-4}	~ 39	0.0997
1986	using (a), for seasonally oscillating data		
	r^2=0.34; P< 0.01; MSE = 2.55x10-4		
	b=0.006g; g=0.0011	> 39	NA
1987	NS		

(b) (SO)

Year	Curve analysis; equations (a), (b) or (c).	(T) month	**(SO)**$_\infty$ (g)
1982	NS		
1983	NS		
1984	NS		
1985	using (b), for asymptotic growth data		
	K=0.070; r^2=0.28; P< 0.01; MSE=1.22x10^{-4}	~ 39	0.0679
1986	using (c), for asymptotic growth		
	and seasonally oscillating data		
	K=0.043; l=0.075g; b = 0.007g	~ 39	0.075
	r^2=0.31; P< 0.01; MSE = 1.46x10-4		
1987	NS		

The analyses for both primary and secondary oral ossicles show a significant seasonal oscillation in oral ossicle weight in the 1986 cohort. Variation in mean oral ossicle weight occurred with maxima in the early winter months (i.e., the significant parameters of equation (c) for (PO) were, (2 x b) = 0.012g (range of seasonal variability) and c = 29 (seasonal maxima which corresponds to March/April) and minima in early summer. This demonstrates an opposing seasonal fluctuation to the cycle found from the analyses of whole body diameter which coincides with gametogenesis (cf. Chapter 5).

3.3.5. Morphometric analyses among three GBR populations.

Three populations from a wide geographic range on the GBR were sampled for whole body diameter, spine ossicle length, and spine pigment band count for comparative morphometry among populations in relation to estimated population density. Additional data from Helix Reef obtained by Kettle (1990) were analysed (with permission) to compare with the results from the population density and mean whole body diameter analyses. Unfortunately, no spine ossicle length data was available from Kettle's study. The populations were categorised as: very high density, Helix Reef (estimated age range 2+ to 4+, see Kettle, 1990); high density, Davies Reef (estimated age range = 2+ to 8+ years); intermediate density, Butterfly Bay, Hook Island (estimated age range 2+ to 9+ years); and low density, Lady Musgrave Island (estimated age range 3+ to 11+ years) (Figure 3.22). A comparison of whole body size in fully mature individuals, excluding individuals with estimated age < 3 years, shows a negative relationship between mean adult body size and population density over the four broad categories described here (Table 3.12).

Table 3.12. Mean whole body diameter and estimated population density in four *A. planci* populations from the GBR Region.

Location	($PDha^{-1}$)	$(BD)_{mean}$ (cm)	SE	n
HE	H $(1276)_2$	38.8	1.293	23
DA	H $(420)_1$	39.2	0.108	1680
HI	I $(50)_1$	43.2	0.670	66
LM	L $(0.3)_2$	50.6	4.209	9

where (PD) = estimated population density

H = high density

I = intermediate density
L = low density
[1] = estimated in this study
[2] = estimated from Kettle (1990)

The data from Kettle's Helix Reef study showed there was a difference in mean body size between a lower density (Davies Reef) and a higher density outbreak population (Helix Reef). There was also a significant correlation coefficient between mean whole body diameter and estimated longevity ($\boldsymbol{r} = 0.903$; $\mathbf{F}_{(\mathbf{ratio})} = 19.6 > \mathbf{F}_{(\alpha 2;0.05;3,3)} = 15.4$; $0.02 < P < 0.05$) where the Davies Reef population was divided in the pre-outbreak and post-outbreak groups (see Chapter 4) and assuming the estimated longevity of the Helix Reef population was 4 years. The morphometric analyses of the GBR populations also revealed differences among the populations:

(a) Comparison of mean whole body diameter in Davies Reef, Helix Reef, Hook Island and Lady Musgrave Reef populations from the GBR.

where Tukey (HSD) comparison of means of BD; LM > HI > DA > HE
ANOVA; $F = 235.8$; $P < 0.01$; $n = 1814$; $MSE = 21.63$

(b) Comparison of spine ossicle length and estimated age using linear regression analyses were made from all estimated classes in Davies Reef, Hook Island and Lady Musgrave Reef. To obtain a consistent method of calculating age in months it was assumed that settlement of larvae occurred during mid summer on all reefs.

Minimal regression model

	Coefficient	SE	T	P
Constant	10.959	0.7989	13.7	< 0.01
(AGE)	0.2530	0.0042	60.7	< 0.01
($HI_{elev.}$)	3.9444	0.7176	5.50	< 0.01
($DA_{elev.}$)	2.7204	0.7672	3.55	< 0.01

	SS	DF	MS	F	P
Regression	20251.5	3	6750.5	1235.9	< 0.01
Error	8870.3	1624	5.4620		
Total	29121.8	1627			

Minimal model analysis

$(S) = (AGE) + (HI_{elev.}) + (DA_{elev.})$

$F = 0.73 < \mathbf{F}_{(\alpha 1;0.01;1,1620)} \approx 3.78$; $P > 0.25$

Therefore 3 parallel linear regressions were formed:

DA $(S) = 14.847 + 0.2539 \times (AGE)$ $r^2 = 0.68$; $P < 0.01$; $n = 1549$; $MSE = 5.473$

HI $(S) = 13.707 + 0.2526 \times (AGE)$ $r^2 = 0.72$; $P < 0.01$; $n = 68$; $MSE = 5.859$

LM $(S) = 12.321 + 0.2379 \times (AGE)$ $r^2 = 0.98$; $P < 0.01$; $n = 11$; $MSE = 1.399$

There were no significant differences in slope, however, there was a significant difference in elevation of the regressions among the three populations. The order of the populations' regressions for increasing elevation (Figure 3.20) does not conform with the order of populations for increasing mean whole body diameter, i.e. while Davies Reef had the highest elevation for the regression between (S) and (AGE) it had the lowest mean whole body diameter. A similar slope among the three regressions also shows there are no significant differences in adult spine ossicle growth.

The differences in elevations of the regressions can be attributed to differences in the mean spine ossicle length attained by the age at maturity in the three populations i.e. there are significant differences in the rate of growth in spines during the juvenile phase among these populations. Therefore, while it appears that increased population density can reduce maximum body size among populations, it coincides with a longer spine ossicle length estimated at full sexual maturity. This suggests that juvenile spine growth rates (and therefore, possibly body growth rates also) are higher in populations with higher densities.

3.3.6. Life-history constants

The extent of invariance in the Beverton-Holt life-history constants was investigated from estimates made from each of the four principal cohorts from the Davies Reef population. The estimates summarised in Table 3.8 were derived from three-parameter von Bertalanffy growth analyses presented in Appendix 3.2 and the coefficients were calculated from the appropriate equation out of the three alternatives offered and are presented in Table 3.13.

Table 3.13. Summary of life history coefficients calculated for four cohorts (1983 - 1986) from the *A. planci* population on Davies Reef.

Cohort	$K_{(S)}$ (mo^{-1})	$(S)_\alpha$ (mm)	$(S)_\infty$ (mm)	$K_{(BD)}$ (mo^{-1})	$(BD)_\alpha$ (cm)	$(BD)_\infty$ (cm)	M (mo^{-1})
1983	0.021	19.2*	46.4	0.054	32.6*	44.0	0.070
1984	0.019	18.5*	48.4	0.064	33.5*	41.9	0.070
1985	0.039	21.5	34.3	0.115	36.0	39.5	0.120
1986	0.052	23.3	31.9	0.096	37.9	39.2	0.133

where * = estimated from a fitted growth curve under the assumption that full sexual maturity occurs at 3 years (35 months).

K = von Bertalanffy growth constant (mo^{-1})

M = mortality rate (mo^{-1})

L_α/L_∞), substitute variables (S) or (BD) for (L).

The correlation between the two growth constants ($K_{(BD)}$ and $K_{(S)}$) was not significant (r = 0.858; $F_{(ratio)} = 13.06 < F_{(\alpha 1;0.05;2,2)} = 19.0$; $0.05 < P < 0.10$) although the relationship was positive, approximating $K_{(BD)} \approx K_{(S)}^{0.72}$, consistent spine growth occurred in the adult age classes while there was no body growth. This is evidence of different modes of growth in these two morphometric parameters. Curve analyses fitted for whole body diameter were only weakly significant ($r^2 < 0.05$) showing that the estimates of $K_{(BD)}$ are less reliable than those for $K_{(S)}$. This also applies to those life-history constants estimated using $K_{(S)}$ instead of $K_{(BD)}$.

There were marked differences in many of the life-history constants between the pre- and post- outbreak cohorts, assuming that full sexual maturity occurred at the same age in all cohorts. The lower asymptotic spine length and whole body diameter in successive cohorts is involved in an apparent trade-off with an increase in the growth constants of approximately 2 - 2.5 times in the outbreak cohorts compared with the pre-outbreak cohorts. Similarly, there is also an increase in mortality rates of between 1.7 and 1.9 times in the post-outbreak cohorts.

A comparison of the pattern of life history coefficients derived from the high density, post-outbreak cohorts with those from the pre-outbreak cohorts show:

(a) higher growth constants, and inferred juvenile growth rates.
(b) higher adult mortality rates interpreted from variation in growth asymptotes.
(c) a more determinate mode of growth ($(\mathbf{BD})_\alpha/(\mathbf{BD})_\infty \rightarrow 1$).

The coefficients presented in Table 3.13 defining growth, mortality and maturation were used to determine the constancy of the life-history constants among the four principal cohorts in the Davies Reef population (Table 3.14).

Table 3.14. Life-history constants calculated for the four principal cohorts (1983 to 1986) in the *A. planci* population from Davies Reef.

Cohort	$K_{(S)}/M$	$K_{(BD)}/M$	$M.\alpha$	$(\mathbf{S})_\alpha/(\mathbf{S})_\infty$	$(\mathbf{BD})_\alpha/(\mathbf{BD})_\infty$
1983	0.300	0.771	2.450*	0.414*	0.740*
1984	0.271	0.914	2.450*	0.382*	0.799*
1985	0.325	0.967	4.200	0.627	0.911
1986	0.391	0.722	4.655	0.730	0.967

where * = assuming that age at full sexual maturity is at 3 years (35 months) in the pre-outbreak cohorts.

The values for the constants calculated for the pre-outbreak cohorts (1983 - 1984) assumed that the age of full sexual maturity is 35 months. This assumption remains untested since few immature or partly mature individuals were collected from the pre-outbreak cohorts between 1988 and 1991. However, if the assumption is true then the life-history constants ($\boldsymbol{M}.\alpha$, $\mathbf{(S)_\alpha/(S)_\infty}$, $\mathbf{(BD)_\alpha/(BD)_\infty}$) are consistently variable between pre-outbreak and the outbreak cohorts, i.e. under variation of environmental conditions through increasing population density and lower resource availability.

The relationship between the life-history constants $\mathbf{(S)_\alpha/(S)_\infty}$, $\mathbf{(BD)_\alpha/(BD)_\infty}$ was also tested where $\boldsymbol{r} = 0.951$; $\mathbf{F}_{\mathbf{(ratio)}} = 39.9 > \mathbf{F}_{(\alpha 1;0.05;2,2)} = 19.0$; $0.01 < P < 0.05$. The large differences in the ratio of body size at full sexual maturity to asymptotic body size is reflected significantly through similar differences found in the analyses using spine ossicle length. The relationship between growth constants and maximum size in both spine ossicle length and whole body diameter was estimated from linear regression analyses (Table 3.15).

Table 3.15. Pearson correlation coefficient analyses of life-history constants for; growth constants using ($\boldsymbol{K}_{(S)}$, $\boldsymbol{K}_{(BD)}$) and mortality rate $\boldsymbol{M}$ and, asymptotic size $\mathbf{(BD)_\infty}$, $\mathbf{(S_\infty)}$ and mortality rate $\boldsymbol{M}$ in the four principal *A. planci* cohorts (1983 to 1986) from Davies Reef.

Variables	Correlation analyses (H_0: $\rho \geq 0$) where $\boldsymbol{r}$ estimates ρ.
(BD_∞); M	$\boldsymbol{r} = -0.928$; $\mathbf{F}_{\mathbf{(ratio)}} = 26.9 > \mathbf{F}_{(\alpha 1;0.05;2,2)} = 19.0$; $0.02 < P < 0.05$; $M \approx \mathbf{(BD_\infty)}^{-0.64}$
(S_∞); M	$\boldsymbol{r} = -0.996$; $\mathbf{F}_{\mathbf{(ratio)}} = 570 > \mathbf{F}_{(\alpha 1;0.01;2,2)} = 99.2$; $P < 0.01$; $M \approx \mathbf{(S_\infty)}^{-0.65}$
	Correlation analyses (H_0: $\rho \leq 0$) where $\boldsymbol{r}$ estimates ρ.
$K_{(BD)}$; M	$\boldsymbol{r} = 0.924$; $\mathbf{F}_{\mathbf{(ratio)}} = 25.5 > \mathbf{F}_{(\alpha 1;0.05;2,2)} = 19.0$; $0.02 < P < 0.05$; $M \approx K_{(BD)}{}^{0.93}$
$K_{(S)}$; M	$\boldsymbol{r} = 0.989$; $\mathbf{F}_{\mathbf{(ratio)}} = 181 > \mathbf{F}_{(\alpha 1;0.01;2,2)} = 99.2$; $P < 0.01$; $M \approx K_{(S)}{}^{0.67}$
	Correlation analyses (H_0: $\rho \geq 0$) where $\boldsymbol{r}$ estimates ρ.
$K_{(BD)}$;$\mathbf{(BD_\infty)}$	$\boldsymbol{r} = -0.949$; $\mathbf{F}_{\mathbf{(ratio)}} = 38.45 < \mathbf{F}_{(\alpha 1;0.05;2,2)} = 19.0$; $P < 0.05$; $\mathbf{BD_\infty} \approx K_{(BD)}{}^{-1.44}$
$K_{(S)}$;$\mathbf{(S_\infty)}$	$\boldsymbol{r} = -0.846$; $\mathbf{F}_{\mathbf{(ratio)}} = 376.4 < \mathbf{F}_{(\alpha 1;0.01;2,2)} = 99.2$; $P < 0.01$; $\mathbf{S_\infty} \approx K_{(S)}{}^{-1.04}$

There is a significant negative relationship between asymptotic size and mortality rate which is allometric for both whole body diameter ($(\boldsymbol{M}) \approx \mathbf{(BD)_\infty}^{-0.64}$) and spine ossicle length ($(M) \approx (S)_{\infty}^{-0.65}$). Therefore, mortality rates increase significantly relative to the decreases in asymptotic size among successive cohorts. There is a positive correlation which is proportional (exponent ≈ 1) between the growth constants for (BD) and mortality rates among cohorts (where the exponent of $K_{(BD)} = 0.93$). Correlation analyses of the growth constant estimates derived from spine ossicle length analyses also show positive allometry (where the exponent of $K_{(S)}$ is 0.67), such that mortality rates increase at approximately two thirds of the rate of spine ossicle growth. Mortality rate changes with respect to both growth constants ((S) and (BD)) among cohorts, such that an increase in one involves a relative increase in the other. The Beverton-Holt dimensionless number (K/M) remains relatively constant among cohorts in the analyses using whole body diameter, but not spine ossicle length.

There are significant negative correlations (i.e. supporting the notion of physiological trade-offs) between asymptotic size and the growth constant for both whole body diameter (the exponent of $K_{(BD)} \approx -1.44$) and spine ossicle length (the exponent of $K_{(S)} \approx -1.04$). Overall, larger maximum sizes in the pre-outbreak cohorts (at least for spine ossicle length) were apparently obtained through lower growth constants and lower mortality rates (i.e. increased longevity).

3.4. **Discussion**

3.4.1. Further support for the SPBC method

The conclusions drawn from the results of the morphometric study using estimated age from pigment band counts are based on an assumption that the SPBC method is valid over the whole range of estimated age classes on Davies Reef. However, additional support for the validity of the method was obtained from independent data obtained from the morphometric study. A *caveat* was imposed on the conclusions arising from this study from failing to validate the method in all band classes which arose from attempting to develop a novel method of age determination without the availability of known age material; see **Discussion** Chapter 2). However, several sources of independent circumstantial evidence are presented which support the assumption of a valid method over a broader range of age classes than those from the recapture results. These additional results are also used to justify the age related analyses in the Davies Reef population.

Firstly, there was consistent, annual incremental growth of spine pigment band counts in the band classes representing the outbreak cohorts (Figure 3.7). Secondly, mean spine ossicle length increased significantly over the study period under conditions of low additional recruitment (i.e. an ageing population). The mean annual rate of growth in spine ossicle length was similar to that calculated from the recapture data (3.5mm) and corresponds to the approximate length of spine used in the development of light and dark band pairs. Thirdly, the estimated von Bertalanffy growth constant for spine ossicle length, which was predicted from the recapture data (0.039mo^{-1}), falls within the range of $\boldsymbol{K}_{(S)}$ values determined for each of the four principal cohorts ($\boldsymbol{K}_{(S)}$ range = (0.019 to 0.052), and the value for the largest outbreak cohort (1985) coincided with the predicted value. Fourthly, the age determined by SPBC method, which corresponds to the first cohort involved in the development of the outbreak on Davies Reef, conforms to the timing of the appearance of the outbreak reported by the annual *A. planci* crown-of-thorns surveys (28/6/87; Johnson et al., 1988).

Assuming that most *A. planci* become apparent for the first time during daylight hours having attained a body size of approximately 20 - 30cm body diameter in their third year (Kettle, 1990; Zann et al., 1990), and by counting back to their settlement date shows that the first cohort of the most recent outbreak episode settled on Davies Reef in the summer of 1984/1985. Therefore, the timing obtained from the SPBC method for initial settlement of the outbreak cohort is the same as that determined by counting back from the timing of survey observations of recruitment to the adult population, made independently of the present study.

3.4.2. Time series morphometric study

3.4.2.1. Population dynamics in the Central GBR

The large numbers of *A. planci* produced in the 1984/1985 spawning season impacted on a large part of the Central Section of the GBR, as shown by the discovery of large numbers of 1+ year juveniles on many of the reefs off Townsville in 1986 (Kettle, Stump and Bell, unpublished). This distinct episode was also reported by Doherty and Davidson (1988) with an estimated 5 000 times "normal" densities of juveniles on a number of reefs between 18° and 19° 53' latitude in 1986 (Figure 3.1). By contrast, few small juveniles were recovered in their surveys undertaken in 1987 suggesting that recruitment was much lower in 1986 relative to 1985. Therefore, it appears that the massive "seed clouds" generated widely over the Central GBR from spawning outbreak populations in December 1984, contributed to the development of the outbreak population on Davies Reef.

The recruitment history on Davies Reef between 1982 and 1991 as determined from the starfish collections, using the SPBC method, shows that recruitment to the adult *A. planci* population (since the SPBC commence at three years) increased consistently each year from 1982 and then decreased after 1988. By 1988 most of the surveyed reefs under outbreak were observed to be south of Davies Reef (Figure 3.1), suggesting a relationship between the northward proximity of outbreaks and massive recruitment resulting in an outbreak of Davies Reef.

Larval dispersal simulations suggest that reef connectivity (i.e. sources and sinks for larvae) is related to local and regional hydrodynamic relationships (long-shelf transport, cross-shelf transport, and source-sink relationships) so that low density populations may persist in the northern region, while the strong southward drift in the central and southern regions means that populations to the south can only be maintained by recruitment from the north (James et al., 1990). Therefore, while the pattern and timing of recruitment, determined from the SPBC analyses, conformed to predictions from the theory of spatial waves of outbreaks moving southward along the GBR from the Northern Section (Moran, 1986; Reichelt, 1990) the results do not support the theory of geographical synchronicity in outbreak populations (Seymour and Bradbury, 1994) between the Northern and Central Sections. Synchronous outbreaks among the GBR Sections may well be interpreted from survey data because of the inherent delays in establishing the distribution of outbreaks when they first occur, the timing of the assumed primary outbreak/s, as well as the likelihood of a highly stochastic long-shelf advection of larvae over distances from the north to the central and southern reefs.

3.4.2.2. Assessment of Davies Reef population estimates

The population size declined throughout the study. The size and therefore, the coefficient of variation of the density estimate are assumed to represent an approximate range which included the number of adults present on the reef at the time the second post-outbreak cohort reached maturity (i.e. the maximum population size during the outbreak phase). Population size and density estimates may have been greater than the actual values because the low recapture rates realised may not have been due wholly to natural dispersion of the marked individuals (an assumption of the method). An increase in the rates of mortality from the handling and marking procedure on released individuals would result in an artificially inflated population size estimate. Although experimental evidence of high survival rates from moderate levels of arm-damage have been found (Butler, personal communication) the marking procedure prior to release involved the amputation of two adjacent arms, a treatment which may have increased mortality from predation or disease.

Several unrelated studies, which were being conducted concurrently on Davies Reef, initiated small scale *A. planci* control programs to reduce coral predation in their particular study sites (C. Johnson, personal communication). Although information on the mark and recapture study was circulated among the scientific community these control exercises may have accounted for some losses of marked starfish. The use of the same release site throughout the study could have attracted predatory species into that area, further exacerbating mortality in marked individuals. Therefore, the actual population density and size may have been closer to the lower end of the range of confidence limits determined from the recapture data. Unfortunately, there were limited opportunities to observe marked individuals following release (due to limited ship time), preventing an assessment of post-marking survival.

The Davies Reef population size and density estimates are relatively low compared with those reported for other outbreak populations. Pearson and Endean (1969) proposed a scale of abundance categories which were considered by Birkeland and Lucas (1990) to be a reasonable fit with most other definitions of outbreaks. The upper boundary of the "low density" category was calculated as approximately $100ha^{-1}$ and an outbreak, being approximately $417ha^{-1}$, was estimated to be able to kill 25% of the coral cover during its course. The density estimate obtained from the recapture data ($420ha^{-1}$ and 95%C.I. $\pm$ $176ha^{-1}$) fits the category of a relatively low density outbreak population, as discussed by Birkeland and Lucas (1990).

3.4.2.3. Davies Reef population characteristics

The preferential sampling from aggregations in the first half of the study and irregular complexity of the reef, promoting a more cryptic behaviour in dispersed starfish, led to biased sampling throughout the study. The bias due to collecting predominantly from those cohorts which settled in higher densities is likely to have contributed the observed variation in the definition of modes representing cohorts in the size frequency distributions. Therefore, there is a need for careful sampling strategies to be implemented over wide areas of patch reefs to obtain representative numbers of individuals from all cohorts within a population. The patchy nature of the distribution of cohorts, and aggregations within cohorts, probably reflects the stochastic nature of larval settlement of cohorts and their aggregation as adults, even under the influence of a massive outbreak episode as was experienced in the Central GBR during the 1980s.

These results highlight the potential for drawing invalid conclusions about life-history characteristics from studies involving samples obtained from a few or one-off collections. This is clearly illustrated by the consistently lower body sizes in successive cohorts which could be interpreted as evidence for an indeterminate mode of growth, without the additional information obtained from repeating the sampling measures over several years. A similar erroneous conclusion was made by Kenchington (1977) while interpreting age from body size in *A. planci* through analyses of combined size frequency data sets cited from a number of high density population studies. In the present study, the longitudinal (time series) sampling strategy identified individual cohorts in each successive sample which showed that the differences in mean body size among the cohorts was due to variation in body growth patterns according to estimated age (i.e. K and L_∞ among the cohorts).

Although relatively small, the significantly lower mean body sizes in consecutive adult cohorts in the Davies Reef population resulted from a decrease in resource availability to developing starfish as the population increased in size and density from 1983 to 1988. Under the conditions of increasing recruitment the pattern of smaller body sizes in successive cohorts appears to support the use of body size modes to estimate age, if modal size differences can be determined, which was similar to the interpretation of size frequency data made by Kenchington (1977). However, the repeated sample analyses of the time course showed that all starfish in the Davies Reef adult cohorts had attained mean asymptotic body sizes during the 38 month study which indicated there was no modal progression with age in adult starfish.

Kenchington (1977) interpreted an indeterminate mode of growth using combined data from a number of GBR populations reflecting a consistent increase in adult body size with age. When different populations and age classes develop under different densities (increasing or decreasing) and resource availability, the habitat conditions impose various levels of constraint on growth and producing a range of size classes, irrespective of age. Therefore, variation in *A. planci* growth is better described at the individual or cohort level rather than for whole or combinations of populations. In this study, the environmental conditions were assumed to be less variable to individual starfish within cohorts than between them, allowing for more reliable estimates of mortality, longevity and spine ossicle and whole body diameter growth rates. This is an important result for the development of population dynamics studies of *A. planci*, but also to the study of other echinoderm species whose mode of body growth can respond to changing environmental conditions.

3.4.2.4. Seasonal and long term variability in cohorts

The large decrease in the level of resource availability significantly influenced the characteristics of the *A. planci* population on Davies Reef, and these effects were stronger in successive cohorts as the outbreak developed (Figures 3.9 to 3.18). The low recapture rate and the variation in search effort between sampling trips (to maximise the number of recaptures for validation of the SPBC method), prevented the use of recapture rates to estimate the changes in relative population size. This would have been useful for showing the timing and extent of the population decline over the study period. However, the significant decrease in live coral cover on Davies Reef interpreted from the results of Ayling and Ayling (1992) meant a profound decrease in food availability by the second year of the study and was followed by a significant decline in *A. planci* numbers. The decline and dispersal of aggregations between 1989 and 1990 resulted in a substantial increase in *A. planci* collection times to obtain sufficient starfish for analyses, and this trend continued to the end of the field sampling program (Table 3.1). A significant reduction in coral cover followed shortly afterwards by a sharp decline in the *A. planci* numbers was also reported for an outbreak population on Helix Reef by Kettle (1990).

Although no overall growth was found in whole body diameter analyses of the combined cohorts, there was a significant seasonal oscillation (Figure 3.9) in body size of 2 to 3cm which conformed with the timing of the annual gametogenic cycle. This oscillation is caused by the expansion of the body wall with maturation of the gonads in the proximal portions of the arms (Birkeland and Lucas, 1990). Kettle (1990) also found a seasonal fluctuation of 2cm in whole body diameter from his Helix Reef study. However, there was skeletal growth in four ossicle variables (S, WS, PO and SO) over the study period in the combined cohort analyses. The relative rates of growth of the oral ossicles were considerably lower than those of the spine and pedicel (Figures 3.11, 3.13, 3.15, 3.17).

A seasonal oscillation in skeletal weight opposed to the variation in whole body diameter was determined from analyses of the second post-outbreak cohort (settled in 1986) in primary oral (range = 0.012g) and secondary oral ossicle weight (range = 0.014g) (Table 3.6). This pattern was not found in the first outbreak cohort which settled in 1985, even though there was a seasonal oscillation in whole body diameter. The differences between the two post-outbreak cohorts probably resulted from the significant increase in resource limitation following the initial outbreak. Kettle (1990) found a pronounced inverse cyclicity between gonadal partitioning and body wall indices in *A. planci* from Helix Reef. Under extreme food limitation, the body wall of *A. planci* yields energy to allow resource partitioning or to allow maintenance in post-spawning winter periods (Kettle, 1990), where organic material is made available first, followed by inorganic material. Therefore, a seasonal variation in skeletal weight occurs as a more extreme response to levels of resource availability and/or seasonal demands on energy partitioning, i.e. high reproductive effort and/or at times when the energy content of seasonally reproductive corals is relatively low (see Babcock et al., 1986).

The priorities for partitioning resources for reproduction under limited food availability was shown by Kettle (1990) to commence with energy from the pyloric caeca and stomach to maintain somatic processes, and ultimately with energy from the body wall for reproduction and maintenance under extreme food limitation. This resulted in a higher ratio of skeletal to soft tissue weights and net shrinkage during starvation. Therefore, the reduction in soft tissues in the body wall occurs due to the energetic demands of gametogenesis (in times of resource limitation), but under more extreme limitation (i.e. in the second outbreak cohort, 1986) there was apparent resorption of the stroma and hard tissues associated with the major internal skeletal ossicles (the oral apparatus). These ossicles are replaced by regrowth during winter, producing the inverse pattern of seasonal oscillation in size to whole body diameter.

Kettle (1990) reported a seasonal fluctuation in mean underwater weight of approximately 25g in the Helix Reef population over a two year period.

A small but significant reduction of skeletal weight was also found in individuals under conditions of starvation for six months in laboratory experiments. *A. planci* maintained unfed showed a significant decrease by 0.28 (paired t test; $t = 13.2$; $n = 6$; $P < 0.01$: Chapter 2) in mean underwater weight at the end of the experiment. Unlike the internal ossicles, there was evidence of growth in the spine ossicles, at least during the early part of the starvation experiment, since fluorescence analyses of spine ossicle samples revealed the tetracycline marker, introduced at the start of the experiment, close to the basal ossicle surface. A significant reduction in skeletal mass over a period of two months was observed in the echinoid species *Diadema antillarum* which showed an ability to reduce metabolic costs under stress (Levitan, 1988). Shrinkage was also interpreted by Ebert (1967) from growth studies conducted on the echinoid, *Strongylocentrotus purpuratus*.

The pattern of individual body growth in the Davies Reef *A. planci* population shows that seasonal variation in soft tissues occurs under competition for resources in those cohorts which had developed in conditions of high coral cover (1983 to 1985). These cohorts had opportunities to develop large reserves of stored energy prior to maturation, which could then be mobilised to offset reproductive demands. The oscillation in oral ossicle weights is a more extreme response to the energetic demands of reproduction from a combination of intraspecific competition for resources and a juvenile growth phase which developed under conditions of low resource availability (i.e. in the 1987 cohort).

3.4.2.5. Mortality in cohorts

High levels of mortality occurred in the population throughout the study period as indicated by the marked increase in collection times (Table 3.1) and the disappearance of large aggregations over most of the reef, particularly during the second year of the study. This period of high mortality coincided with the pattern of attenuation of spine ossicle and whole spine appendage growth in the outbreak cohorts. The assumption here is that the growth history of the individual is reflected in the incremental growth of the skeletochronometer (spine ossicle), reflecting the condition of the starfish. The switch from obtaining samples from aggregations to more solitary individuals in the second and third year of the study is indicated in Figures 3.11 and 3.13 by the apparent sharp increase in spine growth following the period of growth attenuation (T = 18 to 24 months for cohort 1985; and T = 25 to 32 months for cohorts 1986 and 1987, respectively). These variations from the major pattern of attenuation was interpreted as reflecting differences in the pattern of spine growth in those individuals living in dispersed conditions. These individuals were not subjected to the same stresses limiting spine growth as had occurred in the starfish from aggregations. Therefore, increased competition for resources resulted in an increase in mortality (as determined by the pattern of attenuation in spine growth) in those individuals obtained from aggregations which was not apparent in those individuals collected from dispersed locations in the same cohorts.

The evidence for different patterns of age-related mortality in aggregating and non-aggregating starfish (Table 3.8) is also interpreted from the attenuation of spine ossicle growth in the 1985 cohort up to the summer of 1989 and 1990 (AGE ≈ 5.0 years) and similarly in the 1986 cohort in the summer of 1990 and 1991 ((AGE) ≈ 4.8 years). Starfish belonging to the earlier, pre-outbreak cohorts approached an asymptote in spine length at an older estimated age towards the end of the study (in the 1983 cohort) or later (in the 1984 cohort). Pre-outbreak cohorts apparently experienced no sudden increase in the rate of mortality during the study period which had been identified in the post-outbreak cohorts living under similar conditions.

3.4.3. Life-history characteristics in the Davies Reef population

The value of the interpretation of the results from the life history analyses in the four cohorts principally relies on the accuracy of the fit obtained from the curve analyses estimating growth rate and asymptotic size. The growth rates of the pre-outbreak cohorts were estimated from incomplete data sets where data collection commenced in 1988 and the cohorts are estimated to have settled in 1983 and 1984. Knight (1968) has drawn attention to the potential for considerable error in estimating parameters of the VBG curve from truncated data, in particular L_∞. However, $\boldsymbol{K}$ and L_∞ are mathematically linked in the VBG equation and $\boldsymbol{K}$, among other things, is a measure of curvature where a large curvature relates to a low L_∞ and *vice-versa* (Knight, 1968). For similar data to have been obtained in all four cohorts, the field study would have had to commence in 1985 and run for seven years to 1991, therefore the interpretations of the analyses may have some inherent limitations through varying levels of truncated data among cohorts.

To control the variability in the curve analyses several steps were undertaken to reduce the number of variables in the three parameter VBG equation used in the analyses of the four cohorts. The VBG equation was reduced to a single unknown variable (the growth constant, $\boldsymbol{K}$) where estimates of the other two factors were considered to be reliable. The accuracy of estimated age in months ($\boldsymbol{t}$) was assumed to be relatively reliable and evidence for this is presented in Chapters 2 and 3. Estimates of (L_∞) were also shown to be reasonable due to the overall low levels of growth recorded for whole body diameter in adult starfish over the study period. In addition, the curve analyses identified well defined asymptotes in spine ossicle growth which were found in most of the cohorts during the 38 month study. Estimates of (t_0) were standardised to 10 months for all cohorts, and therefore held constant. This coefficient estimates the age when the phase of von Bertalanffy growth begins following the initial exponential growth response to the switch from coralline algae to feeding on hard corals (after approximately 6 months post settlement (Yamaguchi, 1974; Lucas, 1984; see also Figure 30, Birkeland and Lucas, 1990). The timing of the switch in growth characteristics was considered to be relatively invariant because under normal conditions it occurs in the first year of life and therefore has little option for variation unless access to coral is limited (see Lucas, 1984).

The growth constant $\boldsymbol{K}$ was estimated from the growth found in each cohort, and because there were relatively greater changes in spine ossicle growth than whole body diameter during the study, the significance of the whole body diameter analyses, particularly in the pre-outbreak cohorts was found to be relatively weak. Therefore, the potential for determining life-history characteristics from analyses of adult spine ossicle growth instead of whole body diameter was investigated. However, there was no significant correlation found between the two growth constants. Possible causes for this lack of correlation include the small sample size (number of cohorts) as well as the relatively poor estimates of whole body growth from the VBG analyses.

The life-history constant for the dimensionless ratio $\boldsymbol{K}_{(S)}/\boldsymbol{M}$ in the four principal cohorts were found to be relatively invariant ($r^2 = 0.98$; $P = 0.01$). However, despite a similar outcome for the analysis of $\boldsymbol{K}_{(BD)}/\boldsymbol{M}$, the result was not significant ($r^2 = 0.85$; $P = 0.08$). The relationship between estimates of mortality rate and the growth constants in the four cohorts (exponent = 0.93) is similar to the same relationship determined from the data presented by Ebert (1975) using echinoid species (exponent ≈ 0.96; Charnov, 1993), maintaining a consistent ratio (isometric) between these variables. Ebert (1975) suggested the underlying reasons for the positive relationship between $\boldsymbol{M}$ and $\boldsymbol{K}$ in echinoid species involve specific adaptations of physiology, structure and behaviour under a consistent mortality regime and their interactions with the environment which determines fitness. The manner in which limited resources are allocated to growth, reproduction and maintenance influence the relationship between $\boldsymbol{M}$ and $\boldsymbol{K}$, and therefore, also an important determinant of life-history characteristics in *A. planci*.

If the age at full sexual maturity had been found to vary between the pre-outbreak and post-outbreak cohorts in a manner that conformed to the theory of life-history constants ($(\mathbf{BD})_\alpha/(\mathbf{BD})_\infty$; $(\mathrm{S})_\alpha/(\mathrm{S})_\infty$; $\boldsymbol{M}.\alpha$) among the cohorts, then estimates of the differences in age at maturity could be made. Recalculation, assuming the Beverton-Holt life-history constants in the pre-outbreak cohorts are similar to the post-outbreak values, shows that the estimated age at full sexual maturity in the pre-outbreak cohorts would have to be delayed to approximately five years, post settlement. No such delays in the age at sexual maturity have been reported for *A. planci*, in fact, the few field studies where age of the cohorts was known (Zann et al., 1987; 1990; Habe et al., 1989) confirm the age at maturity found in laboratory experiments using starfish from the GBR and Japan (Yamaguchi, 1973; 1974; Lucas, 1984). At this time, there is no information concerning reproduction in low density populations which have developed in conditions of abundant food resources, therefore, the assumption remains that the age at full sexual maturity is at 2+ years. Further discussion on age at maturity is undertaken in Chapter 5 where fecundity is analysed from samples obtained from populations in several regions.

A theoretical approach to the prediction of age and size at maturity in species as the outcome of resultant forces from the characteristics of their life histories was first attempted by Gadgil and Bossert (1970). They stated that maturity occurred when reproductive effort became > 0, after a maximum had been reached between fitness and body size. Maturation can be delayed under conditions of exponentially increasing fecundity with body size (Bell, 1980) and increased juvenile mortality rates (Stearns and Koella, 1986). An exponential fecundity/body size relationship has been described in a number of *A. planci* populations and large variation in juvenile mortality rates is characteristic of many benthic invertebrates. However, these theories are dependent on the implicit assumptions of optimisation, including a stable age distribution which does not necessarily apply to *A. planci* populations. The species exhibits many colonising attributes so that populations are normally decreasing in size with variable recruitment rates (see Zann et al., 1990). The Davies Reef population analyses showed relative variation in mortality and growth constants among cohorts, suggesting that the curvature of $\boldsymbol{K}$ values is linked to physiological stresses, as suggested by Pauly (1979), and subsequently higher mortality rates ($\boldsymbol{K}_{(BD)}$; $\boldsymbol{M}$ ($\boldsymbol{r} = 0.924$; $P < 0.05$; $n = 4$), and $\boldsymbol{K}_{(S)}$; $\boldsymbol{M}$ ($\boldsymbol{r} = 0.989$; $P < 0.01$; $n = 4$)).

The life-history constant $\boldsymbol{M}.\alpha$ was discussed by Charnov (1993), who first considered that age at maturity is selected for when the net reproductive rate $\boldsymbol{R}_0$ is maximised to maintain an overall stable population size (i.e. $\boldsymbol{R}_0 = 1$) and therefore, can be considered in theoretical terms of evolutionary stable strategies (ESS) (reviewed by Stearns, 1992) and life history trade-offs. In this context, the value $\boldsymbol{M}.\alpha \approx$ the exponent at the ESS which maximises $V_{(\alpha)}$ (the reproductive value, the number of offspring produced during the lifetime, at maturity) (Charnov, 1993). Therefore, variances in $\mathbf{M}.\alpha$ in *A. planci* populations which increase with increasing density and decreasing resource availability, imply there are similar variances in trade offs involving growth and/or reproductive processes, i.e. size at maturity.

Variations in the Beverton-Holt constants ($(\mathbf{BD})_\alpha/(\mathbf{BD})_\infty$ and $(\mathbf{S})_\alpha/(\mathbf{S})_\infty$) in the Davies Reef population resulted from differences in size at maturity where the ratio increased with lower asymptotic sizes in both whole body diameter and spine ossicle length. The pattern described smaller sizes at maturity for those starfish which achieved larger asymptotic sizes, i.e. the smaller the maximum size the more determinate the mode of growth becomes. A similar result was found by Vøllestad et al. (1993) in their analyses of brown trout populations.

The pre-outbreak cohorts of *A. planci* on Davies Reef achieved larger asymptotic sizes at a later stage in the study than the pre-outbreak cohorts, and at an older estimated age. This suggests there were substantial differences in the growth, and perhaps other life-history characteristics between the two groups. The fact that the relationship between length at maturity and the theoretical asymptotic length is constant within some taxa but not others may be of some interest (Vøllestad et al., 1993) for this variable relationship suggests there is certain plasticity in the life-history traits of *A. planci* related to these estimates.

3.4.4. Mode of body growth in *A. planci*

If we assume that rates of respiration, feeding and assimilation were similar in all four cohorts, then the allocation of resources between maintenance, growth and reproduction must differ between the pre-outbreak cohorts and the post-outbreak cohorts for the observed differences in growth characteristics to have occurred. Between 1987 and 1988 Keesing (1990) monitored seasonal feeding rates and movement in large ((BD) > 40cm) and small ((BD) < 40cm) adult *A. planci* on Davies Reef. The arbitrary separation of size classes made by Keesing can be interpreted as a similar distinction to that made in the present study between the pre and post-outbreak groups (determined from SPBC analyses, where mean body diameter was 41.9cm and 38.9cm respectively). He found a significant positive relationship between feeding rate and body size, with no difference in the number of feeds per day between the two body size groups, except in the early part of his field study prior to the commencement of the present one. On Davies Reef, the overall mean rate of coral cover killed in < 40cm group was 155cm.d^{-1} (mean (BD) = 32.5cm, or approximately 1340g mean whole wet weight) and in the ≥ 40cm group was 314cm.d^{-1} (mean (BD) = 48.5cm, or approximately 3520g (WET)) (Keesing, 1990). Calculation from these data yields the relationship between feeding rate (FR) and (WET);

$$(FR) \propto (WET)^{0.73} \qquad (3.7)$$

This relationship is similar to the general hypothetical relationship for feeding rates and body size, $(WET)^{0.75}$ (Peters, 1983), showing there was no significant difference in the relative rate of feeding between the two size classes on Davies Reef. This type of allometric relationship also supports an asymptotic growth pattern in both groups. If we assume that the same resources were available to all starfish over the adult body size range sampled by Keesing (1990), then feeding rate was a relative estimate of the amount of energy available for maintenance, growth and reproduction. In general terms, the proportion of the energy budget allocated to growth and reproduction declines with increasing body size (Reiss, 1989). Therefore, when fecundity increases exponentially with body size, i.e. in *A. planci* (Kettle and Lucas, 1987; Kettle, 1990; Birkeland and Lucas, 1990), there is relatively much less energy available for growth and maintenance and so there is a tendency to a determinate mode of growth and a shortened lifespan (Kettle, 1990). In species that show determinate growth, the proportion of the energy budget devoted to growth must decline to zero in adults (Reiss, 1989).

The results in this study have shown that growth is influenced by habitat conditions (i.e. density and food availability) and can vary among age classes within a population. The mode of growth in *A. planci* has been discussed thoroughly (Lucas, 1984; Moran, 1986; Kettle, 1990; Birkeland and Lucas, 1990), and well-defined asymptotes have been found to occur in a number of studies. However, the question remains as to how some *A. planci* in low density populations reach very large body sizes in conditions of solely intrinsic limitation to growth (i.e. limited by the rate of energy intake). Although the field data required to assess this problem is not yet available, several possible explanations include:

(a) a similar growth rate to that in high density populations with an extended period of growth from lower reproductive effort throughout the adult phase (indeterminate growth).

(b) increased growth rate to attain maximum size within the juvenile and young adult growth phases to (AGE) = 3+ years, i.e., the same period of growth as reported in higher density populations and in experimental studies (determinate growth).

(c) *A. planci* has the capacity for indeterminate growth; however, many populations experience limiting habitat conditions in moderate to high densities or low food resources which promotes a determinate-type mode of growth as a variant of an underlying potential for indeterminate growth.

Growth rates and final sizes of marine invertebrates are often constrained by environmental conditions rather than by genetics, i.e. they are plastic ontogenetic responses to local conditions (Sebens 1987) resulting in a capacity to exhibit a wide range of body sizes in various habitats. Paine (1976a) found that intraspecific competition (i.e. density dependence) had a clear effect on growth rate and ultimate size in *Pisaster ochraceus*, which exhibited indeterminate growth by reaching a much larger size in uncrowded populations and an abundance of suitable prey, presumably from less competition. However, Lucas (1984) favoured the argument that variation in genotype or environment results in a broad range of ultimate sizes in *A. planci*, yet ultimate size is clearly determinate under experimental conditions. The results from this study also demonstrated a determinate growth pattern in *A. planci* under outbreak conditions (Figure 3.9). The analyses from the four principal cohorts found there was asymptotic growth because both pre and post-outbreak groups experienced a shortage of resources at the same time, but at different estimated ages. The mean body sizes of the pre-outbreak cohorts were significantly larger, reaching asymptotes at a later stage of the study, and suggesting they exhibited a more indeterminate-type mode. Therefore, the mode of growth is apparently not just determinate or indeterminate but more like a continuum between the two extremes of habitat dependence and asymptotic final size as suggested by Sebens (1987), depending on the degree of plasticity in growth, exhibited in the adult stage. Therefore, it is predicted that an individual of 100cm whole body diameter, having a similar growth rate to that determined from the pre-outbreak cohorts on Davies Reef, would take at least 11 years to achieve that size.

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

3.4.5. An alternative assessment of body growth

If individual growth histories are preserved in ossicle growth increments as indicated by the relationship found between whole body diameter and spine ossicle growth, then past body growth rates can possibly be estimated from skeletal ossicle analyses. The use of chronometric morphometry to estimate past growth rates has been suggested for fish species by the assessment of otolith growth (Radke, 1987).

There was a positive relationship (but weak coefficient of determination) between spine ossicle length and whole body diameter (Table 3.1) in combined samples of the Davies Reef adult population (AGE > 3 years: $r^2 = 0.04$; $P < 0.01$, $n = 1270$; MSE = 13.27). Larger starfish generally have longer spines for the same estimated age. There is an approximate three fold increase in the spine ossicle growth constants $\boldsymbol{K}_{(S)}$ in the post-outbreak cohorts (1985 and 1986) compared with the pre-outbreak cohorts (1985 and 1986). Therefore, there is a correlation between increasing population density and the estimated growth rates determined from the spine ossicle growth constants. A positive correlation between increased growth rates and population density may be achieved by behavioural differences in starfish from intraspecific stimulation to form feeding aggregations, and *stress* increasing the rate of the growth constant and decreasing the asymptotic body size (i.e. a net decrease in overall production from *stress*) due to increased competition for resources.

By extending this hypothesis to other populations on the GBR a consistent argument can be used to explain the apparent inverse correlation among populations for mean spine ossicle length at age and mean body size among GBR populations (where a Tukey (HSD) test for mean spine length at estimated age found Davies Reef > Hook Island > Lady Musgrave Reef (Figure 3.20b) and; mean whole body diameter, Lady Musgrave Reef > Hook Island > Davies Reef > Helix Reef) (Table 3.6; Figure 3.19). Mean spine ossicle length at estimated age is lower in low density populations despite a negative relationship between mean whole body diameter and estimated population density (reflecting resource availability). Thus spine ossicle growth constants are lower in low density populations. Therefore, the significant positive relationship between spine ossicle length and whole body diameter at estimated age found in the Davies Reef population does not necessarily apply to the inter population analyses because there are differences in the mode of spine ossicle growth between these populations.

The assumption of the SPBC method, for simplicity, that settlement occurred in December/January in all three populations may not be realistic because cooler water temperatures prevail in early summer with increasing latitude and therefore, is likely to delay the timing of spawning and settlement in the southern GBR region. However, this would not affect the significance of the differences found among the populations. The latitudinal influence on settlement dates would only serve to displace the regressions for Hook Island and Lady Musgrave Reef populations towards the right hand side of the plot and therefore, increase the significance of the analyses. An inverse relationship between growth constants and mean adult body size in *A. planci* is evidence for a range of growth patterns from determinate to indeterminate modes. However, confirmation of this variability must await intensive low density population studies.

3.4.6. Longevity in populations from the GBR

A smaller spine length at full sexual maturity (i.e. at age 35 months, see Lucas, 1984) was interpreted as a slower growth rate in the juvenile phase and therefore, resulted in significant differences in the elevation of the GBR population regressions for spine ossicle length and estimated age. These morphometric differences may be caused by variation in behaviour under a range of population densities and differences in mean annual water temperature. Although spine growth rates in the adult phase were found not to differ among the three populations (i.e. regressions are parallel), water temperature influences growth throughout the life cycle. Therefore, annual spine ossicle growth was maintained in adult starfish despite shorter periods of seasonally elevated water temperatures (summer) in the southern populations, slowing overall growth. The longevity estimates were greater in the Hook Island and Lady Musgrave Reef populations than for Davies Reef, which therefore supports the hypothesis relating increased lifespan with slower growth rates, although without more data it still remains speculative for this species.

Ebert (1982) found a positive relationship between survival probability and relative body wall size in 17 species of echinoids from the Indo-West Pacific, supporting the hypothesis that survival is related to the allocation of resources to protection and maintenance, and this relationship may also apply to *A. planci*. In relation to echinoids, the greater the unpredictability of recruitment (or juvenile survival) then the longer the species' lifespan (Ebert, 1982). Although the two *A. planci* outbreak episodes on the GBR showed consistently high recruitment over a number of years this pattern may be atypical for the species. Longer term studies on Suva Reef by Zann et al. (1987) and in Southern Japan (Habe et al., 1989) described the recruitment of *A. planci* as irregular and provides the selective pressure for very high fecundity (see Birkeland and Lucas, 1990). The estimated lifespan found in the three GBR populations ranged from 4.8 years in the outbreak cohort of Davies Reef to approximately 12 years in the Lady Musgrave Reef population, i.e. a positive relationship between longevity and mean body size for those populations ($\boldsymbol{r} = 0.903$; $n = 5$; $0.02 < P < 0.05$). If body size is determined by environmental conditions (i.e. food availability and population density) then the link between habitat type and the life-history characteristics related to body size (i.e. fecundity) may be found in the mortality regime of populations (Stearns, 1992).

Figures

Figure 3.10 Plot of mean and SE of whole body diameter (BD) in each sample and (T) joined by straight lines in each cohort (1983 to 1988) over the study period on Davies Reef (October, 1988 to December, 1990).

Figure 3.11 Plot of linear regressions (dotted) for spine ossicle length (S) and (T) in the principal cohorts (1984 to 1987) and overlay of combined means and SE with a cubic spline fit (dashed) and linear regression fit (solid), over the 38 month study on Davies Reef (October, 1988 to December, 1990)

Figure 3.12 Plot of mean and SE of spine ossicle length (S) in each sample and (T) joined by straight lines in each cohort (1982 to 1988) over the study period on Davies Reef (October, 1988 to December, 1990).

Figure 3.13 Plot of linear regressions (dotted) for whole spine appendage length (WS) and (T) in the principal cohorts (1984 to 1987) and overlay of combined means and SE with a cubic spline fit (dashed) and linear regression fit (solid), over the 38 month study on Davies Reef (October, 1988 to December, 1990)

Figure 3.14 Plot of mean and SE of whole spine appendage length (S) in each sample and (T) joined by straight lines in each cohort (1982 to 1988) over the study period on Davies Reef (October, 1988 to December, 1990).

Figure 3.15 Plot of linear regressions (dotted) for primary oral ossicle weight (PO) and (T) in the principal cohorts (1984 to 1987) and overlay of combined means and SE with a cubic spline fit (dashed) and linear regression fit (solid), over the 38 month study on Davies Reef (October, 1988 to December, 1990).

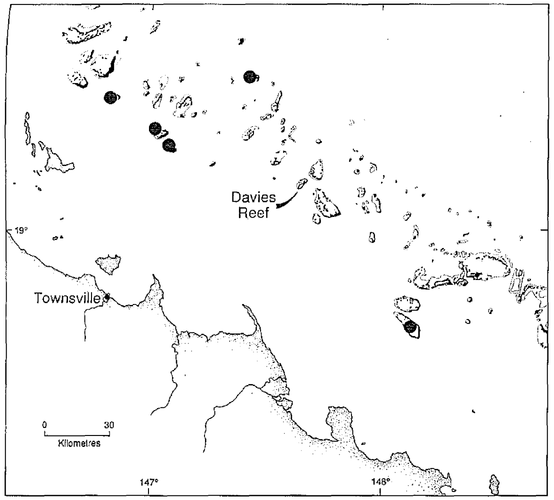
Figure 3.16 Plot of mean and SE of primary oral ossicle weight (PO) in each sample and (T) joined by straight lines in each cohort (1982 to 1987) over the study period on Davies Reef (October, 1988 to December, 1990).

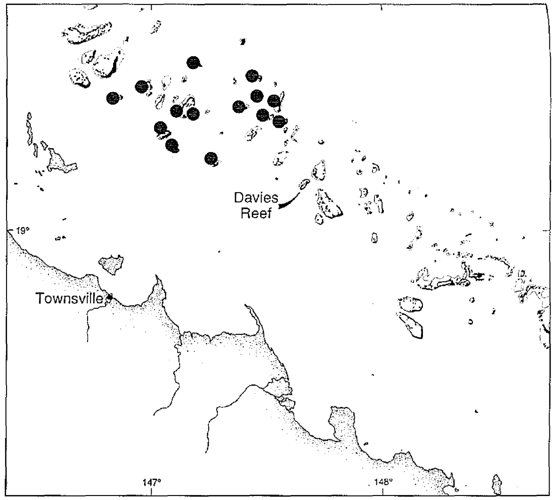
Figure 3.17 Plot of linear regressions (dotted) for secondary oral ossicle weight (SO) and (T) in the principal cohorts (1984 to 1986) and overlay of combined means and SE with a cubic spline fit (dashed) and linear regression fit (solid), over the 38 month study on Davies Reef (October, 1988 to December, 1990).

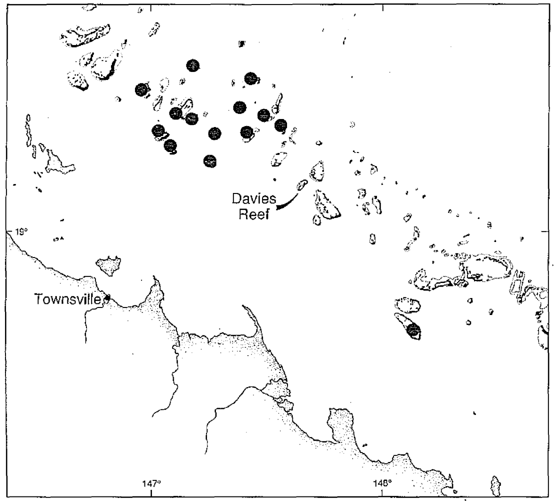
Figure 3.18 Plot of mean and SE of secondary oral ossicle weight (PO) in each sample and (T) joined by straight lines in each cohort (1983 to 1987) over the study period on Davies Reef (October, 1988 to December, 1990).

Figure 3.19. Linear regression analysis of mean whole body diameter (cm) and estimated population density (ha.$^{-1}$) in four populations from the GBR region: Helix Reef (from Kettle, 1990); Davies Reef; Butterfly Bay, Hook Island; and Lady Musgrave Reef.

Figure 3.20 Linear regression analyses of spine ossicle length (S) and estimated age (AGE) in three populations: Davies Reef (n = 1549); Butterfly Bay, Hook Island (n = 68); and Lady Musgrave Reef (n = 9).


Davies Reef
19°
Townsville
0
30
Kilometres
147°
148°


Davies Reef
19°
Townsville
147°
148°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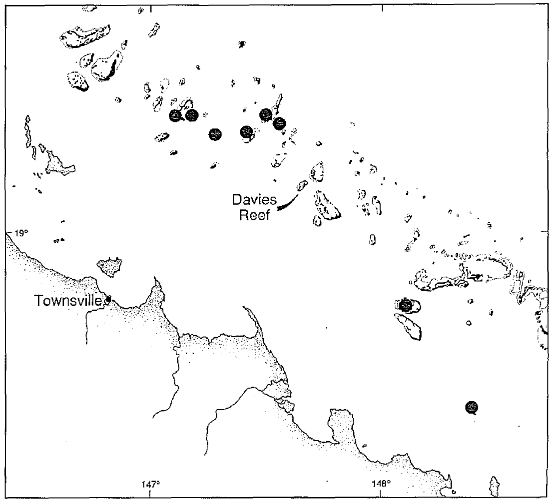
19°
Townsville
147°
148°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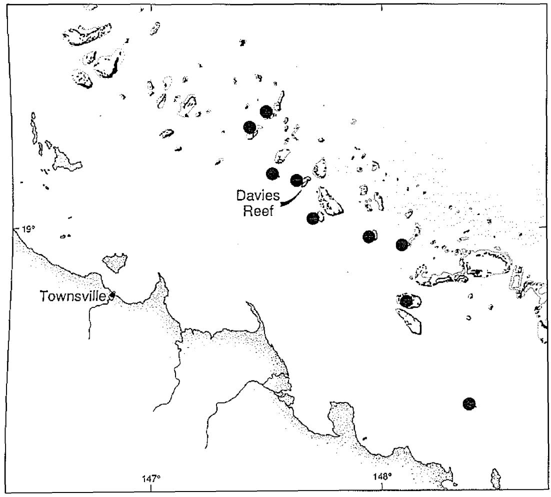
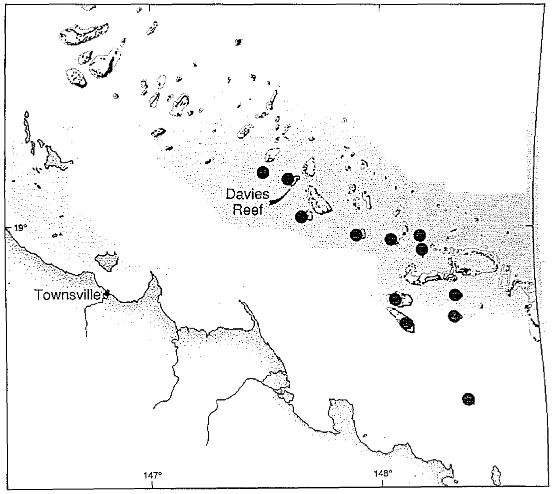
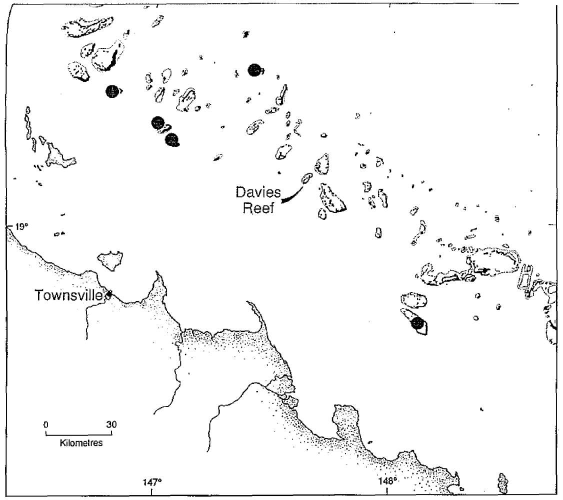
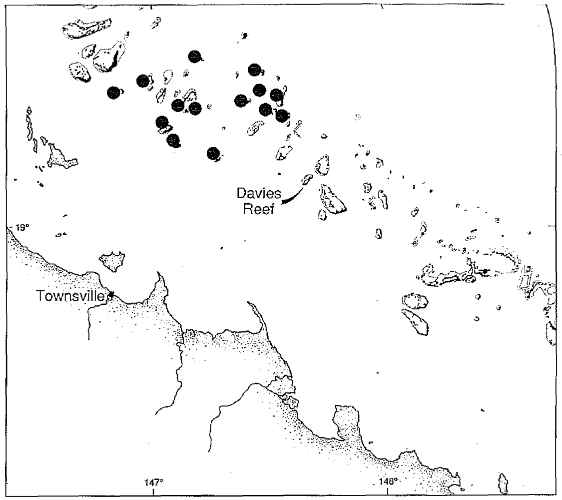
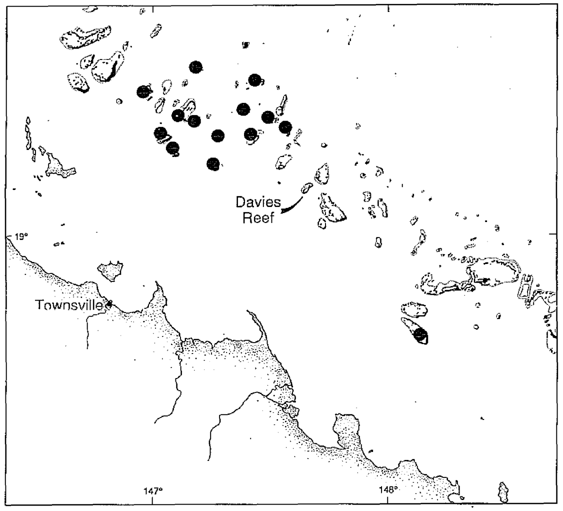
19°
Townsville
147°
148°


Davies Reef
19°
Townsville
147°
148°


Davies Reef
19°
Townsville
147°
148°


Davies Reef
19°
Townsville
0 30
Kilometres
147°
148°


Davies Reef
19°
Townsville
147°
148°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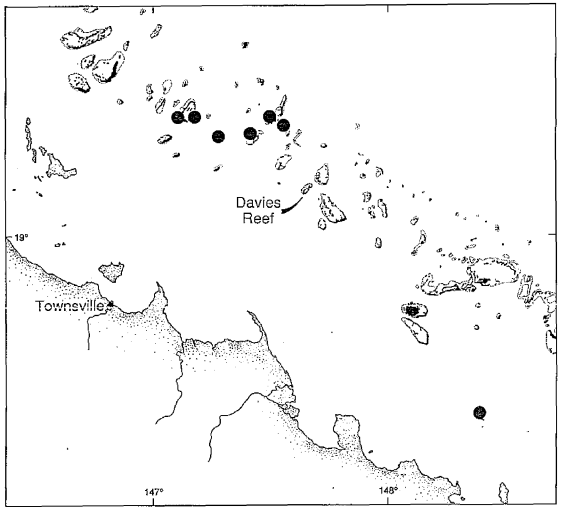
Townsville
147°
148°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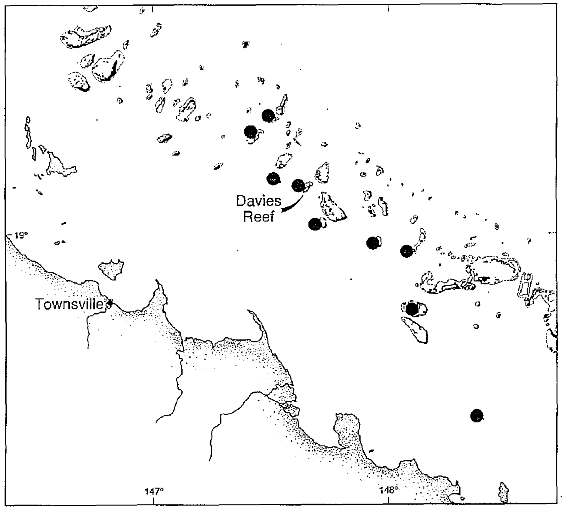
Townsville
147°
148°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19°
Townsville
147°
148°

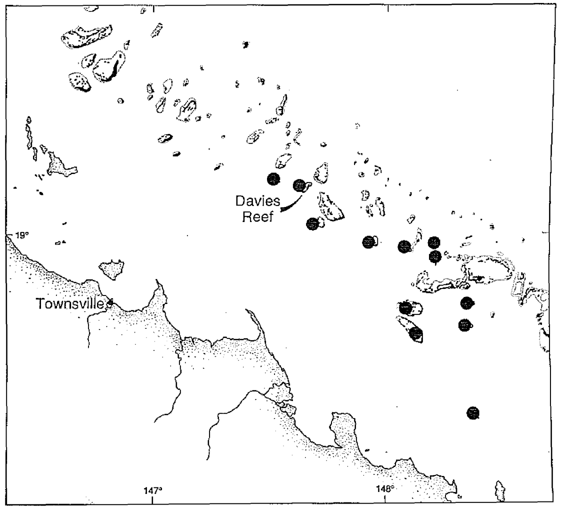

Davies Reef
19°
Townsville
147°
148°

FIGURE 3.2

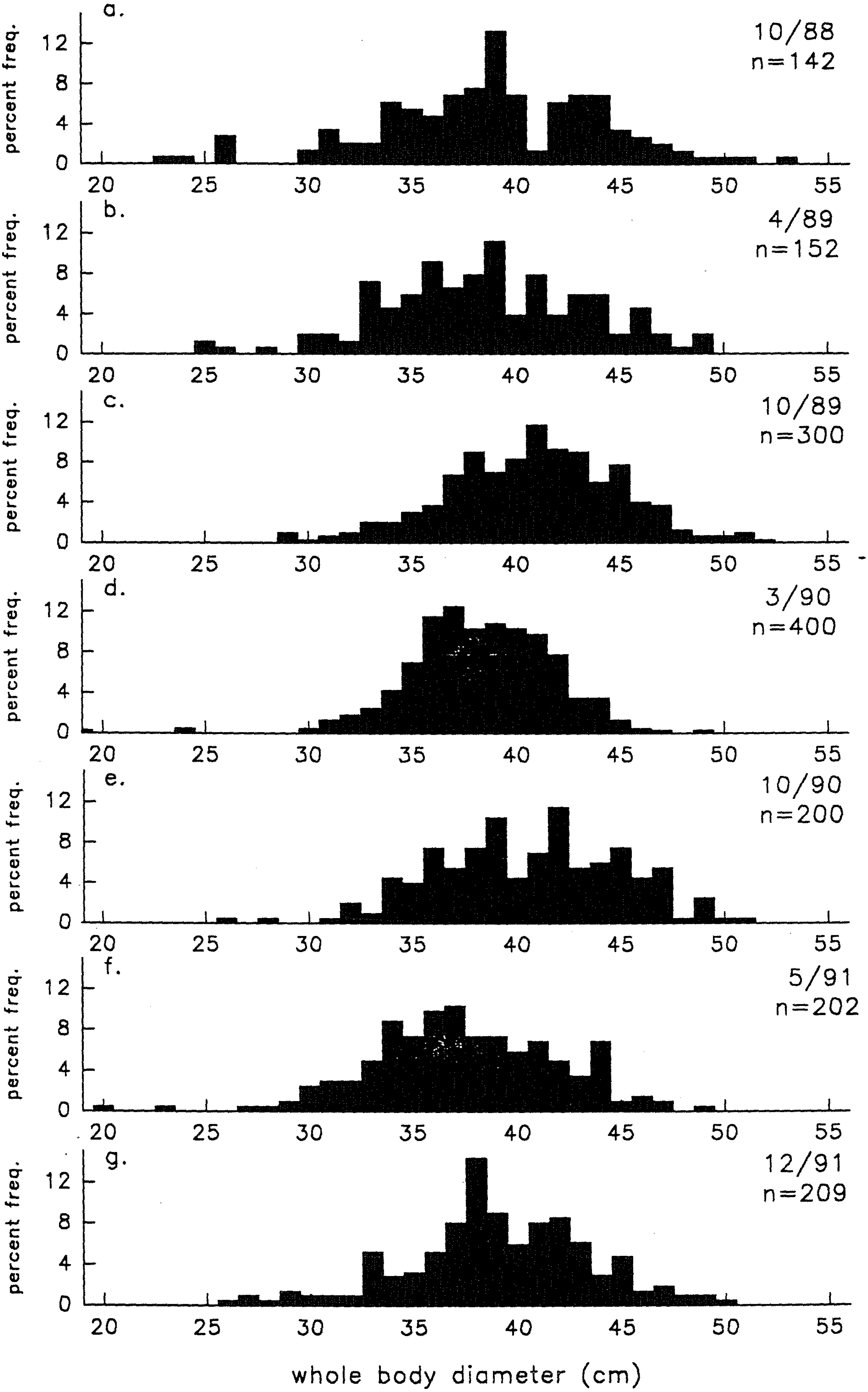
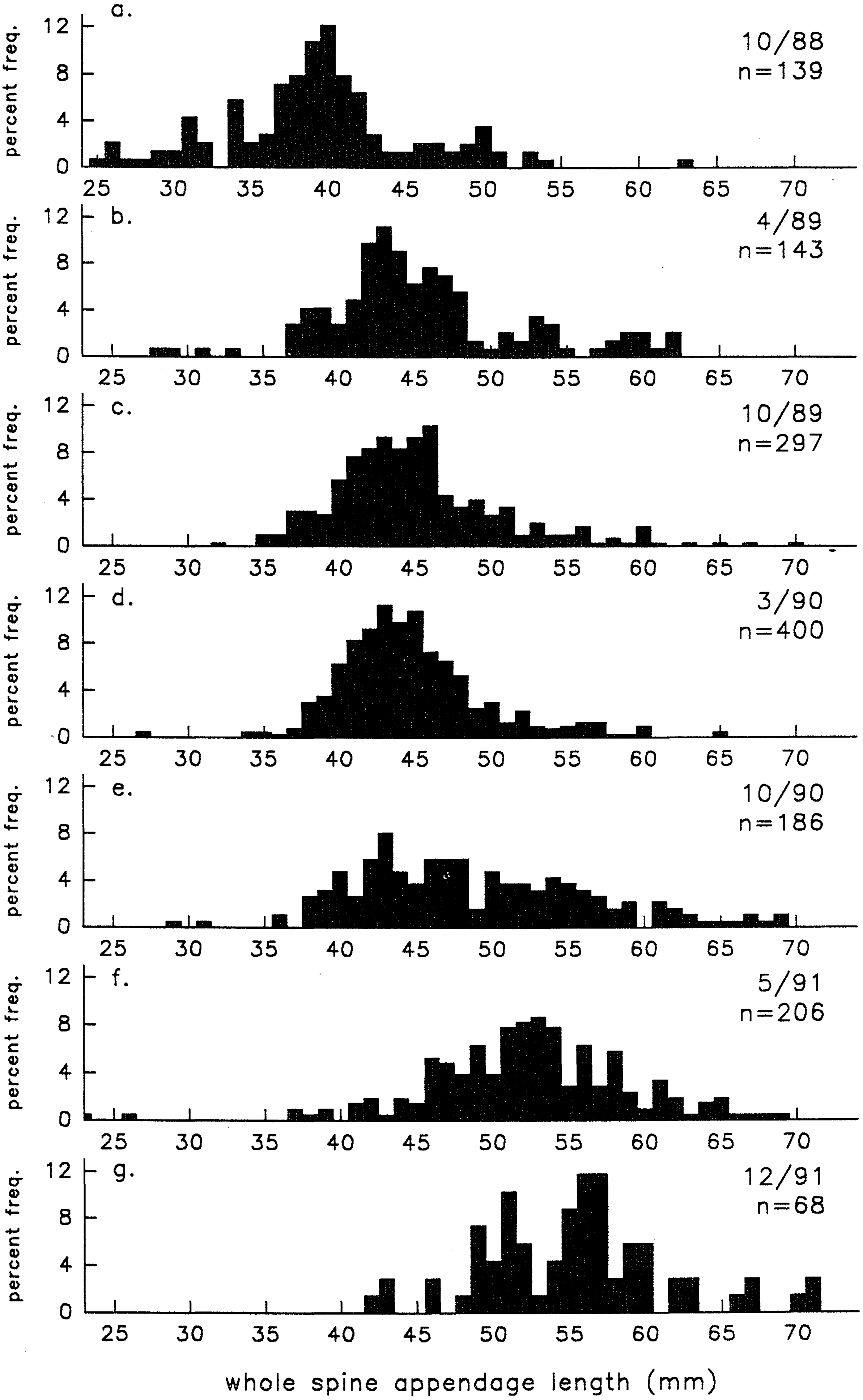

a.
10/88
n=142
b.
4/89
n=152
c.
10/89
n=300
d.
3/90
n=400
e.
10/90
n=200
f.
5/91
n=202
g.
12/91
n=209
percent freq.
0
4
8
12
20
25
30
35
40
45
50
55
whole body diameter (cm)

FIGURE 3.4



a.
10/88
n=139
b.
4/89
n=143
c.
10/89
n=297
d.
3/90
n=400
e.
10/90
n=186
f.
5/91
n=206
g.
12/91
n=68
percent freq.
0
4
8
12
25
30
35
40
45
50
55
60
65
70
whole spine appendage length (mm)

FIGURE 3.5

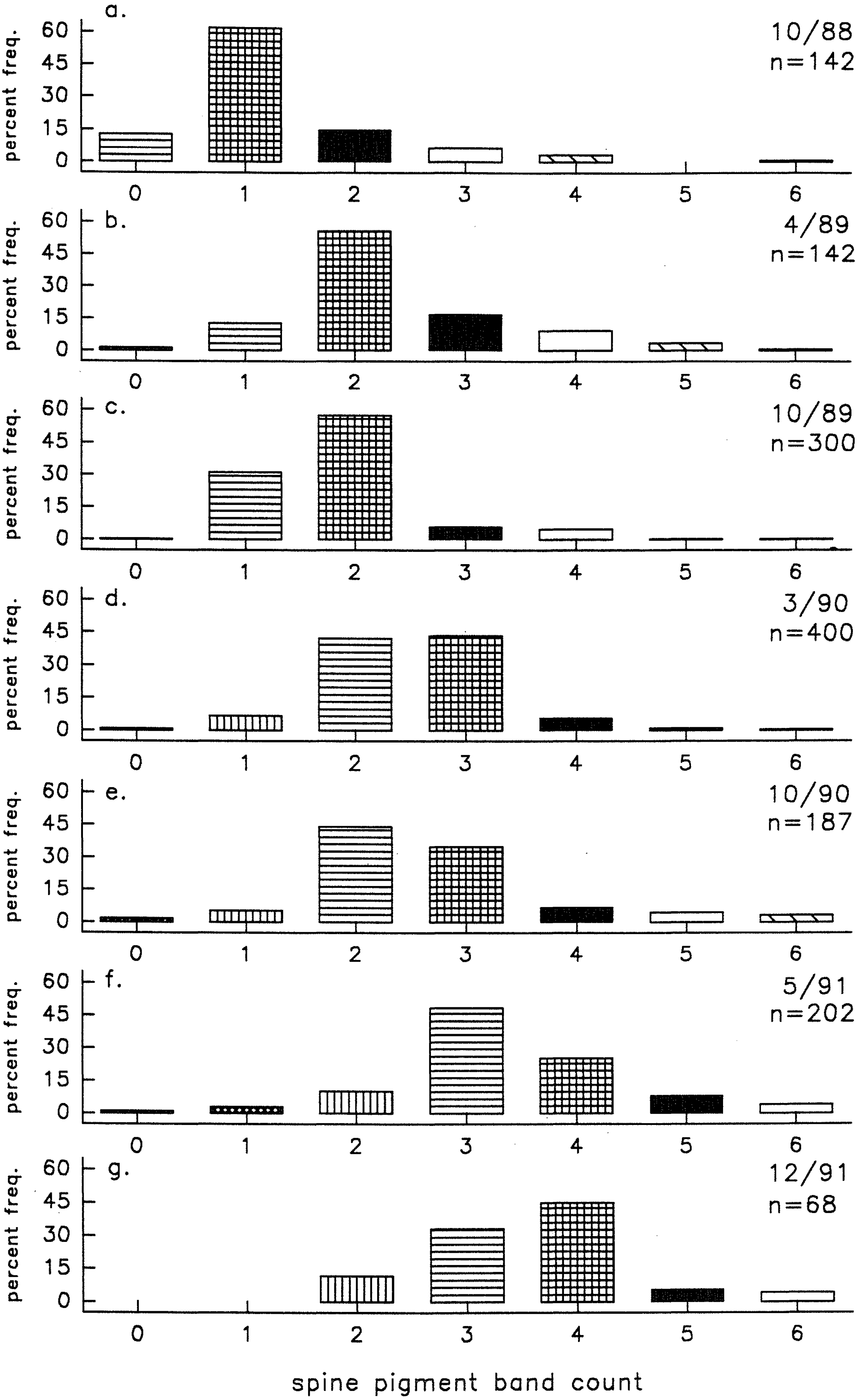

a.
10/88
n=142
b.
4/89
n=142
c.
10/89
n=300
d.
3/90
n=400
e.
10/90
n=187
f.
5/91
n=202
g.
12/91
n=68
percent freq.
0
15
30
45
60
0
1
2
3
4
5
6
spine pigment band count

FIGURE 3.6

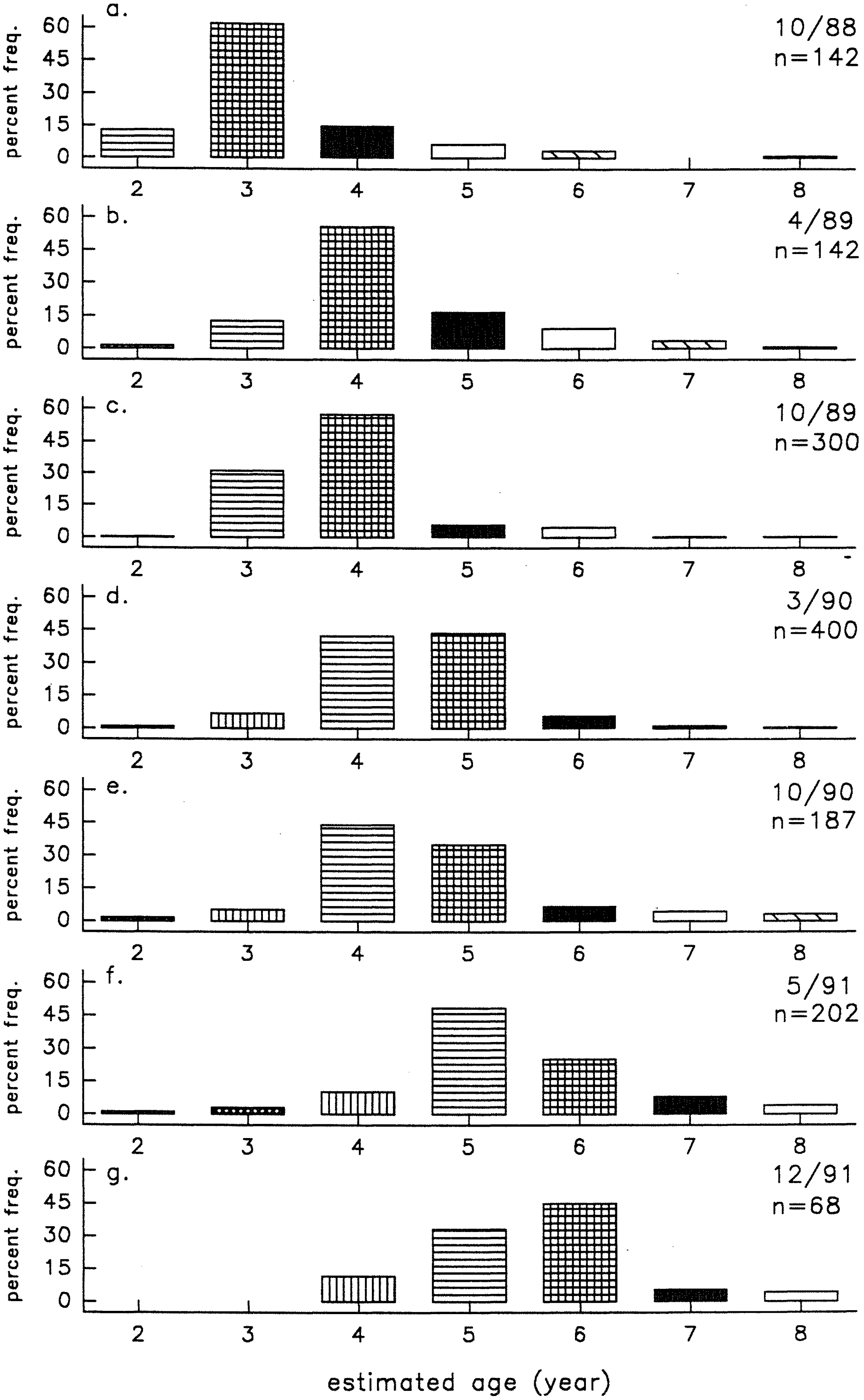

a.
10/88
n=142
b.
4/89
n=142
c.
10/89
n=300
d.
3/90
n=400
e.
10/90
n=187
f.
5/91
n=202
g.
12/91
n=68
percent freq.
0
15
30
45
60
2
3
4
5
6
7
8
estimated age (year)

FIGURE 3.8

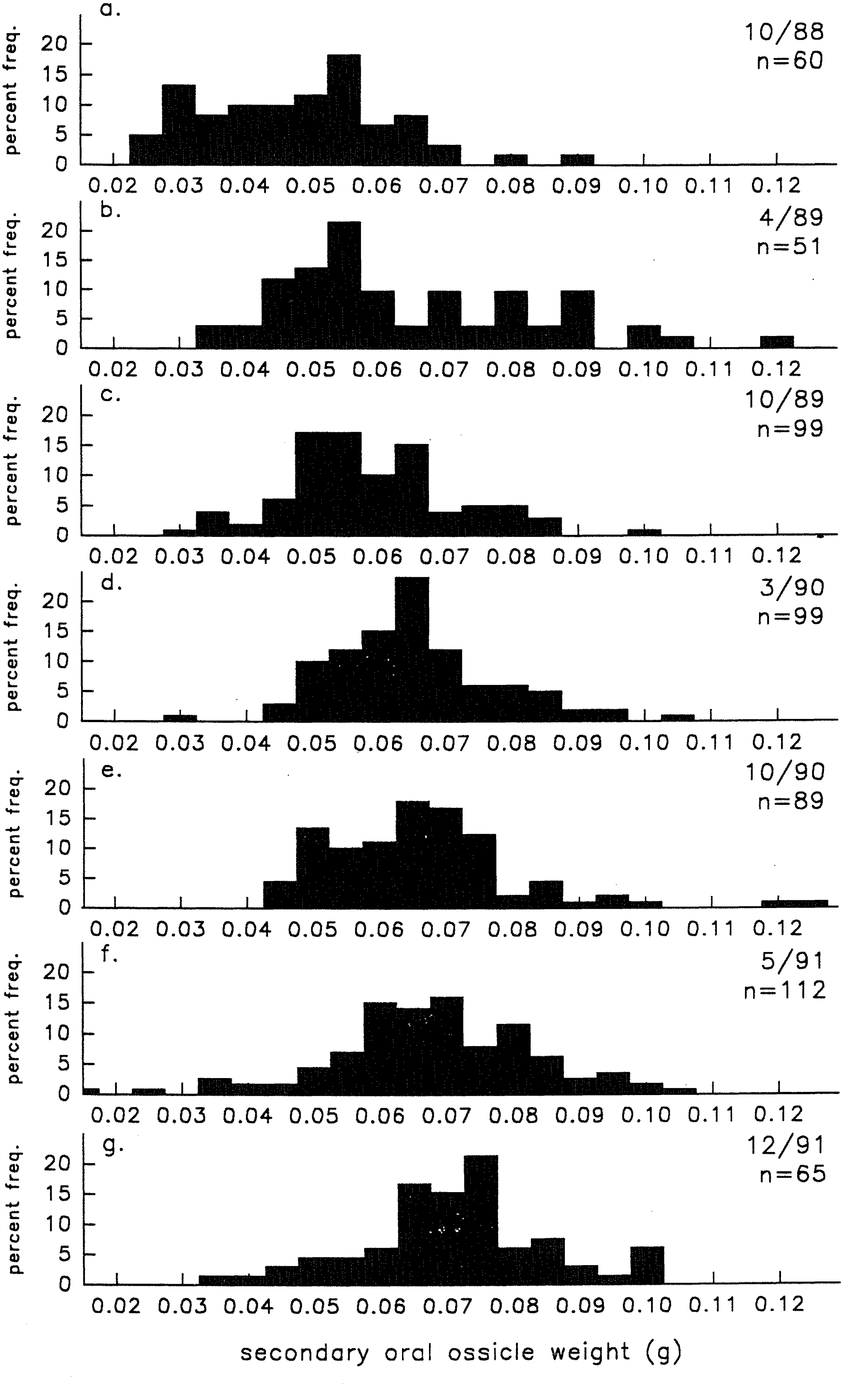

a.
10/88
n=60
b.
4/89
n=51
c.
10/89
n=99
d.
3/90
n=99
e.
10/90
n=89
f.
5/91
n=112
g.
12/91
n=65
percent freq.
0
5
10
15
20
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
0.11
0.12
secondary oral ossicle weight (g)

FIGURE 3.9

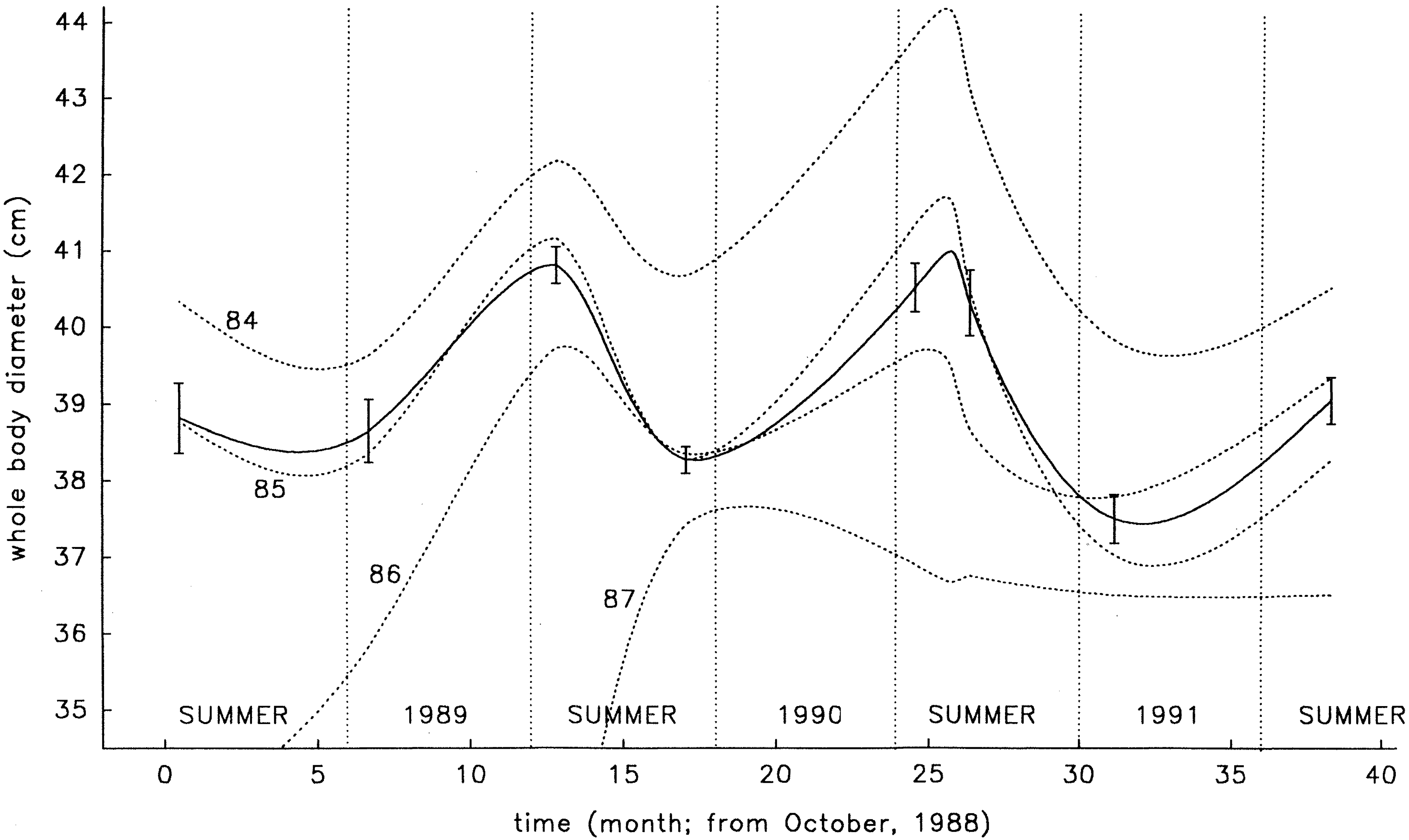

44
43
42
41
40
39
38
37
36
35
whole body diameter (cm)
84
85
86
87
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.10

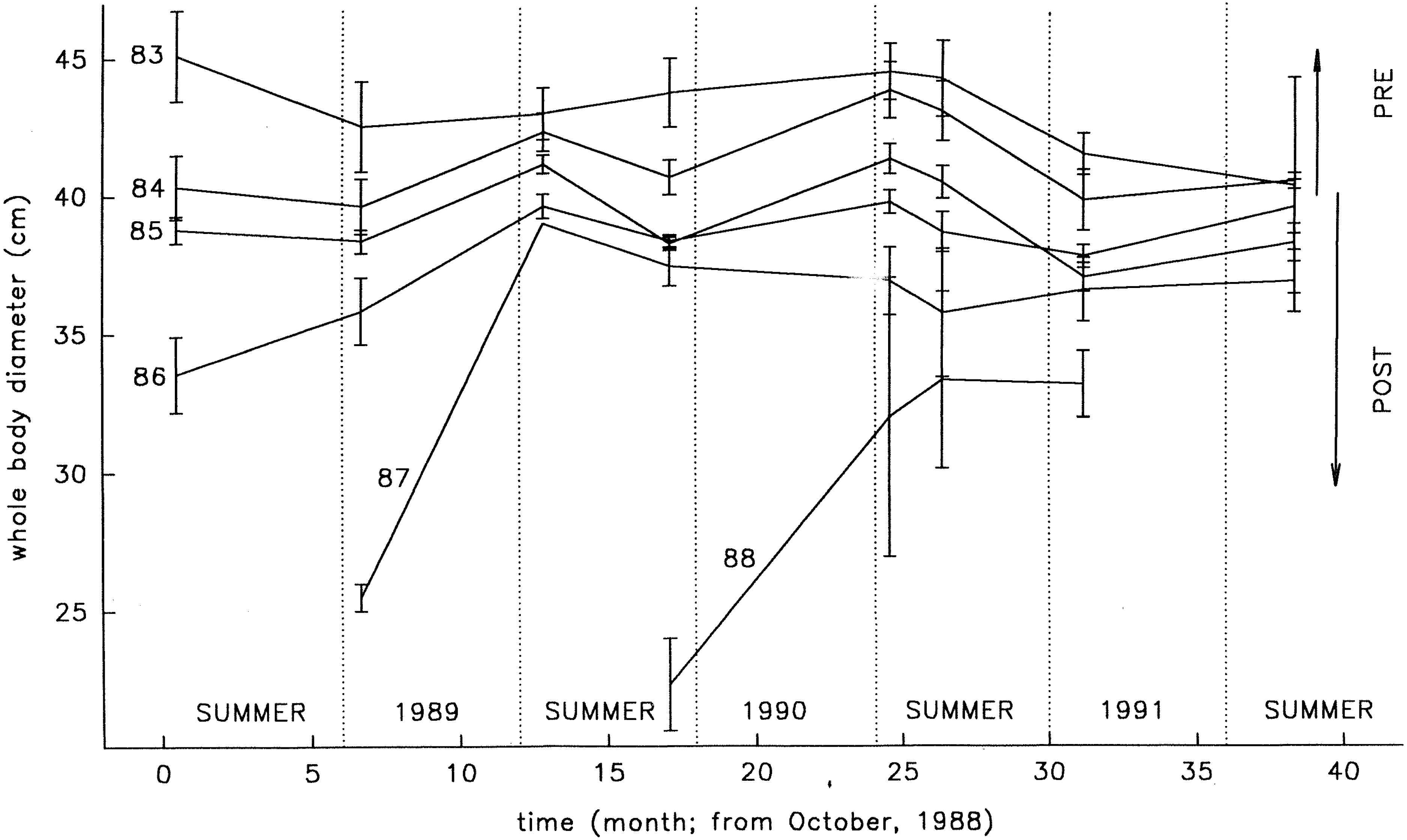

whole body diameter (cm)
45
40
35
30
25
83
84
85
86
87
88
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
PRE
POST
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.12

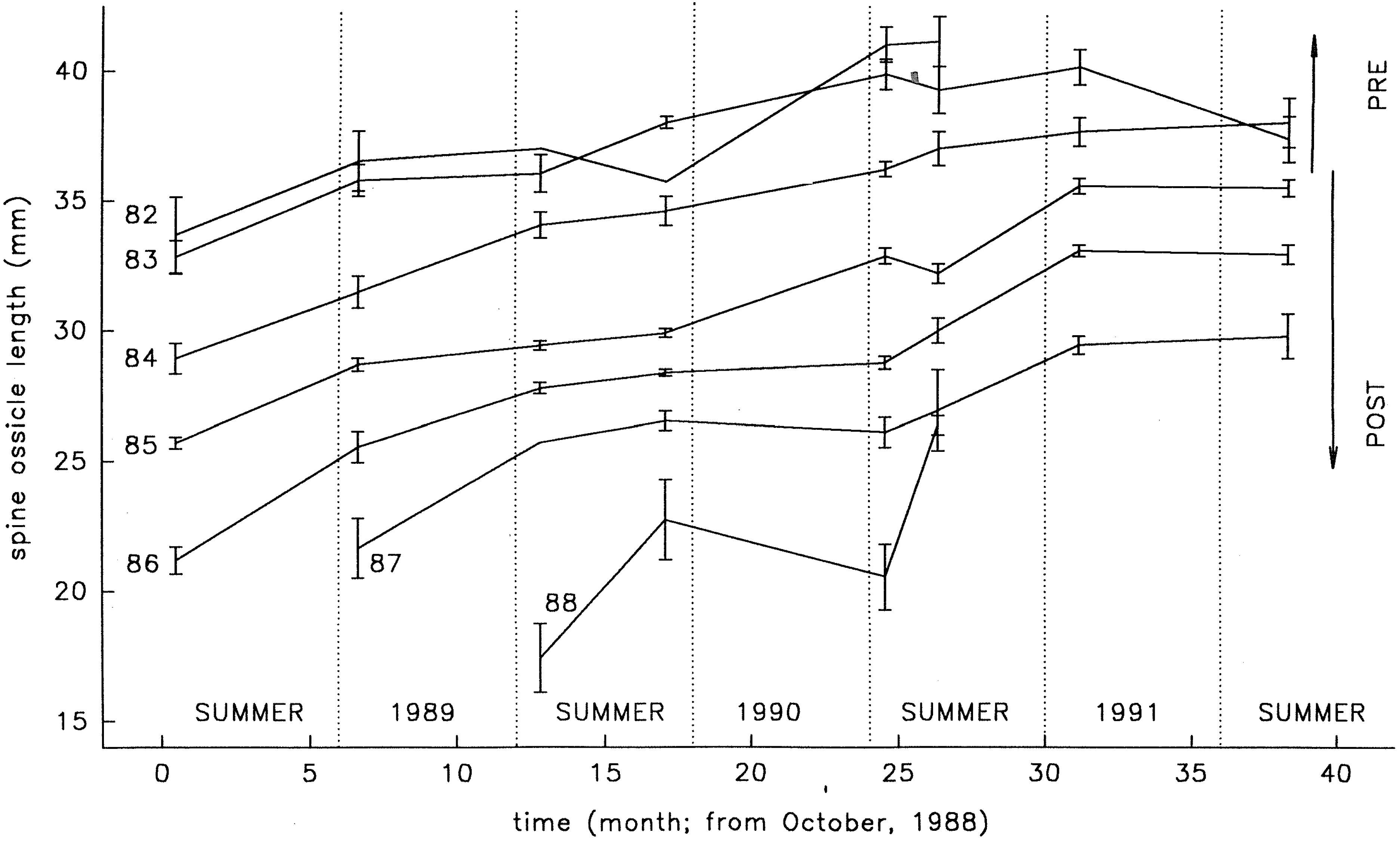

spine ossicle length (mm)
time (month; from October, 1988)
40
35
30
25
20
15
0
5
10
15
20
25
30
35
40
82
83
84
85
86
87
88
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
PRE
POST

FIGURE 3.13

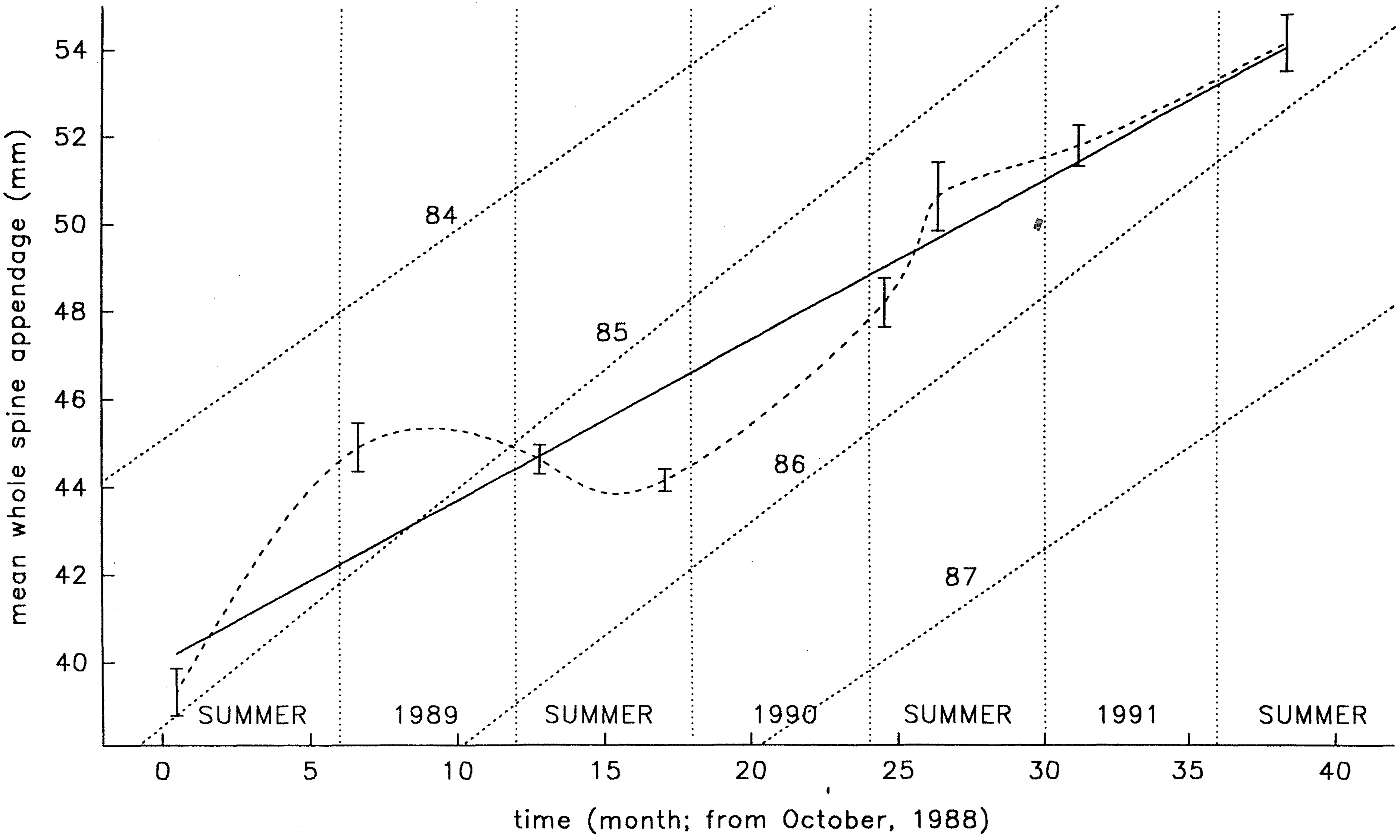
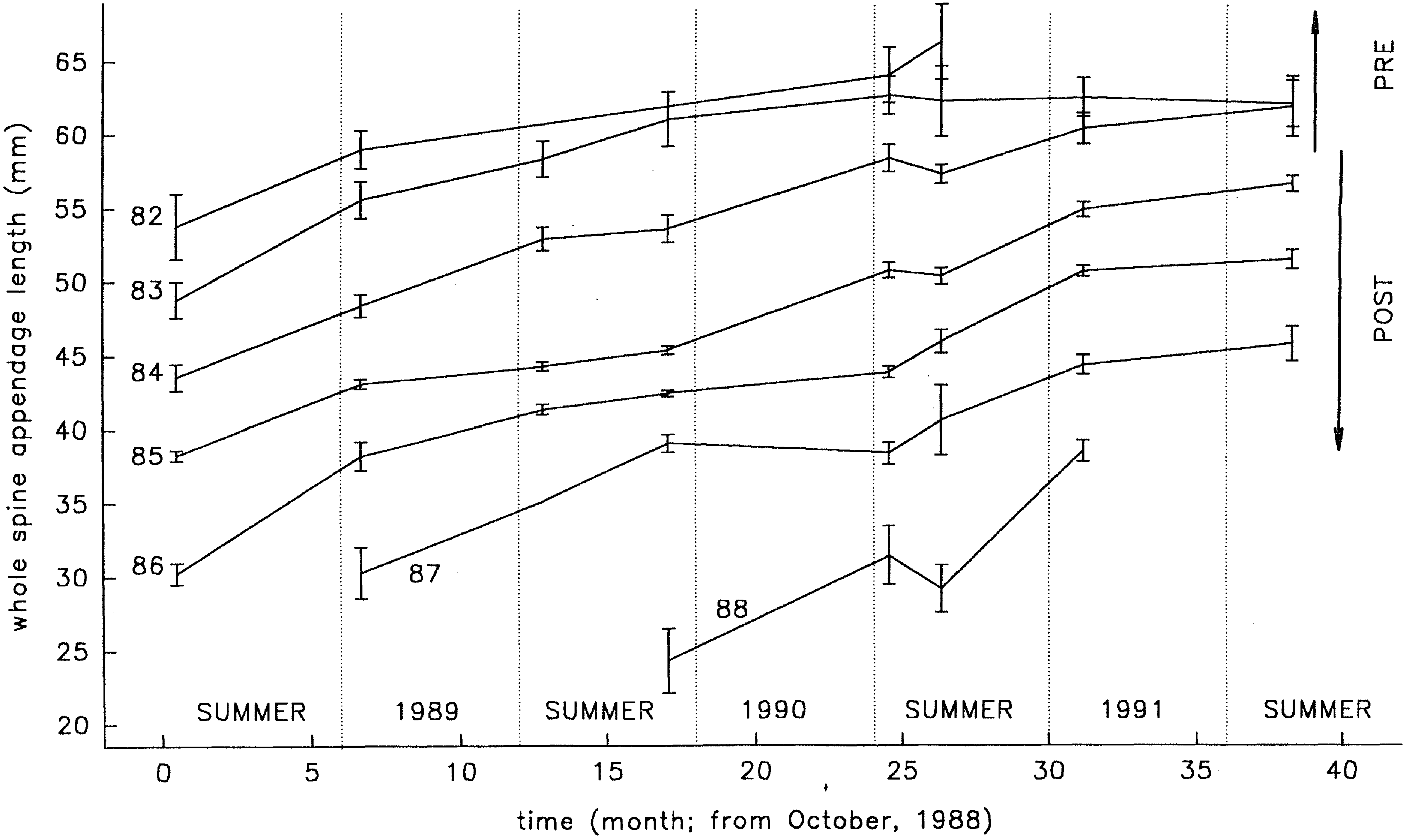
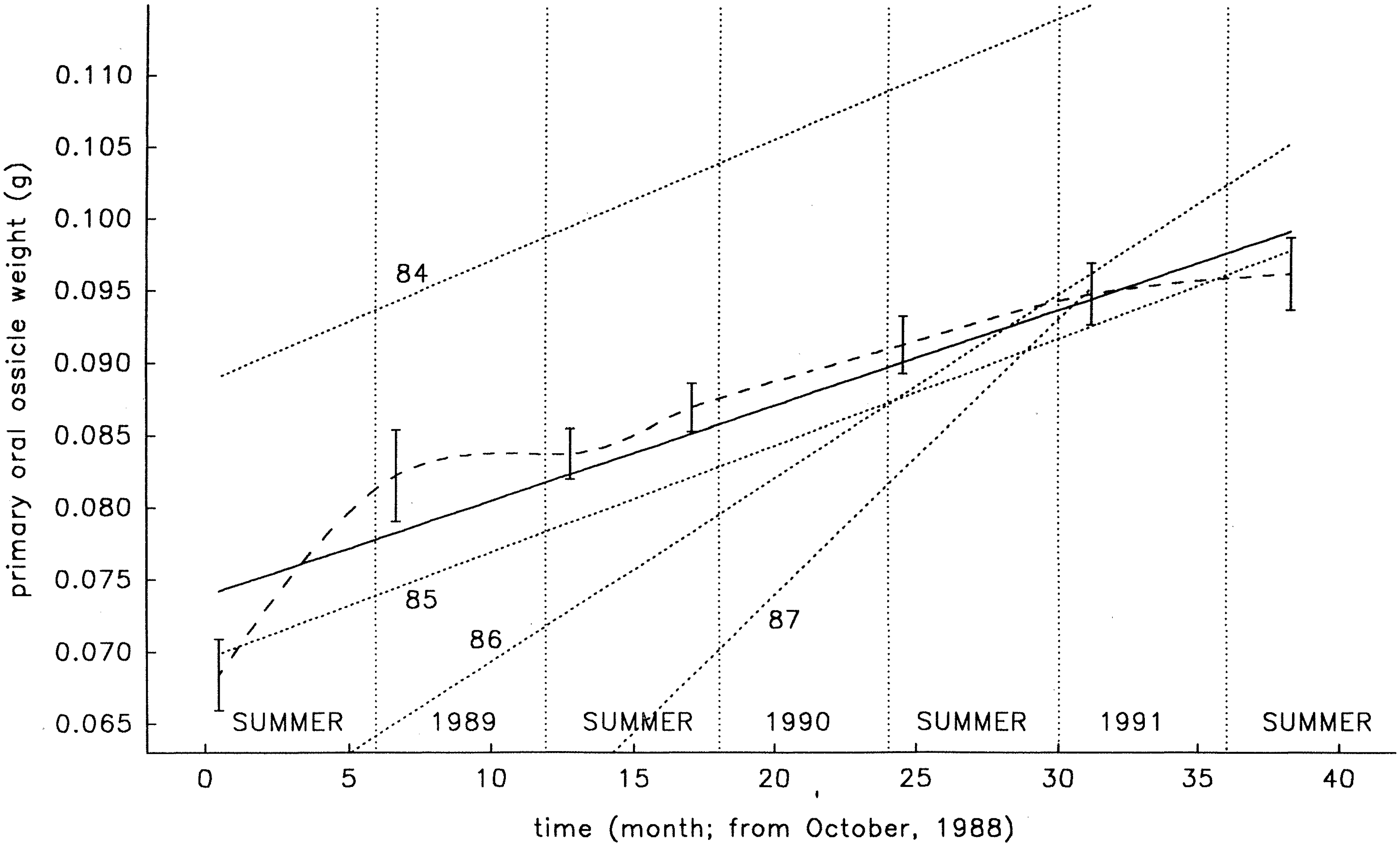

mean whole spine appendage (mm)
54
52
50
48
46
44
42
40
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)
84
85
86
87
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER

FIGURE 3.14



whole spine appendage length (mm)
65
60
55
50
45
40
35
30
25
20
82
83
84
85
86
87
88
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
PRE
POST
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.15



primary oral ossicle weight (g)
0.110
0.105
0.100
0.095
0.090
0.085
0.080
0.075
0.070
0.065
84
85
86
87
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.16

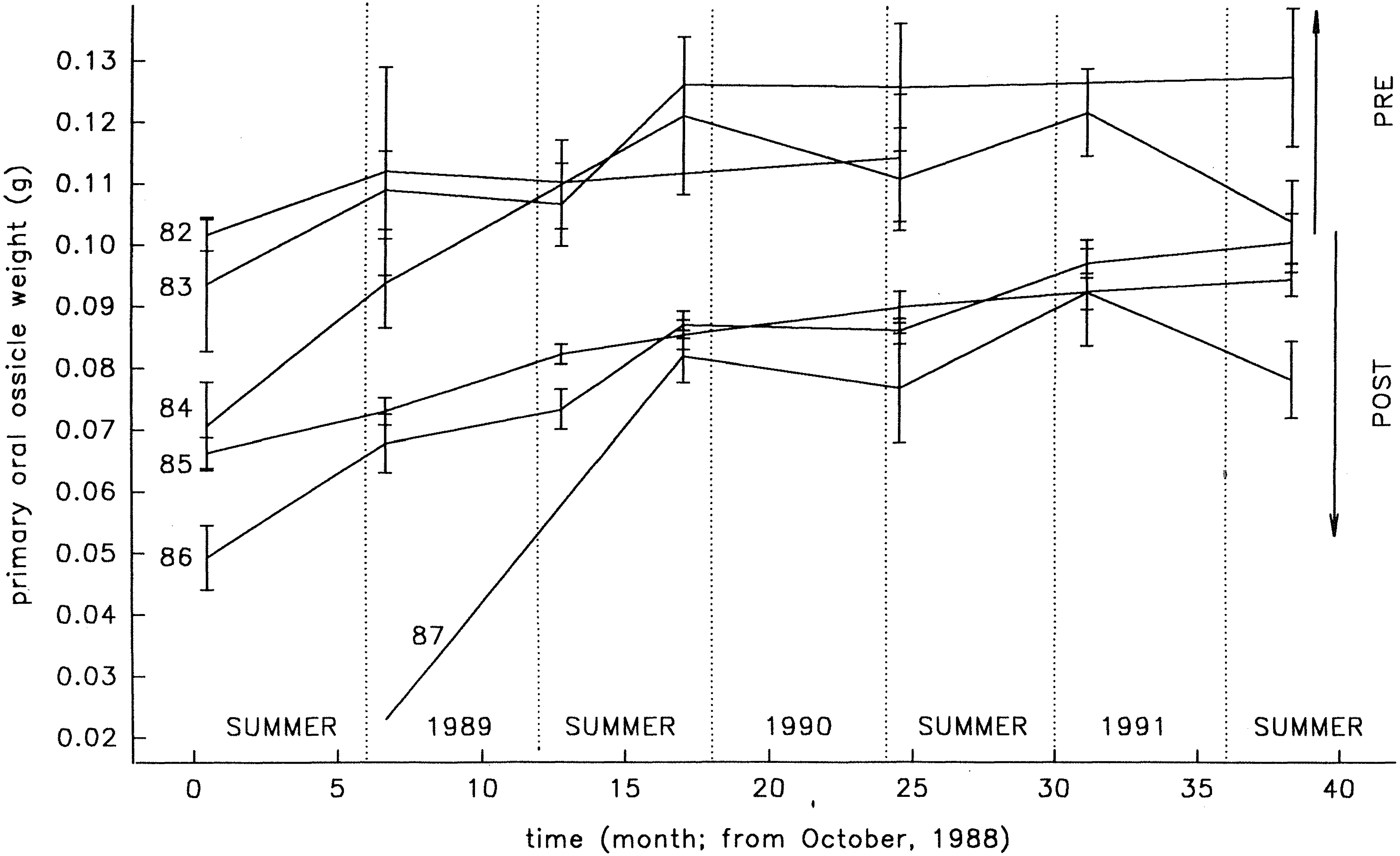
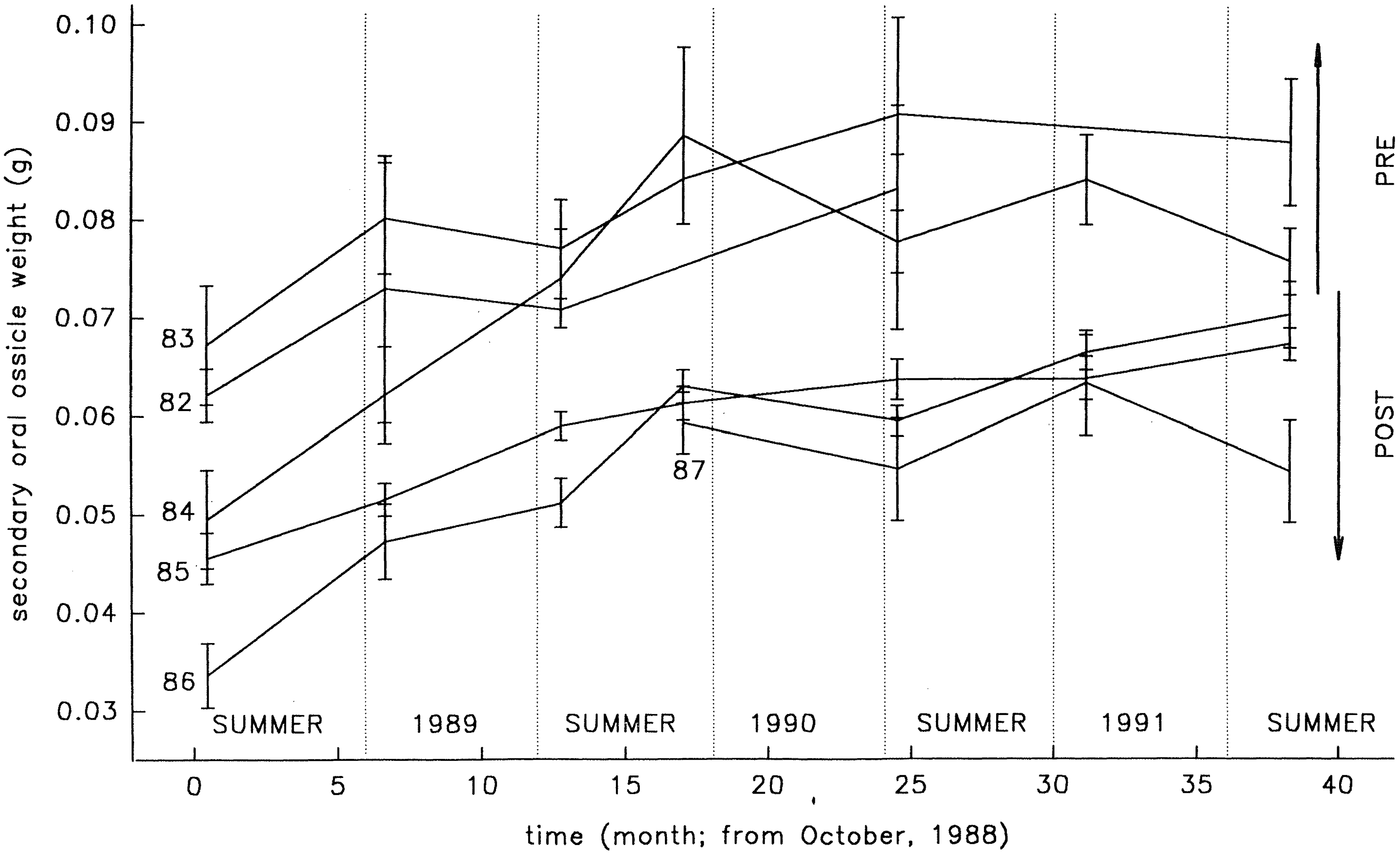
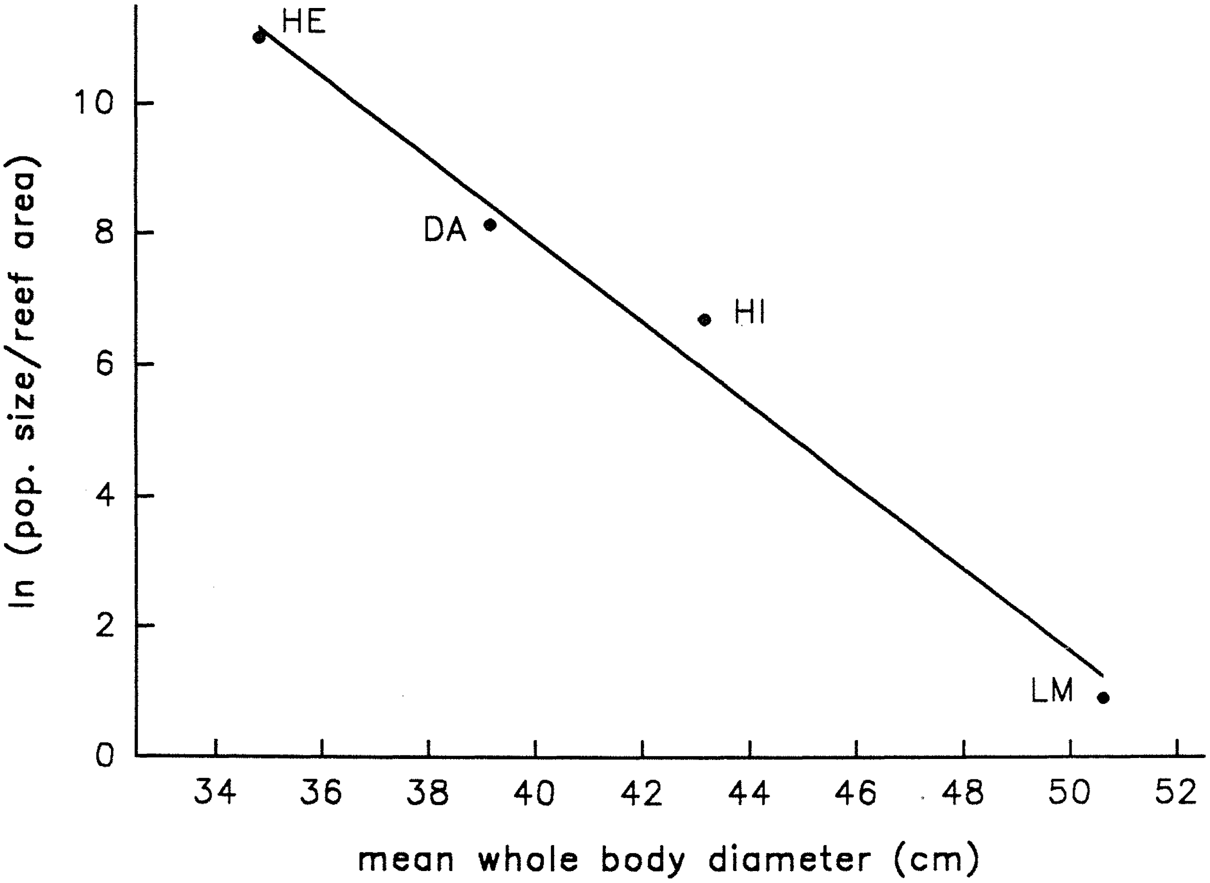

primary oral ossicle weight (g)
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.10
0.11
0.12
0.13
82
83
84
85
86
87
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
PRE
POST
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.18



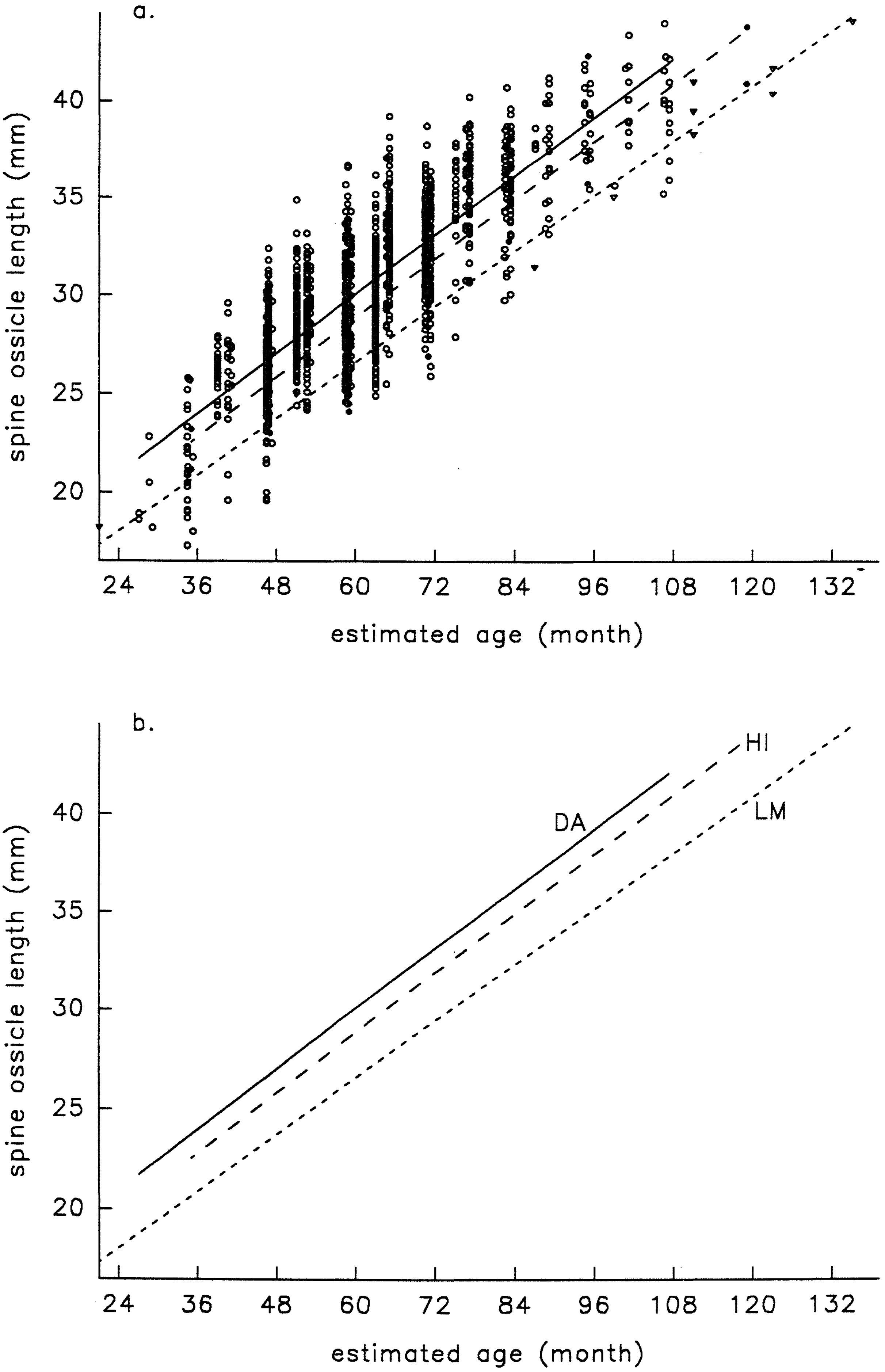
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
secondary oral ossicle weight (g)
83
82
84
85
86
87
SUMMER
1989
SUMMER
1990
SUMMER
1991
SUMMER
PRE
POST
0
5
10
15
20
25
30
35
40
time (month; from October, 1988)

FIGURE 3.19



HE
DA
HI
LM
ln (pop. size/reef area)
0
2
4
6
8
10
34
36
38
40
42
44
46
48
50
52
mean whole body diameter (cm)

FIGURE 3.20


a.
spine ossicle length (mm)
20
25
30
35
40
24
36
48
60
72
84
96
108
120
132
estimated age (month)
b.
spine ossicle length (mm)
20
25
30
35
40
24
36
48
60
72
84
96
108
120
132
estimated age (month)
DA
HI
LM