THE ECOLOGY OF *FRAGUM ERUGATUM* (MOLLUSCA, BIVALVIA, CARDIIDAE) IN SHARK BAY, WESTERN AUSTRALIA

by

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COVER. *Fragum erugatum* shells from a recent storm ridge. Note a recently dead shell which is still articulated and shells with black colouration, long dead, which have been buried in the infratidal coquina. Inset is of living symbiotic zooxanthellae from *F. erugatum* tissue.

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Summary

Fragum erugatum populations were sampled every second month over two consecutive years between June 1994 and June 1996 in Hamelin Pool, Lharidon Bight and Freycinet Harbour (at Nanga), which are representative of the metahaline and hypersaline regimes of Shark Bay. Salinities ranging from 46.8‰ in Freycinet Harbour to 75.8‰ in Hamelin Pool were recorded. Water temperatures were also extreme, ranging from 13.3°C to 30.8°C. The substrate on which *F. erugatum* occurs was found, in most cases, to be a coquina composed largely of the shells of this species, many of which remain articulated and closed.

Surveys recording presence/absence of living *F. erugatum* in Hamelin Pool and Lharidon Bight, indicate an extensive distribution on the infratidal platforms between a depth range of approximately 1.2 m to 6.5 m. Living *F. erugatum* does not occur in the intertidal zone or deep basins. From digitised maps the areas of the infratidal platforms at the depth at which *F. erugatum* occurs were estimated to be 110 km^2 and 262 km^2 for Lharidon Bight and Hamelin Pool respectively.

Microscopic examination of crushed *F. erugatum* tissue revealed dense aggregations of endosymbiotic, unicellular zooxanthellae (green algae) which are most abundant in the mantle and gills. The presence of these symbiotic autotrophs probably contributes a significant energy subsidy to *F. erugatum* and thus to the apparently nutrient deficient, relatively closed ecosystems of Hamelin Pool and Lharidon Bight. It probably also accounts for the maximum depth distribution of *F. erugatum*, which would be limited by availability of light

Morphometric analysis showed that shell shape of the population from Hamelin Pool differs from that of the Lharidon Bight, Freycinet Harbour and Dampier Archipelago populations, in which shell shape was similar. The greater ratio of shell inflation to shell height in Hamelin Pool specimens results in a characteristic rounded shape. The maximum shell size attained is smallest in the Hamelin Pool populations (inflation 8.45 mm, height 11.73 mm), compared with the Lharidon Bight (11.26 mm, 13.95 mm), and Dampier Archipelago (12.02 mm, 19.38 mm) populations respectively.

Histological examination of the gonads revealed that *F. erugatum* is a synchronous hermaphrodite, i.e. male and female gametes develop simultaneously. Single, distinct settlements of juveniles recorded between June 1994 and October 1994 and modality of the population size distributions indicates that *F. erugatum* spawns once a year between winter and spring. However, in 1995 settlements were recorded at all sites (except Nanga) in April, suggesting a broader and possibly more variable period of reproductive activity.

At the sites sampled over the two year study period, the mean densities of live animals and production rates of shell were 576/m^2 and 65.0 g/m^2/year at Flagpole Landing, 382/m^2 and 33.3 g/m^{2}year at Carbla, 4319m/^{2} and 415.0 g/m^{2}year at Lharidon Bight and 998/m^2 and 170.8 g/m^{2}year at Nanga. In Hamelin Pool and Lharidon Bight the populations typically comprised two distinct year classes (0+ and 1+) and in some instances a very low proportion of 2+ animals. At the Nanga site the population comprised only a single cohort.

Comparisons of shell size distributions of the living populations, recently dead specimens from the infratidal coquinas and recently washed ashore in the storm/tidal strandline, and from the supra-tidal coquina suggest that although some shells are washed ashore continuously, these are not necessarily the product of recent mortality and large-scale deposition of the accumulated shells, i.e. the infra-tidal coquinas, probably occurs in major storm events.

On the basis of the shell production rates and the total areas of suitable infra-tidal habitat determined in this study, the mean annual rate of shell deposition per metre of coastline is estimated to be 64 kg (≡ 0.096 m^3) in Hamelin Pool and 467 kg (≡ 0.70 m^3) in Lharidon Bight. (This assumes that 90% of shells are washed ashore annually and that deposition is uniformly distributed). This may be further extrapolated to total annual rates of beach deposition of 11,840 tonnes (≡ 17,778 m^3) for Hamelin Pool and 41,096 tonnes (≡ 61,706 m^3) for Lharidon Bight. These are rough approximations only and must be treated with extreme caution because they include the assumptions that the production rates estimated at the study sites are applicable throughout the infra-tidal platform where *F. erugatum* occurs and that 90% of the shell production is washed ashore.

Introduction

Fragum (Afrocardium) erugatum (Tate, 1889) is a small bivalve endemic to Western Australia, where live animals occur from the Dampier Archipelago to the Houtman Abrolhos. Fossils have been recorded from various localities further south, including Rottnest Island and Windy Harbour, and east along the south coast to Yorke Peninsula in South Australia, the type locality (Wilson and Stevenson 1977).

Wilson and Stevenson (1977) describe *F. erugatum* as an extremely variable species, but (on the basis of an unpublished study by B.R.Wilson and G.W.Kendrick) consider the trapezoidal form from Hamelin Pool, which Iredale (1949) named *Fragum hamelini*, to be an ecophenotype of hypersaline conditions.

Fossil *F. erugatum* form a relatively minor component in most parts of the Pleistocene Dampier Limestone at Shark Bay (Kendrick 1990). However, this species dominates the molluscan fauna of the modern hypersaline embayments, Hamelin Pool and Lharidon Bight (Figure 1). Vast accumulations of its dead shells form the associated Hamelin Coquina (Hagan and Logan 1974, Hocking et al. 1987).

Playford (1990) describes the Hamelin Coquina around the shores of Hamelin Pool and Lharidon Bight as consisting of a succession of beach ridges, in a belt up to 1 km wide and 4 m thick. The ridges are composed almost entirely of single, loose shells, but become progressively more cemented to coquinite away from the modern shoreline. The loose shells have been excavated for a variety of purposes, particularly at Lharidon Bight. The weakly lithified coquinite has been quarried for use as building blocks and some of the historic buildings in the Shark Bay area are constructed of this unique building material.

The main objective of this study was to provide basic ecological information on living *P. erugatum* in Shark Bay, with a view to complementing geological investigation of the age and rate of deposition of the Hamelin Coquina. In particular, the aim was to establish whether the present living populations are continuing to produce shell at a rate similar to that which resulted in formation of the Hamelin Coquina.

Methods

The spacial distribution of *F.erugatum* in Hamelin Pool and Lharidon Bight was determined from the shore and from a vessel using a small dredge, and recording the presence/absence of living specimens. The dredge used was made from a piece of boiler pipe 10 cm in diameter and 25 cm long which, when towed, sampled approximately 1000 cm^2 of the surface substrate. Because of the total areas of Hamelin Pool and Lharidon Bight (1310 km^2 and 347 km^2 respectively) and limitations in the range of the vessels available, the entire embayments could not be sampled comprehensively. The areas and length of coastlines of Hamelin Pool and Lharidon Bight were derived using GIS analysis of digitised maps. In the case of Hamelin Pool, the area of the infratidal platform inhabited by *F. erugatum* was estimated using depths derived from a bathymetric chart. As bathymetric data are not available for Lharidon Bight, the extent of the infratidal platform was estimated using Landsat TM imagery.

The *F. erugatum* population was sampled for biological information every second month over two consecutive years. Using SCUBA, samples were taken from June 1994 to June 1995 at two transects in Hamelin Pool (one at Flagpole Landing, adjacent to the Old Telegraph Station and one at Carbla Point) and at one transect in Lharidon Bight (adjacent to the public access area to the Shell Beach). From August 1995 to June 1996 the same regime was followed, except that sampling of the Carbla transect was discontinued after June 1995.

All transects were adjacent to extensive beach coquina deposits and within the optimum depth range (1.5 to 5.5 m) of *F. erugatum*. Each transect was approximately 1 km in length, running at right angles to the shore. Along each a pair of randomly selected samples about 30 m apart was taken at approximately 500 m intervals using a quadrat measuring 25 by 25 cm; i.e. 6 sample quadrats in total per transect. The entire substrate, to a depth of approximately 2 cm, was removed in a metal dustpan that exactly fitted the quadrat, and deposited in a calico bag.

The sampling positions were determined and relocated using a handheld GPS unit, probably to within 100 m at most.

Sampling was also undertaken in Freycinet Harbour, but no living *F. erugatum* were detected until October 1994, when a small, newly settled population was found close to shore at the Nanga Beach Resort and subsequently sampled bimonthly. As this population was distributed over a distance of only about 35 m between extensive seagrass beds and the shore, two quadrats only were taken until June 1996 when 4 quadrats were sampled because of the much reduced population density.

Each sample was sorted and all living specimens of *F. erugatum* removed, measured to 0.01 mm and recorded (using digital calipers connected directly to a laptop computer). Measurements taken were shell height (maximum distance from umbo to posterior margin) and inflation (maximum distance between the two valves). The latter measurement was used as the standard measurement of size in this investigation. Inflation of shells from the supratidal coquina and storm ridges was determined by doubling the measurement of single valves (*F. erugatum* is bilaterally symmetrical). Specimens were preserved in the field in a 10% buffered formaldehyde solution. Because of the uniformity of distribution, the six samples from each transect were combined to estimate the mean density along each transect. Dry flesh and shell weight was determined in the laboratory by drying to constant weight at 60°C. Weights were measured on an electronic balance to three decimal places.

Ten specimens from each sampling site were retained from the bimonthly samples for histological examination of the gonads. However, histological examination was only undertaken of the Lharidon Bight samples, as this did not prove to be particularly useful for precisely establishing the timing of spawning. The whole animals were fixed in 10% formaldehyde solution, removed from their shells and embedded in paraffin wax. Sections 5μ thick were cut through the gonads, stained with haematoxylin and eosin and used to assess reproductive state, by classification into the following four microscopic stages of development:

Stage 1 - Inactive

Female: Follicles absent (collapsed) or small with oogonia and small oocytes around margins. Male: Follicles absent (collapsed) or small and lined with spermatocytes.

Stage 2 - Developing

Female: Follicles with oocytes of varying sizes, but most attached to the follicle wall; a few detached oocytes. Male: Follicles with spermatocytes, spermatids and few spermatozoa towards the centre.

Stage 3 - Ripe

Female: Large follicles with numerous oogonia in varying stages of development, but a high proportion detached. Male: Follicles more than two thirds full of spermatozoa radiating towards the centre.

Stage 4 - Recently spawned

Female: Similar to Stage 1 but with some large, residual oocytes, both attached and free, of which some are undergoing cytolysis. Male: Similar to Stage 1, but with spermatids and a few spermatozoa.

The classification of stages of gonad development described above is based on one used for the hermaphroditic cockle, *Clinocardium nuttallii* by Gallucci and Gallucci (1982).

Production in *F. erugatum* was calculated using Crisp's (1971) method as modified by Chalmers and Milne (1975). Size frequencies of individual year classes, were isolated mathematically from multimodal size frequency distributions.

Examples of other co-occuring organisms were also preserved for identification.

Temperature and salinity were determined at each sampling site.

Positions of the sampling sites are as follows:

Transect	**Inner**	**Middle**	**Outer**
Flagpole Landing	26° 23'34"S, 114° 08' 44"E	26° 23'11"S, 114° 08' 58"E	26° 23'23"S, 114° 08'34"E
Carbla Point	26° 15'37"S, 114° 12'19"E	26° 15'37"S, 114° 12' 34"E	26° 15'37'"S, 114° 11' 53E
Lharidon	26° 12'32"S, 113° 46' 36"E	26° 12' 16"S, 113° 46' 37"E	26° 12'01"S, 113° 46'40"E
Nanga	26° 15' 28"S, 113° 48' 06"E		

Results

The Physical Environment

A summary of the physical environment of Shark Bay is given by Logan and Cebulski (1970) and includes bathymetric zonation, climate, winds, waves, tides, salinity, water temperature and hydrologic structure. Hamelin Pool and Lharidon Bight constitute their "hypersaline" zone, with salinity and temperature ranges of 56-70‰ and 17-27°C. Freycinet Harbour is representative of their "metahaline" zone, with salinity and temperature ranges of 45-48‰ and 17-25°C. As is evident from Figure 1 and Table 1 below, the present study involves populations of *F. erugatum* from two slightly different hypersaline regimes (Hamelin Pool and Lharidon Bight) and a metahaline environment in Freycinet Harbour (Nanga). Salinities at Hamelin Pool were consistently higher than those at Lharidon Bight and both were significantly higher than in Freycinet Harbour (Nanga). The temperature ranges recorded are large, 16.5°C-30.8°C in Hamelin Pool, 16.5°C-28.9°C in Lharidon Bight and 13.3°C-28.0°C in Freycinet Harbour (Nanga).

Table 1. Bottom water temperatures (°C) and salinities(‰) respectively at sampling sites (1994/95 followed by 1995/96 data).

		June	August	October	December	February	April
Flagpole	°C	-, 16.5, 21.5	-, 19.8	25.5 -	27.0, 26.7	29.0,30.8	24.5, 26.0
	‰	-, 67.5, -	68.8, 64.7	72.4, 65.2	75.8, 68.5	73.2,66.9	74.3, 68.2
Carbla	°C	-, -, -	19.7, -	25.5, -	27.1, -	28.5,-	-, -
	‰	-, -, -	69.5, -	69.3, -	66.0, -	72.5, -	70.2, -
Lharidon	°C	-, 16.5, 21.7	-, 19.8	25.2, 20.3	27.3, 24.1	27.2, 28.9	22.2, 26.2
	‰	-, 64.0, 58.3	61.3, 61.4	62.3, 61.2	61.3, 69.0	61.3, 66.9	62.6, 58.1
Nanga	°C	-, 13.3, 21.5	-, 19.5	19.8, 17.5	22.8, -	27.4, 28.0	21.5, 23.5
	‰	-, 48.3, 46.8	-, 46.8	57.3, 55.7	58.1, 63.2	52.1, 47.9	52.7, 47.2

The optimal depth range of *F. erugatum* on the gently sloping sublittoral platforms of Hamelin Pool and Lharidon Bight was found to be approximately 1.5 m to 5.5 m. The total areas of the sublittoral platforms between this depth range, as calculated from the digitised maps, are 262 km^2 and 110 km^2 respectively. (For Lharidon Bight this figure excludes some areas of seagrass beds which were not inhabited by *F. erugatum*). The total areas of Hamelin Pool and Lharidon Bight were determined to be 1,313 km^2 and 347 km^2 and the lengths of their coastlines are 185 km and 88 km respectively (excluding the extensive sand spits in Lharidon Bight).

The substrate of the sublittoral platforms of Hamelin Pool and Lharidon Bight ranges from fine to course calcareous sand containing sparse articulated and disarticulated *F. erugatum* shells, to coarse coquinas of articulated and disarticulated shells with interstitial calcareous sand particles and Foraminifera. Some of the articulated shells are from recently dead animals, but in others, long dead, the valves are held together by cementation. At the Hamelin Pool sampling sites this infratidal coquina overlies a cemented pavement about 3-5 cm thick (also containing embedded *F. erugatum*), sometimes as a thin veneer only a few centimetres thick, but usually as a layer 10-30 cm thick. The coquina at the Carbla sampling site is thinnest and also has the highest foraminiferal and sand content. At the Hamelin site small erosional depressions or "blow-outs" occur, in which the pavement is exposed or even fractured. The coquina at Lharidon Bight is thickest (about 30 cm), does not overlie a cemented pavement, and has the lowest sand and foraminiferal content. Associated with the coquina at all these sites are ephemeral microbial mats, the green alga, *Polyphysa peniculus* and a variety of other filamentous green algae. The calcareus stalks of dead *P. peniculus* form a conspicuous interstitial component of coquina, particularly at the Carbla and Lharidon Bight sampling sites.

The substrate at the Nanga sampling site is composed of fine to medium grained sand with sparse single *F. erugatum* and other bivalve shells. There was a thin, overlying microbial mat in October 1995 in which the newly settled *F. erugatum* were embedded.

Morphometrics

The linear relationships between shell height (y) and shell inflation (x) (the maximum distance between the two valves) for each sampling locality and from a population from Rosemary Is. in the Dampier Archipelago, are given below and illustrated in Figure 4. (The Dampier data, taken from museum specimens are included for comparison, being representative of a population from a "normal" marine salinity regime).

Flagpole Landing $y = 1.1427x + 1.2303$

R^2=0.90, N=197,range = 2.78 mm-7.55 mm.

Carbla Point $y = 1.1857x + 1.2221$

R^2=0.66, N=360, range = 3.3 mm-7.23 mm.

Lharidon $y = 1.4773x + 0.5811$

R^2=0.92, N=305, range = 2.34 mm-10.26 mm.

Nanga y = 1.4464x + 0.8175

R^2=0.94, N=150, range = 2.29 mm-6.01 mm.

Dampier y = 1.4721x + 0.7173

R^2=0.91, N=167, range = 3.9 mm-12.0 mm

95% confidence limits for these regressions are given in Appendix Table 1.

The relationship between dry shell weight (y) and shell inflation (x) for the Hamelin Pool (Flagpole Landing) and Lharidon Bight populations are given below and illustrated in Figure 5.

Flagpole Landing logy=2.621471*logx-2.85238

R^2=0.99, N=122, range = 1.84mm-8.13mm

*Lharidon logy=2.809966*logx-2.93991*

R^2=0.99, N=155, range = 1.56mm-9.2mm

95% confidence limits for these regressions are given in Appendix Table 1.

The relationship between dry flesh weight (y) and shell inflation (x) for the Hamelin Pool (Flagpole Landing) and Lharidon Bight populations are given below.

Flagpole Landing logy=2.163896*logx-3.7496

R^2=0.87, N=122, range = 1.84mm-8.13mm

*Lharidon logy=1.961731*logx-3.39356*

R^2=0.87, N=155, range = 1.54mm-9.2mm

95% confidence limits for these regressions are given in Appendix Table 1.

The relationship between shell inflation and height is very similar at the two Hamelin Pool sampling sites and differs markedly from that in the Lharidon, Nanga and Dampier population, in which it is almost identical.

The mean ratio of shell inflation to shell height is greatest in the populations from hypersaline water at Flagpole Landing (0.73, n=197) and Carbla Point (0.70, n=360) in Hamelin Pool. The ratio of the population from Lharidon (0.60, n=305), in a lower hypersaline regime, is identical to that in the metahaline regime of the Nanga population (0.60, n=150) and similar to that of the Dampier population in 'normal' seawater salinity (0.63, n=111).

The maximum shell size attained is smallest in the Hamelin Pool populations (inflation 8.45 mm, height 11.73 mm), compared with the Lharidon Bight (11.26 mm, 13.95 mm), and Dampier Archipelago (12.02 mm, 19.38 mm) populations respectively. The difference in maximum size attained by the Hamelin Pool and Lharidon Bight populations is also reflected by their maximum mean total dry weight weights :- 0.35 g vs 0.42 g respectively).

Zooxanthellae

The general colour of the flesh of living *F. erugatum* is brown and this can also be seen through the translucent, largely unpigmented valves. Microscopic examination of crushed tissue revealed that this is due to dense aggregations of endosymbiotic, unicellular zooxanthellae which are most abundant in the mantle and gills (Fig.6). The mean diameter of the zooxanthellae is 10µm with a range of 8-13µm.

Zooxanthellae are symbionts of a wide variety of marine invertebrates - Protozoa, Porifera, Cnidaria, Platyhelminthes and Mollusca (Muscatine 1980). Well documented as inhabitants of the mantles of giant clams (Tridacnidae), (Norton and Jones 1992), zooxanthellae have infrequently been recorded in other bivalves, but have been reported by Kawaguti (1950, 1968 and 1983) in the cardiids *Corculum cardissa*, *Fragum unedo* (Linnaeus) and *Fragum fragum* (Linnaeus), and by Morton (1982) in the Trapeziid *Fluviolanatus subtorta* Dunker.

Spacial Distributions

Sampling for presence/absence of living *F. erugatum* in Lharidon Bight and Hamelin Pool indicates that the species is widely distributed over the entire sublittoral platforms at a depth between approximately 1.2 m and 6.0 m (Figures 2 and 3). The intertidal zone and deep basins are devoid of living specimens, but numerous single valves demonstrate that dead shells are transported both inshore and offshore from the sublittoral platform. The maximum depth range of *F. erugatum* is probably limited by the light penetration required for photosynthesis by its zooxanthellae. *Gaffrarium intermedium*, which does not have endosymbiotic zooxanthellae, was recorded live in deep basins devoid of *F. erugatum* at 8.5 m.

Settlment, Size Distributions and Growth

Densities and size distributions at Flagpole Landing, Carbla, Lharidon Bight and Nanga are summarised in Tables 2-7.

An essentially bi- or tri-modal size distribution was apparent at all sites except Nanga where it was uni-modal throughout. Newly settled *F. erugatum* were first recorded at Lharidon in June 1994, at Hamelin in August and at Carbla and Nanga in October. By following the modal progression of this and the cohorts of larger animals it is apparent that animals in the Hamelin and Carbla populations persist for two years, with the possibility that a very low number may live into their third year. At Lharidon an indistinct third mode or, skewness of modes to the right, indicates persistence of a larger proportion of the population into the third year. In 1995, new settlement was recorded earlier, in April at all sites except Nanga where none occured. In 1996 a very small settlement was detected in June at Lharidon Bight only.

Density, Biomass and Production

Density, biomass and production at Flagpole Landing, Carbla, Lharidon Bight and Freycinet Harbour (Nanga) are summarised in Tables 8-13 respectively. (All weights are dry weights).

At Flagpole Landing the mean total production rate over the two consecutive years sampled was 68.7 g /m^2/year, of which 65.0 g /m^2/year was shell and 3.7 g /m^2/year was flesh. The mean total biomass (standing crop) was 70.0g/m^2 of which 66.1g/m^2 was shell. The mean annual turnover rate (P/$\bar{B}$) ratio was 0.98. Mean density was 576/m^2. The standard errors of the mean density estimates ranged from ± 11-46 % with a mean of 31 %.

At Carbla total production rate was 34.96g/m/year^2, of which 33.25g/m^2/year was shell and 1.70g/m^2/year was flesh. The mean total biomass (standing crop) was 55.6g/m^2 of which 52.56g/m^2 was shell. The P/$\bar{B}$ ratio was 0.63. Mean density was 382/m^2. The standard errors of the mean density estimates ranged from ± 21-29 % with a mean of 25 %.

At Lharidon Bight the mean total production rate over the two consecutive years sampled was 446.3g/m/year^2 (dry weight), of which 415.0g/m^2/year was shell and 31.3g/m^2/year was flesh. The mean total biomass (standing crop) was 483.0g/m^2 of which 445.7g/m^2 was shell. The P/$\bar{B}$

ratio was 0.92. Mean density was $4319/m^2$. The standard errors of the mean density estimates ranged from ± 8-30 % with a mean of 15 %.

At Nanga total production rate was $185.39 g/m/^2$ (over the first 12 months, and contributed by a single cohort), of which $170.78 g/m^2$ was shell and $14.61 g/m^2$ was flesh. The mean total biomass (standing crop) over the same period was $68.26 g/m^2$ of which $62.00 g/m^2$ was shell. The $P/\bar{B}$ ratio was 2.72. Mean density was $998/m^2$.

Age curves, expressed as increase in mean shell inflation derived from a composite of modal progression, are given for the four sampling sites in Figure 8. The von Bertalanffy growth equation: $Lt=L\infty[1-e^{-K(t-t_0)}]$ (Ricker 1968) was used to describe these growth curves where: Lt=length at age t (months)

$L\infty$=asymptotic or maximum mean shell inflation

K=rate of change in shell inflation

t_0=age at which growth theoretically begins

In order to describe post-settlement growth, the equation should be used in the form: $Lt+4=L\infty[1-e^{-K(t-t_0)}]$

	Flagpole	Carbla	Lharidon	Nanga
$L\infty$	7.652	5.943	9.437	6.453
K	1.036	2.119	0.640	1.708
t0	0.114	0.066	0.027	0.141
r^2	0.978	0.983	0.991	0.969

Size Distributions of Shells in Coquinas

As levels of predation are apparently extremely low in the hypersaline, generally low energy, environments of Hamelin Pool and Lharidon Bight, large numbers of shells of dead *F. erugatum* accumulate to form the coquina substrates described above. Some of these shells are obviously from animals long dead as the valves are held together by cementation and their interiors are filled with sediment. However, the valves of others, clearly more recently dead, are held together by persistence of the ligament and/or the interlocking hinge teeth and are not filled with sediment. Figures 9-11 present the size distributions and densities of these relatively recently dead (uncemented), articulated shells, and living animals in April 1995. They show that: (i) at all sampling sites, over the larger size range, the densities of dead shells exceeded that of living animals, but the reverse was true over the smaller size range. (Moreover, the density of dead shells would have been underestimated, as they frequently become disarticulated in the sorting process); (ii) if the new settlement is ignored, the modality of the living and dead shells shows a fair degree of correspondence, and at Lharidon Bight the peak of dead shells in the 3.5-3.9 mm size class may possibly reflect mortality of the living year class represented by the modal peak in the 4.5-4.9 mm size class. These results suggest that a high proportion of animals that die remain with valves closed *in situ* and lie undisturbed for a considerable length of time. Transportation and deposition onshore of the majority of these shells, particularly from deeper water, is therefore most likely to occur irregularly in association with high energy storm events.

Size distributions, expressed as percentages, of shells from the most recent storm/tide ridge (i.e. recently washed up, see Figure 7) and from the adjacent living population sampled the same month are illustrated for Lharidon Bight and Flagpole Landing in Figures 12 and 13. At both sites the size distribution of the shells of dead animals approximates to a normal distribution and bears little resemblance to the tri-modal distribution of the living populations. The shells comprising storm/tide ridges are the accumulations of shells (many of which are articulated) which wash ashore in small numbers daily. They may originate from the shallowest extreme of the depth range of *F. erugatum* where the substrate is subject to scour under moderate conditions of wave energy. These results also suggest that *F. erugatum* which die are not rapidly deposited on the shore.

The size distributions, expressed as percentages, of shells of *F. erugatum* sampled at Lharidon Bight from the supratidal coquina at a distance of about 75 m inland from the present shore-line, the most recent storm/tidal ridge, and the adjacent recently dead (articulated) infratidal coquina are compared in Figure 14. It is apparent that the both the recent storm ridge and supratidal coquina shell approximate to normal distributions, with the full size range represented although the distribution of the latter is slightly skewed to the right. Neither bears a close correspondence to the modality of the distribution of the recently dead infratidal coquina, but there is a close correspondence in the size ranges. However, it seems likely that sampling of the infratidal coquina would have underestimated the numbers of smaller specimens, as these do not remain as strongly articulated on death as larger ones. (The distributions of shells in the storm ridge and supratidal coquina were determined from single valves).

Reproduction

Histological examination revealed that *F. erugatum* is a synchronous hermaphrodite, i.e. male and female follicles develop in phase.

The single, distinct new settlements recorded between June 1994 and October 1994 and bimodality of the populations suggests that *F. erugatum* spawns once a year, generally between winter and spring. However, the April 1995 settlements at all sites (except Nanga) indicates a broader and possibly more variable period of reproductive activity.

Discussion

As described by Wilson and Stevenson (1977), the morphology of Hamelin Pool populations from the most hypersaline conditions is trapezoidal, i.e. shell inflation to shell height ratio is high. Maximum overall size attained is also smaller than in lower salinity regimes of Lharidon, Nanga and Dampier. Although there is a correlation between salinity and shell morphology and maximum size, the difference in salinity between the Hamelin Pool and Lharidon populations is only about 10‰-15‰. This suggests that if this is a causal relationship, the salinity experienced by the Hamelin Pool phenotype may be close to its maximum tolerance limits.

Differences in shell morphometrics within the Hamelin Coquina may prove useful in detecting different salinity regimes that may have existed in the past in Hamelin Pool.

Lower densities in new settlements (cohort 0+) than in the previous year's settlement (cohort 1+) at Hamelin and Carbla, and difference in timing of settlement indicates that settlement strength is variable and erratic - possibly affected by local hydrological conditions. Logan and Cebulski (1970) commented that living *F. erugatum* in the hypersaline basins "appears in vast numbers only at certain times" and were abundant in 1956 and 1957, absent in February 1965, but very abundant again a year later. They conjecture that recruitment is from reproductive populations outside the hypersaline zone.

The origin of larval recruitment to the hypersaline, relatively "closed" basins of Hamelin Pool and Lharidon Bight is unknown. However, histological examination of the gonads showed that *F. erugatum* is reproductively active within them. This question will only be resolved through study of the genetic affinities of various populations within Shark Bay and from elsewhere in its distribution. Material has been collected for such a study, but it will not form part of the present investigation.

The high standing crop and dominance of *F. erugatum* in the hypersaline basins seems most likely to be attributable to its physiological tolerance of the conditions, lack of competitors and, more particularly, lack of predators. In Freycinet Harbour the usual teleost and elasmobranch predators of bivalves are common and crabs and paguroids were observed feeding on recently settled *F. erugatum* at Nanga. None of these predators occur in the hypersaline basins where the main cause of mortality is unknown.

Levels of primary productivity in the hypersaline basins of Shark Bay appear to be low. In the only study of its plankton, Kimmerer et al (1985) found that in the hypersaline Hamelin Pool, the phytoplankton showed lowest species diversity and largely comprised dinoflagellates, many unpigmented, and few diatoms. Similarly, compared with elsewhere in Shark Bay, the zooplankton diversity was lowest in Hamelin Pool, with abundance of a similar magnitude to that of the deep sea and 100-fold below typical surface oceanic values. Production by seagrasses is also very low in the hypersaline basins (Walker 1990) and detritus derived from them and other sources seems unlikely to constitute a significant food source to suspension feeders in the low physical energy environment which prevails. *F. erugatum* as a filter-feeder is presumably sustained by fine detrital particles originating from cyanobacterial mats and green algae (particularly the ubiquitous *Polyphsa*), probably enriched by diatoms and bacteria. However, in the low physical energy environment which prevails, little of this detritus appears to be in suspension, or when it is, to remain so for long. *F. erugatum* must therefore exploit the water column a few centimetres above the surface of the substrate and depletion of suspended detritus would be rapid. However, the conditions of low turbidity in relatively shallow water with high insolation levels must be conducive to primary production by the zooxanthellae which occur within *F. erugatum*. The presence of these symbiotic autotrophs probably contributes a significant energy subsidy to *F. erugatum* and thus to the apparently nutrient deficient, relatively closed ecosystems of Hamelin Pool and Lharidon Bight. It probably also accounts for the maximum depth distribution of *F. erugatum* which would be limited by light penetration.

In a study of the nutrient budget for Shark Bay as a whole, Smith and Atkinson (1984) suggest that in this and other relatively closed marine ecosystems, net community production is P limited and not N limited, as are open ecosystems. Atkinson (1987, 1990) further presents evidence that the incorporation of P into $CaCO_3$ of shells is the major sink for P in Shark Bay. The existence of endosymbiotic zooxanthellae in *F.erugatum* was unknown to these authors and needs to be considered in any future modelling of the unique Hamelin Pool and Lharidon Bight ecosystems.

The difference in the mean total production rate recorded Lharidon Bight was substantially higher than that in Lharidon Bight (446.3g/m/year^2 vs 68.7g/m^2/year at Flagpole Landing and 35.0g/m/year^{2}at Carbla). This is largely attributable to the much higher densities recorded consistently throughout the study at Lharidon, rather than differences in growth rates or maximum sizes attained. In particular, the density of the new settlement at Lharidon in April 1995 (2,500/m^2) and the subsequent persistence of high densities of this cohort resulted in the much higher production rate recorded in 1995/96 than the previous year in Lharidon Bight and accentuated the difference in production estimates there and for Hamelin Pool. It should be noted that density after settlement for this and other cohorts showed an increasing trend over several months before declining due to mortality. This could be due to sampling error (which seems unlikely because of the trend) or migration of *F. erugatum* from settlement areas into its optimal depth range.At Nanga it was recorded to settle in a cyanobacterial mat which is unlike the coquina substrate on which the *F. erugatum* population was sampled in Lharidon Bight. *F. erugatum* is capable of active movement, but judging by the appearance of live animals embedded in the infra-tidal coquina, they remain static for long periods. The only actively migrating animals observed were in an erosional blowout, apparently attempting to escape from this unfavourable situation.

On the basis of the shell production rates and the total areas of suitable infra-tidal habitat determined in this study, the mean annual rate of shell deposition per metre of coastline is estimated to be 64 kg (≡0.096 m^3) in Hamelin Pool and 467 kg (≡0.70 m^3) in Lharidon Bight. (This assumes that 90% of shells are washed ashore annually and that deposition is uniformly distributed). (The Hamelin estimate is based on a production rate of 50g/m/year^2 i.e. an arbitrary figure between the respective Flagpole Landing and Carbla estimates of 65.0g/m/year^2 and 33.25g/m/year^2). This may be further extrapolated to total annual rates of beach deposition of 11,840 tonnes (≡17,778 m^3) for Hamelin Pool and 41,096 tonnes (≡61,706 m^3)for Lharidon Bight. These estimates are rough approximations only and must be treated with extreme caution because they include the assumptions that the annual production rates estimated are representative of "typical" years, that production rates estimated at the study sites are applicable throughout the infra-tidal platform where *F. erugatum* occurs, and that 90% of the shell production is washed ashore. While the latter assumption is clearly not true in the short term, in a greater time frame and in terms of deposition of the Hamelin Coquina it does not seem unreasonable, as the infratidal was never found to be greater than about 30 cm deep. It is therefore concluded that a very high proportion of it, if not all over time, must be washed ashore in periodic major storm events.

References

Crisp, D.J. 1971. Energy flow measurements *In*: Holme, N.A. and McIntyre, A.D. *eds*. Methods for the study of marine benthos. Oxford, Blackwell: 197-279.

Chalmers, M.R. and Milne,H. 1975. The production of *Macoma pelagica* (L.) in the Ythan estuary. *Estuar. Coast. Mar. Sci.*,**3** : 443-456.

Gallucci V.F. and Gallucci B.B. 1982. Reproduction and ecology of the hermaphroditic cockle *Clinocardium nuttallii* (Bivalvia: Cardiidae) in Garrison Bay. *Marine Ecology Progress Series*. **7**: 137-145.

Hagan, G. M. and Logan, B.W. 1974. Development of carbonate banks and hypersaline bars, Shark Bay, Western Australia. *In* Logan B.W., Read, J.F., Hagan, G.M., Hoffman, P., Brown, R.G., Woods, P.J. and Gebelein, C.D., 1974. Evolution and diagenesis of Quaternary carbonate sequences, Shark Bay, Western Australia. *American Association of Petroleum Geologists Memoir.* (22) : 61-139.

Hocking, R.M.,Moors, H.T. and van Graaff, W.J.E. 1987. Geology of the Carnarvon Basin, Western Australia. *Geol. Survey West. Aust. Bull* **133:** 1-289.

Kawaguti, S. 1950. Observations on the heart shell *Corculum cardissa* and its associated zooxanthellae. *Pacific Science*. 4: 43-49.

Kawaguti, S. 1968. Electron microscopy on zooxanthellae in the mantle and gills of the heart shell. *Biological Journal of Okayama University*. **14**: 1-11.

Kawaguti, S. 1983. The third record of association between bivalve mollusks and zooxanthellae. *Proceedings of the Japan Academy Series B, Physical and Biological Sciences*. **59**: 17-20.

Logan, B.W. and Cebulski D.E. 1970. Sedimentary Environments of Shark Bay, Western Australia. *American Association of Petroleum Geologists Memoir* (13): 1-37.

Morton, B.S. 1982. The biology, functional morphology and taxonomic status of *Flaviolanatus subtorta* (Bivalvia: Trapeziidae), a heteromyarian bivalve possessing "zooxanthellae". *Journal of the Malacological Society of Australia*. **5** (3-4):113-140.

Norton, J.H. and Jones, G. W. 1992. *The Giant Clam: An Anatomical and Histological Atlas.* Australian Centre for Agricultural Research, Canberra. 142pp.

Playford, P.E. 1990. Geology of the Shark Bay area, Western Australia. Research in Shark Bay. *Report of the France-Australe Bicentenary Expedition:* 13-31.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations *.Bull.Fish.Res.Bd.Can., (119):1-300*

Tate, 1889. *Transactions of the Royal Society of South Australia.*, **11**: 62.

Iredale, 1949. *Proc.R.zool.Soc.N.S.W.* 1947-48: 18-19.

Wilson B.R. and Stevenson S.E. 1977. Cardiidae (Mollusca, Bivalvia) of Western Australia. Western Australian Museum Special Publication No. 9: 1-114.

Kendrick G.W. 1990. A Pleistocene molluscan fauna with *Anadara trapezia* (Dehayes) (Bivalvia: Arcoida) from the Dampier Limestone of Shark Bay, Western Australia. Research in Shark Bay. *Report of the France-Australe Bicentenary Expedition*: 33-48.

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Tom Stewart of the Zoology Department, University of Western Australia did the histology and took the photomicrographs of zooxanthellae.

Brent Wise of the Fisheries Department fitted the von Bertallanfy growth curves and Nick Caputi of the same Department provided advice on sampling.

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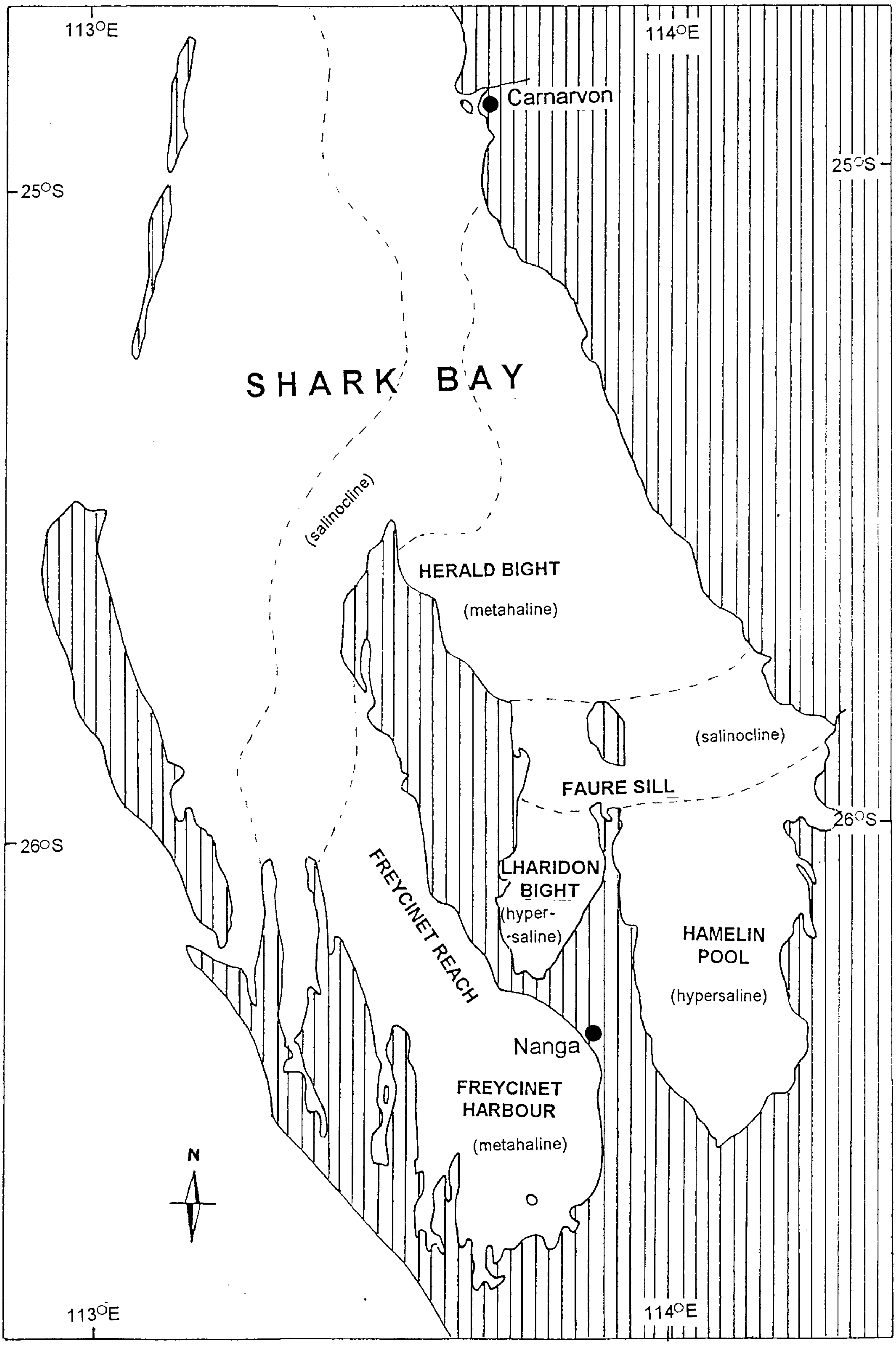

Figure 1. Shark Bay showing the salinity regimes.

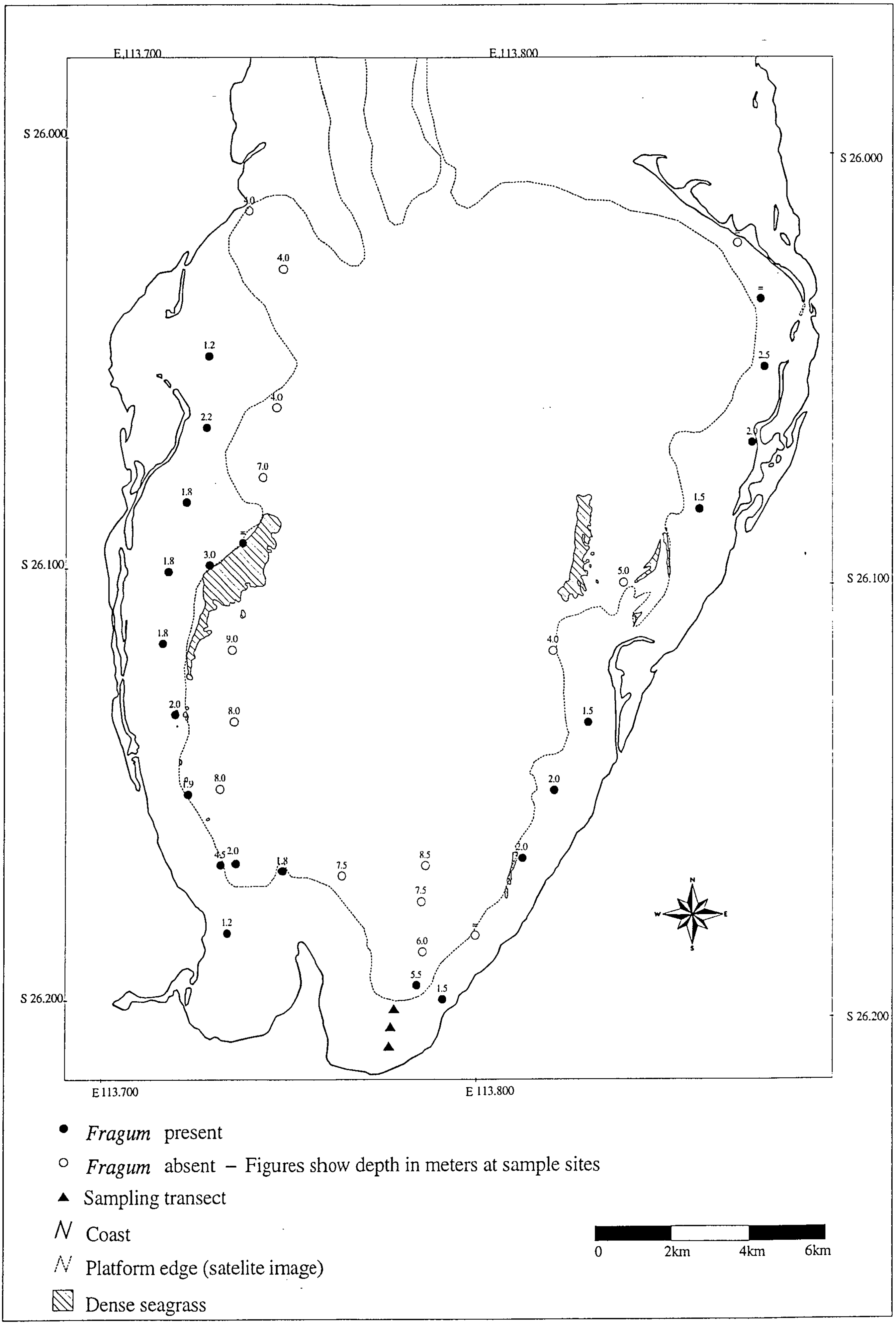

Figure 2. Presence/absence of living *Fragum erugatum* in Lharidon Bight.

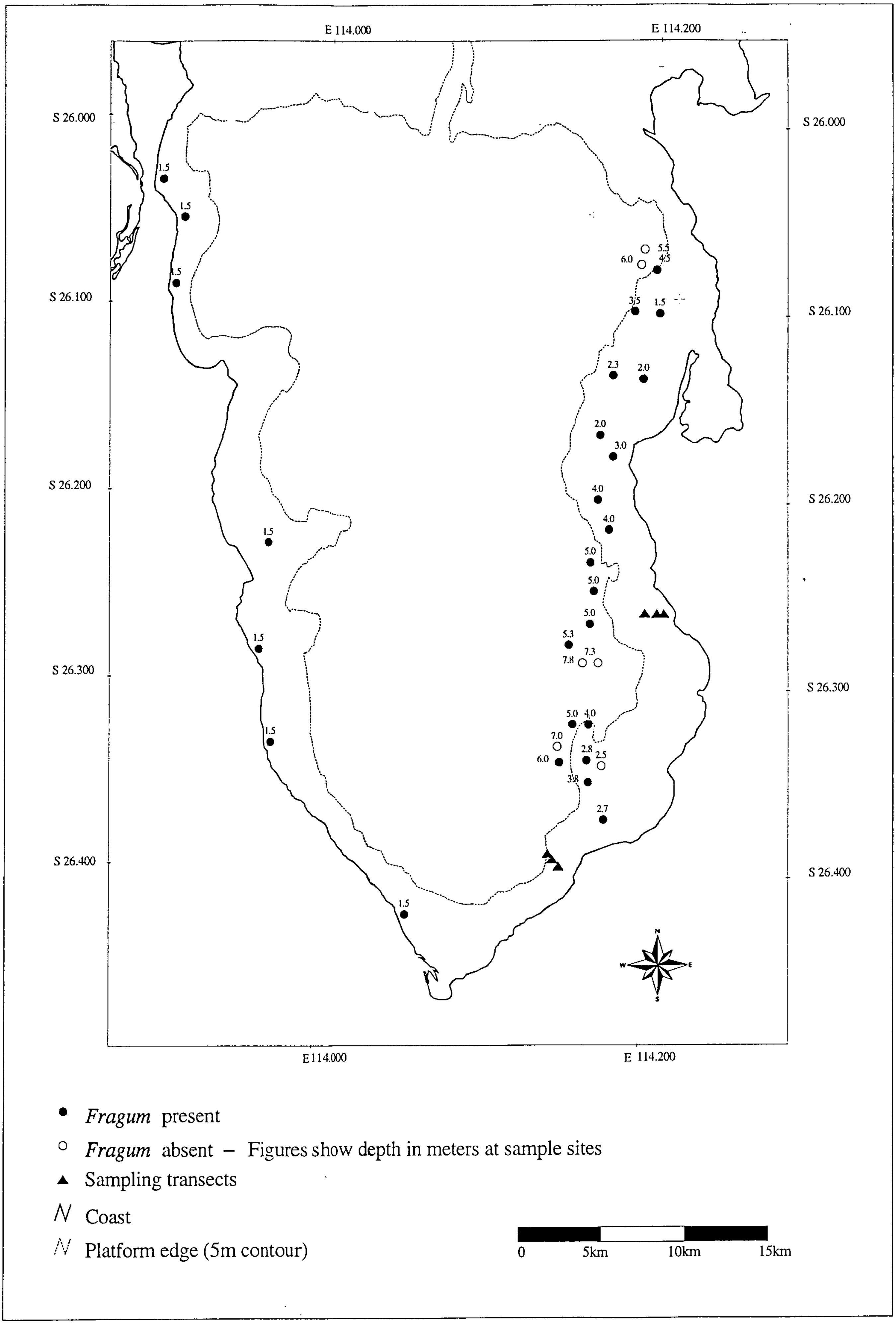

Figure 3. Presence/absence of living *Fragum erugatum* in Hamelin Pool.

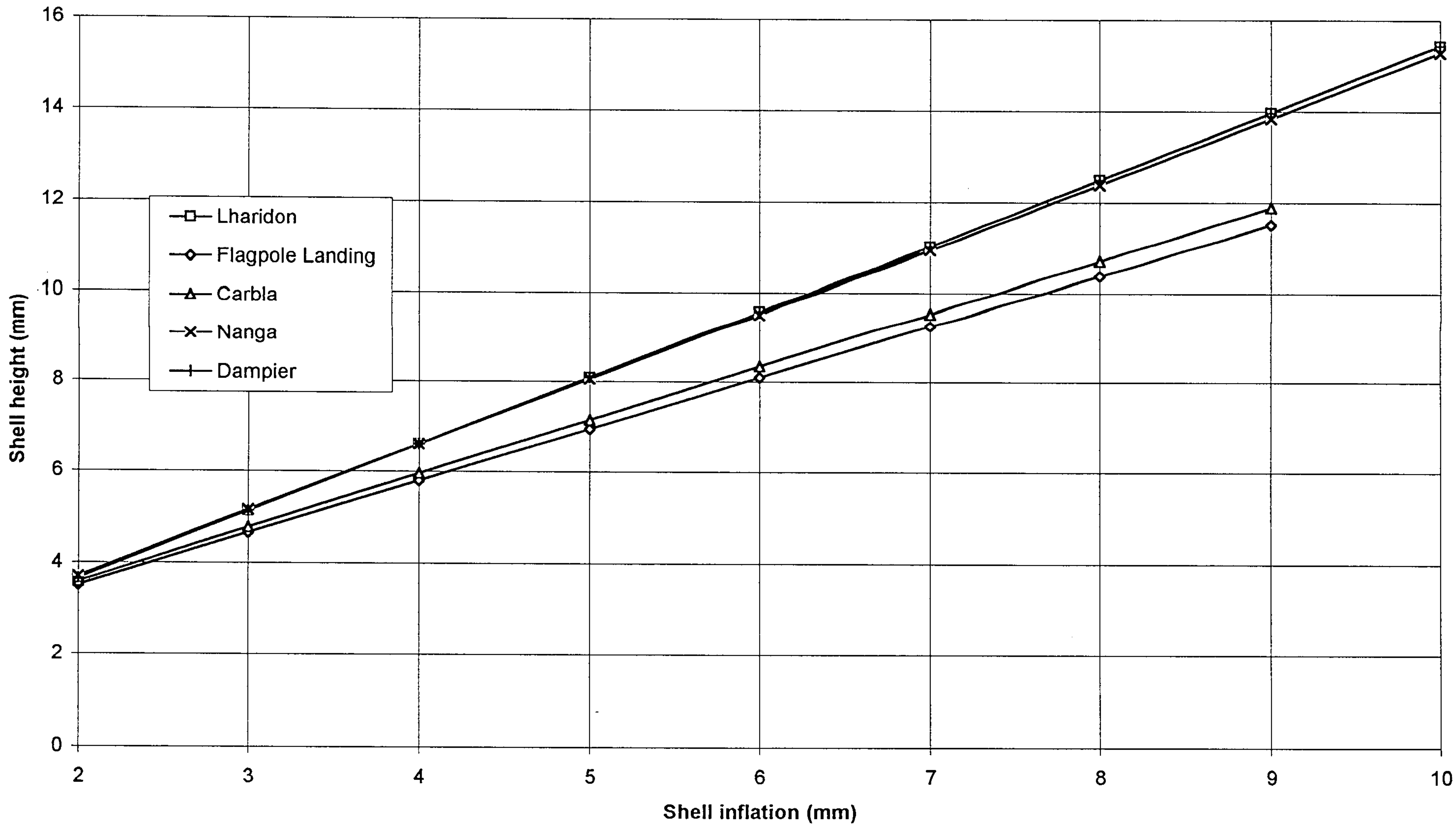

Figure 4. Relationship between shell inflation and shell height in populations of *Fragum erugatum* from Hamelin Pool (Flagpole Landing and Carbla) and Lharidon Bight, Freycinet Harbour and Dampier Archipelago (Lines for the last three are coincident).

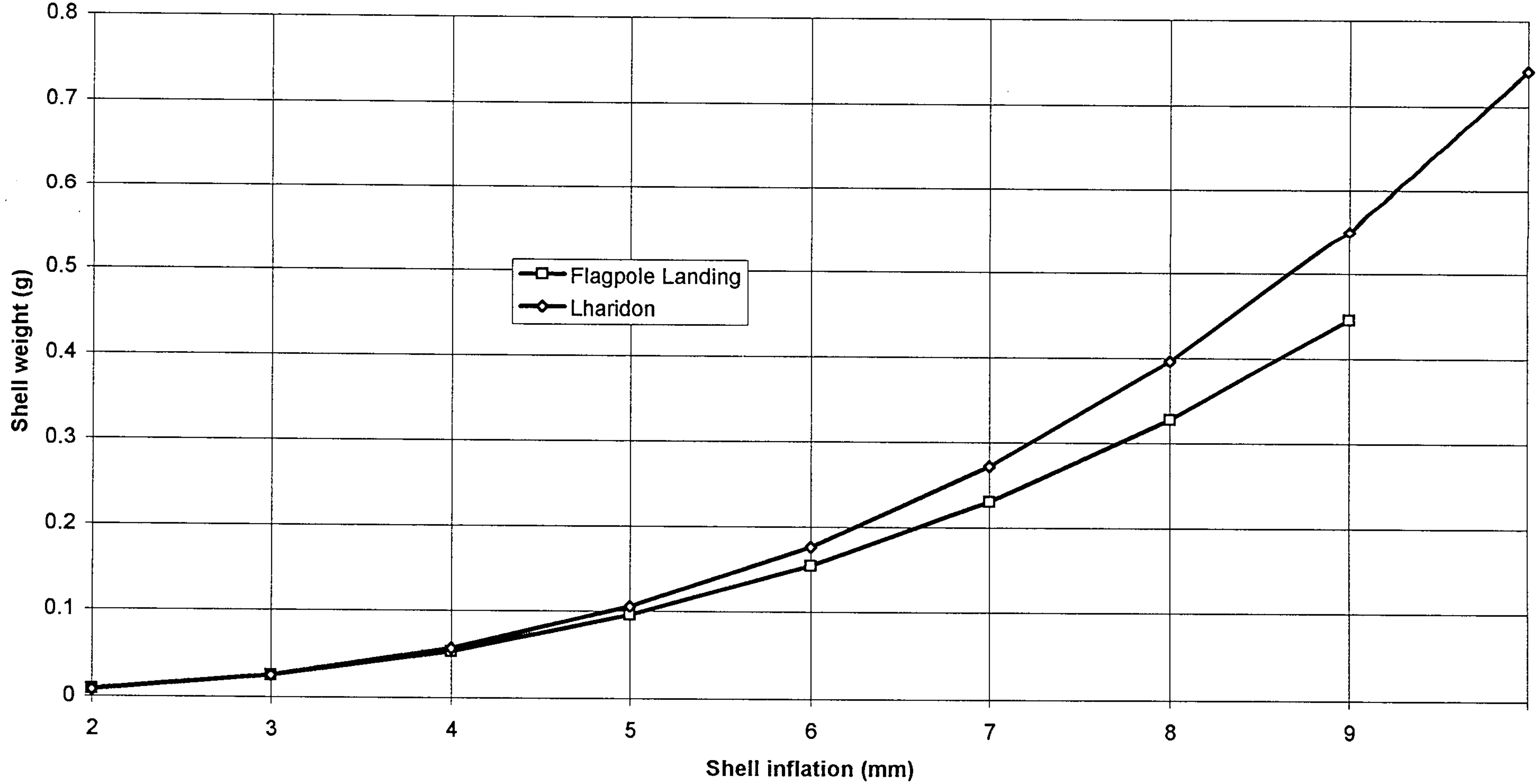

Figure 5. Relationship between shell inflation and shell weight of *Fragum erugatum* in Hamelin Pool and Lharidon Bight.

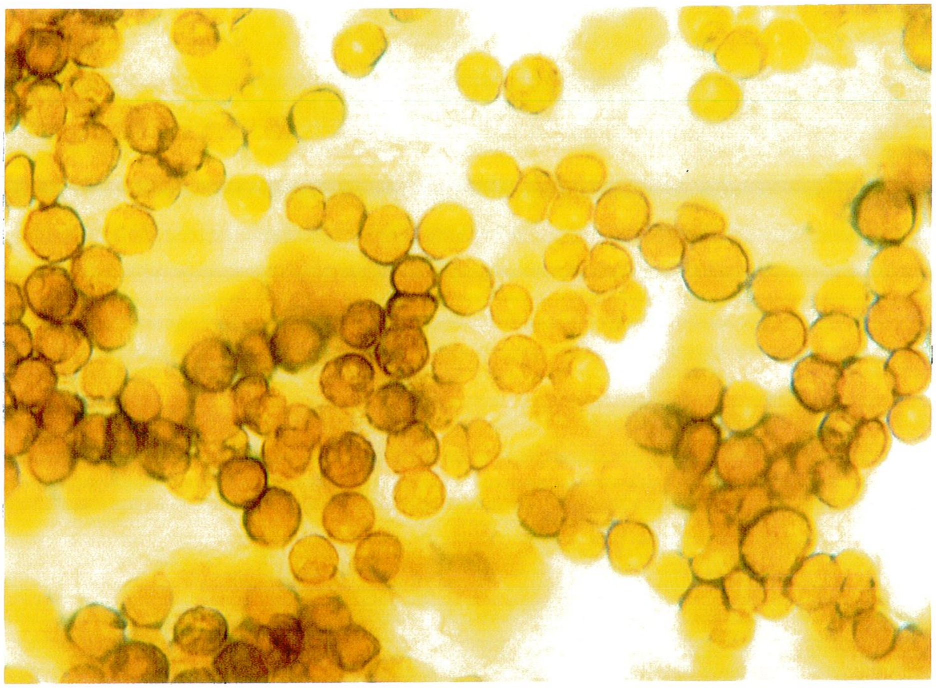

Figure 6. Crushed mantle tissue of *Fragum erugatum* showing endosymbiotic zooxanthellae. (The diameter range of zooxanthellae is 8 - 13μm).

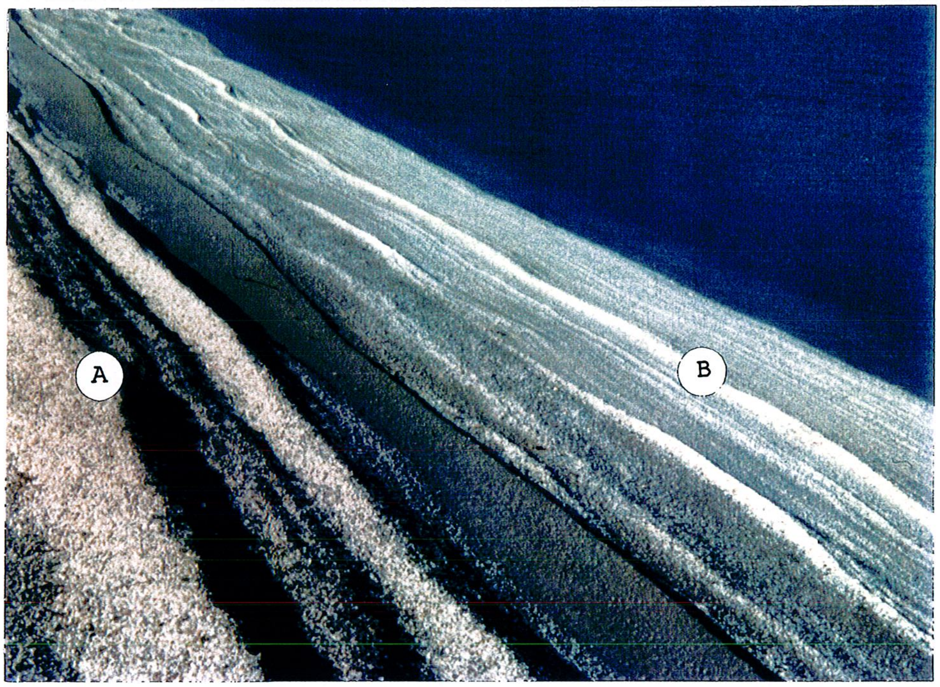

Figure 7. Most recent intertidal storm/tidal ridge (A)of accumulated *Fragum erugatum* shells and smaller tidal ridges (B) in which a high proportion of shells are closed or still articulated at Lharidon Bight.

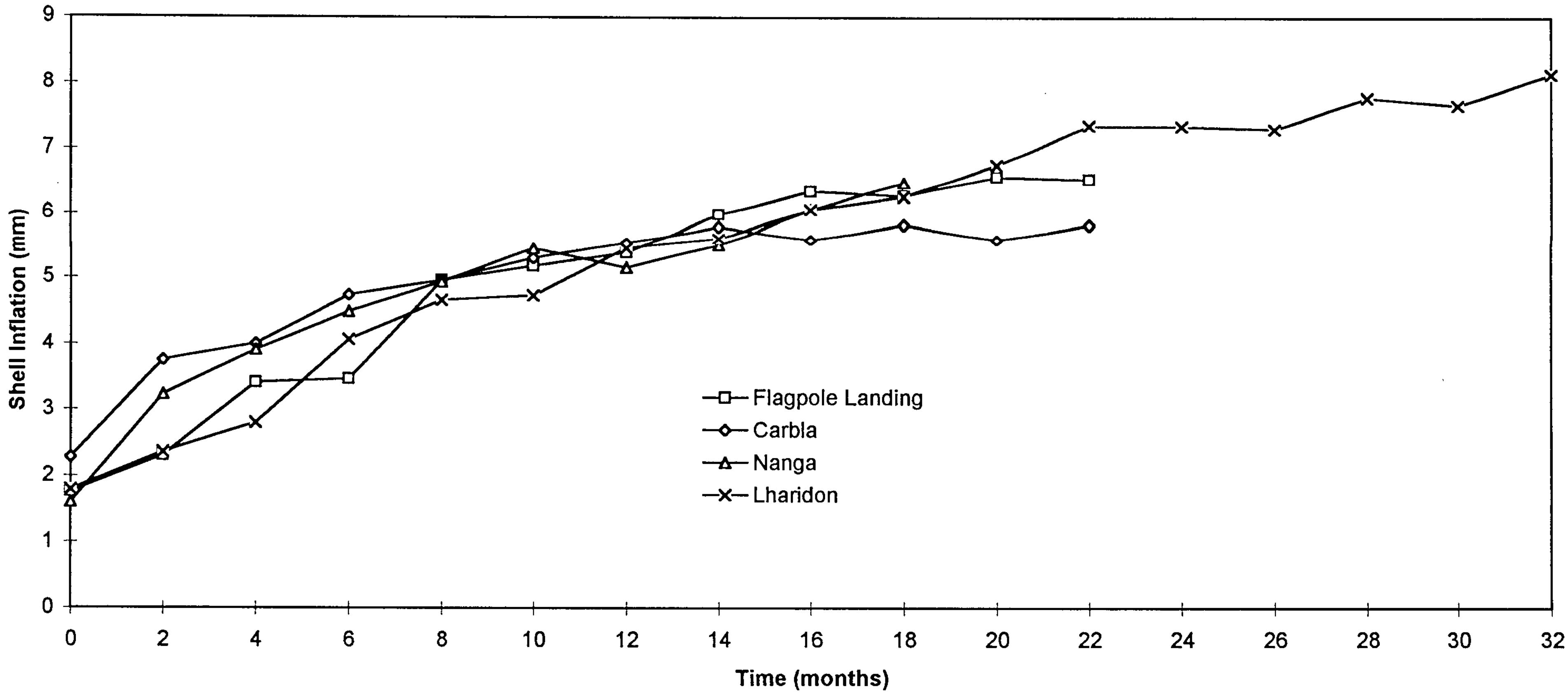

Figure 8. Growth of *Fragum erugatum* based on mean shell size of cohorts.

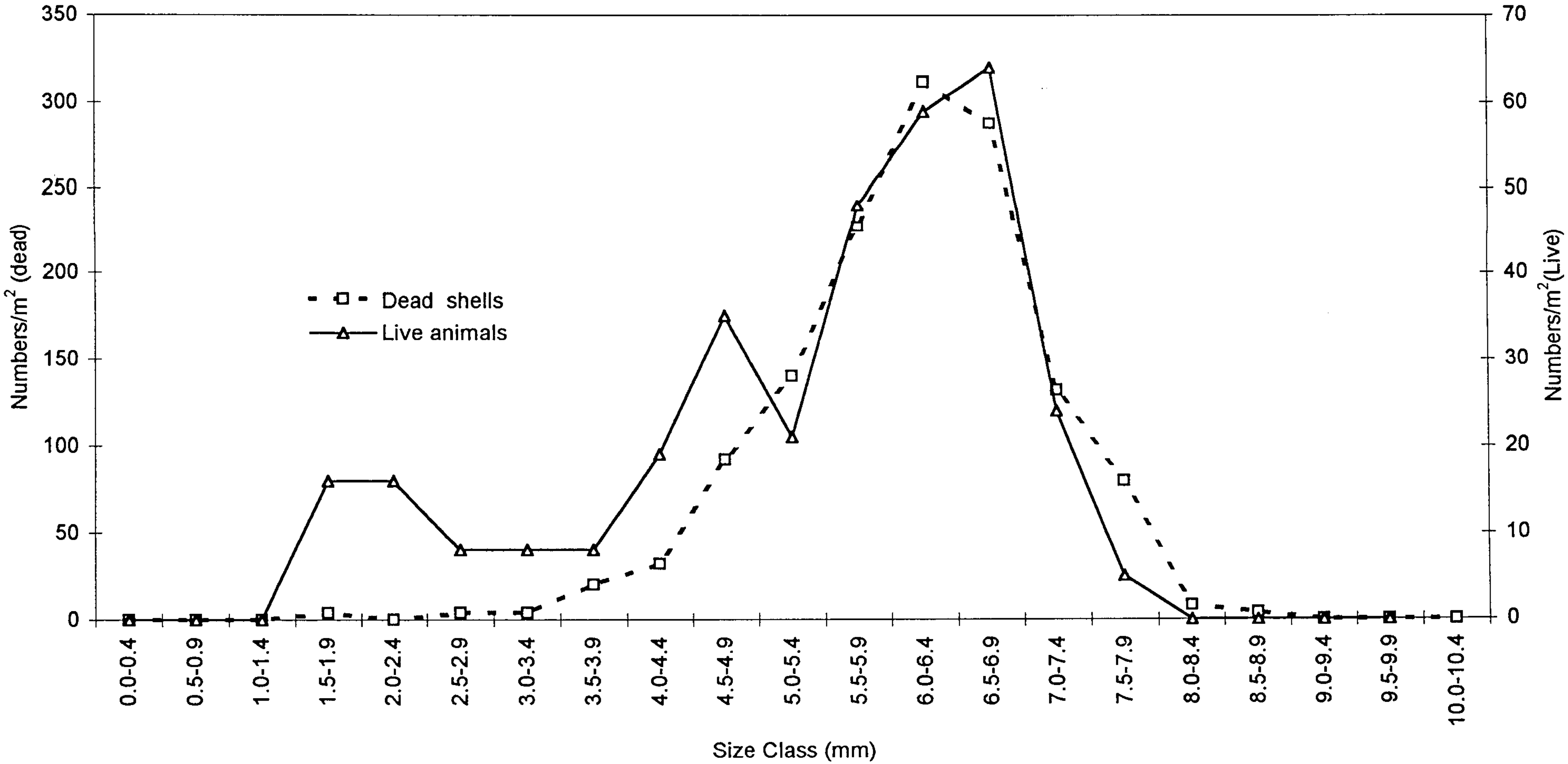

Figure 9. Size distribution of dead, articulated shells and live animals at Flagpole Landing, April 1995.

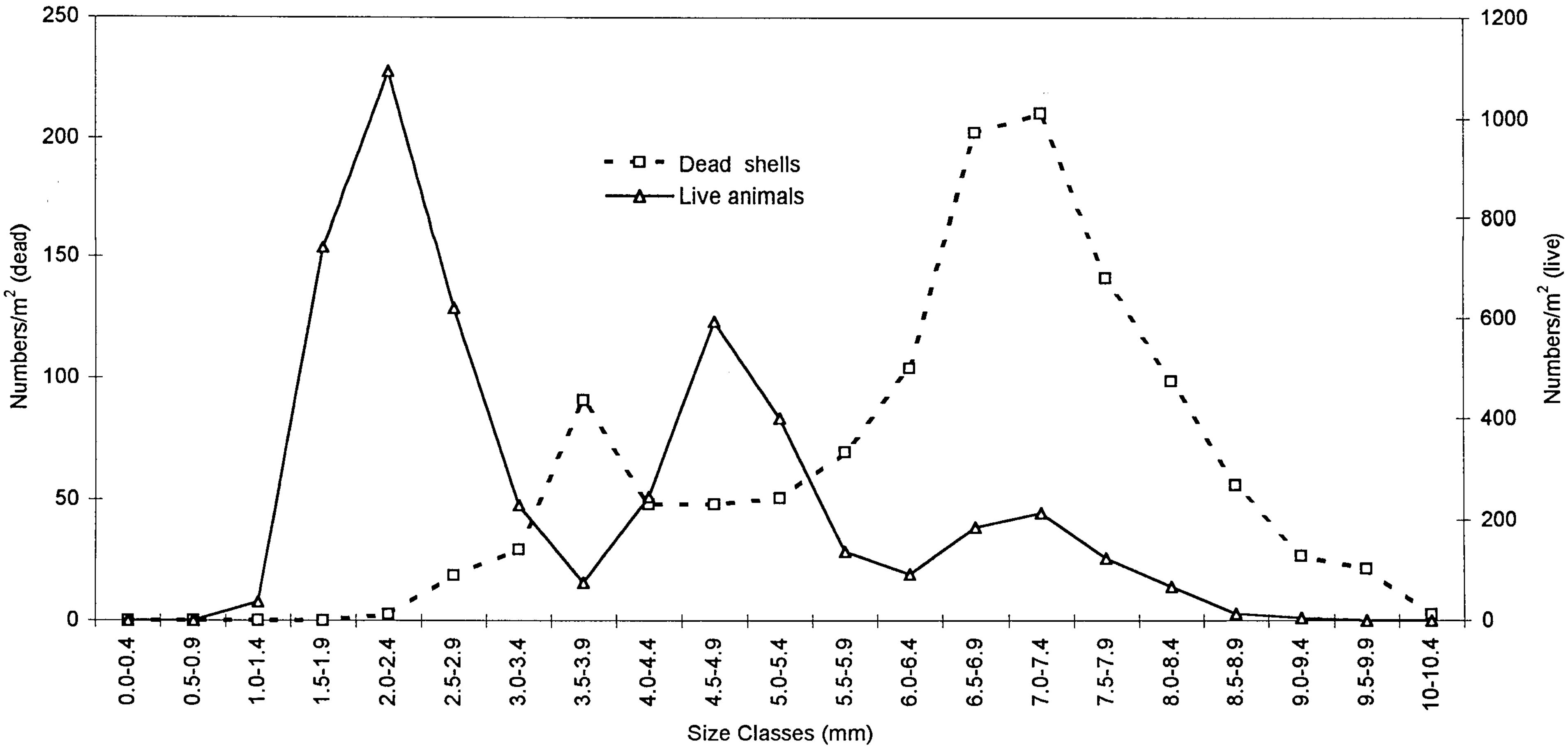

Figure 10. Size distributions of dead, articulated shells and live animals at Lharidon Bight, April 1995.

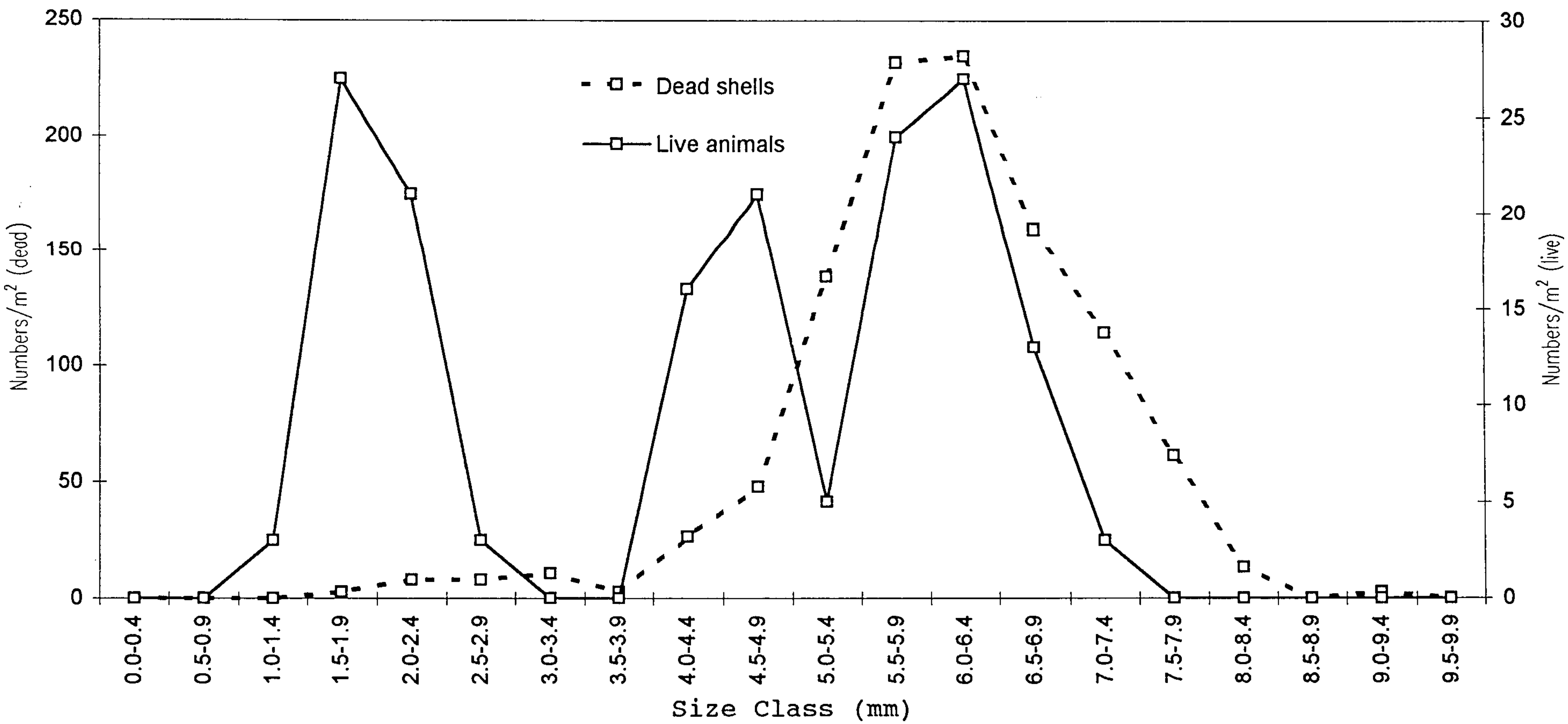

Figure 11. Size distributions of dead, articulated shells and live animals at Carbla, April 1995.

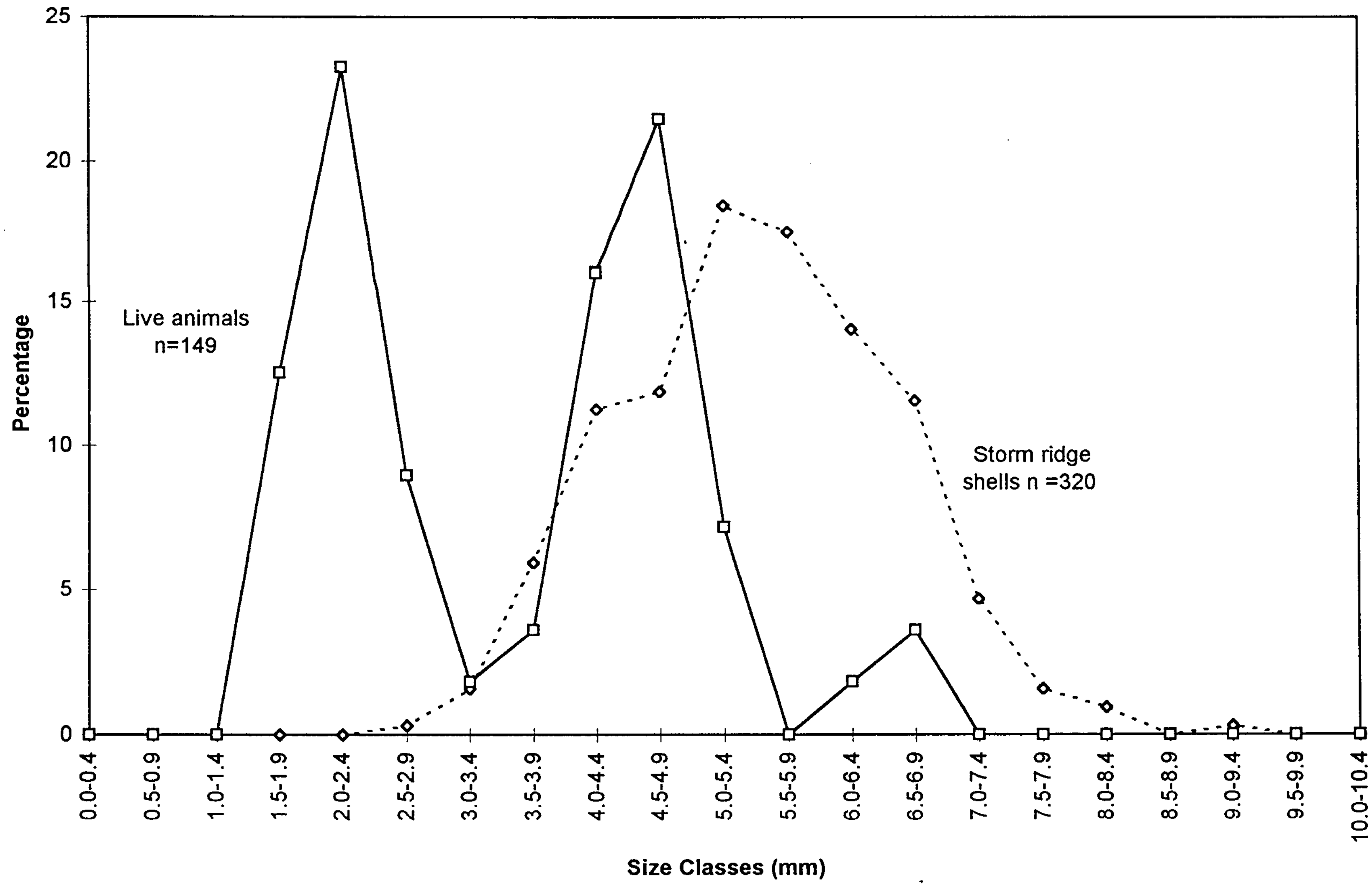

Figure 12. Size distributions of living animals and shells from the most recent storm ridge at Flagpole Landing, June 1995.

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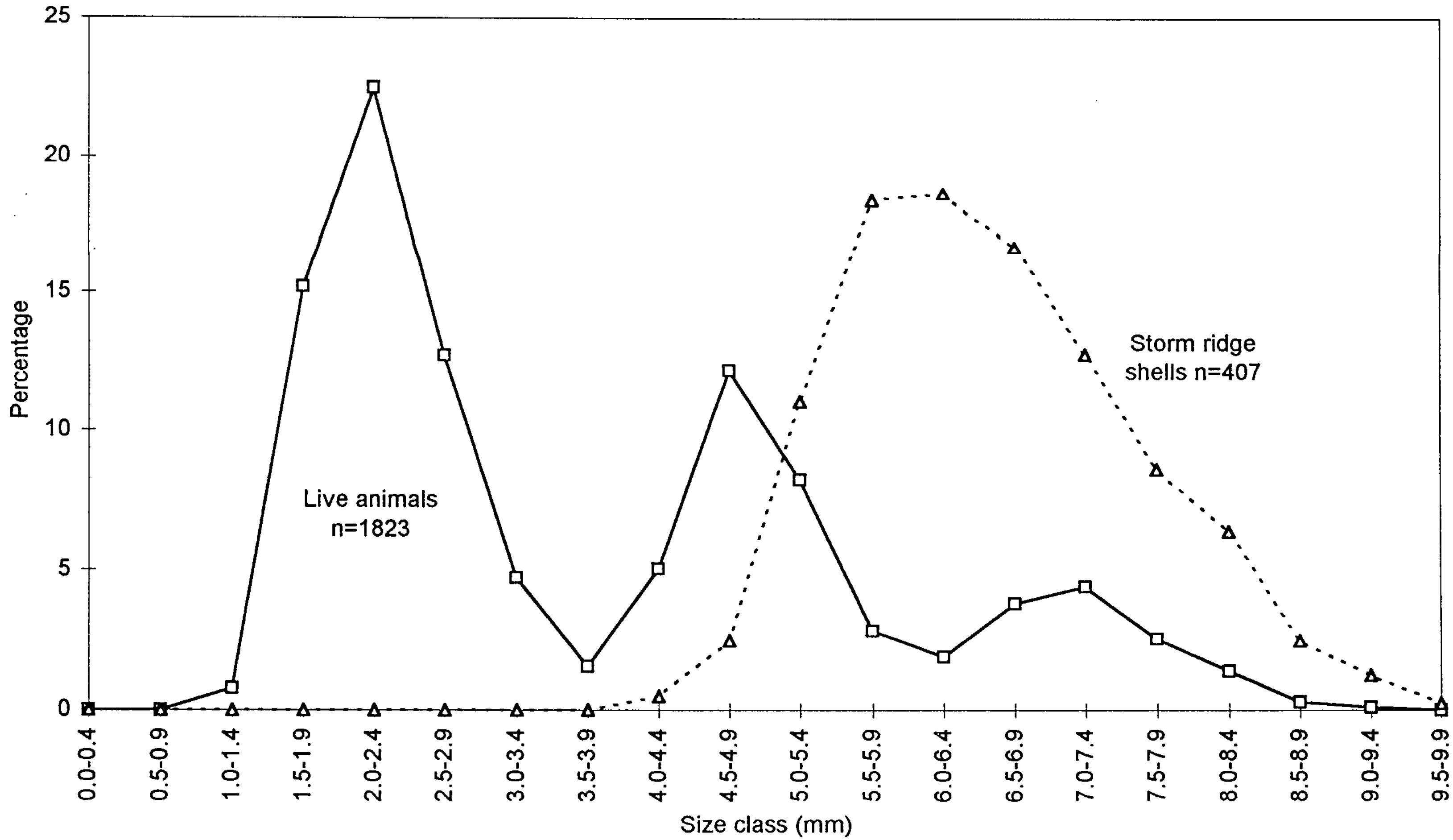

Figure 13. Size distributions of living animals and shells from the most recent recent storm ridge at Lharidon Bight, April 1995.

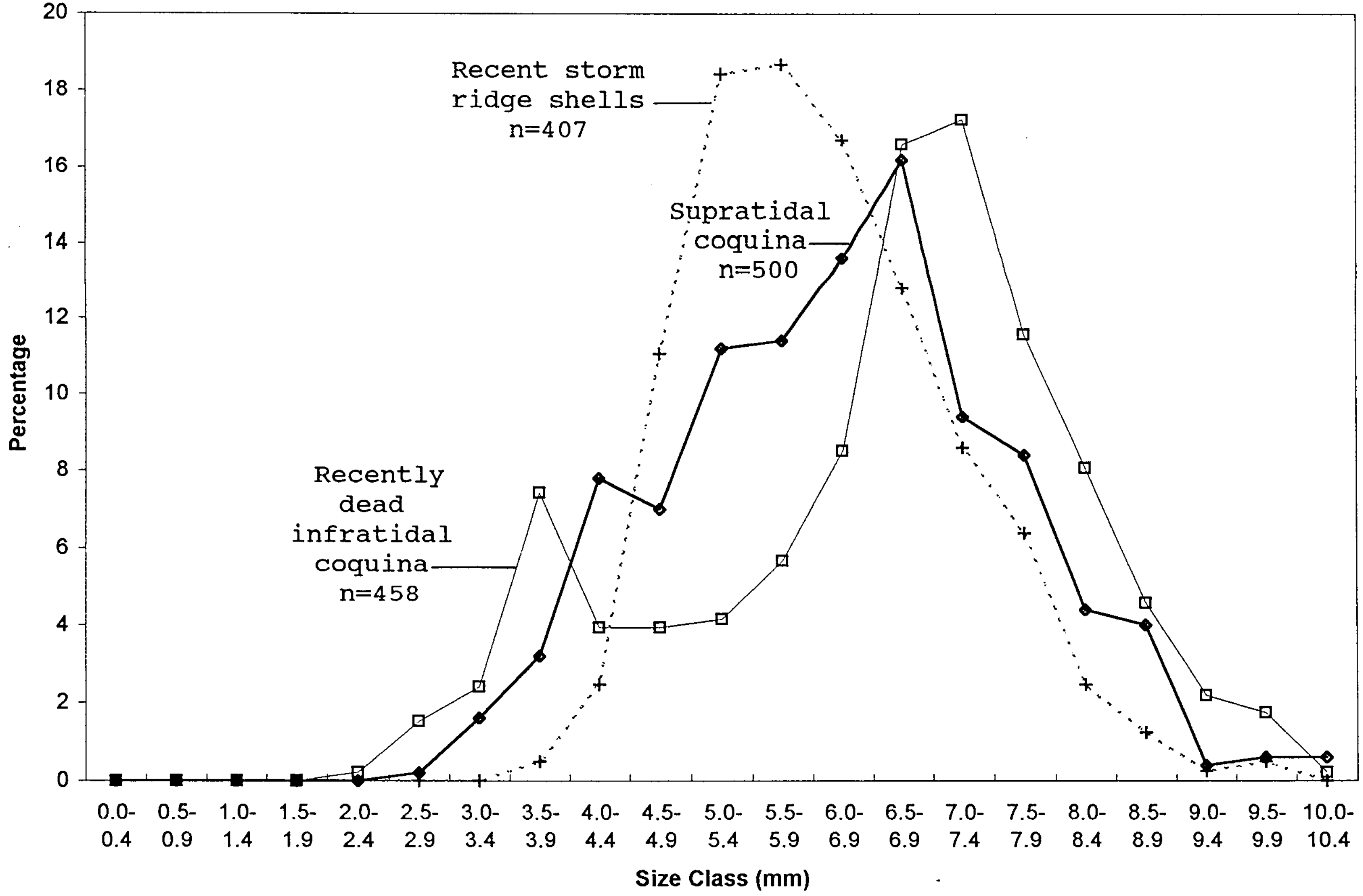

Figure 14. Dead shell size distributions at Lharidon Bight, April 1995.

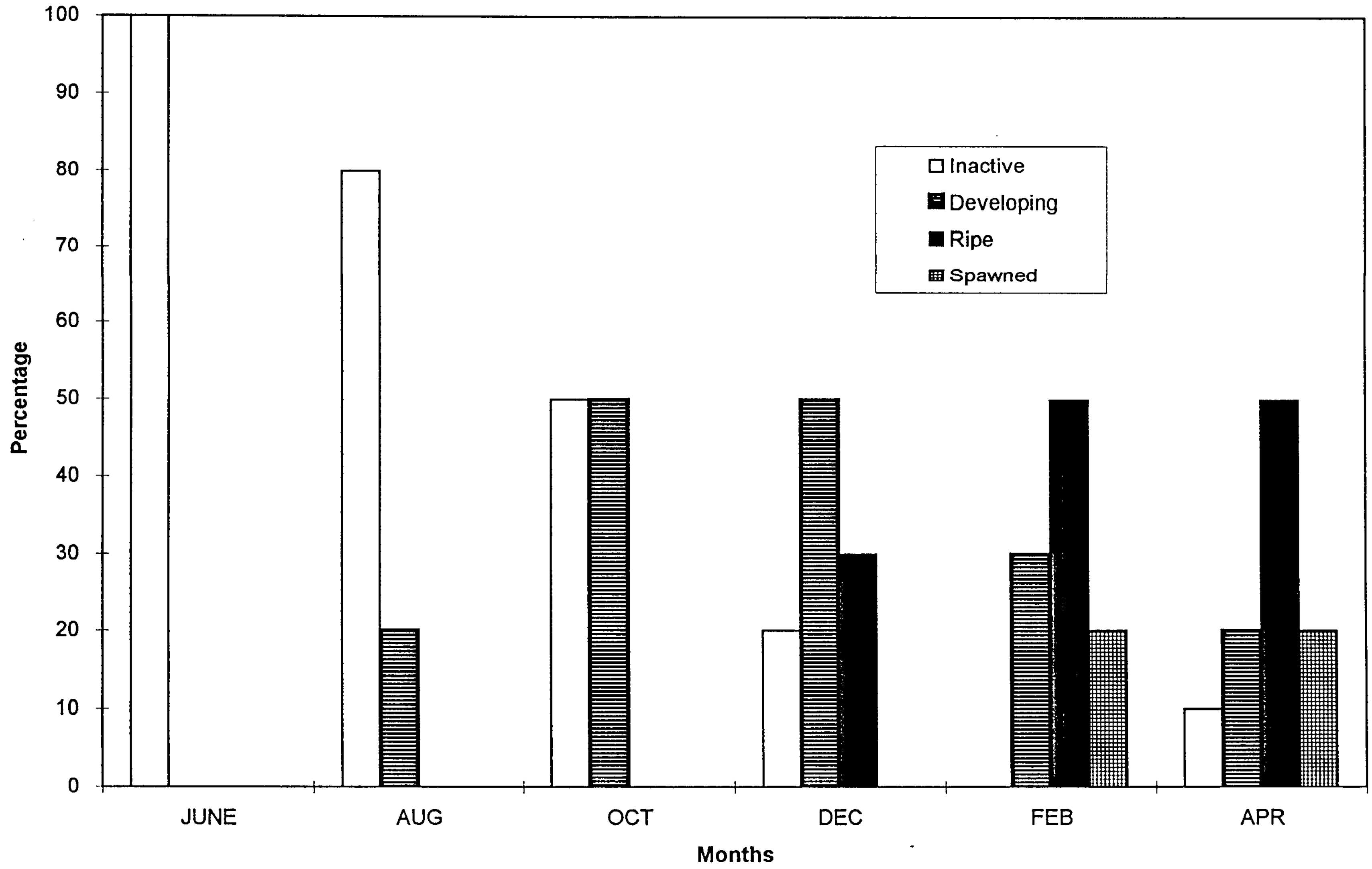

Figure 15. Gonad development in *Fragum erugatum* at Lharidon Bight , 1994/95.

Table 2. Size Frequency Distributions at Hamelin, June 1994-April 1995.

			Numbers /m^2 (±SE, n=6)			
Size class (mm)	June	August	October	December	February	April
0.0-0.4	0	0	0	0	0	0
0.5-0.9	0	0	0	0	0	0
1.0-1.4	0	53	0	0	0	0
1.5-1.9	0	107	16	3	0	16
2.0-2.4	0	51	13	0	3	16
2.5-2.9	3	8	16	19	13	8
3.0-3.4	3	24	3	32	48	8
3.5-3.9	8	24	0	6	40	8
4.0-4.4	24	48	5	13	37	19
4.5-4.9	112	272	19	6	11	35
5.0-5.4	165	421	88	45	27	21
5.5-5.9	93	352	211	131	131	48
6.0-6.4	21	181	176	230	205	59
6.5-6.9	5	45	93	202	141	64
7.0-7.4	0	8	13	74	85	24
7.5-7.9	0	8	5	6	13	5
8.0-8.4	0	0	0	3	8	0
8.5-8.9	0	0	0	0	0	0
9.0-9.4	0	0	0	0	0	0
9.5-9.9	0	0	0	0	0	0
10.0-10.4						
Totals	435±144	1603±361	659±286	778±254	763±348	331±143

Table 3. Size Frequency Distributions at Hamelin, June 1995-June 1996.							
			Numbers /m^2 (±SE, n=6)				
Size class	June	August	October	December	February	April	June
(mm)							
0.0-0.4	0	0	0	0	0	0	0
0.5-0.9	0	0	0	0	0	0	0
1.0-1.4	0	0	3	0	0	0	0
1.5-1.9	19	8	19	0	0	0	0
2.0-2.4	**35**	35	40	0	3	0	5
2.5-2.9	13	**45**	83	3	16	0	5
3.0-3.4	3	35	**125**	19	35	5	5
3.5-3.9	5	19	123	40	59	13	13
4.0-4.4	24	19	69	**99**	133	40	13
4.5-4.9	**32**	32	48	45	**245**	**125**	56
5.0-5.4	11	**40**	**61**	27	88	88	**85**
5.5-5.9	0	24	53	**59**	67	19	51
6.0-6.4	3	19	37	43	35	8	16
6.5-6.9	**5**	16	19	13	21	3	3
7.0-7.4	0	8	13	11	8	0	0
7.5-7.9	0	0	8	3	0	0	0
8.0-8.4	0	**3**	0	3	3	0	0
8.5-8.9	0	0	0	0	0	0	0
9.0-9.4	0	0	0	0	**3**	0	0
9.5-9.9	0	0	0	0	0	0	0
10.0-10.4	0	0	0	0	0	0	0
Totals	149±43	301±98	701±200	363±40	716±214	301±91	253±90

Table 4. Size Frequency Distributions at Lharidon, June 1994 - June 1995							
			Numbers /m^2 (±SE, n=6)				
Size class (mm)	June	August	October	December	February	April	June
0.0-0.4	0	0	0	0	0	0	0
0.5-0.9	0	0	0	0	0	0	0
1.0-1.4	58	16	0	0	0	37	11
1.5-1.9	**178**	253	11	0	0	739	360
2.0-2.4	68	**317**	227	2	0	**1093**	800
2.5-2.9	18	189	**339**	43	0	619	**1072**
3.0-3.4	0	72	200	158	13	229	733
3.5-3.9	6	40	32	379	64	75	211
4.0-4.4	14	13	24	**400**	248	245	139
4.5-4.9	30	32	32	187	**280**	**592**	224
5.0-5.4	122	91	131	69	219	400	**395**
5.5-5.9	**128**	**109**	339	105	152	136	243
6.0-6.4	60	88	**413**	185	235	91	125
6.5-6.9	36	64	227	**203**	**315**	184	**203**
7.0-7.4	**48**	**77**	**240**	176	296	**213**	192
7.5-7.9	28	40	205	**183**	184	123	101
8.0-8.4	22	24	128	130	88	67	37
8.5-8.9	2	5	40	62	40	13	3
9.0-9.4	6	0	3	30	21	5	5
9.5-9.9	0	**3**	**8**	2	5	0	3
10.0-10.4	2	0	3	**5**	**8**	0	3
N	826±69	1435±194	2600±805	2320±698	2168±378	4861±706	4859±651

Table 5. Size Frequency Distributions at Lharidon, June 1995- June 1996.						
			Numbers /m^2 (±SE, n=6)			
Size class	August	October	December	February	April	June
(mm)						
0.0-0.4	**3**	3	0	0	0	0
0.5-0.9	0	0	0	0	0	0
1.0-1.4	8	0	0	0	0	0
1.5-1.9	216	128	11	0	0	0
2.0-2.4	747	635	251	5	0	4
2.5-2.9	1160	1072	771	187	8	**16**
3.0-3.4	**1200**	1227	936	709	189	4
3.5-3.9	653	**1264**	941	1237	557	16
4.0-4.4	240	709	**984**	1613	896	20
4.5-4.9	237	283	624	**1749**	**901**	136
5.0-5.4	**349**	280	325	1125	499	484
5.5-5.9	243	**347**	485	667	421	**776**
6.0-6.4	99	259	**552**	427	405	672
6.5-6.9	91	176	251	229	309	284
7.0-7.4	**109**	152	96	85	104	56
7.5-7.9	80	112	83	37	29	44
8.0-8.4	27	77	35	16	21	16
8.5-8.9	8	8	19	16	5	8
9.0-9.4	8	**11**	3	0	0	8
9.5-9.9	0	0	3	0	0	4
10.0-10.4	0	0	0	0	0	0
N	5477±41	6739±120	6368±59	8104±1406	4347±851	2548±216

Table 6. Size Frequency Distributions at Carbla, 1994/95.							
			Numbers /m^2 (±SE, n=6)				
Size cl	June	August	Oct.	Dec.	Feb.	April	June
(mm)							
0.0-0.4	0	0	0	0	0	0	0
0.5-0.9	0	0	0	0	0	0	0
1.0-1.4	0	0	3	0	0	3	3
1.5-1.9	0	0	27	0	0	**27**	12
2.0-2.4	0	0	**75**	2	0	21	27
2.5-2.9	0	0	40	0	0	3	**29**
3.0-3.4	11	0	3	2	5	0	9
3.5-3.9	37	3	5	**21**	29	0	0
4.0-4.4	120	13	11	16	**45**	16	6
4.5-4.9	**296**	91	59	16	24	**21**	**21**
5.0-5.4	237	**155**	187	110	**59**	5	11
5.5-5.9	104	104	**195**	**199**	51	24	36
6.0-6.4	29	24	91	123	43	**27**	45
6.5-6.9	11	5	21	27	16	13	**48**
7.0-7.4	8	0	5	11	8	3	6
7.5-7.9	0	0	3	2	0	0	0
8.0-8.4	0	0	0	2	0	0	0
8.5-8.9	0	0	0	0	0	0	0
9.0-9.4	0	0	0	0	0	0	0
9.5-9.9	0	0	0	0	0	0	0
10.0-10	0	0	0	0	0	0	0
N	853±228	395±89	723±168	533±131	280±82	163±34	253±78

Table 7 . Size frequency distributions at Nanga

					Numbers/m^2						
Size class (mm)	October	December	February	April	June	August	Oct-95	Dec-95	Feb-96	Apr-96	Jun-96
0.0-0.4	0	0	0	0	0	0	0	0	0	0	0
0.5-0.9	0	0	0	0	0	0	0	0	0	0	0
1.0-1.4	544	0	0	0	0	0	0	0	0	0	0
1.5-1.9	**1168**	16	0	0	0	0	0	0	0	0	0
2.0-2.4	80	112	8	0	8	0	0	0	0	0	0
2.5-2.9	0	608	40	16	16	0	0	0	0	0	0
3.0-3.4	0	**1264**	160	56	64	0	1	1	0	0	0
3.5-3.9	0	560	**472**	152	88	0	2	2	0	0	0
4.0-4.4	0	64	320	256	256	32	9	14	0	0	0
4.5-4.9	0	0	120	**296**	**272**	48	22	58	0	0	0
5.0-5.4	0	16	8	128	112	**80**	**27**	121	18	0	0
5.5-5.9	0	0	0	56	24	**80**	20	**120**	31	16	12
6.0-6.4	0	0	0	8	16	40	7	68	**34**	16	**84**
6.5-6.9	0	0	0	0	0	16	1	13	16	8	68
7.0-7.4	0	0	0	0	0	8	0	2	8	16	24
7.5-7.9	0	0	0	0	0	0	0	0	0	0	12
8.0-8.4	0	0	0	0	0	0	0	0	0	0	8
8.5-8.9	0	0	0	0	0	0	0	0	0	0	0
9.0-9.4	0	0	0	0	0	0	0	0	0	0	0
9.5-9.9	0	0	0	0	0	0	0	0	0	0	0
10.0-10.4	0	0	0	0		0	0	0	0	0	0
N	1792	2640	1128	968	856	304	89	397	106	56	208

Table 8. Density, production and biomass at Hamelin in 1994/95

COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Apr-95	0.0010		0.011		37					0.026	0.456	0.482
Jun-95	0.001	0.000	0.017	0.005	77	57	0.019	0.296	0.315	0.103	1.280	1.382
TOTALS							0.019	0.296	0.315	0.129	1.735	1.864
											P/B=	0.34
COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Jun-94	0		0		0							
Aug-94	0.001	0.000	0.007	0.008	247	124	0.03	0.94	0.98	0.16	1.68	1.84
Oct-94	0.001	0.001	0.014	0.007	48	148	0.08	1.05	1.13	0.06	0.67	0.72
Dec-94	0.003	0.001	0.037	0.022	57	53	0.08	1.17	1.25	0.15	2.13	2.28
Feb-95	0.003	0.000	0.038	0.008	139	98	0.00	0.77	0.77	0.37	5.24	5.61
Apr-95	0.006	0.003	0.100	0.039	141	140	0.46	5.40	5.86	0.84	14.08	14.93
Jun-95	0.005	-0.001	0.081	-0.019	64	103	-0.09	-1.97	-2.06	0.32	5.16	5.49
TOTALS							0.56	7.36	7.92	1.91	28.96	30.87
											P/B=	1.54
COHORT 1+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Jun-94	0.006		0.107		435					2.1663	46.197	48.3633
Aug-94	0.007	0.001	0.120	0.013	1356	896	0.54	11.50	12.04	9.51	163.14	172.64
Oct-94	0.009	0.002	0.156	0.036	610	983	1.70	35.53	37.24	5.33	95.44	100.77
Dec-94	0.010	0.001	0.182	0.025	498	554	0.64	14.00	14.63	4.93	90.50	95.42
Feb-95	0.010	0.000	0.178	-0.004	624	561	-0.10	-2.01	-2.11	6.06	111.16	117.22
Apr-95	0.011	0.001	0.198	0.020	152	388	0.36	7.79	8.15	1.62	30.13	31.75
Jun-95	0.010	0.000	0.194	-0.004	8	80	-0.01	-0.35	-0.37	0.08	1.55	1.63
TOTALS							3.13	66.46	69.59	27.54	491.91	519.44
											P/B=	0.80
TOTALS OF ALL COHORTS							3.71	74.12	77.83	29.57	522.61	552.18

Table 9. Density, production and biomass at Hamelin in 1995/96

	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
COHORT 0+												
Aug-95	0.002	0.000	0.020	0.003	123	100	0.025	0.344	0.369	0.195	2.467	2.662
Oct-95	0.002	0.001	0.032	0.012	395	259	0.194	3.140	3.333	0.923	12.711	13.634
Dec-95	0.004	0.002	0.059	0.026	189	292	0.452	7.726	8.178	0.735	11.099	11.834
Feb. 96	0.005	0.001	0.084	0.026	680	435	0.576	11.177	11.753	3.541	57.350	60.891
Apr-96	0.009	0.004	0.102	0.018	301	491	1.942	8.713	10.655	2.759	30.732	33.492
Jun-96	0.006	-0.003	0.102	0.000	253	277	-0.845	0.078	-0.767	1.548	25.903	27.451
TOTALS							2.344	31.178	33.522	9.702	140.263	149.965
											P/B=	1.34
	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
COHORT 1+												
Aug-95	0.007	0.002	0.117	0.037	176	120	0.211	4.410	4.621	1.201	20.669	21.870
Oct-95	0.007	0.000	0.121	0.003	307	242	0.031	0.748	0.779	2.133	37.004	39.137
Dec-95	0.009	0.002	0.153	0.032	173	240	0.382	7.748	8.131	1.478	26.438	27.915
Feb-95	0.012	0.004	0.235	0.083	35	104	0.380	8.593	8.974	0.427	8.241	8.668
Apr-96	-	-	-	-	0	-	-	-	-	-	-	-
Jun-96	-	-	-	-	0	-	-	-	-	-	-	-
TOTALS							1.004	21.500	22.504	5.239	92.351	97.590
											P/B=	1.4
	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
COHORT 2+												
Aug-95	0.016	0.006	0.335	0.141	3	6	0.033	0.776	0.809	0.049	1.005	1.05
Oct-95	-	-	-	-	0	-	-	-	-	-	-	-
Dec-95	-	-	-	-	0	-	-	-	-	-	-	-
Feb-95	-	-	-	-	0	-	-	-	-	-	-	-
Apr-96	-	-	-	-	0	-	-	-	-	-	-	-
TOTALS							0.033	0.776	0.809	0.049	1.005	1.054
											P/B=	0.77
TOTALS OF ALL COHORTS							3.381	53.454	56.835	14.990	233.618	248.609

Table 10. Density, production and biomass at Carbla in 1994/95

COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m²	Mean No between samples	Flesh production (g/m²)	Shell production (g/m²)	Total production (g/m²)	Total flesh biomass (g/m²)	Total shell biomass (g/m²)	Total biomass (g/m²)
Apr-95	0.0009		0.0096		53		0	0	0	0.046	0.508	0.554
Jun-95	0.001	0.000	0.015	0.006	80	67	0.024	0.372	0.396	0.099	1.213	1.312
TOTALS							0.024	0.372	0.396	0.099	1.213	1.312
COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m²	Mean No between samples	Flesh production (g/m²)	Shell production (g/m²)	Total production (g/m²)	Total flesh biomass (g/m²)	Total shell biomass (g/m²)	Total biomass (g/m²)
Jun-94												
Aug-94												
Oct-94	0.001		0.013		148					0.162	1.885	2.047
Dec-94	0.003	0.002	0.046	0.034	32	90	0.190	3.037	3.226	0.288	4.183	4.471
Feb-95	0.004	0.000	0.054	0.008	64	48	0.021	0.371	0.392	0.175	2.602	2.777
Apr-95	0.005	0.002	0.085	0.031	27	46	0.074	1.389	1.463	0.240	3.855	4.095
Jun-95	0.006	0.001	0.087	0.002	31	29	0.017	0.064	0.081	0.170	2.521	2.691
TOTALS							0.302	4.861	5.162	0.873	13.162	14.035
COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m²	Mean No between samples	Flesh production (g/m²)	Shell production (g/m²)	Total production (g/m²)	Total flesh biomass (g/m²)	Total shell biomass (g/m²)	Total biomass (g/m²)
Jun-94	0.006		0.097		852					5.009	82.806	87.816
Aug-94	0.007	0.001	0.113	0.016	395	624	0.513	10.077	10.590	4.179	70.675	74.854
Oct-94	0.007	0.001	0.129	0.015	575	485	0.351	7.371	7.722	3.601	62.347	65.948
Dec-94	0.008	0.001	0.144	0.015	501	538	0.396	8.296	8.692	4.391	77.456	81.847
Feb-95	0.008	-0.001	0.133	-0.010	216	359	-0.189	-3.763	-3.952	2.737	47.851	50.588
Apr-95	0.008	0.001	0.148	0.014	83	150	0.103	2.157	2.260	1.244	22.111	23.356
Jun-95	0.010	0.002	0.182	0.035	142	113	0.202	3.884	4.086	1.139	20.523	21.662
TOTALS							1.377	28.022	29.398	17.292	300.963	318.254
TOTALS OF ALL COHORTS							1.703	33.254	34.957	18.263	315.338	333.601
											P/B	0.6

Table 11. Density, production and biomass at Lharidon Bight in 1994/95

COHORT 0	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Apr-95	0.002	0.002	0.011	0.011	2504	1252	2.458	14.293	16.751	4.915	28.586	33.501
Jun-95	0.003	0.001	0.022	0.011	3272	2888	2.995	30.567	33.561	9.816	71.984	81.800
TOTALS							5.453	44.859	50.312	14.731	100.570	115.301
COHORT 0	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Jun-94	0.001		0.007		322					0.427	2.131	2.558
Aug-94	0.002	0.001	0.015	0.008	896	609	0.593	4.983	5.575	2.060	13.261	15.321
Oct-94	0.003	0.001	0.023	0.008	829	862.5	0.727	6.649	7.376	2.605	18.660	21.265
Dec-94	0.006	0.003	0.063	0.040	1262	1045.5	3.476	41.868	45.344	8.161	78.944	87.106
Feb-95	0.008	0.002	0.090	0.027	861	1061.5	2.032	28.680	30.711	7.216	77.122	84.338
Apr-95	0.009	0.000	0.097	0.008	1768	1314.5	0.511	10.144	10.655	15.505	172.009	187.514
Jun-95	0.010	0.001	0.119	0.022	864	1316	1.619	28.570	30.189	8.640	102.816	111.456
TOTALS							8.958	120.894	129.852	44.187	462.812	507.000
											P/B=	4.155
COHORT 1	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Jun-94	0.011		0.139		346					3.942	47.988	51.930
Aug-94	0.012	0.001	0.151	0.012	320	333	0.225	3.934	4.159	3.862	48.163	52.025
Oct-94	0.014	0.002	0.186	0.036	1176	748	1.447	26.656	28.104	16.470	218.907	235.376
Dec-94	0.015	0.001	0.201	0.015	343	760	0.633	11.279	11.912	5.089	68.942	74.031
Feb-95	0.017	0.002	0.250	0.049	1024	684	1.632	33.463	35.094	17.638	255.953	273.591
Apr-95	0.020	0.003	0.318	0.068	589	807	2.553	54.938	57.491	12.010	187.345	199.355
Jun-95	0.018	-0.002	0.275	-0.043	720	655	-1.564	-28.191	-29.756	12.960	198.000	210.960
TOTALS							6.490	130.270	136.760	55.070	779.309	834.378
											P/B=	0.983
COHORT 2	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Jun-94	0.020		0.322		156					3.194	50.293	53.488
Aug-94	0.020	0.000	0.314	-0.008	219	187.5	-0.056	-1.521	-1.577	4.419	68.827	73.247
Oct-94	0.023	0.003	0.372	0.058	595	407	1.054	23.689	24.742	13.547	221.627	235.174
Dec-94	0.022	-0.001	0.359	-0.013	711	653	-0.394	-8.492	-8.886	15.759	255.590	271.348
Feb-95	0.025	0.003	0.421	0.062	275	493	1.319	30.505	31.825	6.831	115.873	122.704
Apr-95	-	-	-	-	0	-	-	-	-	-	-	-
Jun-95	-	-	-	-	0	-	-	-	-	-	-	-
TOTALS							1.923	44.181	46.104	43.750	712.210	755.961
											P/B=	0.366
TOTALS OF ALL COHORTS							22.822	340.205	363.027	157.739	2054.901	2212.640

Table 12. Density, production and biomass at Lharidon Bight in 1995/96

	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
COHORT 0+	0.003		0.021		24					0.073	0.503	0.577
COHORT 0+												
Aug-95	0.004	0.001	0.029	0.007	4320	3796	3.796	25.281	29.077	17.280	123.811	141.091
Oct-95	0.005	0.001	0.043	0.014	5664	4992	4.083	70.317	74.401	27.289	242.113	269.402
Dec-95	0.006	0.001	0.063	0.020	5360	5512	8.196	111.646	119.842	33.795	337.685	371.480
Feb-96	0.008	0.002	0.088	0.025	7741	6551	12.066	165.472	177.538	63.066	683.236	746.302
Apr-96	0.008	0.000	0.083	-0.006	3320	5531	-1.504	-30.462	-31.966	26.145	274.743	300.888
Jun-96	0.011	0.003	0.109	0.027	2404	2862	9.185	75.999	85.184	26.647	262.778	289.424
TOTALS							35.822	418.254	454.076	194.221	1924.367	2118.589
											P/B=	1.286
COHORT 1+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Aug-95	0.011	0.001	0.124	0.005	672	768	0.768	3.840	4.608	7.392	83.328	90.720
Oct-95	0.014	0.003	0.193	0.069	573	623	2.118	43.140	45.258	8.252	110.762	119.014
Dec-95	0.015	0.001	0.212	0.019	792	683	0.693	12.870	13.563	12.211	168.030	180.241
Feb-96	0.019	0.003	0.284	0.072	360	576	1.970	41.546	43.516	6.782	102.344	109.125
Apr-96	0.016	-0.003	0.228	-0.056	1024	692	-1.864	-39.032	-40.897	16.531	233.352	249.884
Jun-96	0.022	0.006	0.305	0.077	120	572	3.354	43.846	47.200	2.641	36.544	39.185
TOTALS							3.685	62.364	66.049	59.809	800.632	860.440
											P/B=	0.461
COHORT 2+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Aug-95	0.018	0.000	0.272	-0.003	485	603	0.000	-1.808	-1.808	8.730	131.920	140.650
Oct-95	0.020	0.002	0.313	0.041	504	495	1.035	20.242	21.277	10.127	157.719	167.846
Dec-95	0.022	0.002	0.365	0.052	219	362	0.857	18.959	19.816	4.919	80.018	84.938
Feb-96	-	-	-	-	0	-	-	-	-	-	-	-
Apr-96	-	-	-	-		-	-	-	-	-	-	-
TOTALS							0.327	9.202	9.530	36.736	567.657	604.393
											P/B=	0.063
TOTALS OF ALL COHORTS							39.835	489.820	529.655	291.270	3293.159	3583.999

Table13. Density, production and biomass at Nanga, October 1994 to June 1996.

NANGA COHORT 0+	Mean flesh weight (g)	Change in mean flesh weight (g)	Mean shell weight (g)	Change in mean shell weight (g)	Mean No/m^2	Mean No between samples	Flesh production (g/m^2)	Shell production (g/m^2)	Total production (g/m^2)	Total flesh biomass (g/m^2)	Total shell biomass (g/m^2)	Total biomass (g/m^2)
Oct. 94	0.001		0.005		1792					1.868	8.150	10.020
Dec. 94	0.004	0.003	0.032	0.028	2640	2216	6.734	61.327	68.061	10.774	85.074	95.848
Feb. 95	0.006	0.002	0.055	0.023	1128	1884	3.516	43.052	46.568	6.708	62.126	68.835
April 95	0.008	0.002	0.083	0.028	968	1048	2.006	28.913	30.919	7.610	80.020	87.629
June 95	0.009	0.002	0.107	0.024	856	912	1.429	22.047	23.477	8.071	91.455	99.526
August 95	0.011	0.002	0.140	0.033	304	580	1.159	19.422	20.581	3.474	42.659	46.133
October 95	0.010	-0.001	0.120	-0.020	89	197	-0.231	-3.985	-4.216	0.912	10.684	11.597
SUB-TOTALS							14.613	170.777	185.390	37.549	372.018	409.567
COHORT 1+											P/B=	2.7
Dec 95	0.012	0.001	0.143	0.023	397	243	0.327	5.470	5.797	4.603	56.570	61.173
Feb 96	0.014	0.002	0.187	0.044	106	252	0.610	11.062	11.672	1.492	19.847	21.339
April 96	0.016	0.002	0.224	0.037	56	81	0.155	18.179	18.334	1.294	18.179	19.473
June 96	0.017	0.001	0.237	0.014	204	130	0.091	30.866	30.957	2.162	30.866	33.028
TOTALS							1.183	65.577	66.760	9.551	125.462	135.014

Appendix Table 1. 95% confidence limits for regressions of shell inflation (x) on shell height (y). (See Figures 1-4)

Hamelin lower limit y = 1.0628x + 0.8139, upper limit y = 1.2227x + 1.6466
Carbla lower limit y=1.0978x+0.7764, upper limit y = 1.2735x + 1.6678
Lharidon lower limit y=1.4265x+0.2780, upper limit y = 1.5280x + 0.8843
Nanga lower limit y = 1.3448x + 0.4105, upper limit y = 1.5480x + 1.2246
Dampier lower limit y = 1.4024x + 0.2169, upper limit y = 1.5418x + 1.2176

Appendix Table 2. 95% confidence limits for regressions of shell inflation (x) on shell weight (y). (See Figure)

Flagpole Landing lower limit logy=2.5656782*logx-2.89099, upper limit logy=2.6772632*logx-2.81376

Lharidon Bight lower limit logy=2.769194*logx-2.97109, upper limit logy=2.850738*logx-2.90873