ASPECTS OF THE BIOLOGY OF THE INTERTIDAL BARNACLE *TETRACLITA SERRATA* DARWIN IN SOUTHERN AFRICA

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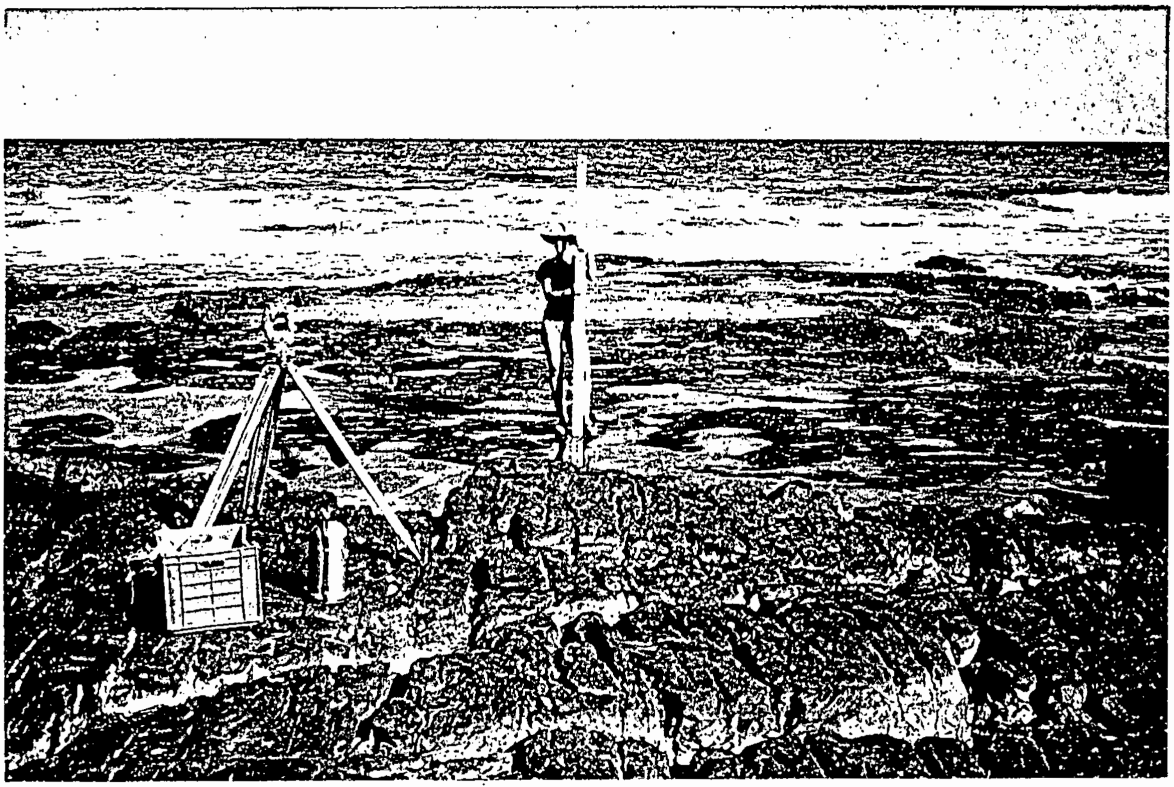
Thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in the Faculty of Science at the University of Cape Town.

August 1987

to Natalia
for unknowingly providing the final boost



FRONTISPIECE: view of the main study site at Dalebrook (False Bay)

ACKNOWLEDGEMENTS

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CONTENTS

GENERAL INTRODUCTION

An important area of research in biology deals with the integration of an organism with its environment. For a long time, interest was focused on the reactions of organisms to their physical milieu (Thiery, 1982). Subsequently, attention shifted to biological interactions such as competition and predation. More recently, biologists have come full circle in that physical aspects are, once again, being more fully investigated (e.g. Kazmierczak et al., 1985; Underwood, 1985).

Shorelines provide an environment perhaps most ideally suited to such investigations. The transition zone between sea and land represents a unique mosaic of physical conditions whose diversity has yet to be fully explored by biologists. This is exemplified by classical models of species distributions involving 'wave action' (see Newell, 1979), a factor which is rarely precisely quantified in biological practice although its individual, hydrodynamic components have long been known to physical oceanographers. The present study of the biology of a rocky intertidal organism, the barnacle Tetraclita serrata Darwin, was carried out in southern Africa between 1976 and 1984 with the specific aim of revealing the most important relationships between this organism and its physical milieu.

The region is ideally suited for this purpose because a number of distinctly different climatic regimes occur along the South African coast. Thus, the cold-temperate western region is influenced predominantly by the cold Benguela Current (Fig. 1), whereas the warm Agulhas Current contributes to the warm-temperate conditions on the south coast, merging into the subtropical environment of the east coast. In addition, an often rugged shoreline provides a multitude of microhabitats in which local physical conditions vary dramatically over very small distances.

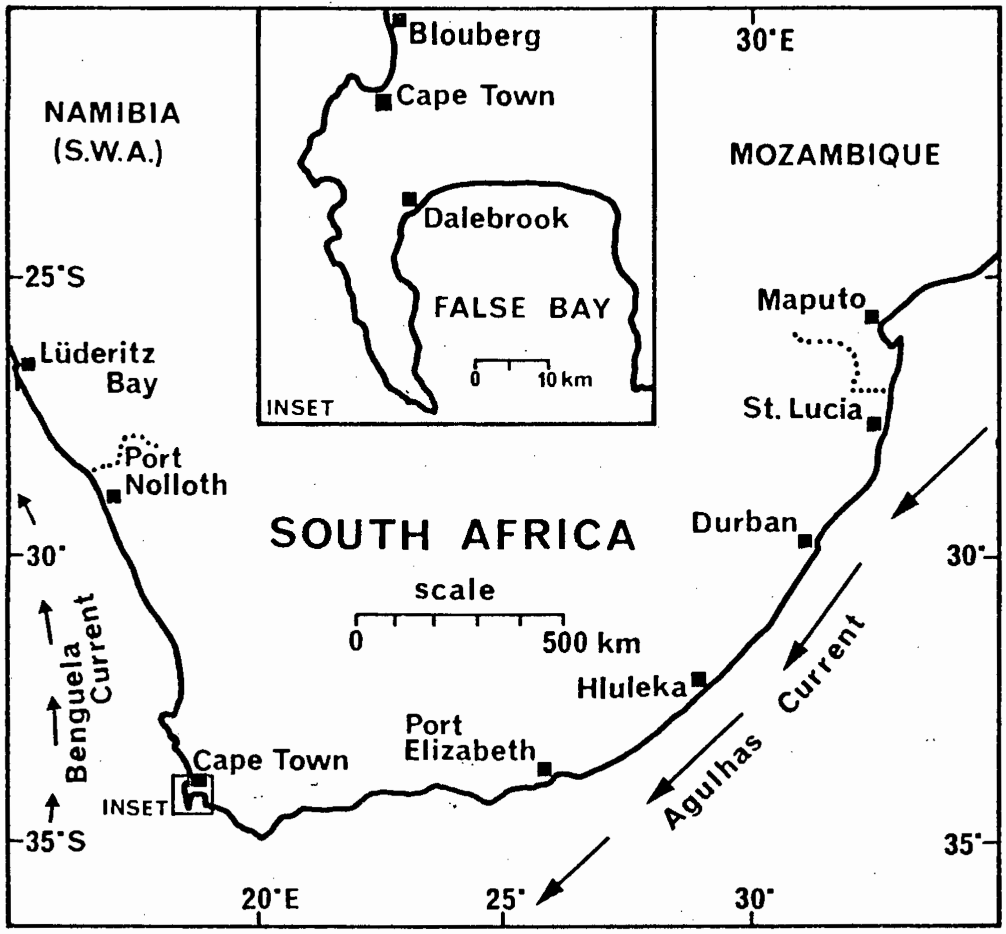

Figure 1. Locality map.

The geographic distribution of the acorn barnacle *T. serrata* encompasses all the regions and settings described above, extending from Port Nolloth in the west to St. Lucia in the north-east (Day, 1974). The study was carried out at five localities, each of which has a different climatic regime. Bloubergstrand in the Cape Peninsula (Fig. 1, inset) is predominantly influenced by the cold Benguela Current, Umhlanga (near Durban) lies in a subtropical environment, whilst conditions at Dalebrook in False Bay and at Port Elizabeth are intermediate between those of Durban and Bloubergstrand. The fifth locality was at Hluleka, a warm-temperate site on the extremely rugged Transkeian coast.

A common member of rocky intertidal communities in South Africa, *T. serrata* is also one of the largest barnacles in the region. It has recently been suggested that, within groups of taxonomically related species, population energy flow per species may be higher in large organisms (refer to Harvey and Lawton, 1986). It is possible, therefore, that *T. serrata* plays a significant role in energy flow through the whole community. As such, the species is worthy of attention within the broad framework of the Benguela Ecology Programme which has been initiated by the South African National Council for Oceanographic Research. Indeed, one aim of this programme is to investigate material transfer through intertidal communities bordering the Benguela Current - one of the major upwelling regions worldwide (Nelson and Hutchings, 1983).

Apart from preliminary investigations of reproduction, production and community structure (Griffiths, 1979; Gibbons and Griffiths, 1986; Bosman et al., 1987), very little is known about the biology of *T. serrata*. The present study commences with a detailed description of population distribution along local tidal gradients in two different regional settings at Dalebrook (False Bay, South Africa; Section 1A) and Hluleka (Transkei; Section 1B) providing contrasting physical conditions. In addition, this work was extended at Hluleka to include two other barnacles co-occurring with *T. serrata*, namely

Chthamalus dentatus Krauss and Octomeris angulosa Sowerby (Section 1B).

The next section (Section 2) deals with patterns of shell accretion and allometry in a local population at Dalebrook (Section 2A). Additional data are provided in an appendix (Section 2B).

The study proceeds with a detailed investigation of reproduction (Section 3). Monthly breeding activity was examined in various regional settings (Section 3A). In addition, size-related reproductive 'effort' (Section 3A) and gonadal histochemistry (Sections 3B and 3C) were studied along local tidal gradients at Dalebrook.

The final section (Section 4) concerns production of T. serrata at Dalebrook. It describes how energy is utilized throughout ontogeny in various facets of production and in the replenishment of somatic reserves.

The study ends with a summarizing discussion which integrates the major findings within the broader framework of the biology and evolution of sessile barnacles.

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Section 1 DISTRIBUTION

SECTION 1A

Effects of topography, wave action and other physical factors on the establishment of *Tetraclita serrata* Darwin (Cirripedia: Thoracica)

Abstract

The occurrence of the post-metamorphosed lifestage of the barnacle Tetraclita serrata Darwin was recorded along an aquatic/aerial gradient in the vicinity of False Bay (South Africa). The juveniles do not settle subtidally, which means that selective settlement accounts for the adults' restriction to the intertidal environment. A literature survey shows that the significance of this aspect of larval behaviour has until recently not been recognized and that little is known of the mechanisms which ultimately control habitat occupation by sessile barnacles, i.e. those factors which control larval behaviour in the water-column.

Within the rocky intertidal environment itself, wave action in conjunction with topography modifies the theoretical submergence regime associated with the still water level and thereby significantly influences population distribution. Only when topographically-induced variability in abundance is averaged at small height increments, irrespective of position on the shore and over a relatively large area (in this instance, total number barnacles counted - 63,000), does it become evident that T. serrata tends to be symmetrically distributed along the submergence gradient. Topography (together with wave action) thus appears to be the most important controlling factor at Dalebrook. Two limiting factors, which act at respectively the lower and upper boundaries of species occurrence, are excessive wave impact during submergence and exposure to air and sunlight during emergence. It is concluded that only by identifying and quantifying the integrated effects of all major controlling factors can a given distribution pattern be correctly interpreted.

Introduction

It has long been recognized that the subtidal and intertidal environments form distinct ecotypes within the marine habitat. Species which are found in one environment are not commonly found in the other. The mechanisms which control the spatial segregation of species along this aquatic/aerial gradient have been the subject of research for over a hundred years.

One aspect which has received considerable attention is habitat occupation by invertebrates which have sessile adults and planktonic larvae. Grosberg (1982) and Wethey (1983) have recently retraced some major concepts developed in the case of barnacles. Two steps along the chain of events which result in the establishment of the adult population have been investigated to date: first, the behaviour of the juvenile during settlement and second, survival after metamorphosis. Surprisingly, the fundamental question of whether the mobile juvenile 'distinguishes' between the subtidal and intertidal environments has only recently been posed. Grosberg (1982) has shown that differential stratification of the larvae in the water-column can predetermine the environment in which they will eventually settle. Thus, the restriction of the adult to the intertidal environment, for example, may be primarily a consequence of pre-settlement events.

This paper discusses the spatial distribution of the intertidal barnacle <u>Tetraclita serrata</u> Darwin along an aquatic/aerial gradient in the vicinity of False Bay, South Africa. The objectives of the study are two-fold: first, to verify whether, as predicted by the findings of Grosberg (1982), juveniles settle only in the intertidal environment and second, to investigate which physical factors, if any, affect the distribution of the adult population within this environment. For convenience, 'juveniles' are defined here as individuals that have only recently settled, i.e. that are younger than 3 months; 'adults' are any individuals above this age.

To achieve these objectives, the habitats occupied initially by the newly settled juveniles and populated subsequently by the adults were investigated. In particular, adults were sampled to determine whether their distribution along the tidal gradient was affected by, among other things, topographic variability, degree of exposure to wave action, etc. Furthermore, the literature dealing with habitat occupation by barnacles is evaluated in order to see whether the fundamental mechanisms which confine a species to either the subtidal or intertidal environments have yet been established.

Study area

The work was carried out in the vicinity of False Bay (South Africa; 34°07'S; 18°30'E; Fig. 1). The main study area at Dalebrook comprised an elevated sandstone platform which measures about 13 m x 25 m and which is situated just above mean sea level. At its seaward limit, it drops vertically by at least 50 cm to a lower terrace, whereas its landward boundary is defined by a vertical step of at least 50 cm to an upper terrace.

Materials and Methods

The topography of the platform was determined by surveying the elevations of 240 randomly spaced points with a tacheometer, resulting in an average of one measurement per 1.4 m^2. This random point grid was then contoured at 5 cm intervals to produce a simplified topographic map. Elevations were expressed as heights above chart datum in order to relate their positions directly to predicted tidal curves.

The occurrence of post-metamorphosed individuals on the horizontal surface of the platform was quantified during the annual period of recruitment in 1980 (March-April; Delafontaine, unpubl. data). Barnacles lying in gullies or on vertical surfaces were excluded from these counts. To facilitate data handling,

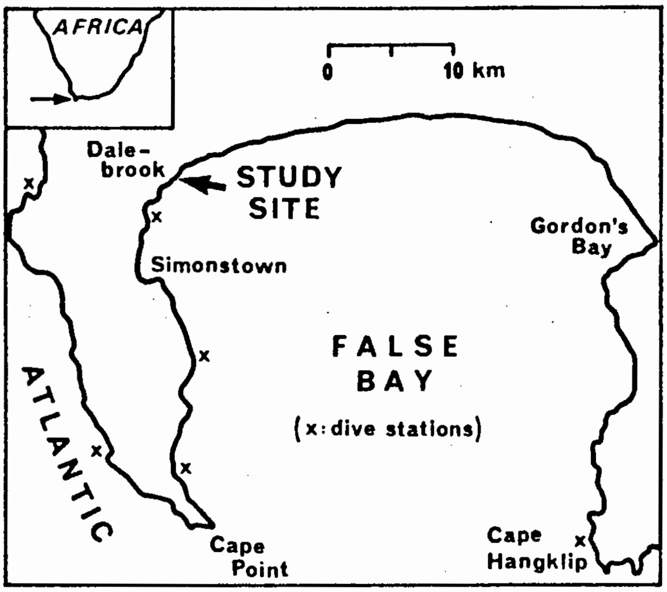

Figure 1. Locality map

the area was divided into a regular grid of rectangles defined by 20 longitudinal and 48 transverse lines. Each rectangle, measuring 50 cm x 60 cm, was photographed and the number of barnacles counted from the projected slide. Since this method was found to be unsuitable for newly settled juveniles, their abundance was determined by _in situ_ counts within random quadrats each measuring 50 cm x 50 cm. Finally, to establish whether post-metamorphosed juveniles occurred subtidally, SCUBA surveys were carried out in False Bay and adjacent areas (Fig. 1).

Results

Topographic survey

Three major types of topographic features interrupt the otherwise even gradient of the platform (Fig. 2). First, there is a shallow depression towards the centre of the platform. Second, the seaward section is dissected by a long, narrow gully which, for the greater part, runs normal to the shoreline. Finally, the edges of the platform are broken by numerous, partly eroded joints.

The theoretical submergence regime associated with the still water level of predicted tidal curves indicates that most of the platform should be inundated at high tide throughout the year (Fig. 3A-C), except at the time of the autumnal neap equinox (Fig. 3D). In effect, the seasonal variation in predicted tidal amplitude has a marked influence on the theoretical submergence/emergence regime at the landward limit of the platform, but not at the seaward limit which lies almost at mean sea level (Fig. 3E, F). Thus, at least the upper third should theoretically remain emerged at the time of lowest neap tides around the autumnal equinox (Fig. 3D). It is evident, of course, that the relationship between the predicted height of the still water level and the actual submergence regime is also a function of, amongst other factors, the local wave climate (e.g. Glynn,

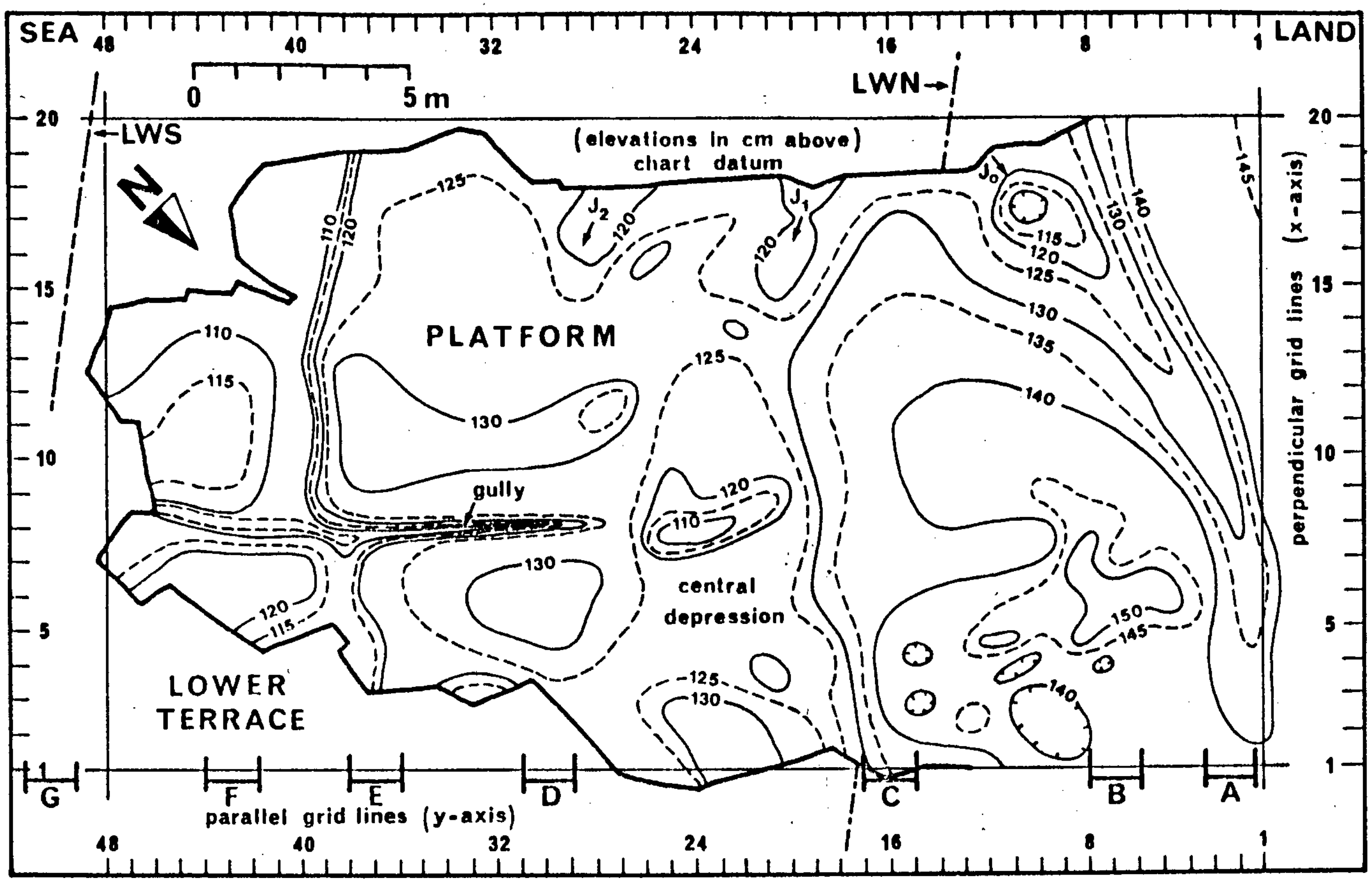

Figure 2. Elevation map of the rock platform at Dalebrook showing major topographical features (J_0-J_2: partly eroded joints; A-G: transverse corridors along which juveniles were recorded *in situ*; a grid system, indicated by numbered lines along X and Y axes, was used for orientation, sampling and data handling; LWN: low water neaps; LWS: low water springs; elevations in cm above chart datum).

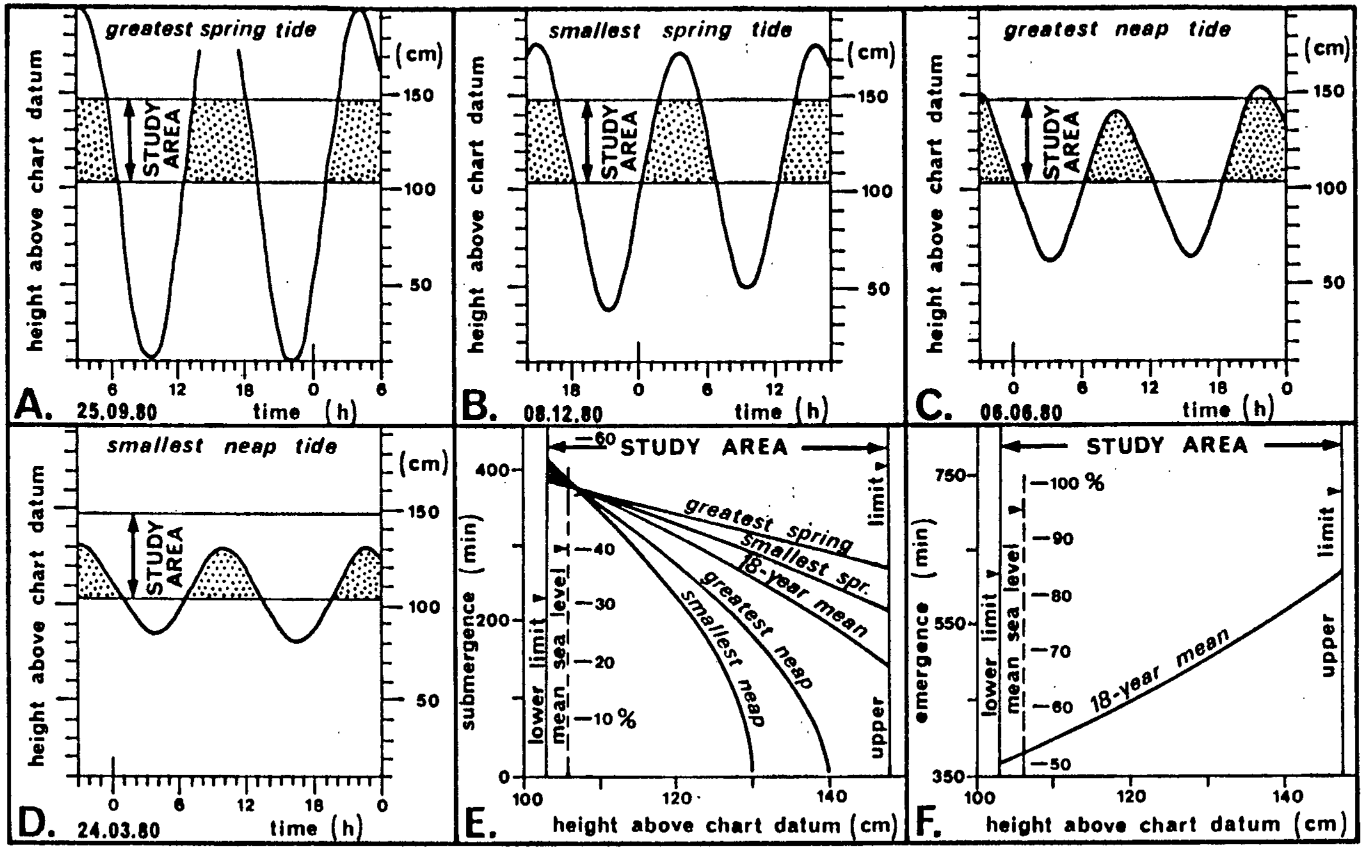

Figure 3. Relationship between platform elevation and the predicted tidal ranges at greatest and smallest neap and spring tides (A-D). Diagrams E and F indicate the relationship between time periods and percentages of submergence and emergence as a function of elevation for different tidal situations (elevations in cm above chart datum; shaded area: zone of occurrence of <u>T. serrata</u> on the horizontal surface of the platform).

1965). Thus, although the landward section of the platform lies well above the highest predicted still water level of the lowest neap tides, it was nevertheless always inundated by waves at high tide, irrespective of the tidal range. Besides this influence of wave action, it was observed that the actual submergence regime was also highly dependent on local topography. The central depression, for example, was always submerged at the same time as the relatively low-lying edges of the platform. Since the submergence regime integrates the effects of the various factors which control the distribution of intertidal organisms, one should expect that wave action in conjunction with topography should have a measurable effect on such distributions. It will be shown below that this is indeed the case.

Spatial distribution

With the exception of unpopulated fringes along the upper and lower margins of the platform, T. serrata occupied most of the horizontal rock surface. Beyond this zone, it also occurred locally along the vertical walls of both the upper and lower terraces. Quadrat counts showed that newly settled juveniles occurred only in areas also occupied by adults. Underwater observations confirmed that adults did not occur subtidally, and newly settled juveniles were never recorded there either.

The suspected influence of wave action and topography on animal distribution and density was investigated in three ways. First, by graphically superimposing the area of the platform occupied by the population over the predicted submergence regime (Fig. 3), it could be shown that the upper distribution limit of T. serrata extended beyond the still water level of high water neap tides (Fig. 3C, D). At this height, the period of continuous exposure can theoretically amount to 5 days (Fig. 4) and, unless the organism can survive such prolonged periods of emersion, it would seem that the upper limit of observed distribution is situated higher up the shore than would be possible without inundation by waves. Nevertheless, in spite of regular inundation of the landward boundary of the platform, the

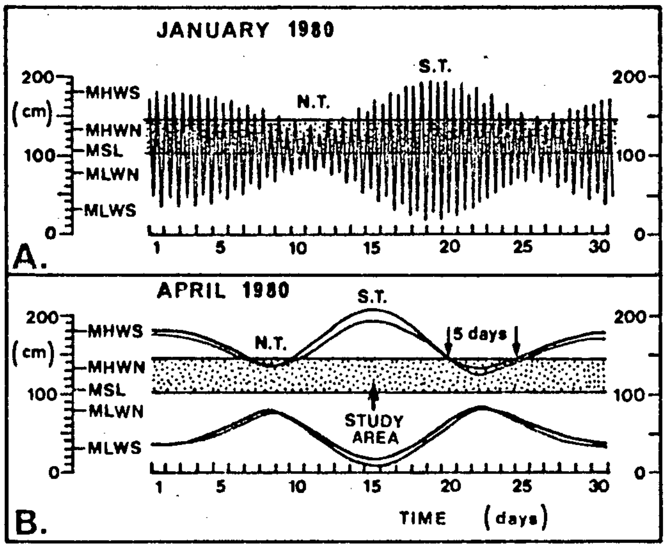

Figure 4. Relationship between platform elevation and the predicted range of consecutive tidal cycles at different times of the year (MHWN: mean high water neaps: MHWS: mean high water springs; MLWN: mean low water neaps; MLWS: mean low water springs; MSL: mean sea level; elevations in cm above chart datum; shaded area: see Fig. 3).

occurrence of T. serrata ceased some distance before the end of the platform, although it could again by found higher up the shore where the vertical wall of the upper terrace was less exposed to direct sunlight (cf. Todd, 1979; Wethey, 1983).

Second, it was investigated whether local differences in wave action correlated with variations in population densities. Even though wave action was assessed only qualitatively, it was noted that T. serrata was absent in places directly facing the full force of the breaking waves, whereas it occupied comparable shore levels in more sheltered positions. This effect was most striking near the lower observed distribution limit, i.e. on the vertical wall of the lower terrace.

Finally, the effect of topographic irregularities was investigated by contouring the density of barnacles per unit area (50 cm x 60 cm). Densities were generally lower than 200 individuals per unit area and higher densities were restricted to localized patches (Fig. 5). By comparing local density patterns with their corresponding topographic setting, it becomes clear that the distribution responds sensitively to local variations in topography (Fig. 6). Some sections of the central depression, for example, yielded low counts with resulting bimodal cross-sectional distributions (Fig. 6A-C), whereas other sections yielded high counts with resulting unimodal distributions (Fig. 6D and see Fig. 5). High densities in the central depression occurred only towards the edges of the platform, not in the centre (Figs. 5 and 6D-E). High densities were also recorded in the vicinity of two eroded joints on the seaward and landward sides of the depression. The cross-sectional distribution curve remains essentially bimodal here, with minor modes being associated with other prominent joints (Fig. 6A) or with the gully (Fig. 6B).

On the basis of these observations, it is concluded that wave action in conjunction with topography modifies the local submergence regime, and thereby influences the distribution of

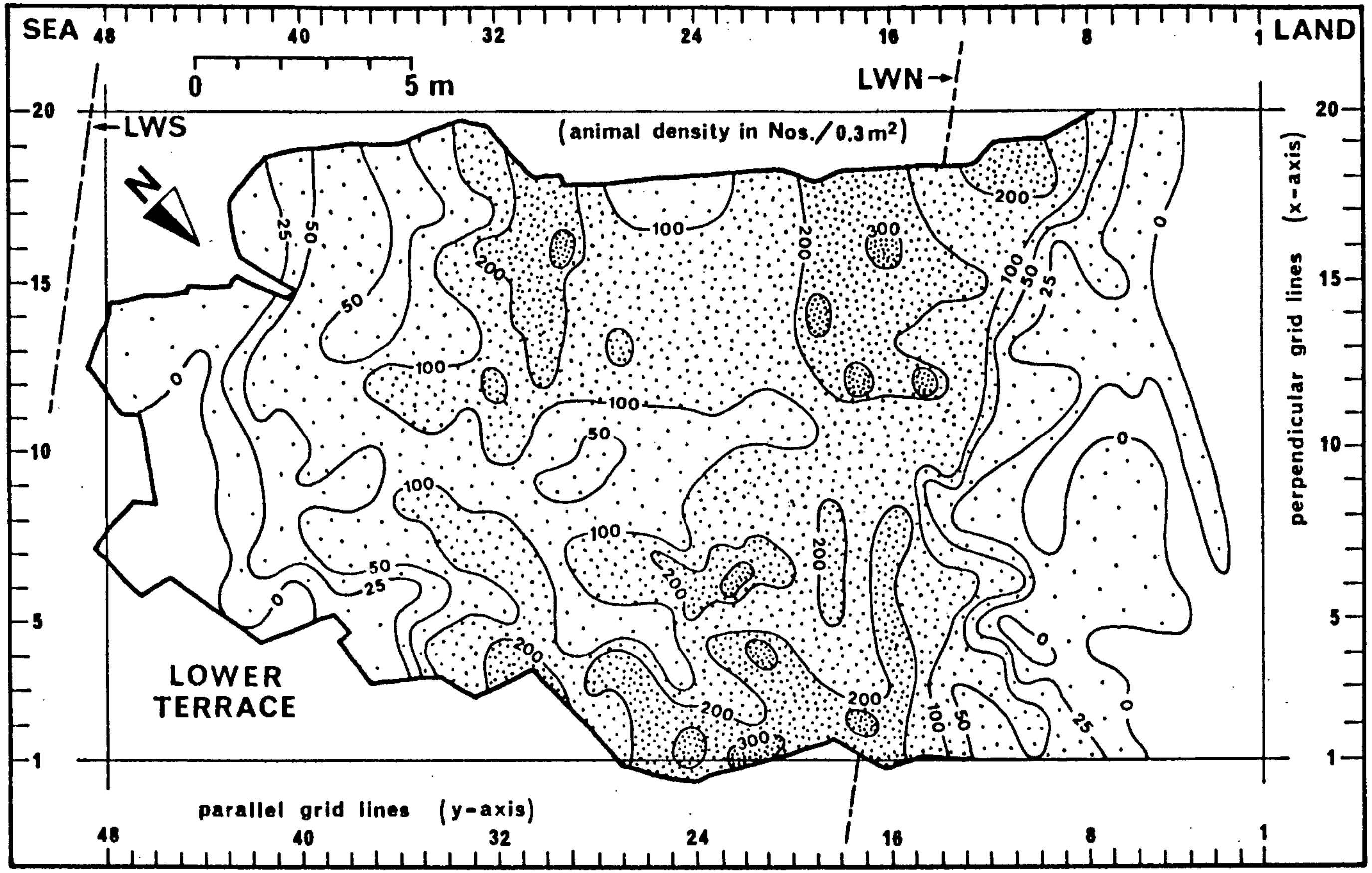

Figure 5. Contour map of density per unit area (50 cm x 60 cm) for *T. serrata*.

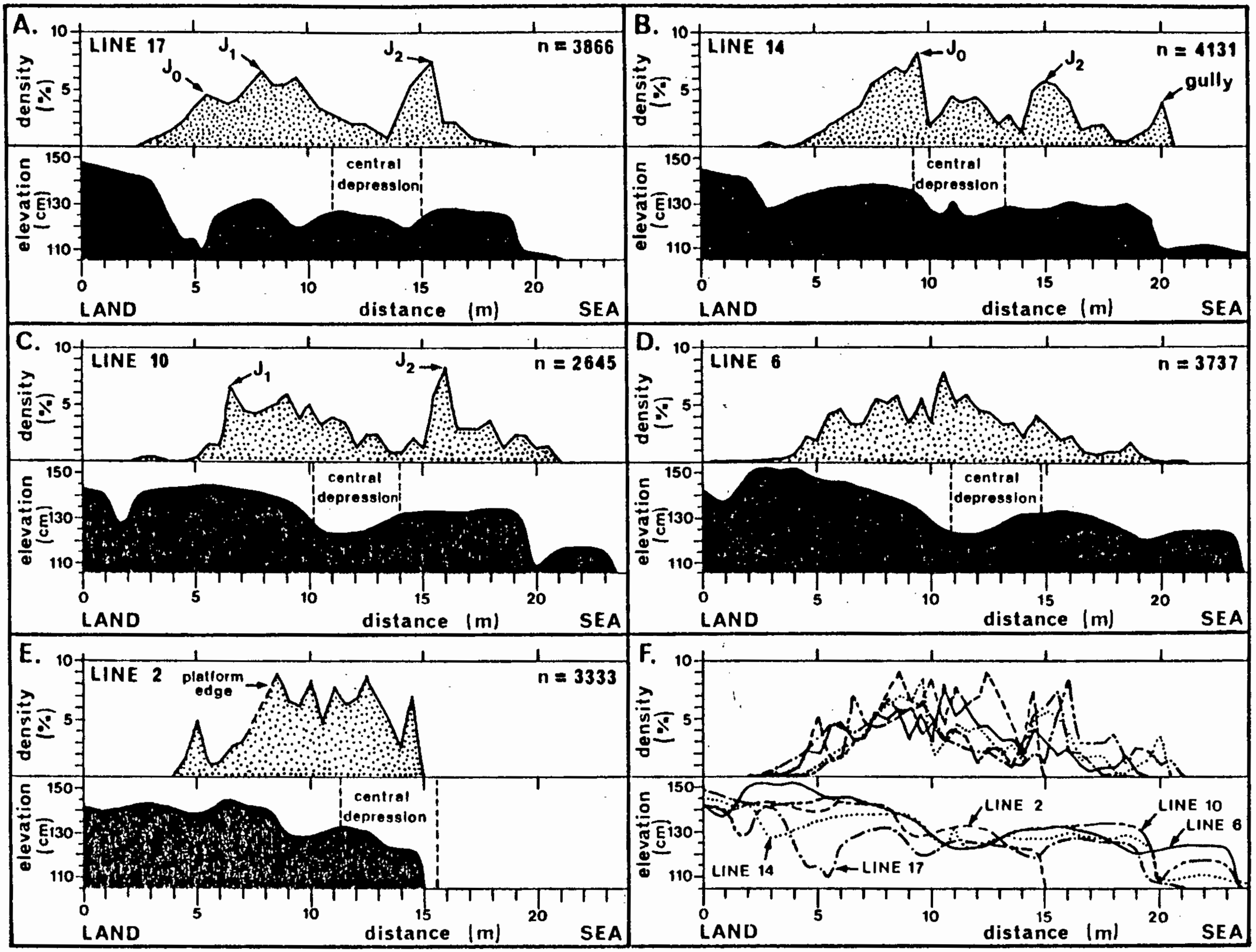

Figure 6. Mean density (percentages of total) as a function of topography along five profiles lying perpendicular to the shore (A-E). A summarizing diagram is shown in F (for the positions of the profiles on the platform, see corresponding perpendicular lines of the grid system in Fig. 2; effects associated with specific topographic features as in Fig. 2).

T. serrata at Dalebrook. This effect is also revealed when plotting average abundances against incrementally measured elevations, irrespective of position on the shore. This facilitates a better comparison between different geographic areas, particularly if mean slope gradients and topographic patterns vary. In effect, Fig. 7 highlights the striking difference in distribution patterns obtained when comparing the above procedure (I) with the more common approach in which density is plotted against elevation at a small number of arbitrarily chosen sampling points (procedure II). As can be seen, the latter procedure totally obscures any potential topographic effects on the distribution.

Notwithstanding these considerations, it is clear that the continuity of the submergence gradient should tend to be restored if topographically-induced variability is averaged over a sufficiently large area. In fact, when pooling the entire data set (Fig. 8A), the distribution curve approaches a symmetrical shape. Successively smaller data sets (Fig. 8B-H), on the other hand, increasingly emphasize local topographic influences on distribution patterns.

Discussion

Larval settlement

In order to investigate whether the mobile larvae of certain species have evolved mechanisms which enable them to return to the habitat of the immobile adults, one should attempt to falsify the hypothesis that they settle only in this environment. Because the juveniles are so small, it may be questionable to equate failure to detect them in situ with an absence of settlement. A possible solution to this problem is to interpret the absence of juveniles in terms of those factors which could affect post-settlement survival. It is difficult to see how conditions in the shallow subtidal environment could cause the elimination of all newly settled juveniles before the young

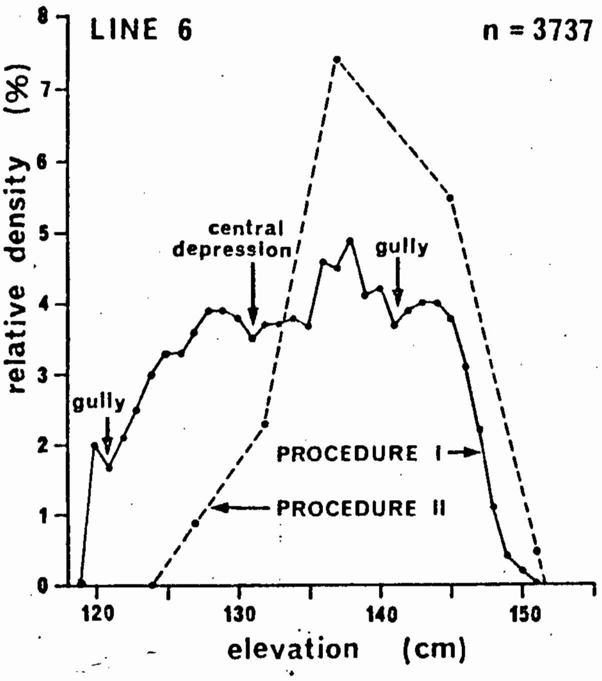

Figure 7. A comparison of distribution curves (animal density vs elevation) obtained when using the two different sampling procedures outlined in the text (see also Fig. 6; elevations in cm above chart datum; line 6 lies perpendicular to the shore; refer to Fig. 2 for the position of line 6 on the platform).

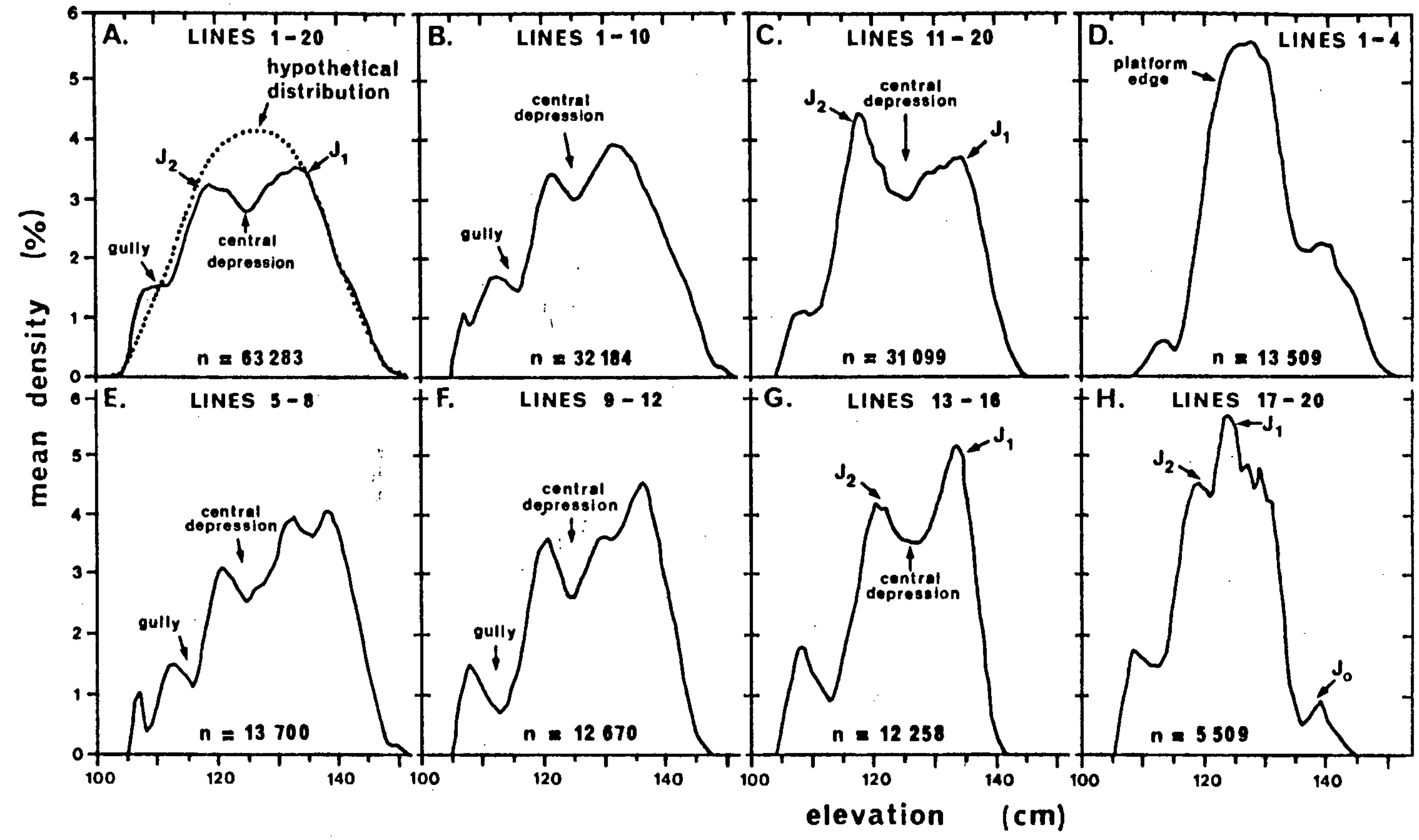

Figure 8. Mean density (percentages of total) as a function of elevation for successively smaller data sets consisting of profiles lying perpendicular to the shore. A: whole platform (lines 1-20); B: one half of platform (lines 1-10); C: other half of platform (lines 11-20); D-H: each corresponds to a group of 4 adjacent profiles (lines 1-4, 5-8, 9-12, 13-16, 17-20) (the positions of the profiles on the platform are indicated by corresponding perpendicular lines of the grid system in Fig. 2; topographic effects indicated by arrows as in Fig. 2; elevations in cm above chart datum; raw data have been smoothed by running means).

become detectable. Their absence from this environment is much more likely due to a lack of settlement (see Brande, 1982). Since juvenile T. serrata have been observed neither on natural (this study) nor artificial substrata (de Chalain, 1979; Henschel, 1981; Fricke et al. 1982) in shallow subtidal areas adjacent to intertidal populations, it is concluded that the planktonic larvae settle only in the intertidal environment occupied by the adult. On the basis of these observations, one might suspect that there is a direct causal relationship between the behaviour of the larvae in the water column and their selective settlement. As shown by Grosberg (1982), this may entail the concentration of the larvae in the upper water layer. In addition, the larvae may inherently be able to 'recognize' the intertidal environment, as suggested by the fact that they do not even settle on floating substrata (de Chalain, 1979). Although the presence of conspecific adults is known to facilitate aggregation in various invertebrates including barnacles (Larman and Gabbott, 1975; Burton and Feldman, 1981), it cannot constitute a prerequisite for habitat occupation since denuded coasts are invariably recolonized (Southward, 1979).

It seems surprising that previous studies have generally failed to recognize the relevance of selective settlement in defining potential adult habitats. Clearly, any factors which may subsequently control adult distribution can have no influence on this process. Only when Grosberg (1982) reported differential larval stratification in the water-column, did the concept of selective settlement receive due attention. Some earlier publications allude to similar processes without, however, providing any direct evidence. For example, Semibalanus balanoides, one of the most widely studied barnacles, is classified as a typical intertidal species, although subtidal populations are known to exist (Lucas, pers. comm.).

If, on the other hand, settlement were not selective and the larvae were to settle in both the intertidal and subtidal environments, they could either survive in both or be eliminated from one. In the latter case, the same factors which eliminate settled juveniles from one environment also explain why the adults occur exclusively in the other. Clearly, any other factors which may then further influence distribution cannot explain why the adult is found in one environment only. As shown in Table 1, research on habitat occupation in barnacles has been biased towards intertidal species. The main findings of this literature survey are: 1) the precise site of larval settlement is generally unknown or unaccounted for (cf. columns 1 and 2; points 18, 28, 29 and 30 show that the larvae of some intertidal populations avoid settling in the subtidal environment, and _vice versa_); 2) research has focused on events which control habitat occupation only within the adult environment (cf. columns 3 and 4). Most of the available information on intertidal species cannot therefore solve the problem of why the adult should be restricted to this environment in the first place.

Spatial distribution

In the course of this study it was demonstrated that environmental factors such as wave action, coupled with topographic variability, obscure the relationship between predicted and actual submergence regimes. It was further shown that _T. serrata_ has a tendency to be symmetrically distributed along the submergence gradient at Dalebrook. Significantly, this was revealed only when abundance per unit area was averaged for small height increments (2 cm), irrespective of position on the shore and over a relatively large area (325 m^2).

The need to account for environmental heterogeneity by choosing an appropriate sampling strategy has often been emphasized in ecological work (Collier et al., 1973; Kimura and Lemberg, 1981), but does not always seem to have been satisfied in intertidal research (see Section 1B). For example, abundance is generally related to mean slope gradients (e.g. Littler et al., 1983; Wethey, 1983), a procedure which, as explained above, preempts the recognition of topographical effects and thereby impairs the resolution and interpretation of distribution patterns. The same applies to another common practice, namely

Table 1. Literature survey dealing with habitat occupation by barnacles. Abbreviations and symbols: A: avoidance of settlement in either subtidal or intertidal environment; C: interspecific competition; D: differential settlement within an environment due to avoidance of competitor or predator; I: intertidal environment; P: predation; S: subtidal environment; *: excluding abiotic factors which influence occupation at the landward limit of intertidal populations; +: yes; -: no; blank: no information provided; ?: present author's query.

SPECIES	STUDY SITE	(1) ADULT OCCURRENCE		(2) LARVAL SETTLEMENT		CONTROL OF HABITAT OCCUPATION			REFERENCE
		I	S	I	S	(3) I		(4) S	
						BIOTIC	ABIOTIC*		
1. Pollicipes polymerus	California	+		+					Barnes and Reese (1960)
	Washington	+		+		C			Paine and Levin (1981)
2. Chthamalus aestuarii	Lagos	+		+		C			Sandison and Hill (1966)
3. Chthamalus dalli	California	+		+					Glynn (1965)
		+		+		C			Loi (1981)
		+		+			+		Littler et al. (1983)
	Alaska	+		+		-			Southward and Southward (1967)
	Washington	+		+		C			Dayton (1971)
4. Chthamalus fissus	Scotland	+	-	+	-?	C		A inferred?	Barnes (1956)
	California	+		+		C			Stimson (1970)
		+		+		C;P			Hines (1979)
		+		+		C			Loi (1981)
		+		+			+		Littler et al. (1983)
5. Chthamalus fragilis	Connecticut	+		+		C			Wethey (1983)
6. Chthamalus microtretus	California	+		+					Glynn (1965)
7. Chthamalus montagui	Ireland	+		+			+		Crisp et al. (1981)
8. Chthamalus panamensis	Panama	+		+					Reimer (1976)

Table 1 (cont.)

SPECIES	STUDY SITE	(1) ADULT OCCURRENCE		(2) LARVAL SETTLEMENT		CONTROL OF HABITAT OCCUPATION			REFERENCE
		I	S	I	S	(3) I		(4) S	
						BIOTIC	ABIOTIC*		
9. Chthamalus stallatus	England	+		+		P?			Morton (1954)
	Scotland	+		+		C			Connell (1961a)
	Britain	+		+		C			Barnes and Barnes (1966)
	Spain	+		+		C			"
	Florida	+		+		[illegible]	+		Bierbaum and Zischke (1979)
	Ireland	+					+		Crisp et al. (1981)
10. Euraphia depressa (Chthamalus depressus)	Mediterranean Sea	+		+		C			Klepal and Barnes (1975); Achituv and Safriel (1980)
	Suez Canal	+		+		C			"
11. Tetrachthamalus oblitteratus	Red Sea	+		+		C			Achituv (1972)
12. Chamaesipho brunnea	New Zealand	+		+		C;P?			Luckens (1970; (1975a)
13. Chamaesipho columna	New Zealand	+		+		C			Luckens (1975a,b)
14. Mitella polymerus	California	+		+					Glynn (1965)
15. Tetraclitella purpurascens	New South Wales	+		+		D			Denley and Underwood (1979)
16. Tesseropora rosea	New South Wales	+		+		D;C			"
17. Tetraclita rubescens	California	+		+					Glynn (1965)
		+		+			+		Littler et al. (1983)

Table 1 (cont.)

SPECIES	STUDY SITE	(1) ADULT OCCURRENCE		(2) LARVAL SETTLEMENT		CONTROL OF HABITAT OCCUPATION			REFERENCE
		I	S	I	S	(3) I		(4) S	
						BIOTIC	ABIOTIC*		
18. Tetraclita serrata	South Africa	+	-	+	-	-	+	A observed	This study
19. Tetraclita squamosa	Florida	+		+		-	+		Bierbaum and Zischke (1979)
20. Tetraclita squamosa rubescens	California	+		+		-?			Hines (1979)
		+		+					Loi (1981)
		+		+		C?			Taylor and Littler (1982)
21. Tetraclita stalactifera panamensis	Panama	+		+					Reimer (1976)
22. Epopella plicata	New Zealand	+		+		C;P			Luckens (1975a, b; 1976)
23. Elminius modestus	New Zealand	+	+	+	+	C;P			Luckens (1970; 1975a, b)
24. Balanus spp.	North West Europe	+		+		C;P			Lewis (1977)
25. Balanus amphitrite	Florida	+	+	+	+				Werner (1967)
	Argentina	+		+		C?			Bastida et al. (1971)
	Suez Canal	+		+					Achituv and Safriel (1980)
26. Balanus amphitrite amphitrite	Fiji	+	+	+	+				Foster (1974)
	Arabian Gulf	+		+		C			Mohammad (1975)
27. Balanus cariosus	Washington	+		+		C			Dayton (1971)
		+		+		C?			Paine and Levin (1981)
28. Balanus crenatus	California	-	+	-	+	A observed			Grosberg (1982)

Table 1 (cont.)

SPECIES	STUDY SITE	(1) ADULT OCCURRENCE		(2) LARVAL SETTLEMENT		CONTROL OF HABITAT OCCUPATION			REFERENCE
		I	S	I	S	(3) I		(4) S	
						BIOTIC	ABIOTIC*		
29. Balanus glandula	Washington	+	-	+	-?	P			Connell (1970)
		+		+		P?			Strathmann and Branscomb (1979)
		+		+		C			Dayton (1971); Paine and Levin (1981)
	California	+		+					Glynn (1965)
		+		+		C;P			Hines (1979)
		+		+					Loi (1981
		+	-	+	-			A observed	Grosberg (1982)
30. Balanus pacificus	California	-	+	-	+	A observed		D;P	Hurley (1973, 1975)
31. Balanus pallidus stutsburi	Lagos		+		+			C?	Sandison and Hill (1966)
32. Balanus trigonus	Florida	-	+	-?	+	A infered?		C	Werner (1967)
33. Semibalanus balanoides (Balanus balanoides)	Scotland	+	+	+	+			C?	Meadows (1969)
		+		+		P			Connell (1961b)
	Wales	+		+		P?			Emson (1977)
	New England	+		+		C			Menge (1976): Lubchenco and Menge (1978)
	Canada	+		+		C;P			Bell (1979)
	Connecticut	+		+		C?			Wethey (1983)
	Massachussetts	+		+		C?			Wethey (1983)
	Ireland	+		+			+		Crisp et al. (1981)
	Isle of Man	+		+		C			Hawkins (1983)

that of computing abundance at irregular and relatively large height intervals. For example, Field and Robb (1970) used intervals which varied from 5 cm to 10 cm elevation, as opposed to the constant 2 cm in this study.

By modifying the local submergence regime, wave action coupled with topography also affects animal distribution at Dalebrook. Other factors reflect conditions which persist during submergence and emergence. Thus, excessive wave impact towards the lower limit, and exposure to air and sunlight towards the upper limit of the population both seem to prevent successful settlement (cf. Connell, 1972; Littler et al., 1983).

The data discussed above do not, of course, reveal how the various controlling factors interact in determining the shape of the distribution curve and its position along the tidal gradient. This can only be achieved by identifying the main factors involved - be they abiotic or biotic - and then quantifying their combined effects. Such combined effects appear of great importance here, and it is felt that this has not been sufficiently appreciated in the past (e.g. Bell, 1979; Creese, 1980; see Bender et al., 1984). At Dalebrook, they must in some manner have been finely balanced to produce the overall symmetrical distribution. It is surmized that topography (in conjunction with wave action) is, in this case, the most important factor which integrates these combined effects.

General conclusion

Three points should be emphasized. First, in order to establish the fundamental mechanisms which control habitat occupation by species whose larvae settle only in the intertidal environment, future research should ultimately focus on factors which control larval behaviour in the water-column (see Keough, 1984). Specific questions include: what are the causes of larval stratification in the water-column (Grosberg, 1982)? Is this only a question of tropism in a physical environment (Young and Chia, 1982; Shanks, 1983), or are the larvae also reacting to potential biotic barriers by, for example, actively avoiding superior competitors (Grosberg, 1981)? A relevant aspect here would seem to be interspecific chemotaxis. Until very recently this has not been investigated during the planktonic lifestage of marine invertebrates (e.g. Cowden et al., 1984), although it has been related to the intertidal zonation of mobile invertebrates (Williams et al., 1983). Whatever mechanisms result in the shoreward transport of the pelagic larvae, how do the larvae then recognize the intertidal environment (see Strathmann and Branscomb, 1979)?

Second, trends in animal distribution along submergence gradients must be determined accurately and correctly before they may be interpreted ecologically. Because conventional monitoring surveys encompass large stretches of coastline and may therefore not account adequately for the effects of local environmental heterogeneity (e.g. Dalby et al., 1978; Jones et al., 1979; cf. Hartnoll and Hawkins, 1980), it would seem preferable to reduce the frequency of sampling sites in favour of fewer but more thorough local studies.

Third, although it has previously been considered that distribution patterns are diagnostic of specific environments (e.g. Lewis and Bowman, 1975; Lewis, Jr., 1977; Tegner and Dayton, 1981), it has generally not been recognized that, in order to relate such patterns to local environmental conditions, the integrated effects of all major potential controlling factors must be taken into account. This would clearly constitute a realistic first approach to the ecological monitoring of key species in intertidal communities (Gray, 1980; Ugland and Gray, 1982; Gray and Christie, 1983). Evidence is presented in Section 1B that the integrated effects of wave impact and the emergence/submergence regime appear to be the prime cause of spatial segregation amongst certain intertidal barnacles, including T. serrata, along the southern African coast.

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SECTION 1B

Physical factors in barnacle community structure: a conceptual model

Abstract

The community structure of temperate intertidal barnacles is commonly attributed to competitive interference between post-metamorphosed animals, with biological/physical disturbance playing an essential role in tipping the competitive balance in favour of competitively inferior species. However, distribution patterns of the barnacles Chthamalus dentatus Krauss, Tetraclita serrata Darwin and Octomeris angulosa Sowerby, observed along the rugged and exposed shoreline of Transkei (Southeast Africa), argue in favour of physical rather than biological control of community structure.

A strong correlation exists between species distribution and two major physical parameters, namely emergence/submergence (E/S) regime and the degree of exposure to wave impact. A two-dimensional conceptual model was derived, in which the habitat of each species is delimited by specific combinations of the two parameters. Thus, C. dentatus occurs under virtually any E/S regime where wave impact is low. O. angulosa in turn occurs where E/S ratios are low, but where wave impact is intermediate to high, whereas T. serrata occupies an intermediate position in terms of both parameters. Although individual habitats overlap over a limited range of physical conditions, there was no evidence that competition controls the distribution or zonation of these species.

The model is consistent with the distribution patterns observed along the entire southeast African coastline and, amongst other things, also explains the occurrence of zonation patterns. Indeed, differential zonation can be predicted on regularly sloping shores and in gullies, where physical gradients are unbroken. In boulder fields, patchy distributions are consistent with physical conditions varying markedly and unpredictably even over very small distances. Circumstantial evidence suggests that the segregative process occurs after the larvae arrive on the shore, but prior to metamorphosis. The model may have implications for other intertidal organisms, including algae.

Introduction

Biologists have long been intrigued by processes which structure living communities (Thiery, 1982). Initially, interest was focused on species-specific requirements for particular physico-chemical conditions. Attention subsequently shifted towards interspecific interactions (predation, competition; e.g. Branch, 1984). Very recently, however, the importance of the physical environment is, once again, drawing more attention (e.g. Littler et al., 1983; Denny et al., 1985; Kazmierczak et al., 1985; Powell and Cummins, 1985; Underwood, 1985; Wethey, 1985; Ruwa and Jaccarini, 1986; Shanks and Wright, 1986; Tamaki, 1987).

The community structure of temperate sessile barnacles is commonly thought to primarily reflect competitive interference between post-metamorphosed animals (Stanley and Newman, 1980; Benton, 1983; Wethey, 1983; Dungan, 1985). Balanoids are considered to exclude chthamaloids from most of the latter's potential habitat. As a result, chthamaloids are said to be restricted to a high-shore refuge from competition where balanoids cannot cope with excessive emergence (competitive exclusion). It is claimed that chthamaloids will reoccupy the remainder of their habitat if balanoid densities are sufficiently diminished by either biological disturbance (such as selective predation) or physical disturbance (a process referred to as 'competitive release' in the present study; Paine, 1981; see also Connell, 1975).

In this paper, evidence is presented which argues against the general applicability of the competitive exclusion/release mechanism to explain barnacle community structure. It was found in a separate study (Section 1A) that both emergence/submergence regimes and wave impact are major factors controlling the distribution of the coronuloid Tetraclita serrata Darwin in False Bay (South Africa). These observations raised the possibility that other barnacles might also respond to the same physical factors. This hypothesis formed the basis for the present study, in which at least three conditions had to be met. Firstly, species distributions had to be examined in as diverse a physical environment as possible. For example, it was found that even minor topographic discontinuities have a marked effect on the distribution of T. serrata (Section 1A). Clearly, if habitat type is found to be species-specific even when topographic diversity is high, then a purely fortuitous relationship between habitat type and species identity could confidently be discarded. Secondly, in order to diminish the effects of, amongst other things, variable larval supplies (Hawkins and Hartnoll, 1982; Caffey, 1985; Gaines et al., 1985; Gaines and Roughgarden, 1985; Geraci and Romairone, 1986; Sutherland and Ortega, 1986), such an investigation had to be carried out in as geographically restricted an area as possible. Thirdly, species distributions had to be related to appropriate measures of the physical environment. Contrary to common practice in rocky shore research, tidal elevation per se and wave 'exposure' were not on their own considered adequate in the present context. One reason for this is that topographic variability has differential effects on the local emergence/submergence regime prevailing at any particular shore level (Section 1A).

In the present study, the distributions of post-metamorphosed T. serrata, Chthamalus dentatus Krauss and Octomeris angulosa Sowerby were investigated in Transkei on the south-east African coast - an area ranked amongst the most exposed in the world (Flemming, 1981). The annual mean percent probability of swells exceeding 4 m in height is almost 35 % and maximum surge velocities in the breaker zone have been estimated on site at over 2 m/sec. In addition, this rugged coastline provides a large diversity of physical conditions, with habitat type changing dramatically even over small distances on the shore.

A conceptual model of community structure is proposed, in which each of the three species occupies a habitat exposed to a different set of physical conditions. The model explains all observed distribution patterns without the need to invoke biotic interactions or physical disturbance.

Study area

The study was carried out along a 500 m stretch of coastline situated at Hluleka (Transkei) on the southeast coast of Africa (see General Introduction, Fig. 1). Figure 1 exemplifies the extremely rugged topography of the region. The species distribution patterns were investigated within three major topographic settings. The first comprised a number of regularly sloping rock platforms which were subjected to a variety of wave regimes.

The second setting comprised large gullies (2-2.5 m deep and 15-30 m long) which dissected the shore at right angles along the entire tidal gradient. Two differently exposed gullies were chosen, one being less, the other more protected from wave action by a large, rocky headland.

The third setting comprised boulder fields on the irregular and rugged open coast. The boulders were of various sizes and shapes. As a result, habitat type changed markedly over distances sometimes as short as a few centimetres.

Materials and Methods

In gullies, species distributions were surveyed with a graduated staff, taking the line between an arbitrary point on the shore (approximately 1.6 m above mean sea level) and the horizon as reference level. In similar manner, the prevailing high and low water levels were determined and, on the basis of this, the mean sea level (MSL) position was subsequently approximated using regional tide tables.

On the open shore outside gullies, species distributions were observed visually and recorded photographically in as large a variety of topographic settings as possible. Relative distribution patterns could then be represented in the form of schematic shore profiles.

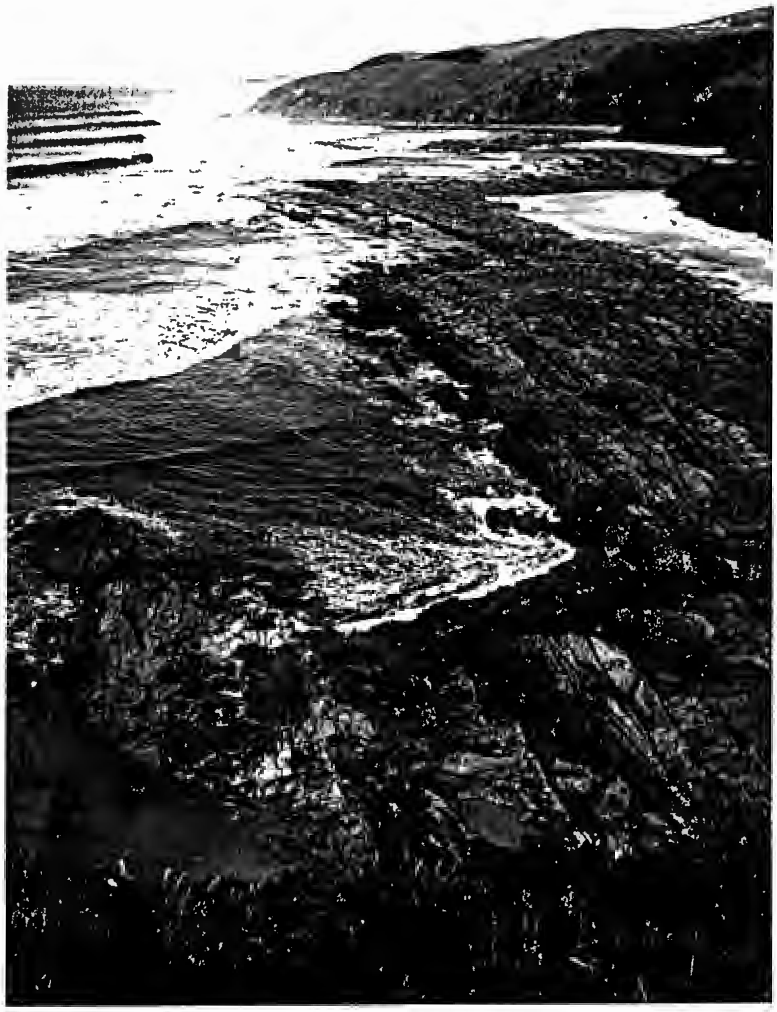

Figure 1. View of the rugged coastline at Hluleka (Transkei, Southeast Africa).

The physical conditions experienced by each species were estimated qualitatively on a relative scale by means of extensive visual observations. Exposure to wave impact on rock surfaces and boulders was gauged in terms of slope, orientation, degree of shelter and tidal elevation. Following the findings of Section 1A, emergence/submergence regimes were estimated in terms of inundation rates as a function of wave action in combination with tidal elevation, and not simply in terms of measured tidal height as is common practice.

Results

On regularly sloping, seaward facing rock surfaces, the barnacles occurred in monospecific, horizontal zones. Individual species were found either alone (monospecific shore profiles) or vertically segregated in groups of two or three. In many cases there was no zonal overlap and individual zones could be separated by as much as several metres along some profiles.

Although the nature of zonal grouping varied, this did not occur randomly but depended on wave regime. Thus, on slopes exposed to relatively little wave action - e.g. in sheltered coves - only C. dentatus was found. Here it occurred under a wide range of emergence/submergence (E/S) regimes, i.e. from low E/S ratios near the mean low water level to high E/S ratios in the splash zone, well above the high water springs (HWS) level.

As wave action increased - e.g. towards the entrances of coves - C. dentatus was found together with O. angulosa. The former, however, no longer occurred as far down the shore as under more sheltered conditions. Instead, O. angulosa now occupied this lower shore region, extending down to the low water springs level. The two species were often separated by a distinct gap where no barnacles occurred.

On slopes exposed to relatively strong wave action near the open coast, O. angulosa once again occupied the lower shore, whilst T. serrata now appeared at mid-shore levels. In this setting, C. dentatus was found high on the shore (above the HWS level) where some protection from direct wave onslaught was provided by large, near-shore rock outcrops. Otherwise, it was not present at all.

On the most exposed slopes directly facing the open sea, only O. angulosa was observed. Here it occupied the whole lower shore, extending some distance above MSL, although never as high as T. serrata did in more sheltered situations.

These observations suggest that each species occurs only under a specific set of physical conditions associated with E/S regimes and wave action. While E/S regimes are relatively easy to assess, wave action is far more difficult to define and quantify, for it incorporates numerous individual fluid dynamic factors such as wave impact, wave surge and wave splash. In an attempt to identify the relevant factor(s) involved, species distributions were investigated at sites at which individual factors locally assumed dominating roles.

In gullies, for example, direct wave impact is essentially restricted to the promontories, which also receive a high degree of splash. Gully walls, on the other hand, are subjected to strong, surging flow accompanied by progressively decreasing wave splash with distance from the gully heads.

In contrast to the vertical segregation patterns observed on regular, seaward facing slopes, the barnacles tended to segregate horizontally in gullies (Fig. 2). Furthermore, species-specific habitats overlapped to some extent. Once again, however, distribution patterns varied depending on wave regime. Thus, whereas all three species were found loosely intermingled near the promontories, only C. dentatus was observed along the whole length of gullies. Under more exposed conditions (Fig. 2A), the other two barnacles extended further into gullies than

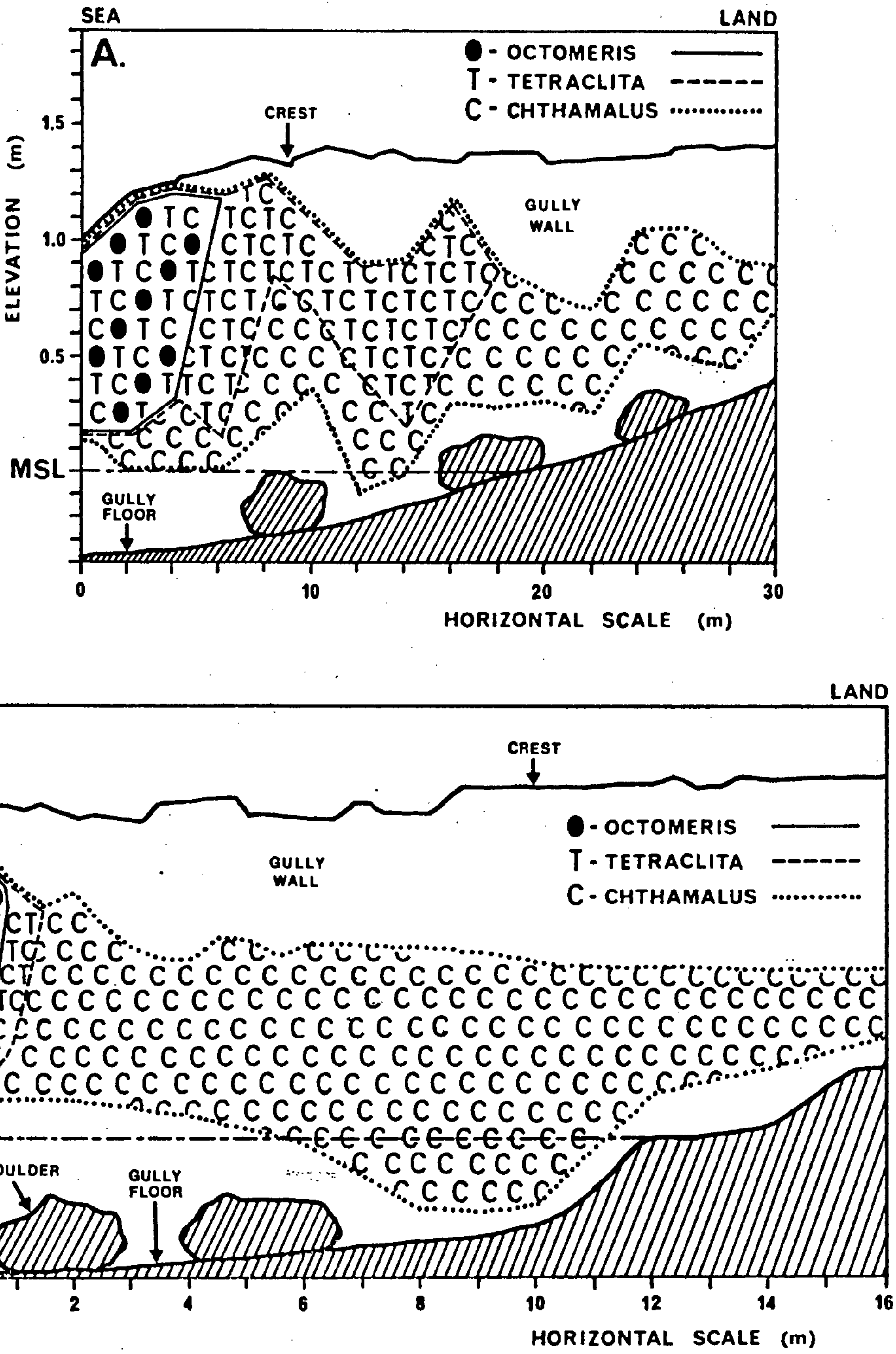

Figure 2. Species distributions in gullies. A: more exposed gully. B: more sheltered gully.

under less exposed conditions (Fig. 2B), T. serrata in both cases more so than O. angulosa. Clearly, species distributions showed greater correlations with wave impact and wave splash than with wave surge.

From the above observations, it was possible to identify species-specific habitats as a function of two major physical factors acting in combination, namely emergence/submergence regime and wave impact. C. dentatus occurs over a wide range of E/S regimes, but is restricted to areas of low impact. O. angulosa is found at low E/S ratios, but over a wide range of impact (though particularly where impact is relatively high). T. serrata occupies an intermediate position in terms of both physical parameters.

Although these habitat types were found to be essentially species-specific, areas of overlap with conditions common to all three species also occurred. No evidence of interspecific competition was observed in such situations.

On the irregular and rugged open coast, and in contrast to the regular seaward facing slopes, there was little evidence of monospecific shore profiles. Likewise, there was no evidence of vertical or horizontal zonation patterns similar to those observed on uniformly sloping rock surfaces and in gullies respectively. Instead, boulder fields showed evidence of discrete, well delimited patches of barnacles. Patches were of various shapes and sizes, and could be separated by as little as a few centimetres (Fig. 3). They were either monospecific or composed of any two, or of all three species. In mixed-species patches (similarly to cases of species overlap in gullies), the species occurred loosely intermingled with each other (Fig. 4). As before, there was no evidence of interspecific competition.

There was no strict relationship between patch type and shore position. Nevertheless, patch distribution was not random, but showed clear correlations with particular micro-environmental conditions. In fact, the relationships between species and habi-

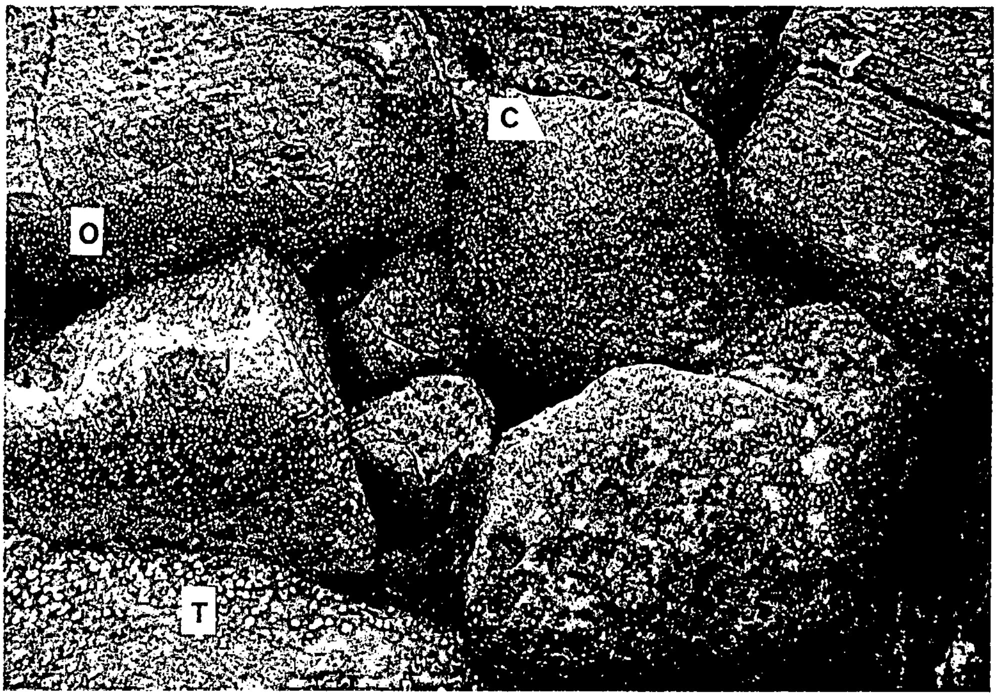

Figure 3. Photograph of monospecific patches of barnacles in a boulder field. C: C. dentatus; O: O. angulosa; T: T. serrata.

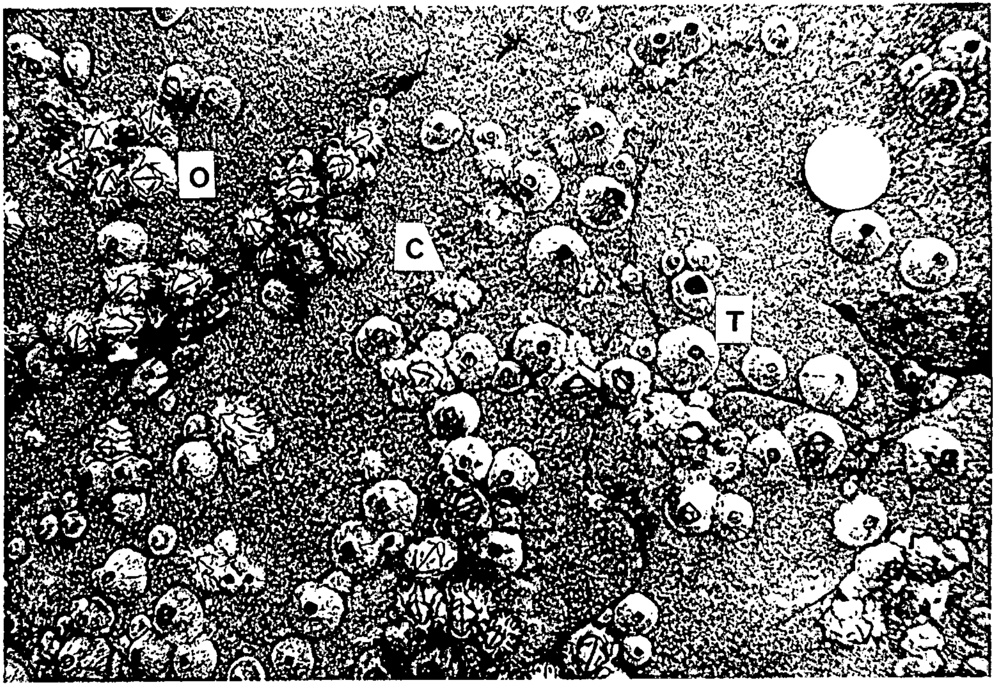

Figure 4. Photograph of loosely intermingled barnacles in a mixed-species patch. Abbreviations: see Fig. 3.

tat types described above persisted in all cases. Thus, small-scale distribution patterns on boulder fields reflected larger scale ones evident on regularly sloping rock surfaces and in gullies. This can be illustrated by a few examples.

Figure 5A shows that patches of O. angulosa occurred only on boulder surfaces which experienced relatively high wave impacts, i.e. surfaces directly exposed to oncoming waves. T. serrata patches were also found on surfaces facing the sea, but only where the full force of the breakers had already been somewhat dampened, i.e. on surfaces situated relatively high up the shore in this case. Furthermore, this species was never found at E/S ratios as low as either of the other two barnacles. At low tidal levels, rock surfaces protected from direct wave impact (e.g. landward facing surfaces) were either occupied only by C. dentatus or by mixed-species patches from which T. serrata was absent. In contrast, high up the shore on boulders that were emerged much of the time, only C. dentatus was observed. Thus, this species was again found over the widest E/S range (Fig. 5B).

The results of the present study demonstrate that species-specific habitats exist and that each is maintained irrespective of the proximity of the other species. Habitats were separated by as much as several metres in the case of monospecific zones on regular slopes, but by as little as a few centimetres in the case of monospecific patches on irregular boulder fields. In both cases, bare rock was common so that the absence of a particular species from any given habitat could not be explained by competitive pre-emption of space.

Discussion

The results presented above were synthesized into a conceptual model of community structure, whereby the habitats of C. dentatus, T. serrata and O. angulosa are each delimited by specific sets of physical conditions involving emergence/

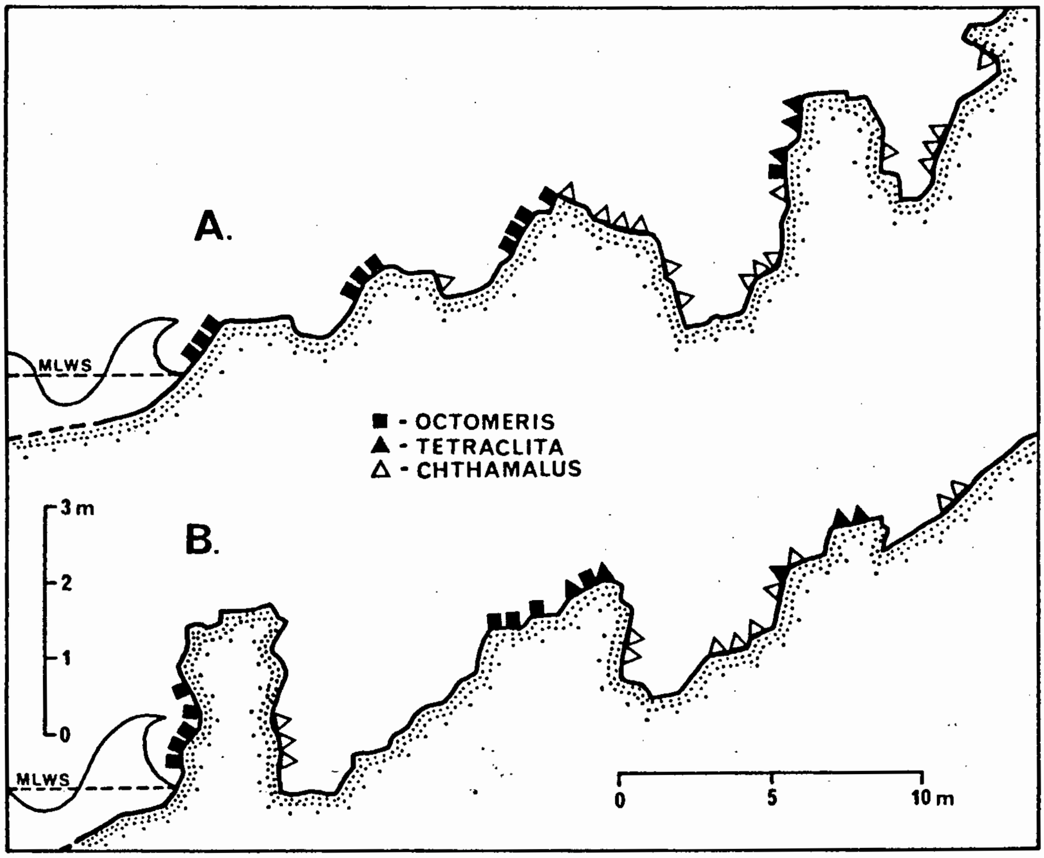

Figure 5. Species distributions along two (A, B) irregular shore profiles (simplified).

submergence regime in combination with wave impact. Pending precise quantification, the two parameters are, for the time being, shown on a schematic, two-dimensional plot of relative scale (Figs. 6, 7). The Y-axis corresponds to E/S ratio, the X-axis to wave impact.

It is emphasized that E/S ratios in this study do not correspond to tidal levels alone, as they would if they were determined from the rise and fall of the still water level (see Section 1A). In this connection, it should be noted that the full range of E/S ratios occurs on every shore, irrespective of tidal range and wave exposure. Wave impact, on the other hand, is entirely a function of exposure to wave action. In any particular situation, therefore, the model corresponds to a specific 'window' which will always cover the full E/S range, but only that degree of impact occurring under the local wave conditions. Such windows are schematically indicated in Fig. 6.

According to the model, C. dentatus occurs under virtually any E/S regime where wave impact is low. O. angulosa occurs where E/S ratios are low, but wave impacts are intermediate to high. T. serrata occupies an intermediate position in terms of both physical parameters. Individual habitats may overlap, but over a limited range of conditions only. Note that, depending on topographic and oceanographic setting, even such conditions of marginal overlap may dominate a shoreline. No evidence of interspecific competition was observed in such situations, probably because animal densities were low (Dungan, 1985; Gaines and Roughgarden, 1985). This is consistent with the finding that at least one species in the present study, namely T. serrata, is symmetrically distributed along the E/S gradient (Section 1A; Fig. 6). In cases where competition does control community structure (Connell, 1975; Wethey, 1983, 1985; Dungan, 1985), barnacle densities are high, bare rock virtually absent at the height of settlement and the overlap between species more substantial than in the present case.

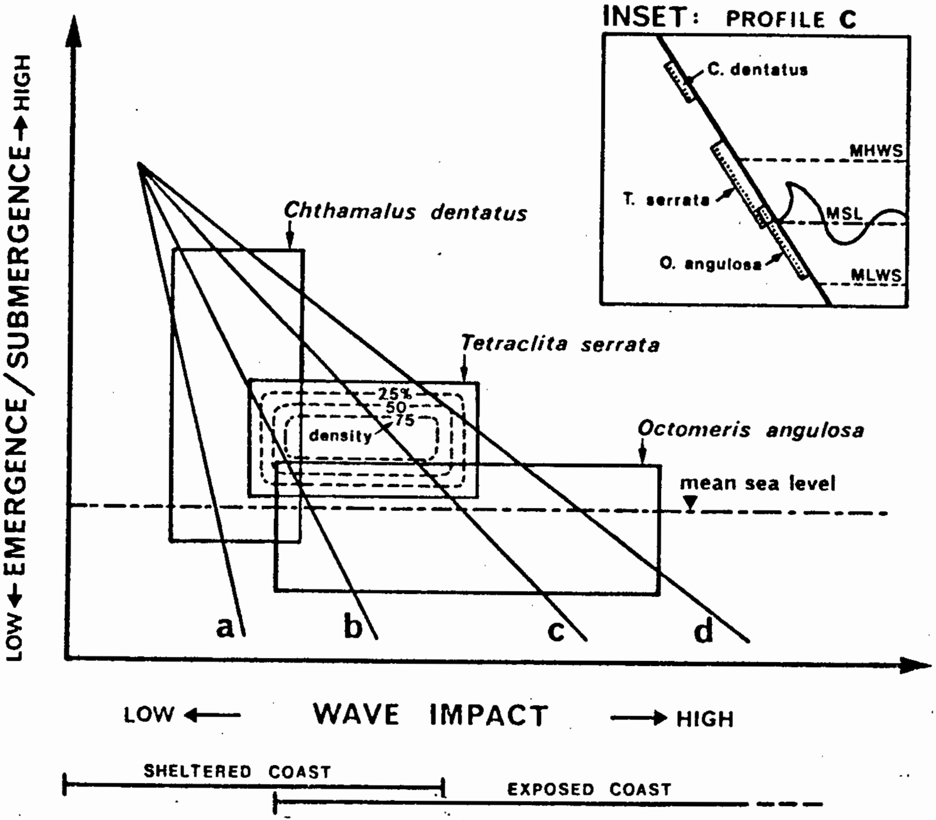

Figure 6. Conceptual model of community structure along regularly sloping shore profiles. Lines a, b, c and d represent the conditions observed along regularly sloping shore profiles in different exposure settings. The inset illustrates the actual shore profile corresponding to line c in the model. Note that, irrespective of the degree of exposure, the physical parameters invariably show regular gradients and that this results in vertical zonation patterns.

Within the physical framework outlined above, all the observed distribution patterns can be accounted for. Furthermore, the model was successfully tested at many other sites along the South African shoreline. Thus, the more regular the shore profile, the less diverse the physical environment in any particular local setting. On an idealized shore, for example, wave impact decreases rapidly with height above still water level (Balsillie, 1985), whereas E/S ratios show the opposite trend. For a particular E/S ratio, however, the degree of impact can vary strongly depending on the local setting. This is most easily demonstrated by conceiving a variety of regularly sloping shore profiles superimposed onto the model (e.g. Fig. 6, profiles a, b, c and d).

Along such regular profiles, the species occupy well defined zones which may overlap in some cases. From Fig. 6, it is clear that the habitat of each species cannot be fully represented along any single profile. For example, landward zonal limits correspond either to minimum levels of wave impact or to maximum E/S ratios beyond which individual species do not occur. The opposite applies to seaward zonal limits, thus questioning the commonly held notion that, for intertidal animals, such limits are usually set by biological conditions (Connell, 1975).

The zonation patterns illustrated by the profiles c and d in Fig. 6 closely correspond to those commonly described for much of the South African coast (Day, 1974; Tietz and Robinson, 1974; Branch and Branch, 1983). If all three species occur together on the shore, then C. dentatus always occupies the most landward, and O. angulosa the most seaward shore position respectively.

Along irregular profiles, by contrast, E/S regimes and wave impact both fluctuate strongly and unpredictably even over small distances. Significantly, no zonation patterns are evident here. Barnacles occur in patches of all shapes and sizes, within which all possible combinations of species are observed. A hypothetical example is illustrated in Fig. 7.

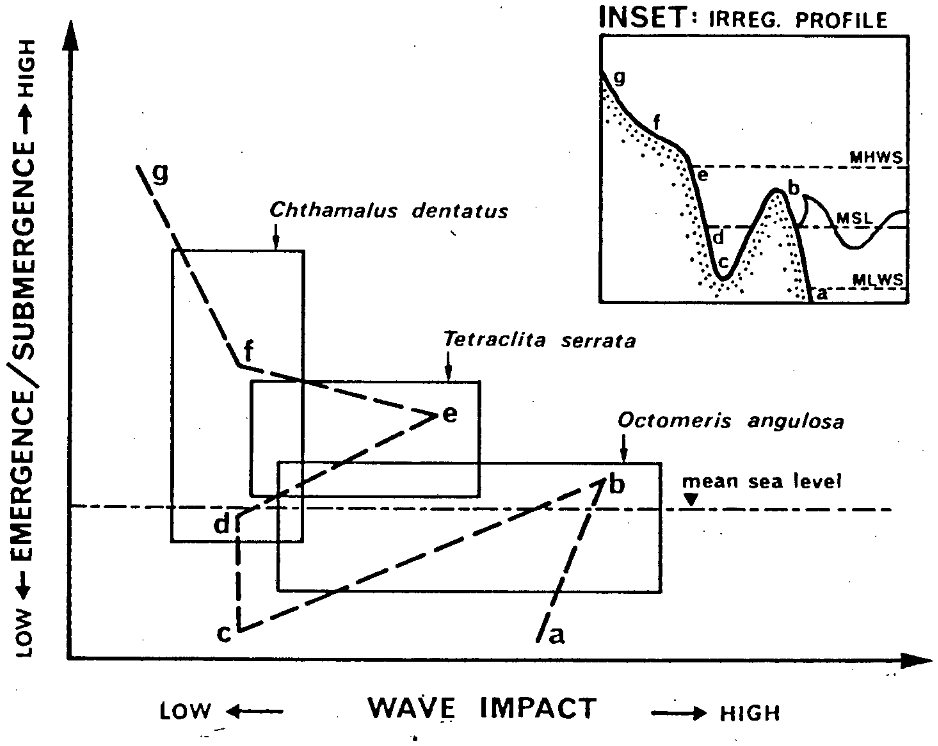

Figure 7. Conceptual model of community structure along irregularly sloping shore profiles. The broken line represents the physical conditions observed along the shore profile illustrated in the inset. In contrast to Fig. 6, the physical parameters in this case do not show regular gradients and, as a consequence, species distributions are patchy.

Although such departures from the "norm" have long been known in rocky shore ecology (Bright, 1938 in the present case), they have remained an unexplained enigma (e.g. Brattström, 1985). The present model, however, provides a rational explanation for this phenomenon.

So far, neither the processes resulting in species segregation nor their influence at different lifestages have been considered. While some effects of emergence and submergence have been established for some barnacles (see Newell, 1979), no equivalent data are available on wave impact (e.g. Schmidt and Warner, 1984; but see Underwood, 1985). In view of the fact that impact pressures on coastal structures can exceed 30 kg/cm^2 (Blackmore and Hewson, 1984), it would indeed be surprising if such enormous forces were not to play an important role in intertidal ecology, particularly in the case of community structure (see also Eckman, 1983; Nowell and Jumars, 1984).

With respect to timing, no evidence for segregative processes was observed in the post-metamorphosed lifestage. It was therefore concluded that segregation took place before the settled larvae metamorphosed. It may, of course, be argued that events occurring during the planktonic lifestage might influence the distribution of the sessile organisms (Grosberg, 1982; Connell, 1985). However it is difficult to conceive how larval stratification in near-shore waters could be maintained within the highly turbulent intertidal environment. It is therefore inferred that the relevant processes come into operation when the larvae arrive on the shore, and not before.

In terms of the proposed model, all the observed species distribution patterns can readily be explained if one assumes that each larval species requires an essentially different set of physical conditions under which to settle and metamorphose. This study has identified two major physical factors defining these conditions, namely emergence/submergence regime and wave impact. However, the manner in which these factors act on the larvae remains to be investigated. Biological interactions may occur at any level discussed in this paper. However, the model does not require such interactions or physical disturbance to explain the fundamental distribution of barnacles in the present community.

In fact, the results of the present study argue strongly against interspecific competition as an important controlling factor. The availability of bare rock and the observed gaps between monospecific zones on regular sloping rock surfaces both make it highly unlikely that zonation is controlled primarily by competition, whereas they are consistent with the proposed physical model. With respect to physical disturbance and to other biological interactions, e.g. selective predation, any arguments questioning the validity of this model must remain speculative until supported by concrete evidence.

The above considerations argue against the propositions that Paine (1981, 1984) has put forward to explain variable patterns of tidal segregation between dominant and subordinate barnacles. As shown in the present study, physical constraints operating differentially on larval assemblages arriving on the shore are consistent with and sufficicent to explain such patterns. Within these constraints, other factors may further influence habitat occupation. These factors include rock type (Hawkins and Hartnoll, 1982; Todd and Turner, 1986; but see Caffey, 1982), sedimentation (Bierbaum and Zischke, 1979), current velocity and turbulence (Crisp, 1974; Bierbaum and Zischke, 1979; Denley and Underwood, 1979; Rittschof et al., 1984; Schmidt and Warner, 1984; Geraci and Romairone, 1986; Todd and Turner, 1986), ambient ionic composition (Rittschof et al., 1986), the presence of conspecifics (Moyse and Hui, 1981; Rittschof et al., 1984), microfloral cues (Strathmann and Branscomb, 1979; Strathmann et al., 1981), bulldozing/predation effects of grazers (e.g. Menge et al., 1986) and space pre-emption by, for example, algae (Denley and Underwood, 1979; Dungan, 1986).

The model presented in this paper provides a rational framework in which to investigate the relative <u>importance</u> (<u>sensu</u> Welden and Slauson, 1986) of physical and biological factors structuring barnacle communities (see also Bradbury et al., 1986). In addition, it is suggested that the model may also be relevant to other intertidal organisms, including algae (see Duggins and Dethier, 1985; Smith and Berry, 1986).

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Section 2   SHELL GROWTH

SECTION 2A

Skeletal growth of the intertidal barnacle *Tetraclita serrata* Darwin (Cirripedia: Thoracica): accretion and allometry

Abstract

Shell and prosomal growth of Tetraclita serrata Darwin (Cirripedia: Thoracica) was recorded on a rocky,intertidal platform at Dalebrook (South Africa). Slow rates of linear accretion of the shell were characteristic of high tidal elevations but were enhanced in areas of greater water-flow near joints in the rock face. On the other hand, fast linear accretion occurred at lower elevations but was depressed in areas of greatest wave impact closest to the sea.

The relationships of shell length vs shell mass, shell height vs shell length and organic carbon level vs animal size were in all cases similar at different elevations on the platform. However, shell allometry differed significantly with tidal level. At lower levels, small barnacles had thicker and more porous shells, with smaller opercular openings and smaller shell internal volumes when compared with comparably sized animals at higher shore levels. The reverse was observed in large conspecifics.

Variation in shell allometry did not affect linear or mass accretion rates of the shell or of the prosoma. In addition, variations in allometry do not seem beneficial in terms of either wave impact or aerial exposure, except perhaps in the case of small barnacles exposed to greater wave impact at lower shore levels. They are, however, potentially important in regulating the growth of body components enclosed by the shell, for thicker shells will have smaller internal volumes. This does not affect prosomal growth but (in a separate study) can be shown to reduce reproductive output.

These results highlight the need to re-evaluate current interpretations of the significance of shell allometry in barnacles, notably in relation to factors such as aerial exposure and predation.

Introduction

The nature of the calcareous skeleton of barnacles was first investigated over a hundred years ago (Darwin, 1854). Since then, biologists have interpreted major physico-chemical aspects of shell growth primarily in terms of competitive and antipredatory abilities (Connell, 1961a, b, 1970; Vermeij, 1978; Stanley and Newman, 1980; Newman and Stanley, 1981; Paine, 1981; Palmer 1982, 1983; Lively, 1986). Notwithstanding extensive and often repetitive investigation of linear accretion, attempts to relate the skeletal growth record to the physical environment have hardly commenced in comparison to other invertebrates (cf. Rhoads and Lutz, 1980; see also Bourget, 1980; Crisp and Bourget, 1985).

The present work attempts primarily to expand our knowledge of skeletal growth, in relation to local topographic gradients which result from prevailing wave and tide regimes. The main abiotic factors affecting the distribution of the coronuloid <u>Tetraclita serrata</u> Darwin were recently shown to be aerial exposure, wave impact and the local submergence regime which is determined by topography in conjunction with wave action (Section 1). It might be expected that the effects of these factors will also be preserved in the skeletal record of barnacles because the shell forms the primary physical barrier to the abiotic environment and it also provides anchorage to the substratum.

The procedure followed here was to examine three interrelated aspects of body growth, the first being ontogenetic changes in shell structure and shape. To interpret any allometric variability in terms of the abiotic factors cited above, it is necessary to establish whether an apparently causal relationship between the two is not purely fortuitous (<u>sensu</u> Williams, 1966), i.e. it could be a coincidental by-product of selection for another feature of shell growth which is affected by allometry. Because allometric growth might affect the trade-off between linear accretion rate and mass accretion rate, a second approach was to monitor the linear accretion rate of the shell in situ in animals of known mass. On the other hand, allometric growth as such need not necessarily be a direct indicator of abiotic environmental pressures or, for that matter, act as a regulator for linear shell growth. In view of recent evidence that the rigid exoskeleton may physically control the growth of the internal soft parts (Palmer, 1981), a third approach was to investigate mass accretion of one such soft part, i.e. the prosoma.

Study area

The study site comprised a 13 m x 15 m rock platform situated at Dalebrook, False Bay, South Africa (34°07'S, 18°30'E; inset Fig. 1). Average sea temperature fluctuates between 19-20°C in summer and 13-14°C in winter (cf. Cliff, 1979).

A detailed account of the topography and population distribution on the platform is provided in Section 1A. Four transverse corridors, each about 3 m wide, were chosen for analysis of barnacles at different tidal elevations and animal densities (Fig. 1). Figure 2 shows the heterogenous nature of the topography within each corridor. Corridor 4 was nearest the sea and had a similar range of elevations to corridor 3, but a lower animal density (Figs. 2 and 3). Corridors 1 and 2 also had comparable elevations but corridor 1, which lay furthest from the sea, had a lower animal density than corridor 2. In relation to the intertidal gradient spanned by T. serrata at Dalebrook, corridors 1 and 2 incorporated high tidal elevations and corridors 3 and 4 had intermediate elevations (Fig. 2).

Materials and Methods

The degree of intraspecific crowding did not markedly influence the relationship between the dry mass (M) and the length (L) of the shell, regressions for grouped and isolated barnacles having

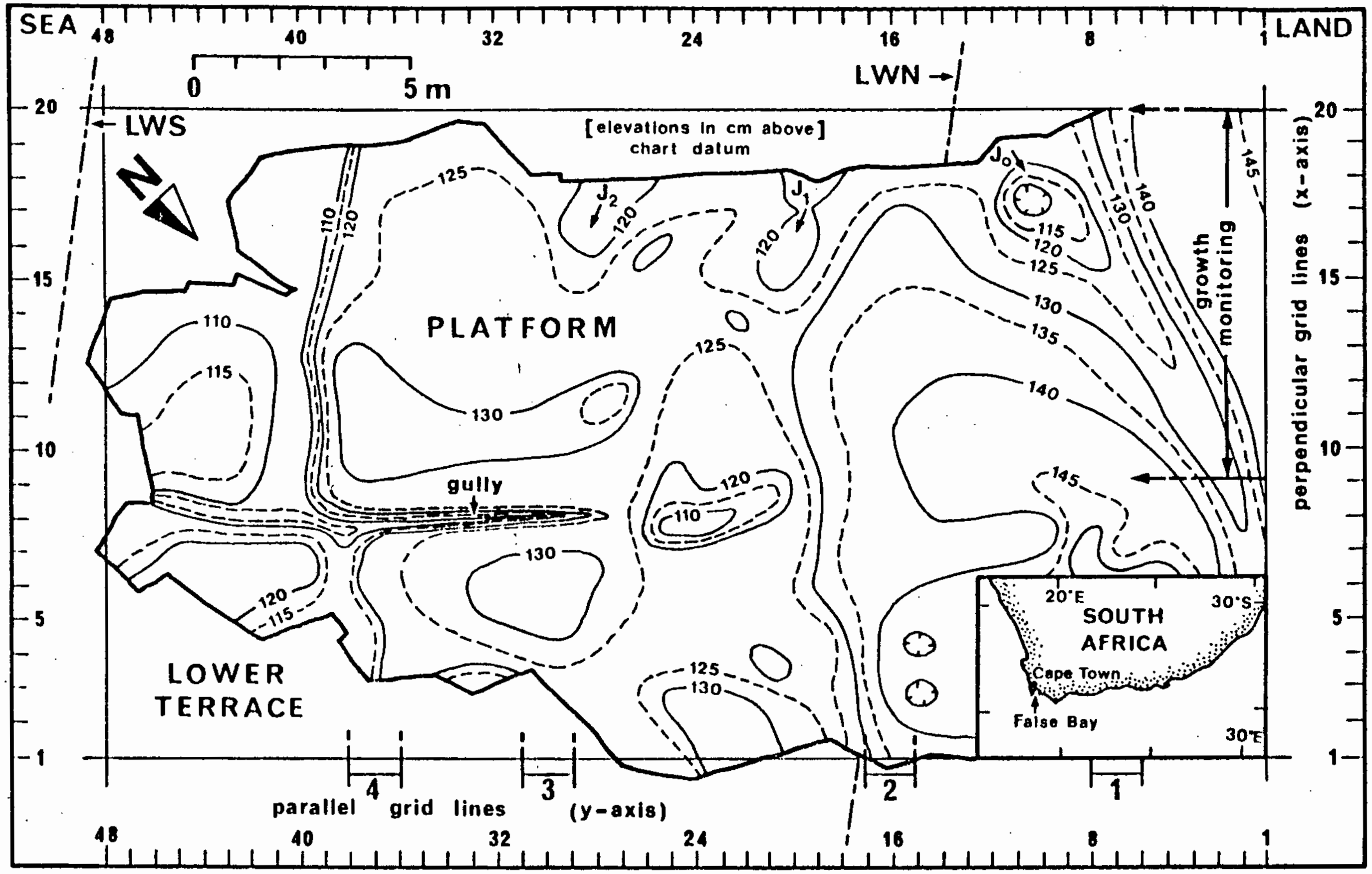

Figure 1. Location of the study area at Dalebrook in False Bay (inset) and elevation map of the rock platform (cm above chart datum) showing major topographical features. Corridors 1 (high shore) - 4 (low shore): transverse study localities on the platform (LWN: low water neaps; LWS: low water springs; for further explanation, see Section 1A).

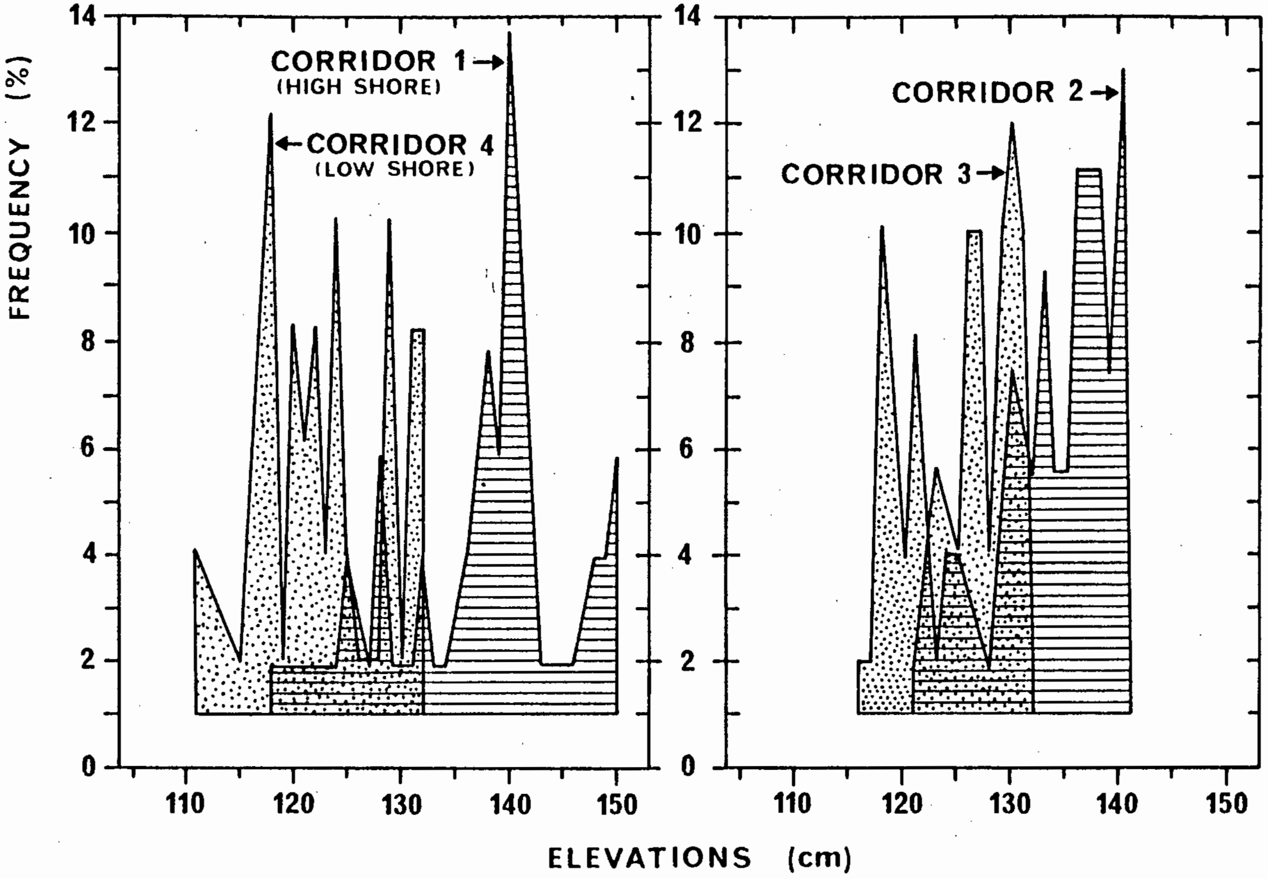

Figure 2. Range of elevation (cm above chart datum) within the transverse corridors, showing the degree of topographic heterogeneity in each corridor.

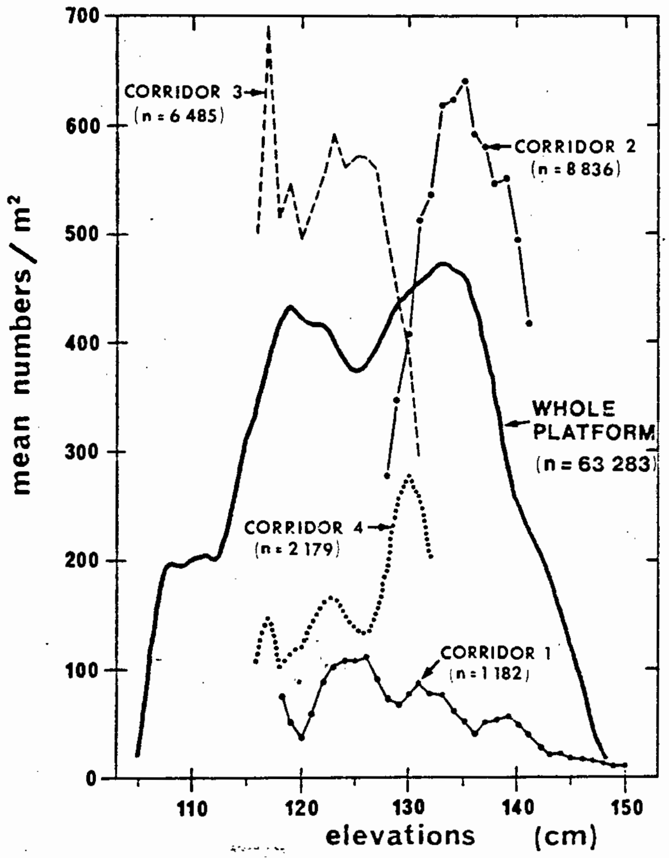

Figure 3. Density of barnacles within each transverse corridor as a function of elevation (cm above chart datum) (for further explanation, see Section 1A).

similar slopes (grouped, M (g) = 0.156 $L^{3.110}$ (cm), r = 0.968, N = 106; isolated, M (g) = 0.138 $L^{3.259}$ (cm), r = 0.971, N = 158; Student's t test, $p > 0.05$). Data for grouped and isolated barnacles were therefore pooled.

Size-frequency distributions of live animals were monitored in 1976 first towards the end of the period during which the planktonic larvae settle (May) and again four months later (September). Barnacles were collected along each corridor and the following dimensions were measured with vernier calipers: length of the shell, length of the opercular opening (in both cases along the rostro-carinal axis), wall thickness at the base of the shell and shell height.

Rates of linear accretion of the shell were monitored at approximately six-weekly intervals for one year from May 1976. Individual barnacles - approximately 50 per corridor - were identified from photographs and the lengths of the shells were measured in situ with vernier calipers. Isolated specimens only were chosen, to avoid dealing with distorted shells (von Gutmann, 1960).

Gravimetric and biochemical analyses were carried out during 1978. A minimum number of 25 barnacles was collected each month in both corridors 1 and 4. Whole specimens were first freeze-dried. The valves were then cleaned in sodium hypochlorite (10-14 %, v/v) and oven-dried at 60° C overnight. Shells, valves and prosomas were weighed on a Mettler ME30 microbalance. Finally, organic carbon was determined in pooled samples of 5-10 shells from barnacles with similar valve masses (see Section 2B for use of valve mass as a convenient indicator of animal size). The shells were ground to a fine powder in a Wig L Bug (Crescent Dental MFG Co.). Replicate subsamples (5-10 mg each) were treated with 0.1 ml conc. HCL to dissolve the carbonates, diluted with 20 ml CO_2-free H_2O (to $pH \simeq 2$) and analyzed in a Beckman Total Organic Carbon Analyzer 915A. A second estimate of organic matter was made by ashing other subsamples in a Muffler furnace at 500° C for 4 hours (Bligh et al, 1984).

The Student's t test was used when necessary to compare regression slopes (Zar, 1974). The rate of linear accretion of the shell was described by the von Bertalanffy equation, $L_t = L_{max} (1 - e^{-k(t-t_o)})$, where L_t = shell length at time t, L_{max} = asymptotic upper limit of length, K = a growth constant, t_o = theoretical age at zero length.

Results

The relative size-frequency distribution was generally bimodal over winter (May - September) except at high elevations where the peak corresponding to the smallest size - class (lengths < 9 mm) was much reduced (Fig. 4). This peak was most pronounced towards the end of the annual settling period in autumn (May) at intermediate elevations. It had generally decreased by the end of winter (September) when it was sometimes merged with a less pronounced peak of slightly larger barnacles. This decrease in the relative frequency of very small, newly settled barnacles by the end of winter is not due to rapid juvenile growth (as shown below, growth rate is in fact slowest during winter). If this were so, a peak representing these recruits should have appeared by September (i.e. 4 months after initial settlement) at a size larger than that of an original recruit, but smaller than that of a one year old animal. These data indicate that few young survive settlement and growth beyond the first winter, the bulk of the population consisting of older animals. At the top of the shore, recruitment was limited but survival of recruits appeared to be higher than it was lower on the shore.

Seasonal variations in linear accretion rates of the shell were slight but significant in small and medium-sized barnacles at intermediate tidal elevations (corridors 3 and 4; Fig. 5). Growth generally increased during summer (October-February) when sea temperatures are highest in False Bay.

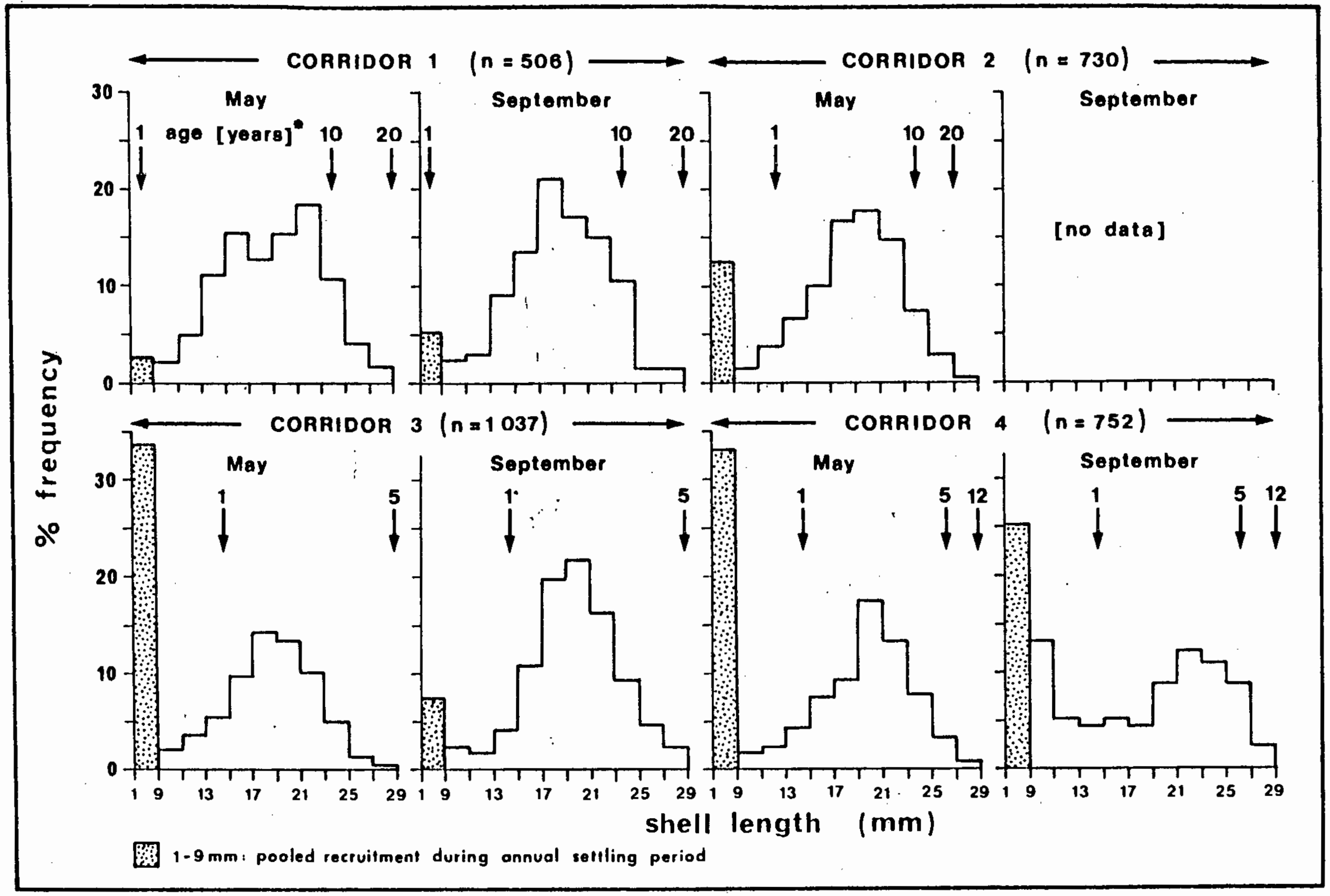

Figure 4. Size-frequency distributions at the end of settling (May) and four months later (September) (*: arrows and figures indicate ages at given sizes, computed from growth curves in Fig. 7).

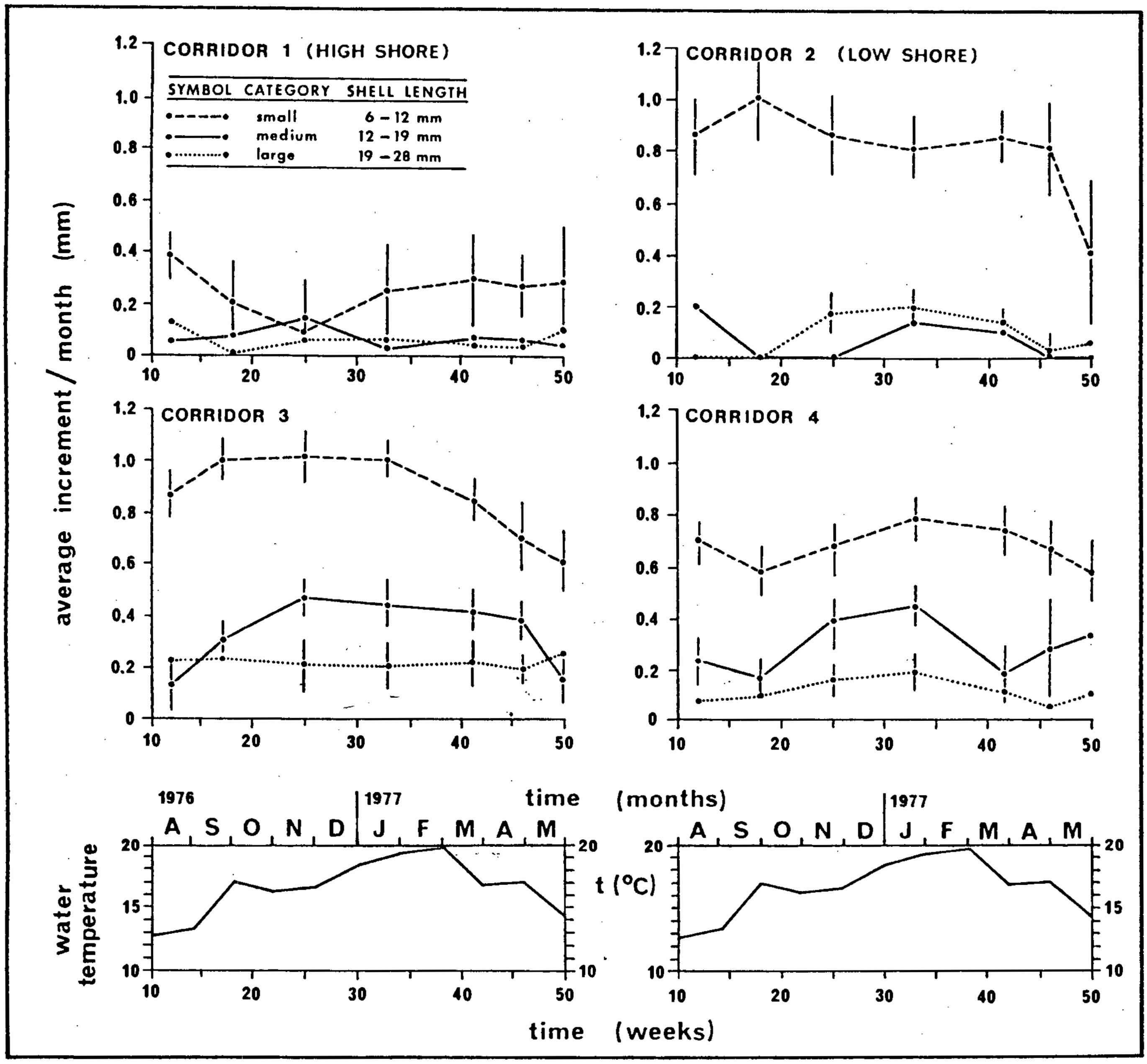

Figure 5. Seasonal patterns of monthly accretion in shell length for various size categories (standard error of the mean shown for all samples with N >5) and of mean monthly sea temperatures at Dalebrook.

By knowing the rates of linear accretion of the shell (Fig. 6) and by estimating a maximum age of 3-4 months for the smallest barnacles whose growth was monitored, it was possible to compute shell length at various ages (Fig. 7) by means of the von Bertalanffy equation (see Materials and Methods). Three trends emerge from these measurements. First, linear accretion rate decreases with age. Second, growth of small barnacles at high tidal elevations is significantly slower than that at intermediate elevations (compare corridors 1 and 2 with 3 and 4 respectively, Figs. 6 and 7; Kruskal-Wallis analysis, Table 1: growth of specimens measuring from 6 mm to 20 mm in length is significantly different between corridors, $p < 0.05$). Third, differences in growth rate between sections of the platform which have a similar range of tidal elevations are clearly associated with the heterogenous nature of the local topography and the horizontal distance from the sea. For example, small barnacles in corridor 2 grew faster than those in corridor 1. Both areas incorporated partly eroded joints along one edge of the platform, but corridor 2 also lay nearer the sea (Fig. 1). Conversely, corridor 4 showed slower growth than corridor 3 despite lying nearer the sea. It was also associated with a long, winding gully, whereas the neighbouring corridor incorporated another distinct joint (Fig. 1).

One explanation for differences in linear accretion rates between individual localities is that the trade-off between linear accretion rates and mass accretion rates of the shell may not be constant over the entire study area. In other words, the value of b may differ in the following equation: shell mass = a $(\text{shell length})^b$. For example, the value of b may be higher in the case of slower linear accretion for high-shore animals. This simply means that shell mass would increase at the expense of linear growth in length. This is clearly not the case at Dalebrook because, for a start, the mass accretion rate was also slower at high elevations (Fig. 8). More importantly, the relationship between mass and length was statistically equal throughout the study area (Fig 9). Therefore, variability in the trade-off between mass accretion of the shell and linear growth

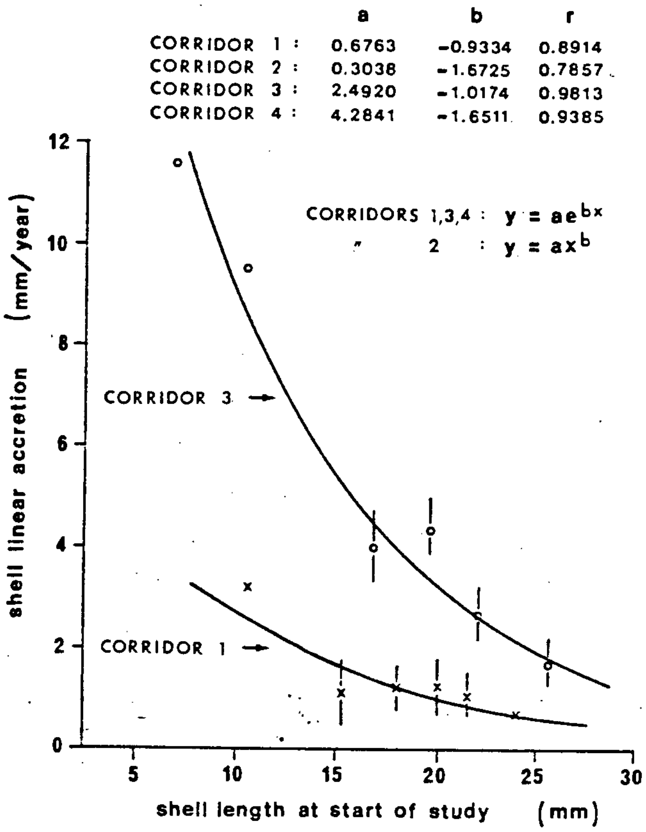

Figure 6. Yearly accretion in shell length in relation to size (standard error of the mean shown for all samples with N >5 at the end of the study period).

	$L_{max.}$	K	t_o	r
CORRIDOR 1 (●) :	30.784	0.1252	-1.3701	0.9974
CORRIDOR 2 (○) :	29.000	0.1786	-1.5621	0.9645
CORRIDOR 3 (◉) :	31.189	0.5112	-0.2693	0.9905
CORRIDOR 4 (×) :	29.000	0.3869	-0.7863	0.9672

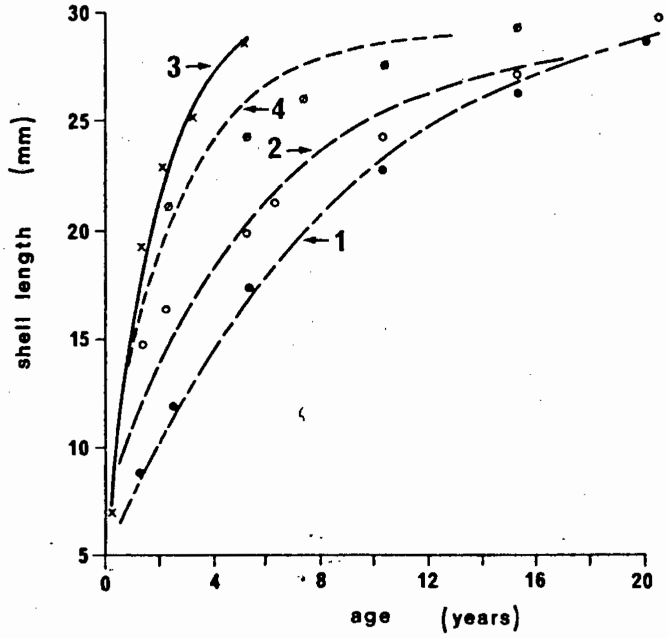

Figure 7. von Bertalanffy curves of linear accretion rates of the shell in corridors 1 (high shore) to 4 (low shore) (see text for further explanation).

Table 1. Kruskal-Wallis one-way analysis of variance to test whether there is a significant difference in linear accretion rate of the shell between corridors (cases of significant difference are underlined for significance level <0.05; df = k - 1)

size class (length, mm)	**number of** **corridors=k**	**H** observed	**probability** $H > H$ observed
6 - 11	4	12.03	$p < \underline{0.01}$
12 - 18	4	8.77	$\underline{0.05}$
19 - 20	4	9.07	$\underline{0.05}$
21 - 22	4	3.83	0.30
23 - 24	4	3.14	0.50
25 - 28	3	4.03	0.20

Table 2. Relationship between shell height (y) and shell length (x) at corridors 1 (high shore), 2, 3 and 4 (low shore) ($y = ae^{bx}$; r = correlation coefficient; N = sample size; slopes $b_1 = b_4$, t test, $p > 0.05$).

corridor	**a**	**b**	**r**	**N**
1	0.569	0.321	0.578	76
2	0.636	0.337	0.602	195
3	0.485	0.421	0.532	236
4	0.726	0.240	0.379	146

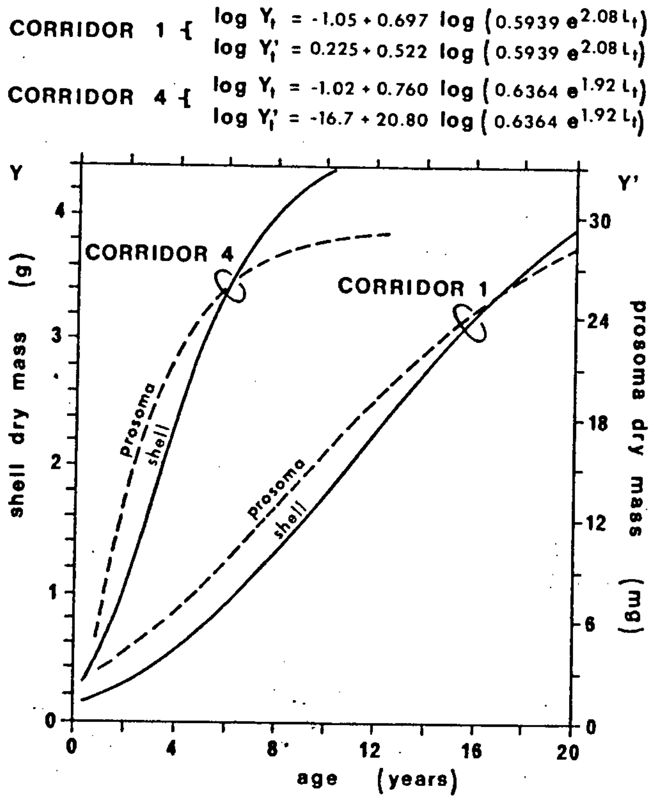

Figure 8. Mass accretion rates of the prosoma and of the shell in corridors 1 (high shore) and 4 (low shore) (see Fig. 7 and text for values of L_t and Section 2B for computation).

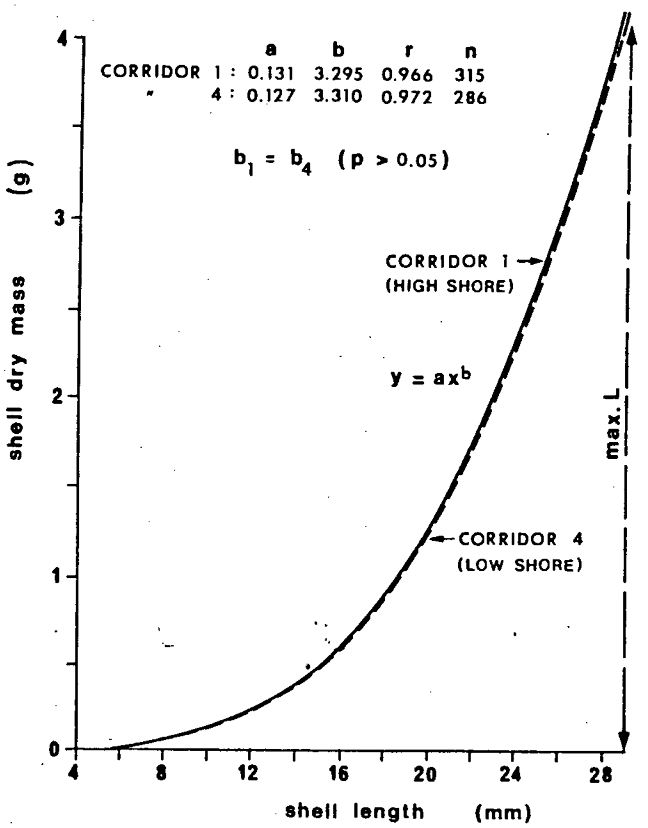

Figure 9. Relationship between the dry mass and the length of the shell in corridors 1 (high shore) and 4 (low shore) (data for 9 monthly samples were pooled in each case; max. L = maximum length observed <u>in situ</u>).

in length of the shell cannot account for differential linear growth in shell length.

It should be emphasized at this point that although the increase in mass per unit length is constant over the platform at a given shell length, this does not mean that the distribution of mass within the shell must also remain constant. In this context, it will be shown below that other allometric features do vary on the platform although the negatively allometric relationship between shell mass and length remains similar. Thus, the distribution of mass within the shell does not as such affect linear or mass accretion.

In order to compare the constitution and the morphology of shells from barnacles that grow at different rates, shell variables of similarly sized animals from high and intermediate tidal elevations were measured. Initially, the following five interrelated variables were compared: organic carbon level, shell height, shell thickness, bulk density (= mass per unit volume) and shell internal volume. Neither levels of organic carbon (and ash) nor height varied relative to position on the platform. Shells of similar length (x) did not differ significantly in height (y) between corridors 1 (high shore) and 4 (low shore) (Table 2). Indeed, the regressions $y = ae^{bx}$ had poor correlation coefficients ($r < 0.60$) in all four corridors. Likewise, levels of organic carbon (and ash) in the shell remained similar between corridors 1 and 4, irrespective of season, animal size and reproductive state (Fig. 10).

Having established the constancy of these two shell variables, it is possible to predict the direct interplay between porosity and thickness (in this study, porosity is inversely proportional to bulk density). It should be evident here that, since the negatively allometric relationship between shell mass and shell length also remained constant over the whole study area (Fig. 9), this interplay can take on two forms only: either the relationship between the two variables follows a constant trend throughout the study area or any decrease (or increase) in the

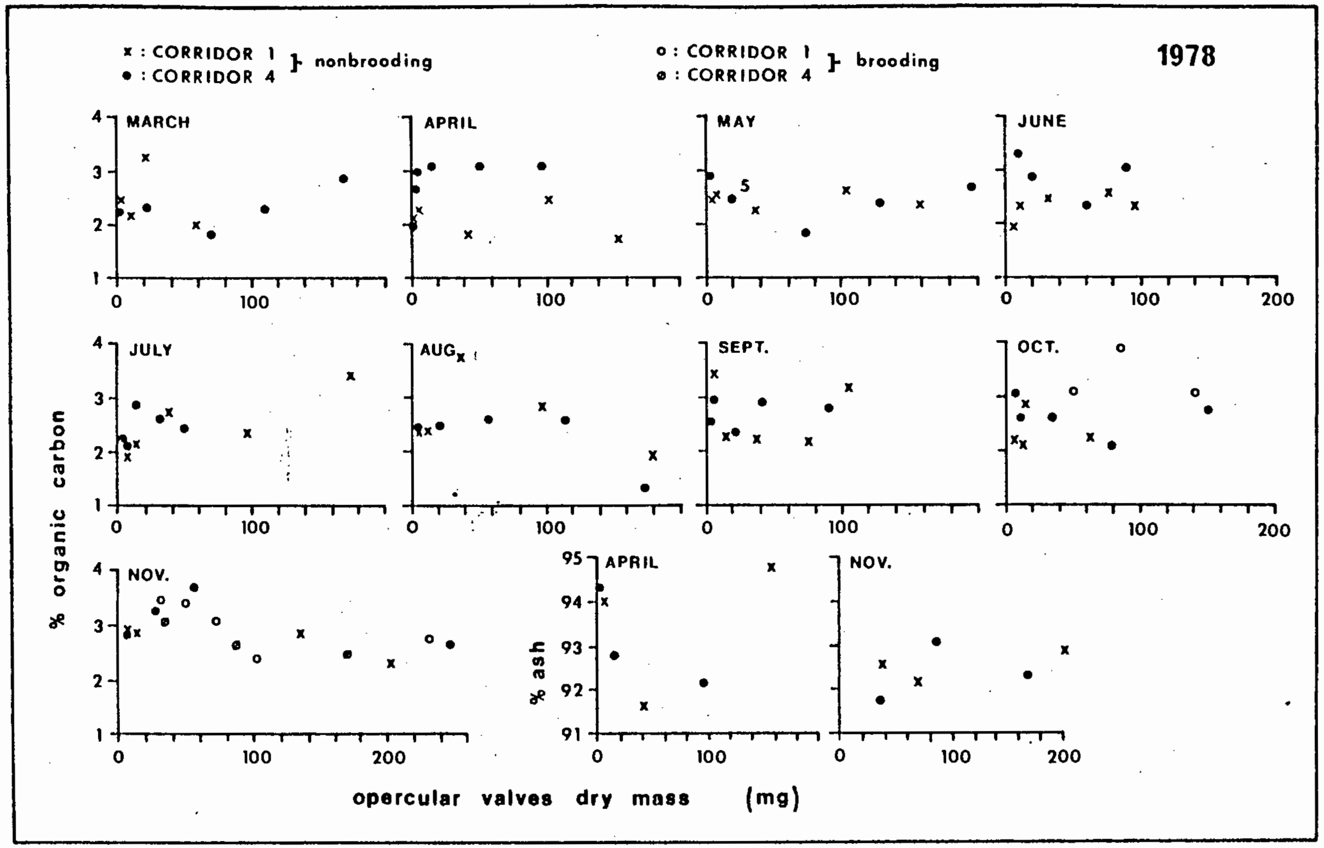

Figure 10. Monthly levels of organic carbon and ash in the shells of barnacles of varying size in corridors 1 (high shore) and 4 (low shore) (animal size was measured as the dry mass of the opercular valves).

one must be counterbalanced by a corresponding decrease (or increase) in the other. Since direct measurements have shown that small shells at high elevations were in fact slightly, but significantly thinner than those at intermediate elevations (Fig. 11), it must be assumed that the bulk density of small shells was greater at high elevations. Conversely, thicker - and hence less dense - shells were evident in large barnacles at high elevations.

The fifth allometric feature to be considered was shell internal volume, because one might suspect this variable to be inversely proportional to shell thickness (cf. Palmer, 1981; Currey and Hughes, 1982). In this case, small barnacles should then have larger internal volumes at high elevations (because of their thinner shells) than lower down the shore, whereas the opposite should hold true for large animals. If the shell physically limits growth of the prosoma, then prosomal size should be proportional to the internal volume of the shell, i.e. small barnacles should have larger prosomas at high elevations than lower down the shore, whereas the opposite should hold true for large animals. In fact, the relationship between prosomal mass and shell length (or mass) was similar for all animals, irrespective of elevation (Figs. 12, 13). This argues against the applicability of the skeletal limitation hypothesis of Palmer (1981) as far as prosomal growth in T. serrata is concerned.

The two remaining morphological features that were investigated are the size of the opercular opening and of the valves which seal it. The correlation between the length of the opening and that of the shell was generally poor (Fig. 14). It is, of course, probable that a single linear measurement provides an inadequate estimate of the size of the opening. Despite this, small barnacles had significantly larger openings at high elevations than lower down the shore, whereas the opposite holds true for large animals (Fig. 14). The relationship between valve mass and shell length did not, however, follow the same trend (Fig. 15). Valve mass was similar in small barnacles,

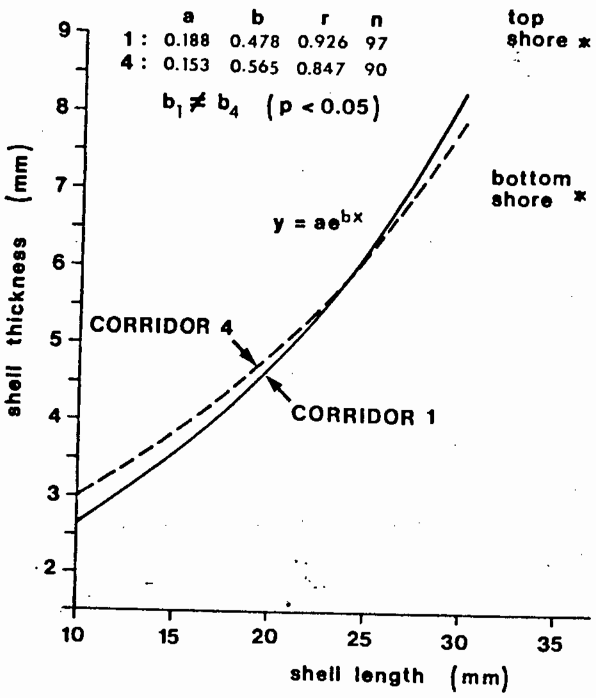

Figure 11. Relationship between the thickness and the length of the shell in corridors 1 (high shore) and 4 (low shore).
* Isolated data points for Tetraclita squamosa rufotincta are extracted from Achituv and Borut (1975).

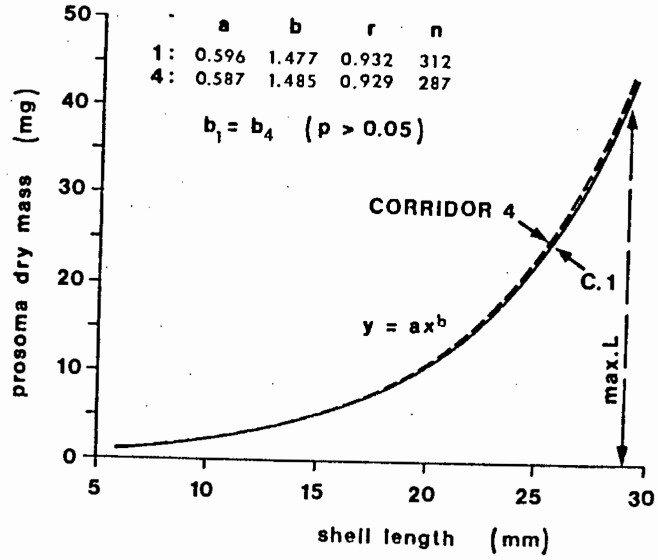

Figure 12. Relationship between the dry mass of the prosoma and shell length in corridors 1 (high shore) and 4 (low shore) (data for 9 monthly samples were pooled in each case; max. L = maximum length observed <u>in situ</u>).

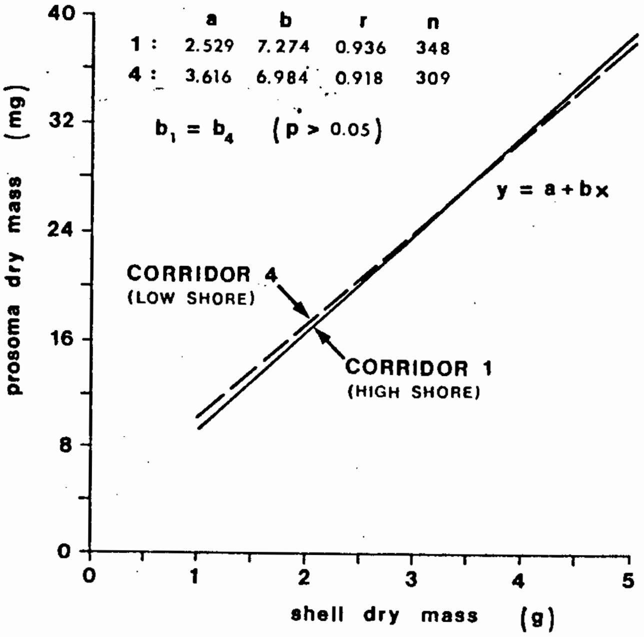

Figure 13. Relationship between the dry mass of the prosoma and of the shell in corridors 1 (high shore) and 4 (low shore) (data for 9 monthly samples were pooled in each case; see Section 2B for individual regressions and further explanation).

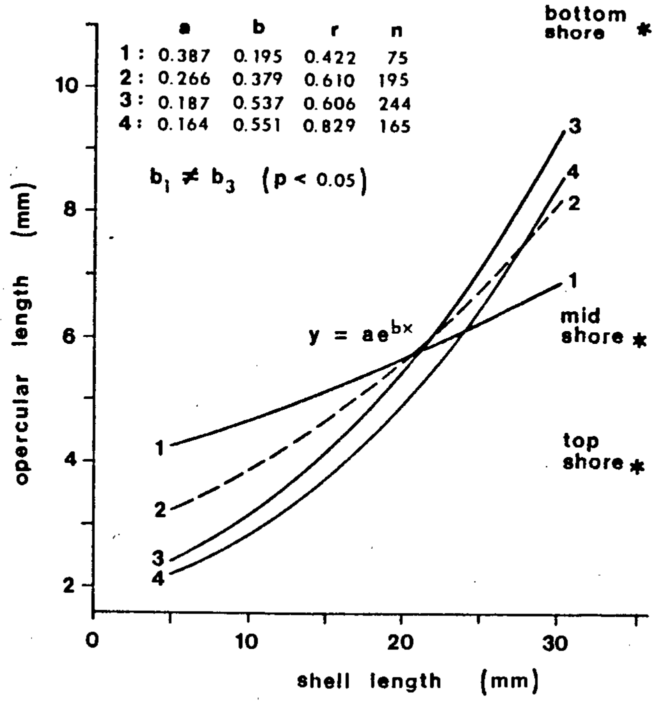

Figure 14. Relationship between the length of the opercular opening and of the shell. * Isolated data points for T. squamosa rufotincta are from Achituv and Borut (1975).

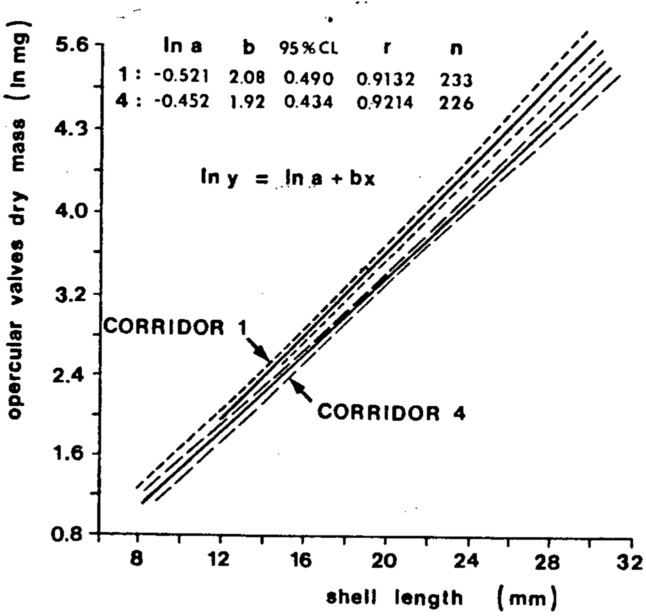

Figure 15. Relationship between the dry mass of the opercular valves and shell length in corridors 1 (high shore) and 4 (low shore (data for 8 monthly samples were pooled in each case; see Section 2B for individual regressions and further explanation; dashed lines indicate 95 % confidence limits).

irrespective of tidal elevation, but large conspecifics had much heavier valves at high elevations.

Discussion

The distribution of T. serrata is influenced by the heterogenous nature of the local topography which, in conjunction with the prevailing wave regime, defines the actual submergence pattern (Section 1). The present study shows that topographic effects also override absolute elevation as a factor influencing linear accretion of the shell. Thus, partly eroded joints along the edge of the platform are regions not only of high barnacle densities but also of enhanced growth. Because the actual submergence regime determines the degree of exposure to environmental conditions prevailing during submersion and emersion, it seems plausible that increased water-flow through joints should result in, for example, greater food availability per unit time. If the submersion period is in addition lengthened, then the time available for feeding and calcification should also increase (see Bourget, 1980). It is therefore easy to see how the proximity of joints could counteract the depression of growth sometimes associated with high population numbers (e.g. Crisp, 1960).

It is clear that growth enhancement near joints will of course depend on the position of the joints on the shore. At some distance from the sea, the positive growth effect should begin to diminish. This has, in fact, been demonstrated in this study. Why then should shell growth also be slower in areas that lie closest to the sea? A plausible explanation seems indicated by the finding that excessive wave impact jeopardizes successful settlement of T. serrata (Section 1). The nature of any causal relationship between wave impact and shell growth remains to be determined but, bearing in mind that linear accretion rate is unaffected by allometric relationships (this study), any future research on this topic should consider wave impact in terms of, for example, feeding efficiency (cf. Crisp and Bourget, 1985).

In view of the evidence that T. serrata is able to modify aspects of shell allometry independently of linear accretion rate and mass accretion rate of the shell, the question arises what then is the functional significance of observed allometric variability? This question is examined below in terms of two major abiotic factors which jeopardize successful settlement and possibly also survival of newly metamorphosed animals, i.e. aerial exposure and wave impact (Section 1 and this study). At this point, allometric variability observed in the present paper is recapitulated: 1) bulk density increases with age and the rate of increase remains constant irrespective of tidal elevation; 2) small barnacles have thinner, denser shells with larger internal volumes and larger opercular openings at high elevations ; 3) large conspecifics have thicker, more porous shells with smaller internal volumes, smaller openings and heavier valves at high elevations. In addition, the decoupling of shell porosity with respect to linear growth is emphasized because it is commonly assumed that increased porosity results in faster skeletal growth (and vice versa; e.g. Stanley and Newman, 1980; Palmer, 1981). As demonstrated here, this holds true only if a change in porosity affects the relationship between mass and linear accretion rates of the skeleton. Therefore, increased porosity in balanoid shells need not automatically result in faster growth which, Stanley and Newman (1980) argue, accompanied competitive exclusion of chthamaloids from the shallow subtidal in the ancestral past.

For a start, an attempt can be made to identify those skeletal features which could provide protection against aerial exposure. It is commonly accepted that porous structures retain water longer, remain cooler longer and are excellent insulators (Johnson, 1975). Porous shells should therefore be ideally suited to intertidal existence. It is indeed difficult to understand why Stanley and Newman (1980) suggested that, in intertidal barnacles which have porous shells, the advantage of competitive superiority resulting from rapid shell growth (but cf. above) should be counterbalanced by the disadvantage of increased susceptibility to aerial exposure. This disadvantage decreases with size (Foster, 1971), but it is again difficult to see how this decrease might result from what these authors have termed 'secondary calcification' (see Darwin, 1854; Pilsbry, 1916; Palmer, 1981).

In addition to porosity, a second variable affecting protection against aerial exposure is the size of the opercular opening. In fact, Achituv and Borut (1975) have reported a negative correlation between opercular diameter and tidal elevation, and a positive correlation between evaporative water loss and opercular diameter in large Tetraclita squamosa rufotincta occurring in the hot, arid environment of the Red Sea (see Fig. 14).

Large animals on the upper shore at Dalebrook have both increased porosity and smaller opercular openings compared to conspecifics lower down, suggesting that they are better equipped against the effects of excessive aerial exposure. Under these circumstances, it is indeed puzzling to observe that small individuals, which are known to be more susceptible to aerial exposure (Foster, 1971), show exactly the reverse trend.

This apparent paradox could be explained in at least two ways. Firstly, small T. serrata may be sufficiently protected against aerial exposure for aperture diameter to be of no significance. This again raises the question of why large barnacles high on the shore should suddenly revert to constructing shells which are more protective, since it is unlikely that they should once again become more susceptible to aerial exposure. Rather, it is possible that the variations in allometry observed in large barnacles by Achituv and Borut (1975) and in the present study are not 'adaptive' in terms of aerial exposure but simply fortuitous; for example, they could be a coincidental byproduct of a response to some other environmental demand. It is also clear from the data on population distribution and structure that the period of larval settlement, and possibly also the first few months following metamorphosis (Section 1A and Fig. 4 in this study) are the most critical survival phases in the life cycle of T. serrata as far as aerial exposure is concerned.

Secondly, one might suggest that small T. serrata have to compromise between any advantage gained from modifying shell morphology to increase protection against aerial exposure and some disadvantage that this protective measure could cause with respect to reproductive capacity, susceptibility to some other environmental factors, etc. (cf. Seed, 1980). If this is so, the compromise seems to fall away in large animals, seeing that they revert back to constructing a more protective shell. Once again, this could simply be fortuitous.

Whatever the solution to the above paradox, the fact is that small barnacles, and probably large conspecifics as well, appear not to be producing shells which serve to provide increased protection against aerial exposure at high tidal elevations. The question remains what the functional significance of observed trends in porosity and opercular size could be. For barnacles which have less porous shells (i.e. small individuals at high shore levels and large individuals lower down the shore), a plausible connection with improving reproductive success seems indicated by the interplay between porosity, shell thickness and shell internal volume on the one hand, and reproducive output on the other hand. These animals have thinner shells (this study) with larger internal volumes (Section 3A) than comparably sized barnacles at the opposite shore level. Likewise, they have larger reproductive outputs, the significance of which is discussed in a separate study (Section 3A) in terms of age at first reproduction and production costs (see also Section 4). The capacity to maximize reproduction by producing thinner shells with larger internal volumes has obvious limits. As suggested by the present findings, these limits are being extended by a concurrent increase in bulk density.

It is known, on the other hand, that an increase in porosity can improve the strength to mass ratio of the shell in, for example, some echinoderms (see Carter, 1980; Crisp and Bourget, 1985). In addition to increasing shock-resistance capabilities (e.g. to wave impact), it seems plausible that, in sessile organisms such as barnacles, more porous shells will have a higher adhesion capacity per unit mass if concurrent increases in shell thickness occur. This will augment the contact between a shell of given mass and the substratum. If these considerations apply to the allometric relationships observed in the present study, they would in part account for the increase in porosity and thickness of small T. serrata towards the lower shore where wave impact is high. Under such conditions, fast growth to large size would also be advantageous. Significantly, shell growth was faster at lower tidal levels in the present study. Large barnacles, which are known to be less susceptible to mechanical forces (Barnes et+ al., 1970), show reverse trends in shell porosity and shell thickness. In terms of reproduction, it may be advantageous for large animals lower on the shore to produce less protective (i.e. less porous and thinner) shells with larger internal volumes because this increases reproductive output (Section 3A and see above). Why comparably sized animals high on the shore revert back to building more protective (i.e. more porous and thicker) shells with smaller internal volumes, which restrict reproduction, remains unclear (Section 3A).

Prior to the present study, the relationship between shell thickness and tidal elevation reported for some other barnacles has been associated with gradients in the intensity of predation (Vermeij, 1978; see also Palmer, 1982, 1983). These data are impossible to re-evaluate here because they include no information on the trade-off between shell thickness and porosity, i.e. on shell mass.

To summarize the main findings of this study, aerial exposure and wave impact influence the distribution of T. serrata at Dalebrook (Section 1), but variations in shell allometry do not appear to be primarily 'aimed' at coping with either of these abiotic influences, except perhaps in the case of small animals exposed to higher wave impact low on the shore (cf. Lowell, 1984). In addition, allometric variability does not affect linear accretion of the shell, or mass accretion of the shell, or mass accretion of the prosoma. On the other hand, it does affect reproductive output (Section 3A). Thus, carbonate skeletons may limit reproduction but not somatic growth in intertidal barnacles, at least in T. serrata (see also Palmer, 1981; Lively, 1986).

Finally, a word of caution seems appropriate. The present interpretations have relied extensively on existing knowledge of skeletal growth in molluscs, the most widely studied marine invertebrates in this regard (Rhoads and Lutz, 1980). Such analogous explanations remain to be verified and expanded upon for barnacles. In the latter case, interspecific comparisons of skeletal growth have focused on linear accretion rates (Fig. 16, Table 3). These rates are generally slowest in chthamaloids, intermediate in coronuloids (though few data are available here) and fastest in balanoids. In addition to functional aspects, the causality of any correlation between skeletal growth and the environment can ultimately be determined only if the integrated effects of at least four other influences on morphology are accounted for, namely phylogenetic constraints, structural limitations, ecophenotypic effects and plain chance (Seed, 1980). Future work on skeletal growth in barnacles should therefore avoid the current tendency to become too strongly biased towards purely functional ('adaptive') considerations, as has been the case in molluscs (Rhoads and Lutz, 1980). For example, the significance of opercular size as a functional indicator of susceptibility to aerial exposure is questioned in this paper.

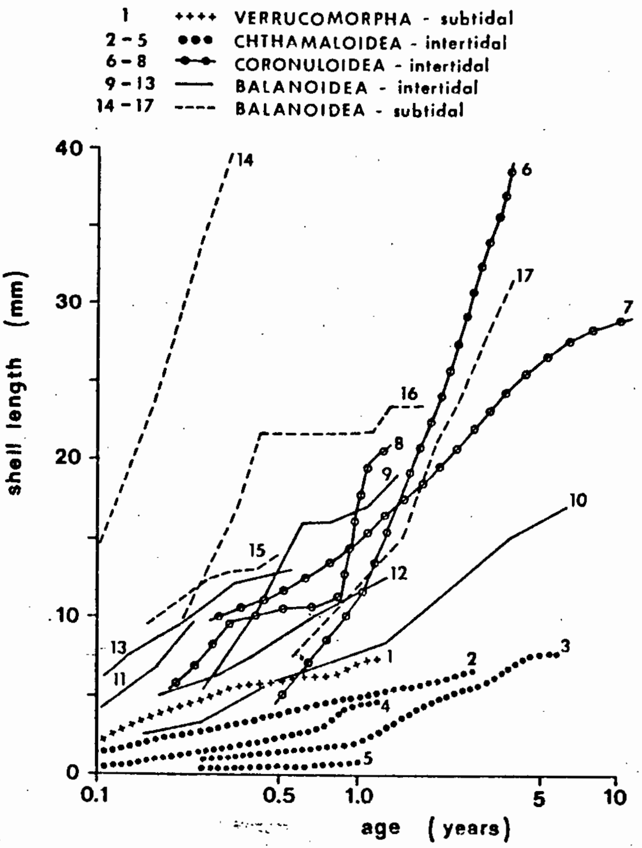

Figure 16. Rates of linear accretion of the shell in barnacles (see Table 3 for references).

Table 3. Literature survey of linear shell growth in barnacles (cf. Fig. 16).

CURVE	SPECIES	LOCALITY	HABITAT	REFERENCE
Verrucomorpha				
1	Verruca stroemia	not given	subtidal	Barnes (1958)
Balanomorpha				
Chthamaloidea				
2	Chthamalus fissus	California	top shore	Hines (1979)
3	Chthamalus dalli	Alaska	intertidal	Southward and Southward (1967)
4	Chthamalus stellatus	Millport?	subtidal transfer	Barnes (1956)
5	Chamaesipho brunnea	New Zealand	top shore	Luckens (1970)
Coronuloidea				
6	Tetraclita squamosa	California	bottom shore	Hines (1979)
7	Tetraclita serrata	South Africa	bottom shore	This paper
8	Tetraclita squamosa rufotincta	Red Sea	intertidal	Achituv and Barnes (1978)
Balanoidea				
9	Semibalanus balanoides	Millport?	bottom and top shore (panels)	Barnes and Powell (1953)
		Woodshole?	mid shore	Barnes and Barnes (1959)
10	Balanus glandula	Vancouver Island	intertidal	Barnes and Barnes (1956)
		Washington	intertidal	Connell (1970)
		California	mid shore	Hines (1979)
11	Balanus eburneus	Trinidad	intertidal (panels)	Bacon (1971)
12	Elminius plicatus	New Zealand	bottom and top shore	Luckens (1976)
13	Elminius modestus	Menai Straits	subtidal transfer	Crisp and Patel (1961)
14	Balanus balanus	not given	subtidal (panels)	Barnes et al. (1963)
15	Balanus trigonus	Miami	subtidal	Werner (1967)
16	Balanus crenatus	Millport?	subtidal (panels)	Barnes and Powell (1953)
17	Balanus porcatus	Irish Sea	subtidal	Crisp (1954)

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SECTION 2B

Appendix

A. To choose a convenient indicator of animal size, the dry mass of the opercular valves of a 'standard' animal (2.5 cm shell length) was monitored throughout the year in corridors 1 (high shore) and 4 (low shore). Values of individual regressions are tabulated below. Because there was no consistent or significant variation in the dry mass of the valves throughout the year (Fig. 1), data for the 8 individual monthly regressions per corridor were pooled (see below and section 2A).

MONTHLY EQUATIONS

Unless otherwise stated in parentheses, ln valve dry mass (mg) = ln a + b shell length (cm) (CL = confidence limits; r = correlation coefficient; N = sample size).

corridor	month	ln a(a)	b	±95 % CL	r	N
	Apr	-0.941	2.29	0.381	0.9471	29
	May	-0.641	2.04	0.378	0.9466	37
	Jun	-1.120	2.30	0.470	0.9450	36
1	Jul	-0.121	1.91	0.411	0.8939	33
	Aug	0.204	1.75	0.468	0.8660	27
	Sep	-0.224	1.92	0.441	0.9050	25
(y=a+bx)	Oct	(-116.0)	94.10	33.60	0.7635	25
	Nov	1.22	1.34	0.365	0.8826	25
	Apr	-0.891	2.10	0.410	0.9430	29
	May	-0.699	2.04	0.389	0.9243	26
	Jun	-0.435	1.86	0.523	0.8646	41
4	Jul	-0.509	1.94	0.365	0.8928	25
	Aug	-0.853	2.07	0.349	0.9554	29
	Sep	-0.309	2.08	0.440	0.8920	27
	Oct	0.265	1.58	0.224	0.9501	25
	Nov	-0.042	1.75	0.398	0.8736	28

COMBINED EQUATIONS

		±95 % CL	r	N	
Corridor 1	$\ln y = -0.521 + 2.08\,x$	0.490	0.9132	233	(1)
Corridor 4	$\ln Y = -0.452 + 1.92\,x$	0.434	0.9214	226	(2)

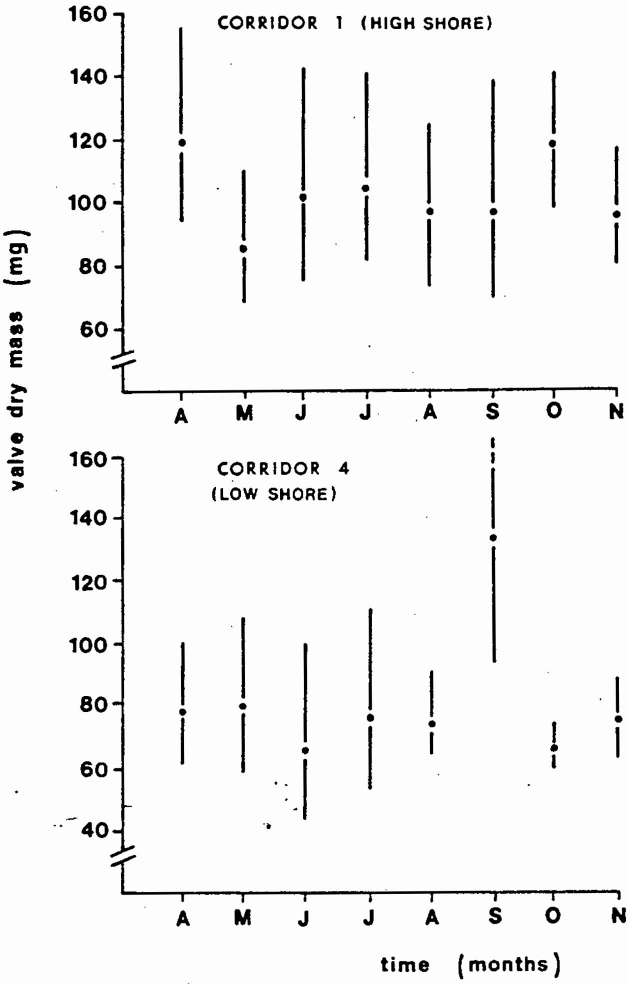

Figure 1. Seasonal variation in the dry mass of the opercular valves of a 'standard' animal (2.5 cm shell length) (95 % confidence intervals are indicated by vertical bars; see text for equations).

B. To compute the mass accretion rates of the shell and of the prosoma in Section 2A, three steps were followed. First, mass was related to animal size every month. A convenient indicator of size was the dry mass of both opercular valves (see A above). For example, log shell (or prosomal) dry mass = log a + b log valve dry mass ,

(3)

Second, the mass of the valves was related to shell length (see equations 1 and 2 above). Third, shell length was related to age (see Section 2A). The results are as follows:

Corridor 1 (high shore)

$\log \text{shell (or prosomal) dry mass}_t = \log a + b \log (0.5939e^{2.08L_t})$

$\text{where } L_t = 3.0784\ (1 - e^{-0.1252}(t + 1.3701)$ (4)

Corridor 4 (low shore)

$\log \text{shell (or prosomal) dry mass}_t = \log a + b \log (0.6364e^{1.92L_t})$

$\text{where } L_t = 2.9000\ (1 - e^{-0.3869\ (t + 0.7863)})$ (5)

The procedure outlined above was also used in Section 4 to compute the mass accretion rates of other body components, i.e. the 'structural' ovary, the 'reserve' ovary, the 'structural' muscle, the 'reserve' muscle, the opercular valves, the semen and the eggs.

Animals could not be aged further once they had reached maximum shell length (see Section 2A). However, opercular valves continued to increase beyond this stage (see Section 2A). In such cases, animals were simply assumed to be 'older' than the age corresponding to maximum shell length (Fig. 2).

There was no consistent or significant variation in the dry mass of the shell or of the prosoma of a 'standard' animal throughout the year (Figs. 3 and 4 respectively). Regressions obtained in December after the breeding period were used to compute mass accretion rates of the shell and the prosoma (see Section 2A).

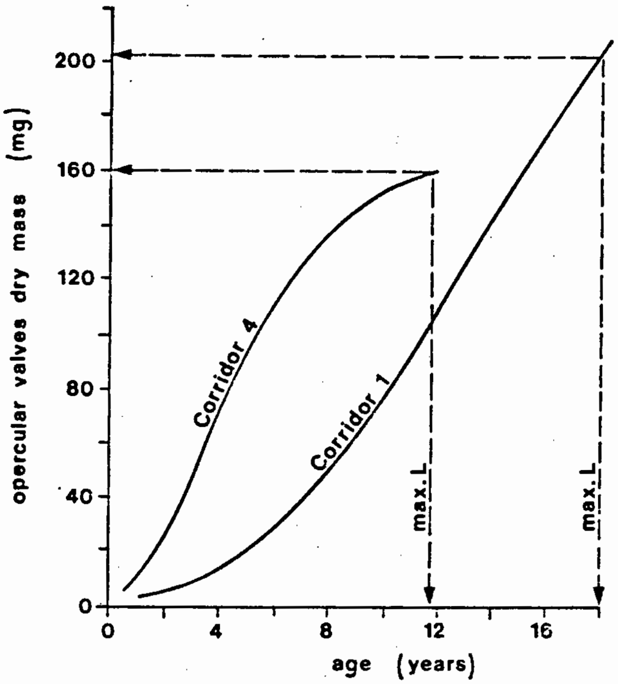

Figure 2. Increase in the dry mass of the valves with age (valve dry $\text{mass}_t = ae^{bL_t}$, see also equations 1 and 2 in text; max. L = maximum shell length observed *in situ*).

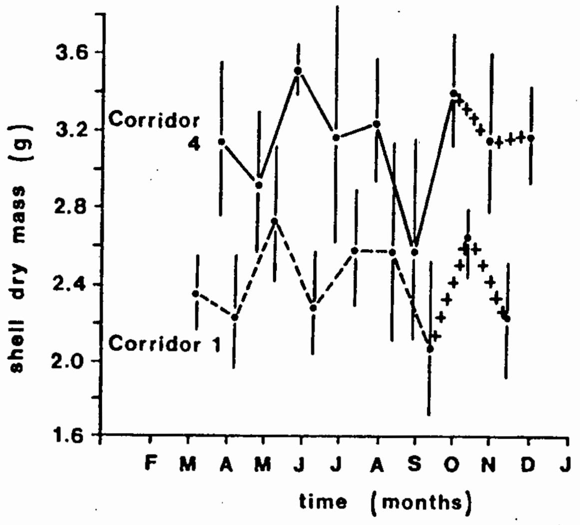

Figure 3. Seasonal variation in the shell dry mass of a 'standard' animal (100 mg valve dry mass) (95 % confidence intervals are indicated by vertical bars; see text for equations; -: non-brooding animals, corridor 4; ---: non-brooding animals, corridor 1; +++: brooding animals, corridors 1 and 4).

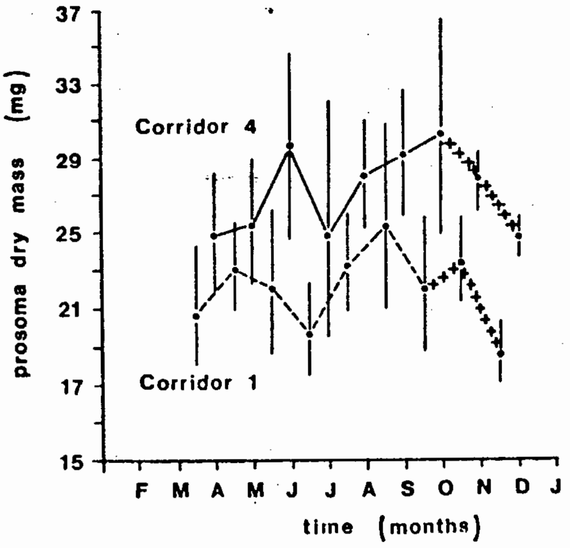

Figure 4. Seasonal variation in the prosomal dry mass of a 'standard' animal (other explanations: idem Fig. 3).

For the relationship of prosomal dry mass vs shell dry mass, data for the 9 individual monthly regressions were pooled (see Section 2A). Values for individual regressions are tabulated below.

PROSOMA

Unless otherwise stated in parentheses, log prosomal dry mass (mg) = log a + b log valve dry mass (mg)(CL = confidence limits; r = correlation coefficient, N = sample size).

corridor	month	log a(a)	b	±95 % CL	r	N
	Apr	-0.070	0.692	0.097	0.9659	31
	May	0.018	0.672	0.075	0.9767	37
	Jun	-0.042	0.693	0.092	0.9602	25
1	Jul	-0.103	0.699	0.086	0.9555	33
	Aug	-0.090	0.728	0.078	0.9602	27
	Sep	-0.056	0.673	0.119	0.9338	26
	Oct	-0.064	0.703	0.099	0.9695	25
	Nov	-0.083	0.643	0.070	0.9597	25
	Dec	0.225	0.522	0.077	0.9487	25
	Apr	-0.035	0.715	0.078	0.9793	29
	May	0.110	0.647	0.092	0.9529	26
(y=a+bx)	Jun	(3.10)	0.265	3.410	0.8803	26
4	Jul	-0.013	0.705	0.103	0.9327	25
	Aug	0.056	0.696	0.076	0.9762	28
	Sep	0.002	0.731	0.077	0.9680	27
	Oct	0.097	0.691	0.113	0.9198	25
	Nov	0.451	0.497	0.084	0.8319	25
(y=a+blogx)	Dec	(-16.7)	20.800	1.780	0.9675	25

SHELL

Unless otherwise stated in parentheses, log shell dry mass (g) = log a + b log valve dry mass (mg) (other information: see above).

corridor	month	log a(a)	b	±95 % CL	r	N
(y=a+bx)	Apr	(0.277)	0.021	0.312	0.9503	31
	May	-1.31	0.828	0.086	0.9798	37
	Jun	-1.22	0.828	0.084	0.9762	25
1	Jul	-1.29	0.824	0.090	0.9644	33
	Aug	-1.29	0.850	0.090	0.9618	27
	Sep	-1.29	0.850	0,119	0.9566	26
	Oct	-1.43	0.873	0.123	0.9695	25
	Nov	-1.21	0.816	0.063	0.9854	25
	Dec	-1.05	0.697	0.106	0.9450	25
	Apr	-1.28	0.887	0.085	0.9839	29
	May	-1.04	0.751	0.078	0.9690	25
(y=a+bx)	Jun	(0.081)	0.034	0.089	0.9950	26
4	Jul	-1.22	0.859	0.092	0.9628	25
	Aug	-1.22	0.864	0.068	0.9874	28
	Sep	-1.34	0.874	0.095	0.9654	27
(y=a+bx)	Oct	(0.159)	0.032	0.426	0.9571	25
	Nov	-1.11	0.803	0.091	0.9602	25
	Dec	-1.02	0.760	0.059	0.9731	25

Section 3 REPRODUCTION

SECTION 3A

The reproduction of the intertidal barnacle *Tetraclita serrata* Darwin: effects of environmental temperature and shell internal volume

Abstract

Reproduction of the barnacle _Tetraclita serrata_ Darwin was investigated at various localities along the South African coast. Brooding is cyclic, occurring during late winter/early summer along the more temperature west coast, and shifting into winter along the subtropical east coast. Ovarian mass varies significantly during the year but the mass of the seminal vesicles remains relatively stable, semen being present in the vesicles throughout the non-brooding period.

In the more temperate regions of the coast, brooding of the population is synchronous irrespective of tidal elevation. Size-adjusted semen production is also similar irrespective of position on the shore. On the other hand, individual brood mass, reproductive 'effort', and the amount of reserves accumulated by the ovary, all vary with tidal level. All three variables have greater values in small _T. serrata_ at higher elevations as compared to lower shore levels. This trend is reversed in all large animals except the very largest ones. A similar set of trends was observed with respect to shell internal volume. It is suggested that allometric relationships involving the availability of internal space may be of primary importance in explaining variations in reproductive output of barnacles along tidal gradients.

Introduction

The intertidal barnacle Tetraclita serrata Darwin occurs in a variety of coastal environments along the southern African shoreline (Day, 1974). The larvae settle successfully under a limited range of physical conditions involving wave impact in combination with emergence/submergence regimes (Section 1). Once settlement has occurred, however, the organism may have to contend with a wide variety of environmental factors. For example, rates of shell growth vary along tidal gradients (Section 2A).

The present work addresses itself to a major event occurring during the post-settlement life-stage, i.e. reproduction. One of its aims was to investigate reproductive patterns along both regional climatic gradients and local, intertidal gradients.

Another aim was to investigate whether reproduction was affected by developmental constraints such as those possibly imposed by body size (Palmer, 1981). Indeed, shells of T. serrata differ in thickness - and presumably also in internal volume - depending on tidal position (Section 2A). If shell internal volume were to limit reproductive output, then one assumption implicit in demographic models - namely, that reproductive traits evolve independently of developmental influences (Stearns, 1976, 1977, 1980) - would be violated.

Study area

One of the study sites was situated at Dalebrook in the temperate environment of False Bay (see General Introduction, Fig. 1). A detailed description of the topography and population distribution at this site is provided in Section 1A. Briefly, a central 13 m x 15 m rock platform rises by at least 50 cm to an upper terrace and drops by at least as much to a lower terrace (Fig. 1). Two corridors were chosen on the platform, each about 5 m wide and lying parallel to the shore. The lower corridor,

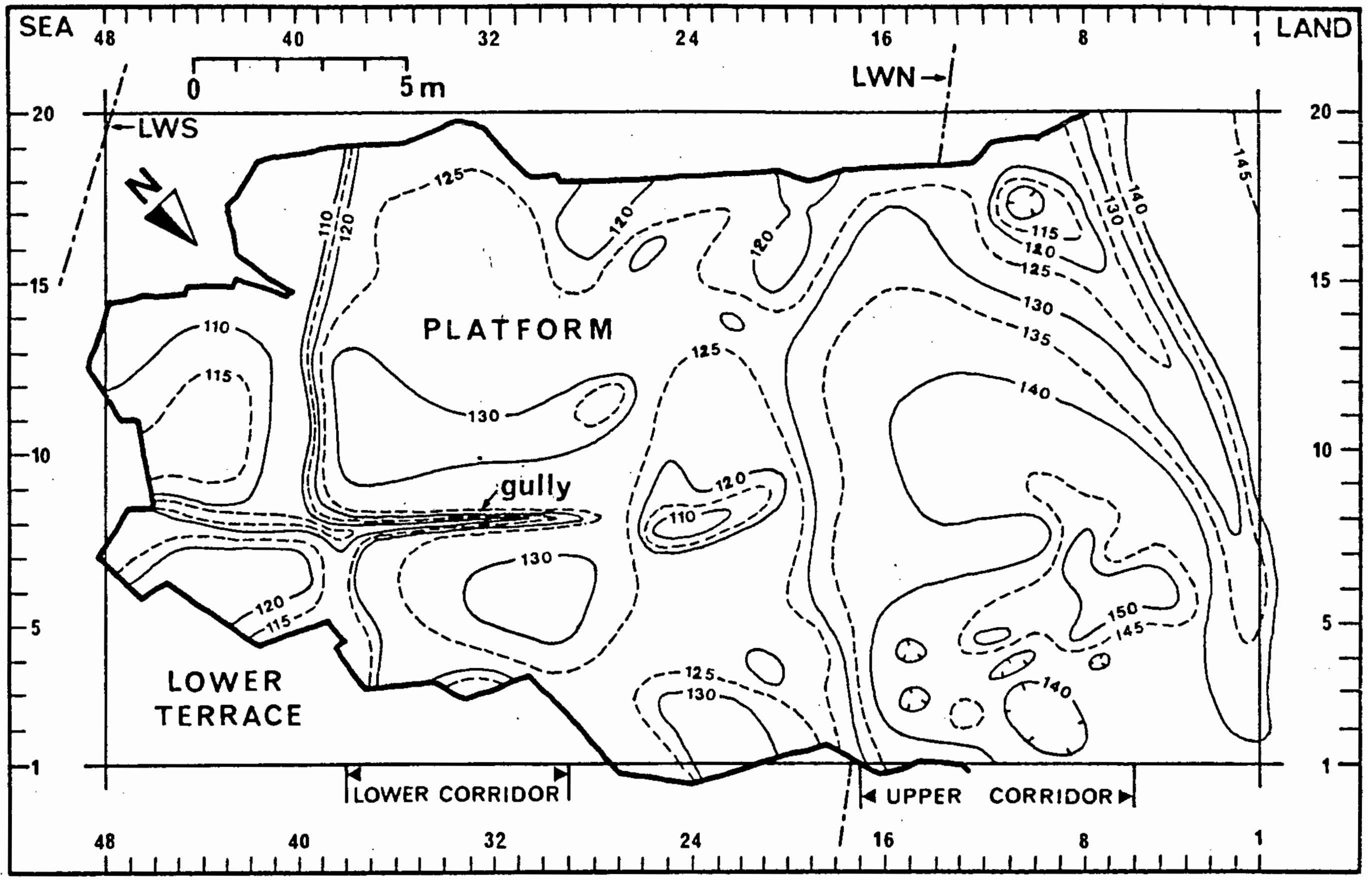

Figure 1. Topography of the main study area at Dalebrook (False Bay), showing the positions of the two sampling corridors on the rock platform (extracted from Section 1A) (LWS: low water springs; LWN: low water neaps; elevation contours are in cm above chart datum).

i.e. the one nearest the sea, spanned a range of relatively low elevations as compared to the upper corridor. Peak animal densities were similar in both corridors but variations in density were greater in the upper corridor (Fig. 2).

The other two research sites were predominantly influenced by the warm Agulhas Current which travels along the south-east coast of Africa (see General Introduction, Fig. 1). One of these sites was situated in the subtropical environment of Durban, the other at Port Elizabeth where conditions are intermediate between those of Durban and False Bay.

Materials and Methods

Barnacle samples were collected every month for at least one year. Animal size was assessed either by measuring the length of the shell (along the rostro-carinal axis) or by weighing both dried opercular valves (see Section 2 for treatment of valves and use of valve mass as an indicator of animal size).

In one series of fresh subsamples, the development of the ovary, the seminal vesicles and the eggs was assessed visually according to the following classification schemes:

1) For the ovary (after Crisp and Patel, 1961):
stage A = not visible; stage B = visible; stage C = well-developed; stage D = profuse.

2) For the seminal vesicles (after Crisp and Patel, 1961):
stages A, B, C as for the ovary.

3) For the eggs (after Sandison, 1954):
stage 1: no embryos in mantle-cavity; stage 2: 2-16 cells, light yellow; stage 3: many cells, appearance of appendage buds; stage 4: eye spot, distinct appendages; stage 5: fully developed with gut, purple-black. In the case of samples from Durban and Port Elizabeth, a simpler classification scheme was used: younger

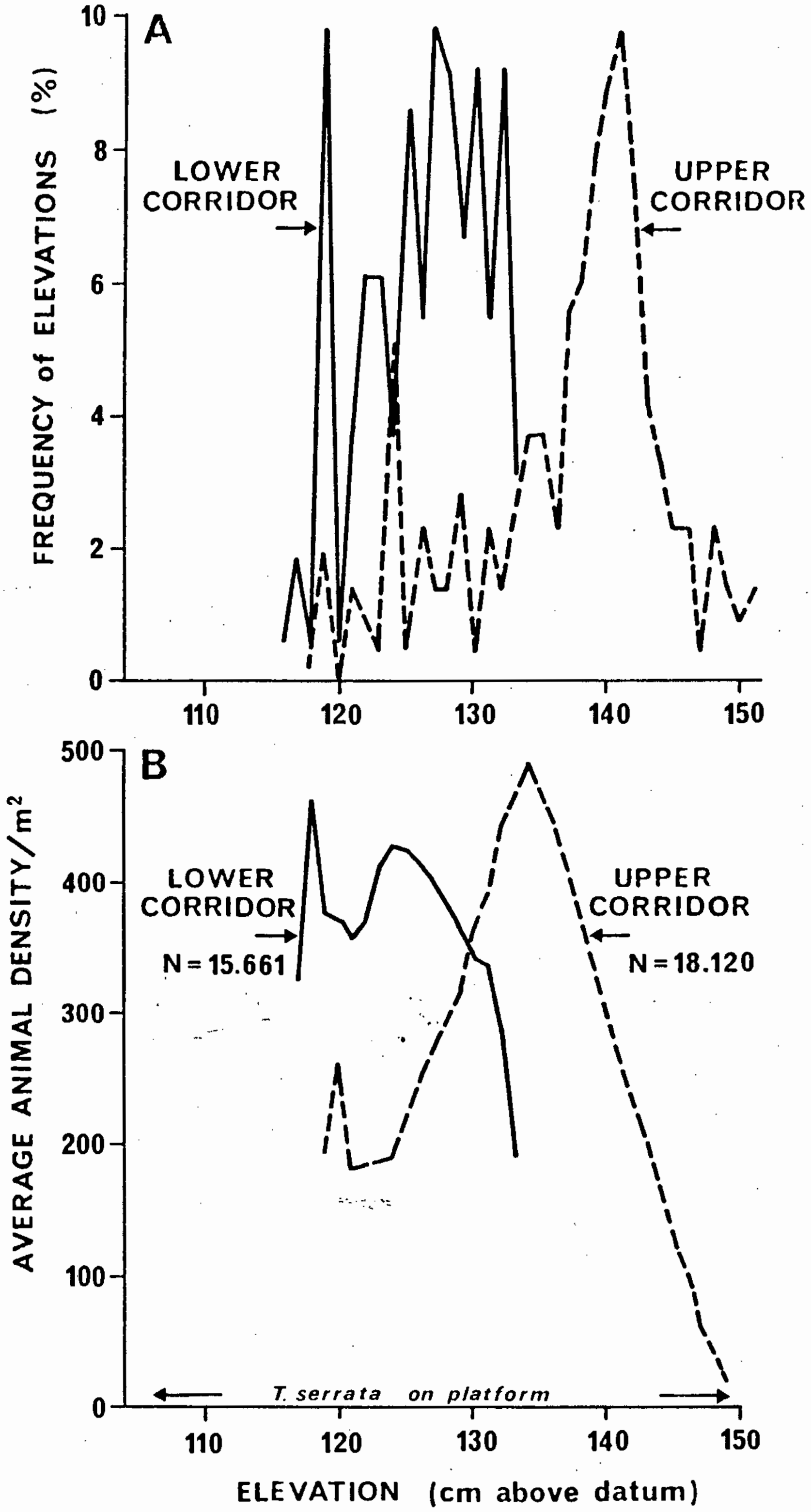

Figure 2. Comparison of elevations (A) and animal densities (B) between the upper and lower corridors at Dalebrook (extracted from Section 1A) (N = sample size).

embryos without eyes were assigned to an early (E) stage (equivalent to stages 2 + 3 above), whereas older embryos with eyes were assigned to a late (L) stage (equivalent to stages 4 + 5 above).

Other subsamples were immediately freeze-dried. The ovary and eggs were subsequently weighed on a Mettler ME30 microbalance. Data on prosomal masses were extracted from Section 2B.

The mass of the seminal vesicles was determined as follows: the vesicles were removed from fresh prosomas in one series of barnacles while, in another series, intact prosomas were retained; after freeze-drying, the prosomas were weighed individually; the difference in mass between intact prosomas and those from which vesicles had been removed represents the mass of the vesicles. Values obtained during the brooding period were considered to provide a fair indication of the minimum amount of semen produced per year. This is based on the assumption that, as in the case of Balanus balanoides (Barnes et al., 1977), the vesicles are depleted of semen during copulation.

The minimum number of broods produced each year was estimated by considering a) the maximum mass the ovary reached immediately before the onset of brooding; b) the residual mass of ovarian tissue which persisted during the non-brooding period ('structural' ovary); and c) brood mass. Assuming that resorption of ovarian material is negligible (Barnes and Achituv, 1976), the difference between a) and b) represents the minimum amount of ovarian material lost in the form of eggs ('reserve' ovary). The minimum number of broods produced per adult per year was then estimated by dividing the mass of the reserve ovary by the mass of a single brood, on the assumption that the number of eggs present in the brood is a fair indication of the number of eggs released by the ovary. In effect, barnacle eggs are enclosed in protective egg-cases the moment they enter the mantle-cavity of the adult (Barnes et al., 1977; Klepal et al., 1977). Values resulting from these calculations were rounded off to the nearest whole number.

Results

Seasonal reproductive patterns

Three main trends were evident in the occurrence of reproduction along the coast. First, brooding was always cyclic (Fig. 3). At least 20 % of the population bore eggs for about 5 months of the year. Secondly, there appeared to be considerable yearly variation in the timing and duration of the brooding period at any particular locality (Fig. 3). Thirdly, in regions which have high sea and air temperatures, brooding shifted into the cooler months (Fig. 4). This latter trend was not associated with any obvious changes in the time span over which the brood developed in the adult. Irrespective of geographic locality, at least some of the embryos were nearly mature within one month of the start of the brooding period (Fig. 4).

At Dalebrook, both brooding activity and ovarian development showed an annual cyclicity (Fig. 5). The ovaries of larger (older) barnacles were visible throughout the year, but they became particularly profuse just prior to the onset of the brooding period. Gonadal reserves began to accumulate 5-6 months before the onset of spawning (Fig. 6; see Table 1A for equations). Smaller (younger) conspecifics, on the other hand, had barely discernible ovaries throughout the year. In fact, most of them did not produce eggs at all (Table 2).

In contrast to the marked cyclicity of ovarian development at Dalebrook, the seminal vesicles remained fully filled with semen throughout the year (Fig. 7). In addition, their mass constituted a persistently high proportion of prosomal mass. For example, the mass of the vesicular semen formed about 30 % of the prosomal mass in large specimens during the brooding season (see August and October, Fig. 8). At the end of the brooding period, semen mass decreased somewhat, although it continued to contribute up to 21 % of the prosomal mass (see May, Fig. 8; equations are given in Table 1B).

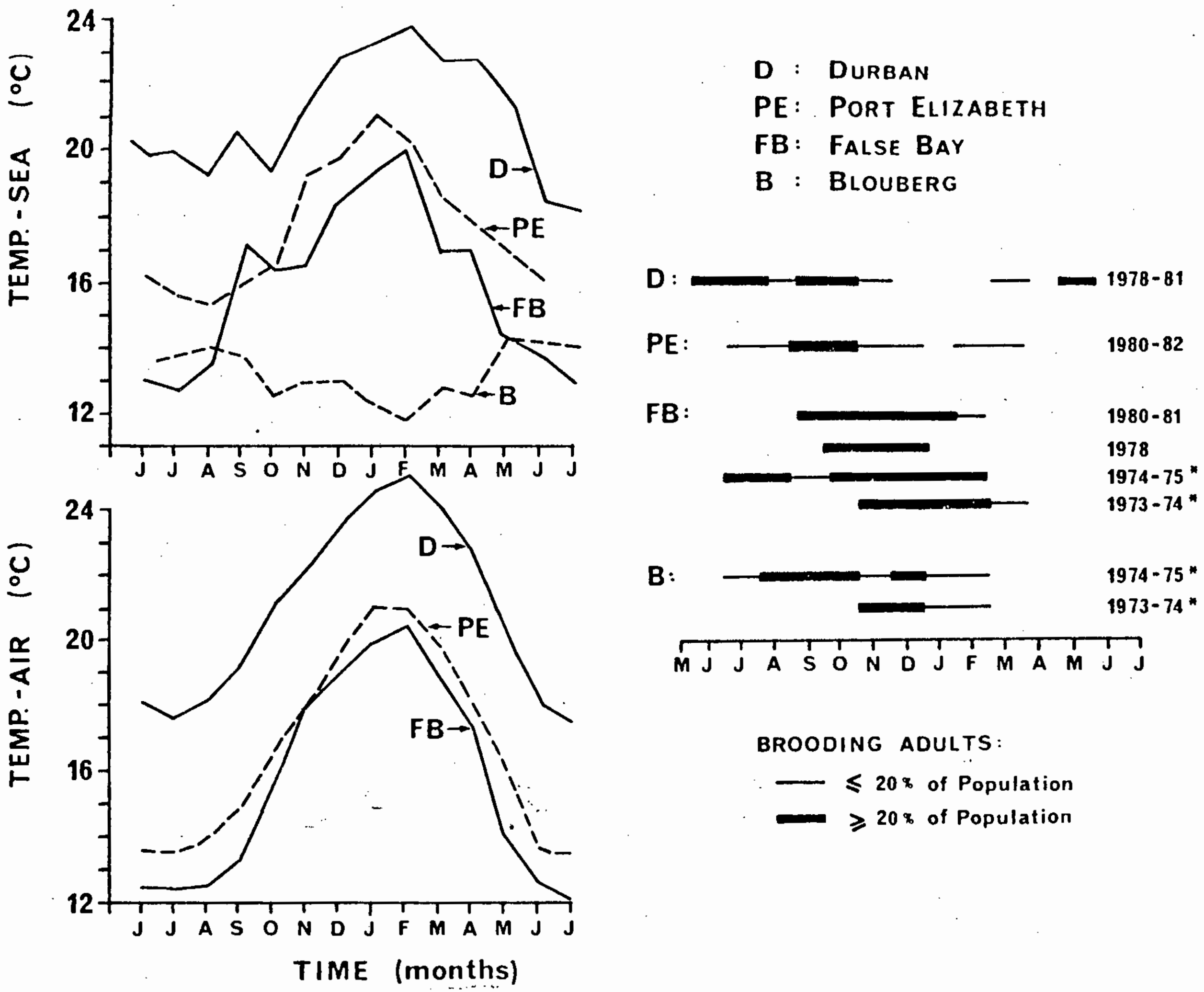

Figure 3. Incidence of brooding adults in local populations along the South African coast (*: extracted from Griffiths, 1979; mean sea temperatures: Griffiths (1979), Beckley (pers. comm.), Maritime Weather Office, Natal Anti-Shark Measures Board; mean air temperatures: Deutsches Hydrographisches Institut; False Bay air temperatures indicate conditions existing at both Dalebrook and Bloubergstrand).

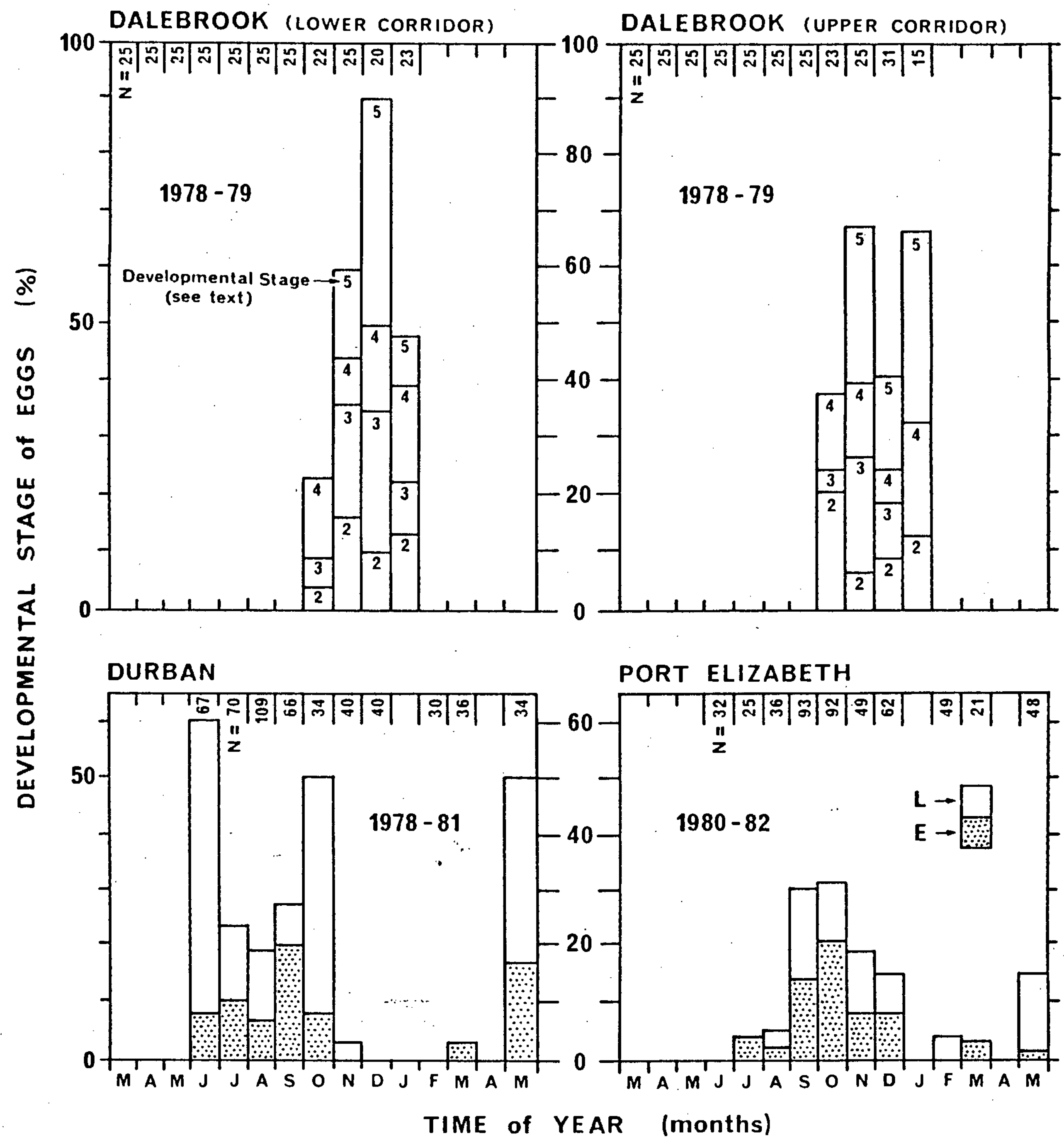

Figure 4. Degree of development of the broods in local populations along the South African coast (developmental stages 2-5: ascending series of egg maturation; developmental stage E: early stage in egg maturation; development stage L: late stage in egg maturation; N = sample size).

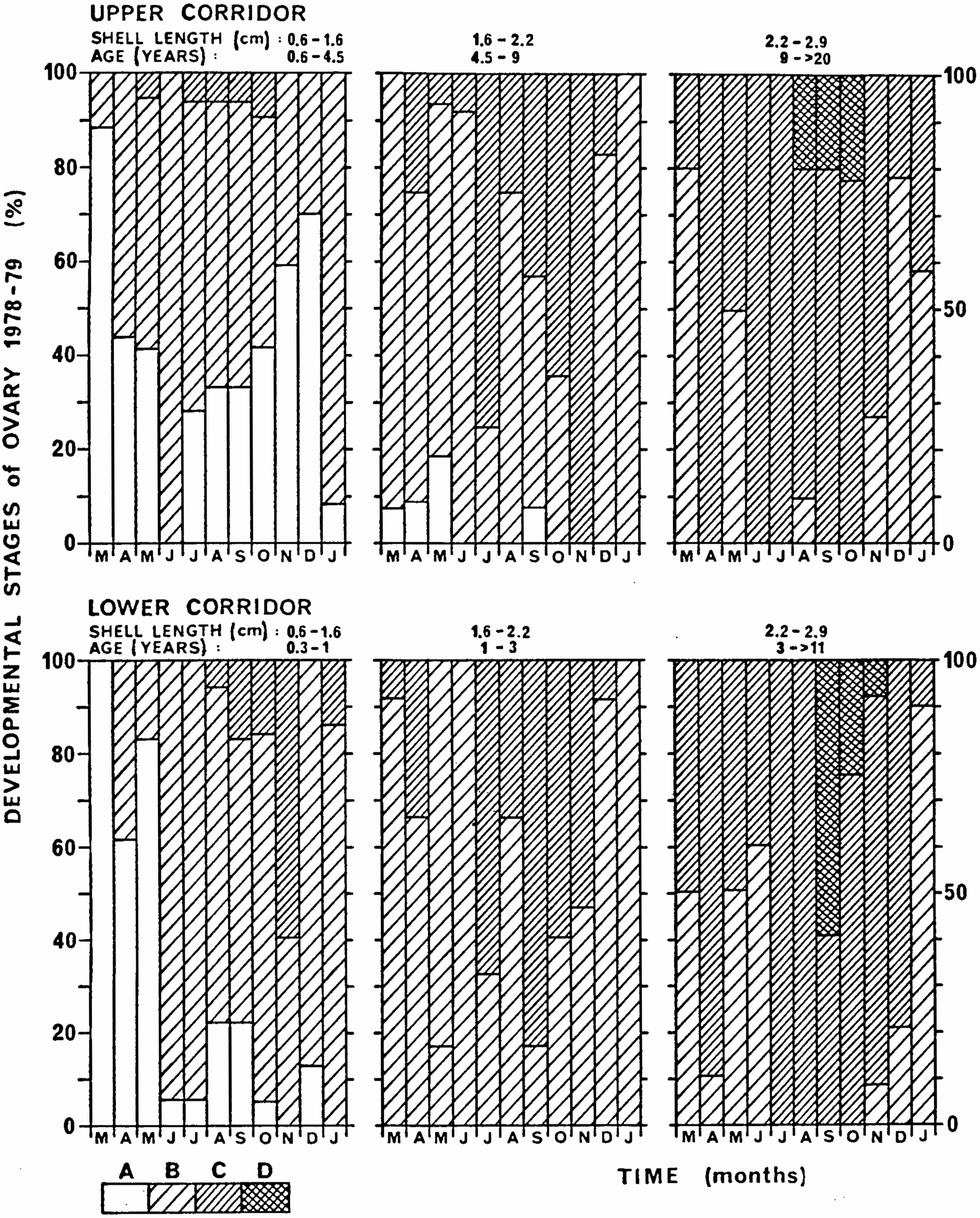

Figure 5. Degree of development of the ovary thoughout the year at Dalebrook (developmental stages A-D: ascending series in ovarian maturation; length vs age relationships extracted from Section 2).

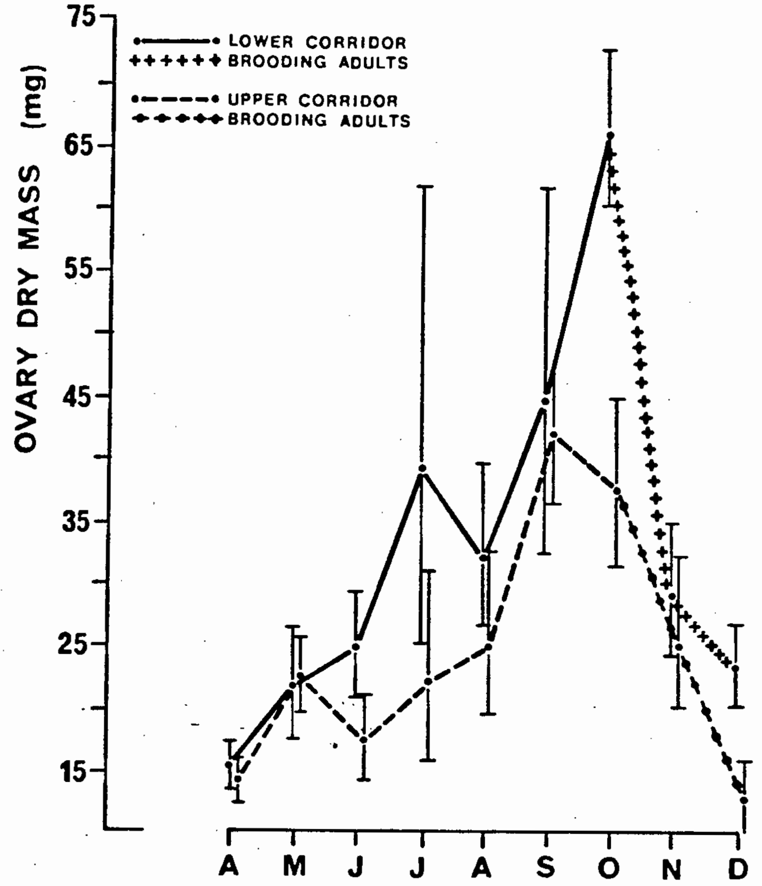

Figure 6. Monthly variation in the mass of the ovary in a 'standard' animal (100 mg valve dry mass) in upper and lower corridors at Dalebrook. 95 % confidence limits are indicated by vertical bars; see Table 1A for equations.

Table 1. Equations relating the masses of various body components to animal size at Dalebrook (measure of size: valve dry mass) (CL = confidence limits; r = correlation coefficient; N = sample size).

A. Ovary dry mass, y (mg) vs valve dry mass, x (mg) (see Fig. ~~7~~ 6; x variable is the mass of both opercular valves)

1978	**upper corridor**	**± 95 % CL**	**r**	**N**
Apr	y = -0.600+0.150 x	3.050	0.9049	30
May	y = -1.610+0.239 x	4.430	0.9241	37
Jun	y = 1.410+0.159 x	4.400	0.8289	24
Jul	log y = -0.310+0.824 log x	0.231	0.8173	33
Aug	log y = -0.169+0.782 log x	0.193	0.7629	22
Sep	y = 3.420+0.383 x	6.820	0.8978	21
Oct	y = 6.050+0.314 x	10.800	0.8532	20
Nov	log y = -0.480+0.936 log x	0.163	0.8136	20
Dec	log y = -0.444+0.317 log x	0.164	0.6181	20

1978	**lower corridor**	**± 95 % CL**	**r**	**N**
Apr	y = -0.185+0.154 x	3.260	0.9116	29
May	y = -29.60+25.70 log x	6.120	0.8550	25
Jun	y = 0.478+0.243 x	3.180	0.8877	26
Jul	log y = -0.307+0.949 log x	0.205	0.8689	21
Aug	log y = -0.187+0.844 log x	0.144	0.8888	21
Sep	log y = -0.374+1.010 log x	0.175	0.8240	22
Oct	y = -4.970+0.708 x	8.480	0.9644	21
Nov	log y = 0.126+0.665 log x	0.124	0.8037	20
Dec	log y = -0.186+0.770 log x	0.122	0.8597	20

B. Seminal vesicle dry mass, y (mg) vs valve dry mass, x (mg) (see Fig.~~9~~8; y variable is the mass of both vesicles; x variable is the mass of both valves) (P = whole prosoma; P' = prosoma from which both vesicles have been removed; S = seminal vesicles; V = opercular valves; dry masses of all components are in mg)

1980	**upper corridor**	**±95 % CL**	**r**	**N**
Oct	log P = 0.240+0.581 log V	0.064	0.9726	30
	log P'= 0.183+0.547 log V	0.062	0.9638	20
	log S = -0.587+0.693 log V		0.9999	14

1980	**lower corridor**	**±95 % CL**	**r**	**N**
May	log P = 0.149+0.629 log V	0.065	0.9555	28
	log P'= -0.135+0.719 log V	0.076	0.9592	26
Aug	log P = 0.168+0.853 log V	0.092	0.9633	31
	log P'= -0.065+0.728 log V	0.060	0.9721	27
Oct	log P = 0.151+0.673 log V	0.057	0.9711	29
	log P'= 0.113+0.615 log V	0.077	0.9391	29
	log S = -0.699+0.834 log V		0.9999	14

C. Egg dry mass, y (mg) vs valve dry mass, x (mg)
(see Fig.9~~10~~; y variable is the mass of both egg lamellae; x variable is the mass of both valves)

UPPER CORRIDOR

egg stages	equation
2 + 3	$\ln y = 0.4949 + 0.5321 \ln x$; $r = 0.7501$; $N = 32$
4 + 5	$\ln y = -0.2329 + 0.6794 \ln x$; $r = 0.7706$; $N = 40$

LOWER CORRIDOR
(regression terms shown to 4 decimal places only)

egg stages	equation
2 + 3	$y = 42.2868 - 3.4620\,x + 0.1282\,x^2 - 0.0021\,x^3$; $r = 0.9112$; $N = 37$
4 + 5	$y = -12.6959 + 1.7253\,x - 0.0542\,x^2 + 0.0009\,x^3$; $r = 0.8949$; $N = 33$

D. Reserve ovary dry mass, y (mg) vs valve dry mass, x (mg)
(see Fig.10~~11~~) (M = maximum ovarian mass prior to spawning; R = reserve ovary; S = structural ovary; V = opercular valves; dry masses of all components are in mg)

1978	**upper corridor**	**r**	**N**
Sep	$M = 3.420 + 0.383\,V$	0.8978	21
Apr	$S = -0.600 + 0.150\,V$	0.9040	30
	$R = 4.014 + 0.233\,V$	0.9999	15

1978	**lower corridor**	**r**	**N**
Oct	$M = -4.970 + 0.708\,V$	0.9644	21
Dec	$S = 3.890 + 0.191\,V$	0.8695	20
	$R = -8.860 + 0.517\,V$	0.9999	15

Table 2. Frequency (%) of brooding within specific age (or size) classes at Dalebrook (size-age relationships were extracted from Section 2; measure of size: dry mass of both opercular valves; N: sample size)

	age (years)	**valve dry mass** (mg)	**% brooding** Oct '78	Nov '78
lower corridor	2	25	-	30
	2-4	25-70	21	71
	4-7	70-127	0	78
	7-11	127-157	33	100
	> 11	> 157	100	67
	N		30	68
upper corridor	3-5	9-20	0	14
	5-10	20-77	40	56
	10-15	77-157	50	79
	> 15	> 157	50	60
	N		30	56

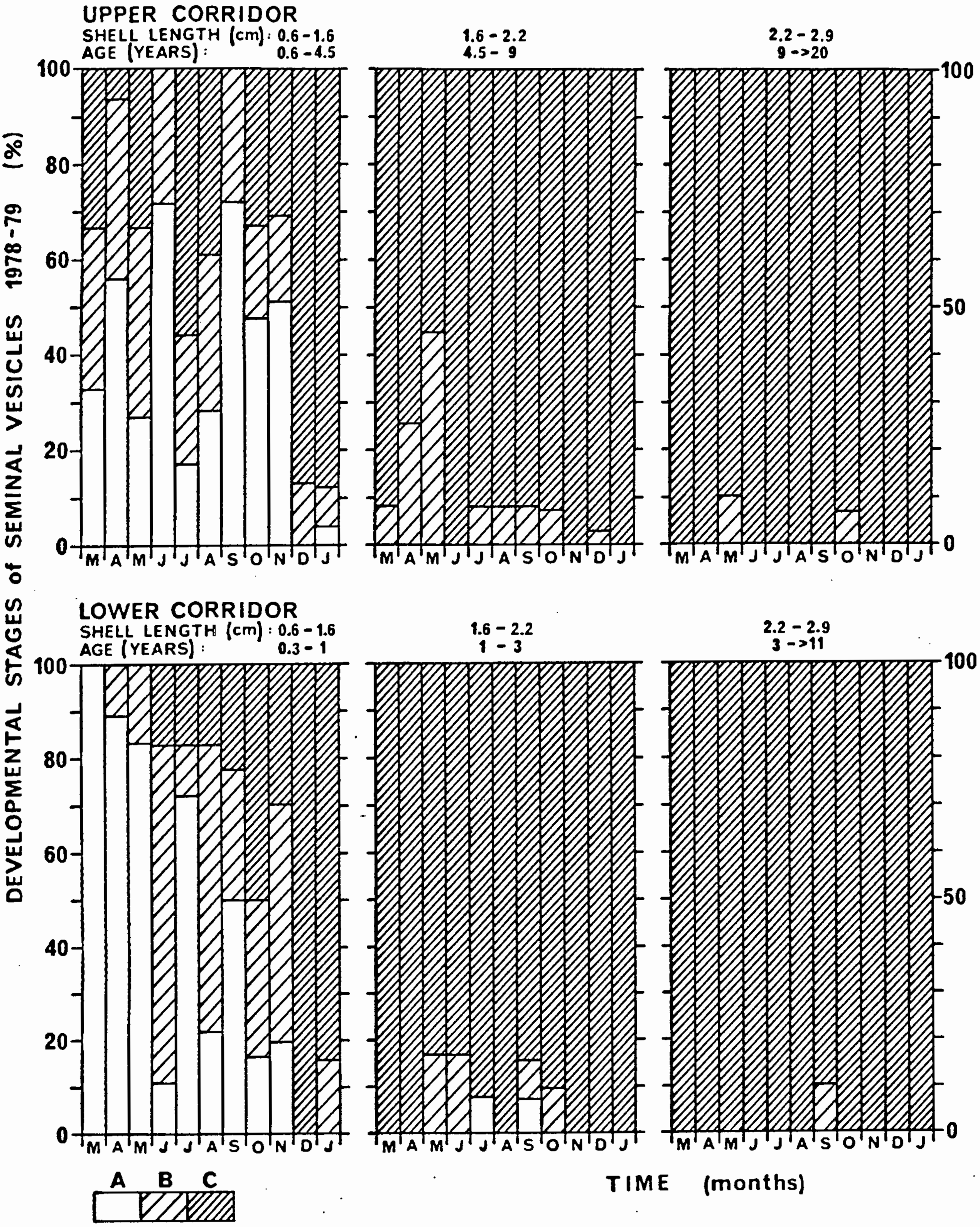

Figure 7. Degree of development of the seminal vesicles throughout the year at Dalebrook (developmental stages A-C: ascending series in vesicular maturation; other information: see Fig. 5).

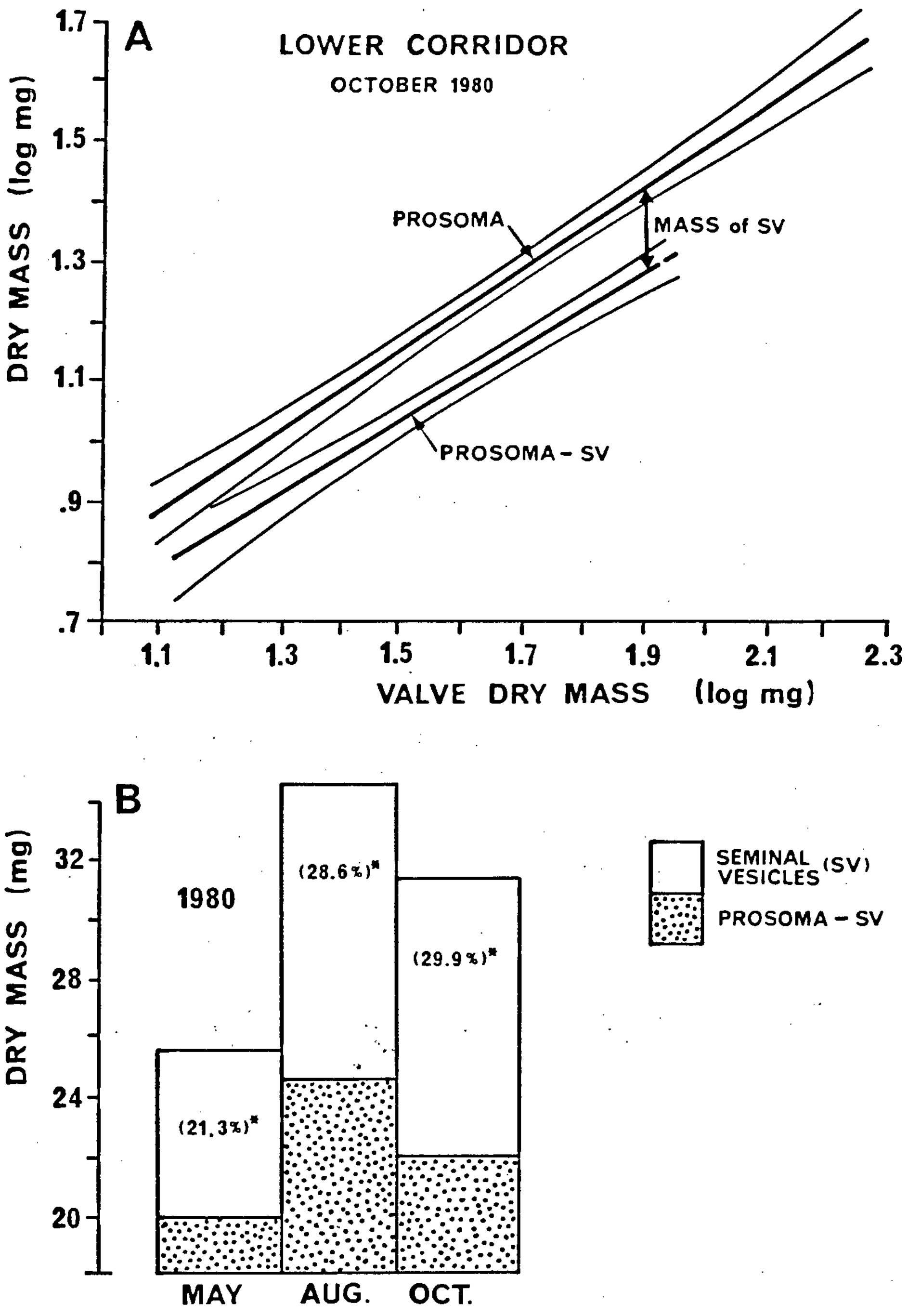

Figure 8. Seasonal variation in the mass of the seminal vesicles in the lower corridor at Dalebrook. A: computation of mass in relation to animal size (i.e. valve dry mass). B: mass in a 'standard' animal (100 mg valve dry mass). 95 % confidence limits are indicated for regressions; see Table 1B for equations; *: mass of both seminal vesicles expressed as % of prosomal mass.

Brooding frequency

By combining, 1) present data on brood and ovarian masses (Figs. 9 and 10) with 2) data extracted from Section 2A concerning the relationship between animal size and age, the annual brooding frequency at a given age was estimated (see also Materials and Methods). The results show that barnacles as young as 2 years accumulated sufficient ovarian reserves to produce a single annual brood in the lower corridor (Table 3; see also Table 2). Initial reproduction was, on the other hand, deferred for an additional year higher up the shore. These upper shore animals continued to produce one annual brood until they were about 12 years old, after which they produced 2 broods per year. Conspecifics in the lower corridor, in turn, produced a second annual brood by their fourth year. By the time they were 12, lower shore animals accumulated enough reserves to produce as many as 3 broods per year. A conservative estimate of 2 annual broods has, however, been utilized in further calculations. Since high shore adults of a given age are much smaller than their counterparts lower down the shore (Section 2A), the lag in reaching first reproduction and maximum brooding frequency observed in the upper corridor could be explained if reproduction were proportional to body size. The relationships between reproductive output and various measures of body size are discussed below.

Reproduction vs valve mass

The relationship between individual brood mass and valve mass (a commonly used measure of size in barnacles) differed substantially between individual habitats on the platform (Fig. 9; equations are given in Table 1C). In the lower corridor, brood masses were positively correlated with valve masses initially. Peak values in brood mass were reached as the valve mass corresponding to maximum shell length was approached. At this point, growth of other major somatic components such as the prosoma, the muscles, etc., also ceased but the valves continued to increase in size as the animal aged further (see Section 2B). On the other hand, brood masses decreased in these large animals

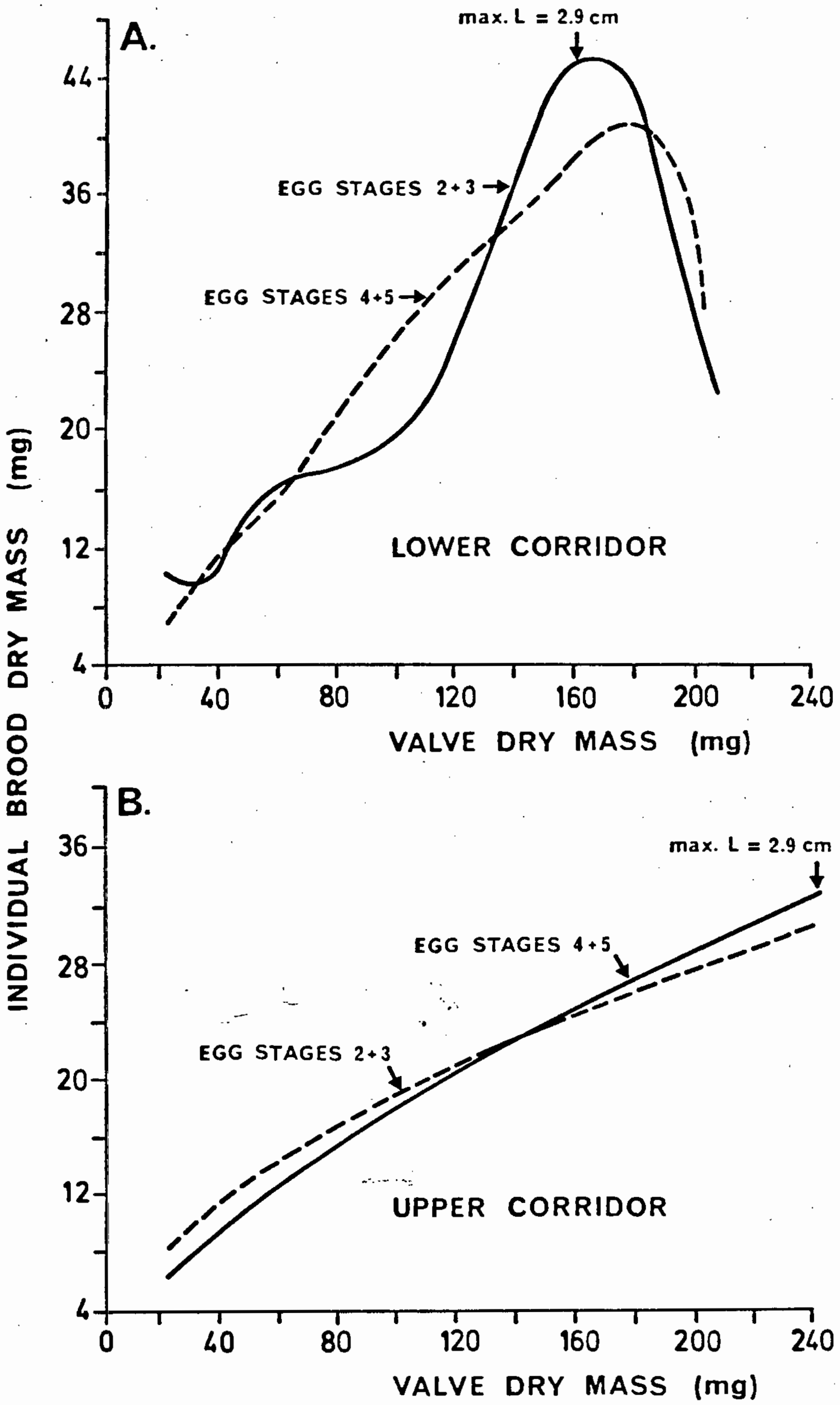

Figure 9. Mass of a single brood in animals of various sizes (i.e. valve dry masses) at Dalebrook. A: lower corridor; B: upper corridor (brood: both egg lamellae; for equations see Table 1C; for developmental stages 2-5 see Fig. 4; max. L: maximum shell length observed *in situ*).

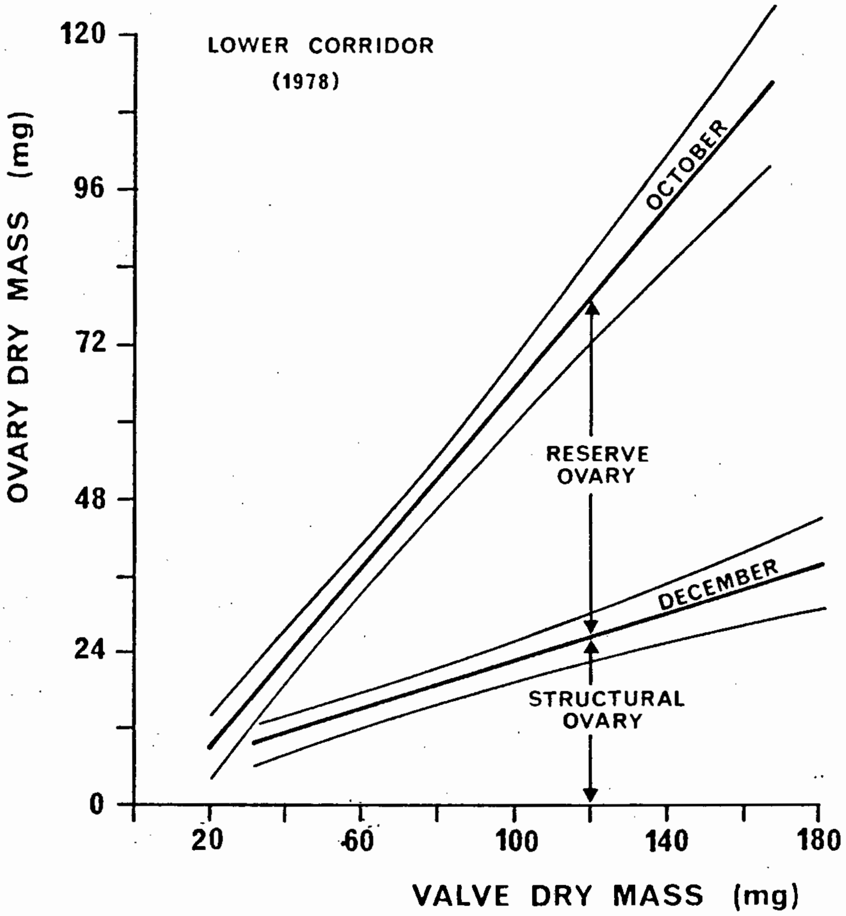

Figure 10. Computation of mass of reserve ovary at a given animal size (i.e. valve dry mass) in the lower corridor at Dalebrook. 95 % confidence limits are shown for regressions; for equations see Table 1D; for further explanations see Fig. 6.

Table 3. Annual brooding frequencies at various ages at Dalebrook. b: calculated frequencies; B: frequencies rounded off to nearest whole number. Size-age relationships were extracted from Seciton 2. *: conservatively estimated as 2 broods per year, see text for explanation.

upper corridor			**lower corridor**		
age (years)	**b**	**B**	**age** (years)	**b**	**B**
2	0	0	2	0.46	1
3	1.16	1	3	1.14	1
4	1.09	1	4	1.58	2
6	1.09	1	6	2.08	2
8	1.19	1	8	1.70	2
10	1.33	1	10	1.62	2
13	1.55	2	>11	2.76	2*
16	1.74	2			
> 18	1.90	2			

(Fig. 9A). In contrast with this pattern, brood masses increased not only less rapidly but also continuously as a function of valve mass in the upper corridor (Fig. 9B).

The various trends discussed above show that, in T. serrata, individual brood mass and valve mass are not related to each other in a fixed manner throughout the intertidal zone. Consequently, valve mass cannot be used as a general indicator of reproduction in this case. On the other hand, reproduction could be consistently proportional to the size of some or other body component not strictly accounted for by valve mass.

Reproduction vs prosomal mass

Fig. 11 shows the relationships between reproductive components and another commonly used measure of body size in barnacles, i.e. prosomal mass (e.g. Hines, 1978). Semen production was related to prosomal mass in a similar manner irrespective of position on the platform. By contrast, production of ovarian reserves and of individual broods differed substantially between the upper and lower corridors (Fig. 11A). As prosomal masses increased, so did production values for the latter two components. Small animals had higher levels of production in the upper corridor than lower down the shore. This trend was subsequently reversed as maximum prosomal mass was approached. However, the largest barnacles showed a sudden decline in individual brood mass in the lower corridor but not higher up to the shore.

The results discussed above mean that, in the upper corridor, the annual reproductive 'effort' (i.e. the ratio between the masses of the male and female reproductive products and of the prosoma) of the small barnacles was greater than lower down the shore (Fig. 11B). The opposite trend occurred in large animals. Evidently, prosomal mass is also not a general measure of reproduction. The question thus arises how reproduction relates to shell size.

Reproduction vs shell internal volume

The simplest measure of shell size which might limit reproductive output is internal volume. To recapitulate the variations in shell allometry (Section 2A) which could affect reproduction, small shells higher on the platform have significantly thinner walls, whereas the reverse applies to large shells (Fig. 12A). Given that shell internal volume can be approximated in terms of a corresponding cone, the thicker walls of small shells in the lower corridor reduced their internal volumes by as much as 24 % in comparison to high shore shells (Fig. 12B). On the other hand, the thinner walls of large shells low on the shore resulted in volume increasing by as much as 12 % in large, low shore barnacles compared to animals higher up the platform.

Trends in shell internal volume discussed above became evident when barnacles from the upper and lower corridors were compared on the basis of shell lengths. Because shell lengths were consistently related to prosomal masses irrespective of position on the platform (Section 2A), it follows that the same trends would be evident if the barnacles were to be compared on the basis of prosomal masses. Recalling the relationships between reproduction and prosomal masses discussed above (Fig. 11), small barnacles higher on the shore not only have larger internal volumes but also accumulate more ovarian reserves, produce bigger individual broods and have higher reproductive 'efforts' than their low shore counterparts, whereas the reverse is true for large animals. The only barnacles which formed an exception to this were the very largest ones.

Discussion

In contrast with other barnacles which have regular brooding cycles, T. serrata retained vesicular semen during the non-brooding period. Because the spermatozoa contain substantial reserves (Section 3B), they should have some degree of metabolic self-sufficiency during their stay in the vesicles prior to

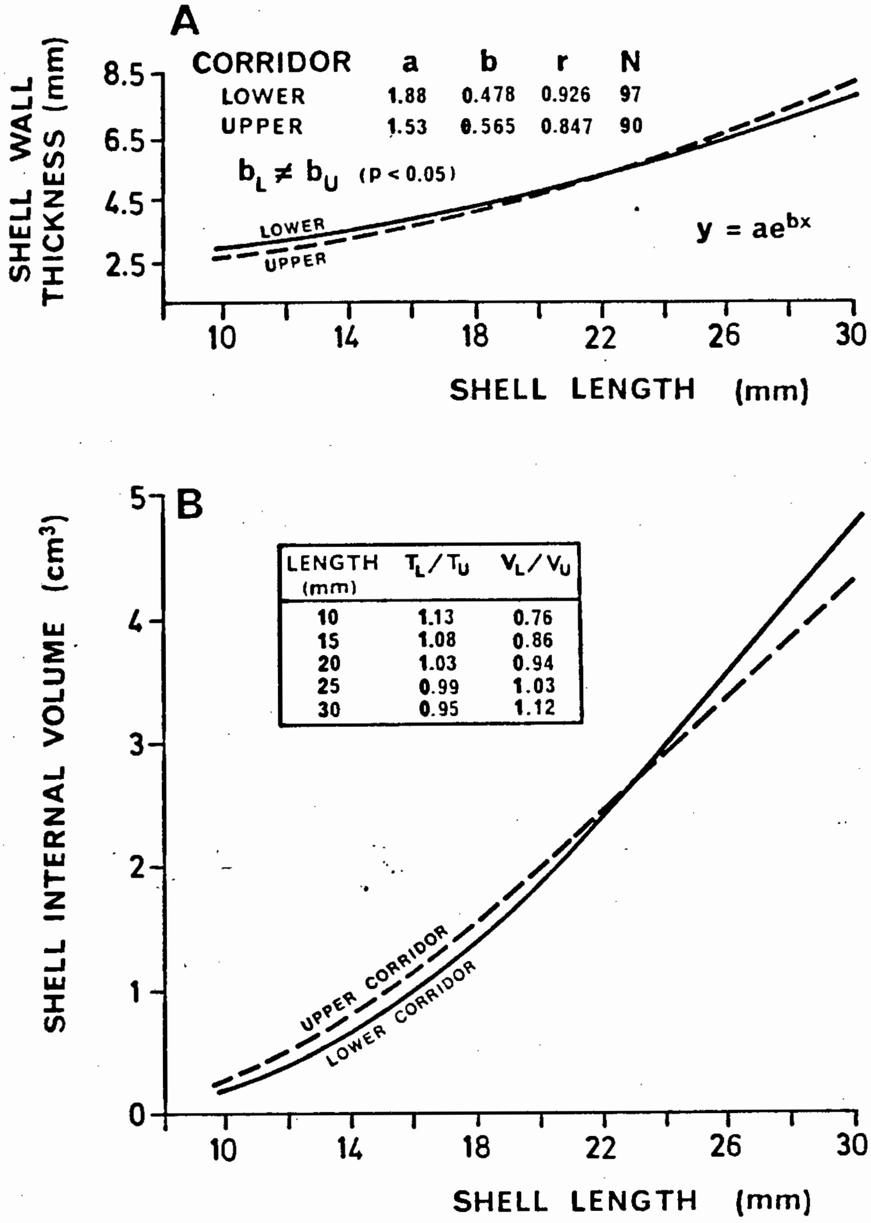

Figure 12. Relationships between shell variables at Dalebrook. A: shell wall thickness *vs* shell length (extracted from Section 2). B: shell internal volume *vs* shell length (r: correlation coefficient; N: sample size; T_L/T_U: ratio between the shell wall thickness of lower and upper shore animals; V_L/V_U: ratio between the shell internal volumes of lower and upper shore animals).

cross-fertilization. Similarly, although the mass of the ovary was much reduced during the non-brooding period, the female gonad also retained mature sex-cells during this time (Section 3C). At this stage, it is not clear why so-called 'acyclic gametogenesis' should occur in a species which breeds only at a certain time of the year. Clearly, any future work on this topic should consider potential causal relationships between environmental instability and variability in brooding activity.

Despite yearly variability in the exact timing and duration of brooding at a given locality, local reproductive patterns remained broadly consistent. Whereas brooding was generally confined to the late winter/early summer months under the more temperate west coast conditions, it shifted into winter in the subtropical south and east coast environments. This shift does not, of course, constitute formal proof that T. serrata was adjusting to different temperature regimes as such (cf. Hines, 1978). However, this view is supported by evidence of concurrent 'homeoviscous adaptation' in which membrane phospholipids alter the degree of saturation of their component fatty acids as a common response to fluctuating ambient temperature (Delafontaine, unpub. data).

In contrast to this evidence of responses to temperature along regional climatic gradients, tidal gradients did not have the same effects on local populations in the temperate environment of False Bay. First, brooding was synchronous over the whole shore. Second, fatty acid profiles did not vary with respect to tidal position (Delafontaine, unpub. data). Third, variations in shell wall thickness had no apparent functional connection with the degree of aerial exposure (Section 2A). On the other hand, the present study showed that shell allometry can affect the reproduction of T. serrata along tidal gradients.

Current attempts to interpret life cycles are largely based on the concept of energetic costs (Calow, 1978). For example, the energy contained in the sexual products may either be compared to the energetic content of the reproducing adult, or it may be incorporated in the organism's energy budget (e.g. Hirschfield and Tinkle, 1975). It is generally conceeded, however, that both procedures provide an inadequate measure of reproductive effort as originally defined by Williams (1966a, b; Stearns, 1977). One major shortcoming in this respect is that physical constraints imposed by body size and/or shape may not be adequately accounted for (Vitt and Congdon, 1978; Reaka, 1979; Stearns, 1980; Corey, 1981; Vitt, 1981; Hines, 1982; Sebens, 1982). Similar criticism has been levelled at studies dealing with interactions between components of somatic growth (Palmer, 1981).

For barnacles, the need to investigate the effect of body size on reproduction was first muted 30 years ago (Costlow and Bookhout, 1957) but this seems to have been overlooked in favour of more 'fashionable' energetic considerations. For example, Wu et al. (1977) suggested that energetic limitations caused shell growth to be favoured at the expense of reproduction in crowded Balanus glandula. However, such 'partitioning' could just as well occur if taller shells impose different volumetric constraints on accretion of 'soft parts'. Such an interpretation would, in fact, be more consistent with the present findings.

In this study, it was found that variations in shell thickness (Section 2A) significantly altered shell internal volumes and, while this had no effect on prosomal masses (Section 2A), it does reflect variations in individual brood masses, ovarian reserves and reproductive 'efforts' for most of the population. By implication, the amount of shell internal volume not occupied by the somatic soft parts should generally be a constant measure of reproduction in T. serrata at Dalebrook.

Only in one instance was reproductive output smaller than expected in terms of volumetric constraints: some of the largest animals in the lower corridor produced relatively small broods. Because these animals had larger valves and were therefore possibly older than otherwise similarly sized conspecifics, it is suggested that the reduction in their reproductive outputs may be an effect of senescence. If this interpretation should prove correct, it would be the first documented case of age affecting reproduction in barnacles since the original observation by Moore (1935) over 50 years ago (see also Crisp, 1954; Lamb, 1977; Calow, 1978).

The reasons why shell wall thickness and shell internal volume vary with tidal position have, as yet, not been considered in terms of reproduction. The capacity to produce thicker shells may be advantageous to small barnacles exposed to higher wave impact low on the shore (Section 2A). But why should thicker shells with smaller internal volumes (which restrict reproduction) be found in large barnacles high on the shore? At least one possible reason has been discounted at this stage, i.e. the need to increase protection against aerial exposure (see Section 2A).

Thinner shells with larger internal volumes maximize reproduction both in large, low shore barnacles and also in small high shore animals. In the latter case, this will alleviate the damping effect that slow volumetric increase will have on reproduction (Section 4). Indeed, it could be one reason why the age at first reproduction was delayed by one year only in high shore barnacles in comparison to the much faster growing, low shore animals.

However, fast growth may incur high costs which adversely affect reproduction (Section 4). At mean adult age, low shore animals had devoted more energy to somatic growth than their high shore counterparts but they had reproduced less. Thinner shells with larger internal volumes which increase reproduction will enable large, low shore barnacles which survive beyond mean adult age to rectify this imbalance.

The capacity to improve reproduction by producing thinner shells has obvious limits. A separate study has shown that T. serrata reduces vulnerability to physical damage by increasing the bulk density of thinner shells (Section 2A). The only other way to maximize space available for the reproductive components would be to minimize the space occupied by the somatic components. Indeed, reserves are accumulated in the ovary at a different time of the year from reserves in the muscles, and the muscles are much reduced in size by the time spawning commences (Section 4).

In view of the above considerations, it is suggested that environmental factors controlling shell growth, in combination with the species capacity to manipulate both the amount and the availability of shell internal volume, may be of primary importance in explaining reproductive variability in barnacles along local tidal gradients. The question remains how these processes are affected by regional climatic gradients in, for example, temperature.

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SECTION 3B

Spermatozoa of <u>Tetraclita serrata</u> Darwin (Cirripedia: Thoracica): continued presence in the seminal vesicle during the extended non-breeding season

Abstract

The spermatozoa of the intertidal barnacle *Tetraclita serrata* Darwin were studied by means of histochemical techniques and electron microscopy at Dalebrook (False Bay, South Africa). The ultrastructure of the male gamete was similar to that previously observed in other barnacles. The accessory droplet contained both protein and carbohydrate moieties, as well as RNA. The compositions of the former two compounds differed from those initially present during the early stages of spermatogenesis. Contrary to the proteins and carbohydrates in the droplet, the protein moiety of these early stages contained no tyrosine, nor did the carbohydrate moiety contain any periodate reactive material.

It is suggested that the accessory droplet of the spermatozoon accumulates organic compounds which, in *T. serrata* at least, facilitate the retention of the sperm in the seminal vesicles even when the adult is not breeding.

Introduction

The intertidal barnacle Tetraclita serrata Darwin has a seasonal reproductive pattern along the South African coast (Section 3A). In the warm-temperate environment of False Bay, site of the present study, the adults bear broods each year, generally from spring (September) to the middle of summer (January). Larval settlement follows during late summer.

The onset of brooding is signalled by decreases in the size of the gonads, expecially in the case of the ovary (ca. 77 % decrease in dry mass) (Section 3A). The seminal vesicles remain visible during the non-brooding period and appear as fully distended, white tubules which contain spermatozoa (Section 3A).

The continued presence of male gametes in T. serrata contrasts with spermatogenic processes observed in other barnacles which also brood periodically. Semibalanus balanoides, for example, has cyclic spermatogenesis and the spermatozoa are resorbed from the seminal vesicles during the non-brooding period (Barnes et al., 1963; Barnes and Barnes, 1967; see also Hines, 1978) or when the adult is starved and prevented from copulating during the breeding season (Barnes and Achituv, 1976). Sperm absorption is associated with the degeneration of the penis in this species (Barnes and Stone, 1972). Conversely, T. serrata retains an elongated penis during the non-brooding season (Delafontaine, unpublished data).

In view of the fact that both copulation and fertilization immediately precede the appearance of eggs in the mantle-cavity of barnacles, the spermatozoa which are present in the seminal vesicles during the non-brooding period are unlikely to be exchanged between contiguous adults. These spermatozoa might therefore constitute a store of potentially active gametes.

The question now arises what processes govern the turn-over of these vesicular spermatozoa during the non-breeding period. For example, what is the rate of spermiogenesis and does partial resorption occur in the seminal vesicles? Another important consideration is whether the spermatozoa are provided with an endogenous nutrient source which could enable them to survive in the seminal vesicles during the non-breeding period. This latter aspect forms the topic of this paper.

Cirripedes are unique among crustaceans in possessing an anterior swelling to the spermatozoon, the 'vesicule de sécrétion' (Bocquet-Védrine and Pochon-Masson, 1969) or accessory droplet (Munn and Barnes, 1970). It has been suggested that this structure contains metabolic substrates and/or enzymes (Barnes et al., 1971). However, no attempt has yet been made to determine its biochemical composition. This paper focuses on the histochemistry of the accessory droplet of T. serrata in the spermatozoa at their site of production in the testis and at their site of storage in the seminal vesicle.

Study area

Barnacles were collected at Dalebrook (False Bay, South Africa; see General Introduction, Fig. 1) during the 1978/1979 and 1980/1981 brooding periods (Section 3A). Samples were processed within a few hours of removal from a rocky, intertidal platform. The topography and animal distribution at this site have been described in a separate study (Section 1A).

Materials and Methods

Histochemistry (light microscopy)

The finely ramified testis adheres to either side of the gut - a part of the prosoma - and is connected to a prominent seminal vesicle. Prosomas of freshly collected adults were removed from the shells and fixed immediately in Bouin's fluid for 12 hours (Culling, 1974), dehydrated through an ascending alcohol series (70 %, 80 % and 96 % alcohol) and transferred to a 1 % solution (v/v) of celloidin in methyl benzoate. Samples were stored in this clearing agent until prepared for sectioning. This entailed embedding in paraplast and serial sectioning at 8 μm with a microtome.

Histochemical tests and their significance are listed in Table 1.

Ultrastructure (electron microscopy)

The seminal vesicles were removed with the aid of fine forceps, fixed in Karnovsky's fixative for 10 hours (Karnovsky, 1965), washed overnight in Millonig's phosphate buffer, postfixed in OsO_4 (1 % in Millonig's phosphate buffer) for 1 hour and finally dehydrated through an ascending alcohol series (50 %, 75 %, 96 % and 100 % alcohol).

The samples were embedded in Spurr's resin (Kay, 1965), polymerised for 10 hours at 60° C and finally sectioned at 500 Å by means of a LKB Ultratome 3. Sections were stained with uranyl acetate (15 minutes) and lead citrate (3 minutes) (Venable and Coggeshall, 1965), and viewed in a Siemens Elmiskop 101 electron microscope.

Terminology

Spermiogenesis refers to the conversion of a spermatid into a spermatozoon; early stages of spermatogenesis refer to all germ-cells excluding the spermatozoa.

Results

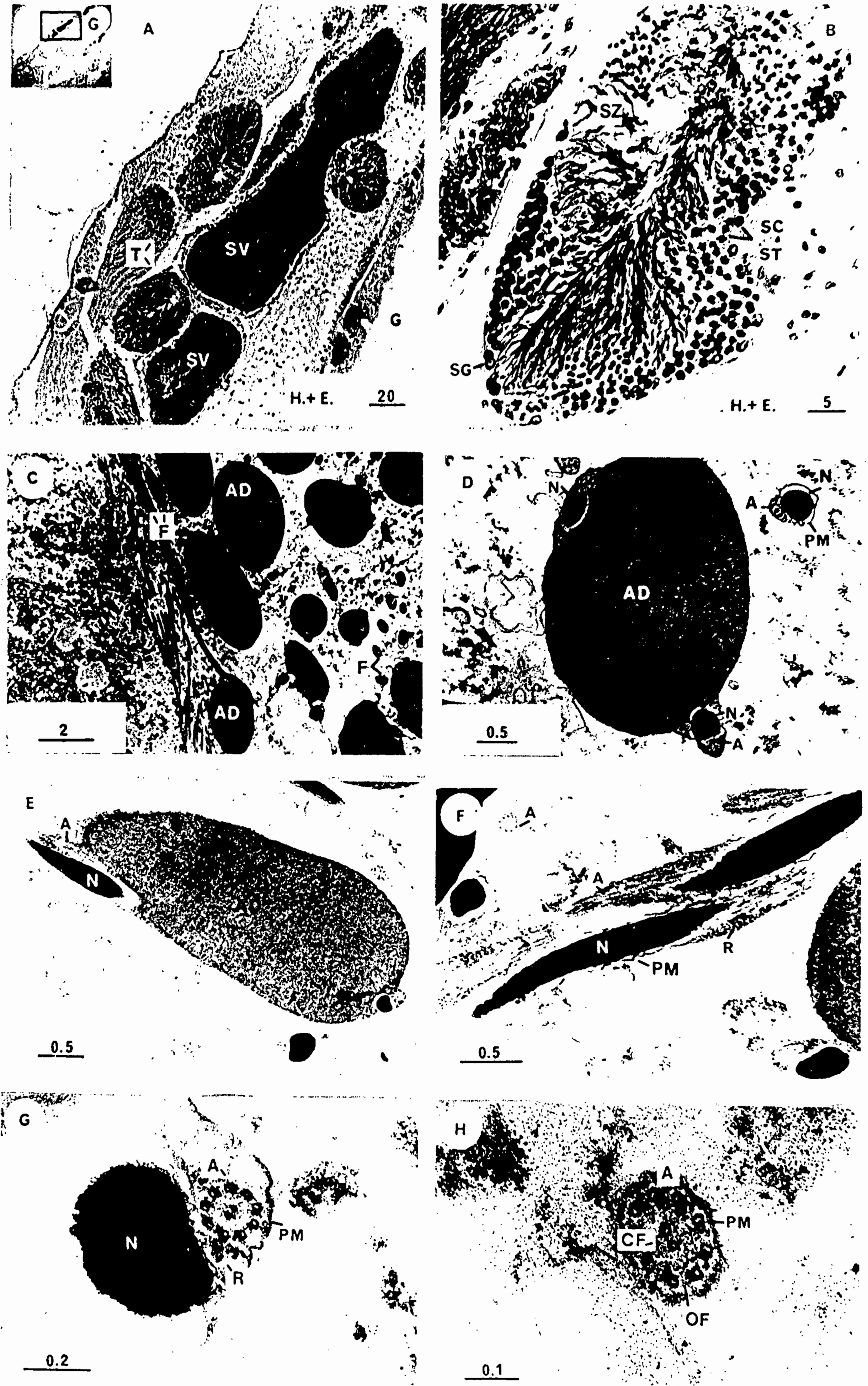
General structure (light microscopy)

Figure 1A shows the position of the convoluted testis and seminal vesicle with respect to the gut. The testis is encased in an outer membrane and contains peripheral spermatogonia,

Table 1. Histochemistry: tests and general information

TEST/CONTROL	SIGNIFICANCE	REFERENCE
GENERAL ORIENTATION		
- haematoxylin/eosin (H+E)	nuclear material/ cytoplasm	Drury et al., 1967
PROTEINS & AMINO ACIDS		
- mercury-bromphenol blue (Bonhag) (BB)	general ($-NH_2$ groups)	Bonhag, 1955; Pearse, 1968
- Million's (Baker) (M)	tyrosine	Pearse, 1968
- thioglycollate-ferric ferricyanide (TFF)	disulphide groups (SS)	Adams, 1956
- 2,2'-dihydroxy-6,6' -dinaphthyl disulphide (DDD)	sulphydryl groups (SH)	Barnett and Seligman, 1952; Culling, 1974
- thioglycollate reduction/DDD (TDDD)	SS and SH groups	Barnett and Seligman, 1952
CARBOHYDRATES		
- periodic acid-Schiff (PAS) (control: acetylation)	general (1,2 glycol groups),excluding acid mucopolysaccharides	Casselman, 1962; Lillie, 1965
- mucihematein (MH)	mucus	Laskey, 1950
- Alcian blue, pH 2.5 (AB 2.5) (control: RNAase)	acid mucopolysaccharides	Steedman, 1950; Pearce, 1968
NUCLEIC ACIDS		
- methyl green-pyronin Y (MG) (control: RNAase)	DNA (green)/RNA (pink)	Kurnick, 1955; Culling, 1974

Figure 1: next page (caption overleaf).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spermatocytes and spermatids. The nuclear contents of these germ-cells are stained dark purple by haematoxylin (Fig. 1B). These early stages of spermatogenesis are easily distinguished from the centrally situated spermatozoa (Fig. 1B). The filiform spermatozoon consists of two main structural entities. The flagellum contains an elongated nucleus which stains dark purple with haematoxylin. The flagellum joins an anterior swelling or accessory droplet which is coloured light pink by eosin. The seminal vesicle encloses a mass of closely packed spermatozoa (Fig. 1A, B). As far as could be ascertained without separating individual gametes, all the vesicular spermatozoa possessed an accessory droplet.

Ultrastructure (electron microscopy)

Observation of the spermatozoon at a higher magnification revealed that the flagellum (diameter: 0.3 μm - 0.6 μm) first joins and then contours the accessory droplet (Fig. 1C-E). The flagellum is encased by the plasma membrane and is traversed longitudinally by the axial filament (axoneme). The axoneme is juxtaposed to the elongated nucleus (Fig. 1E-F) and to a reticulum of narrow tubules (Fig. 1F-G) in the anterior section of the flagellum (i.e., that section which joins the accessory droplet). The axoneme contains an array of fibres in the characteristic (9+2) configuration (Fig. 1G-H) (Munn and Barnes, 1970). The nine outer fibres have a double structure (Fig. 1H). The ovoidal accessory droplet measures approximately 2.5 μm (width) by 4 μm (length) (Fig. 1D-E). The outer membrane encloses an apparently homogenous ground substance.

Histochemistry of the accessory droplet

The results of the histochemical tests for the accessory droplet are listed in Table 2 (abbreviations for tests are given in Table 1) and are discussed below.

Table 2. Histochemistry of the accessory droplet

TEST	RESULT	INTERPRETATON
GENERAL ORIENTATION		
H/E	-/+++	cytoplasm pink
PROTEINS		
BB	+++	protein present (-NH_2 groups)
M	+	some tyrosine present
TFF	++	SS groups present
DDD	++	SH groups present
TDDD	++	SS and SH groups present
CARBOHYDRATES		
PAS	+++	periodate reactive material present (1,2 glycol)
acetylation- PAS	-	reactive groups blocked by esterification
MH	+	mucus present
AB 2.5	+++	acid mucus present
RNAase-AB 2.5	+	positive reaction due partly to RNA
NUCLEIC ACIDS		
MG	+(pink)	RNA present
RNAase-MG	+ (?)	not clear why positive reaction not blocked

+, ++, +++: intensity of positive staining
-: negative staining
Abbreviations of tests: see Table 1.

Proteins

The presence of a protein moiety is indicated by a strong BB reaction (Fig. 2A). The protein contains both -SS- and -SH- groups (TFF, DDD and TDDD tests all positive). Tyrosine concentration is low (weak reaction for M test).

Carbohydrates

The presence of 1,2 glycol groups of carbohydrates is indicated by a strong PAS reaction (Fig. 2B). This result is supported by the blockage of the reactive groups by esterification (acetylation-PAS). Carbohydrates present in the accessory droplet include acid mucopolysaccharides, as suggested by strong AB 2.5 (Fig. 2C) and weaker MH reactions.

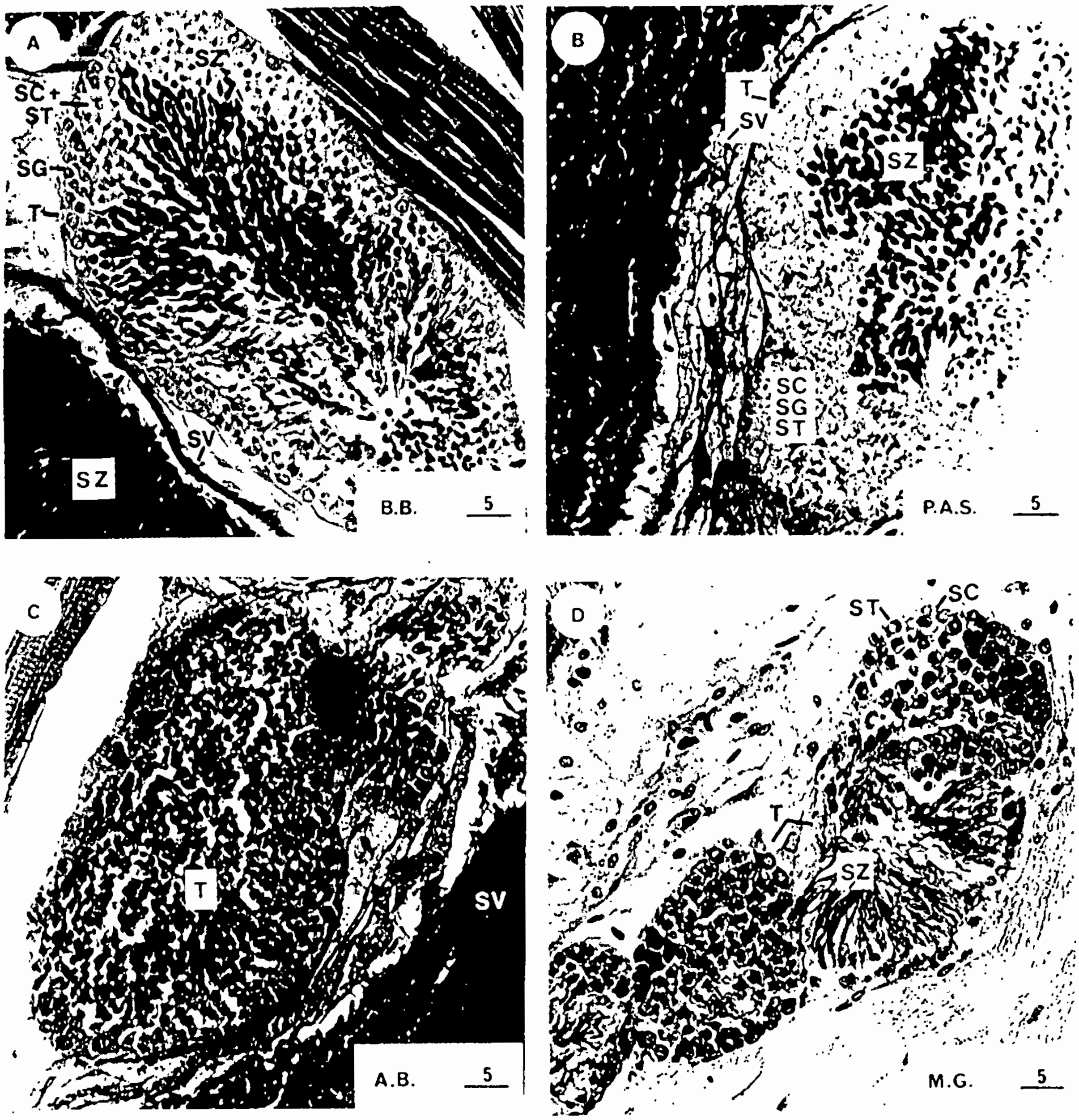
The RNAase control in the test for acid mucopolysaccharides (RNAase-AB 2.5) is only weakly positive, suggesting the strong AB 2.5 reaction to be due partially to RNA. The efficiency of this control is demonstrated by the strong reaction retained by cellular structures which are expected not to contain RNA - for example, certain sections of the gut (pers. obs.; Rainbow and Walker, 1977).

Nucleic acids

The preliminary indication that RNA is present in the accessory droplet (see above) is supported by a weakly positive (pink) MG reaction (Fig. 2D). It is not clear why this positive reaction was not blocked by the appropriate control (RNAase-MG).

In summary, the accessory droplet contains a) a protein moiety which includes amino acids with non-ionized, polar substituents such as -OH (tyrosine), -SH (possibly cysteine) and -SS- (possibly cystine); b) a carbohydrate moiety which includes periodate reactive material and a minor acid mucopolysaccharide component; and c) RNA.

Figure 2: next page (caption overleaf).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5

Histochemistry of the early stages of spermatogenesis

The results of the histochemical tests for the early stages of spermatogenesis are listed in Table 3 and are discussed below.

Proteins

There is little protein in the early stages of spermatogenesis (weak BB reaction; Fig. 2A). Contrary to that subsequently accumulated by the accessory droplet of the spermatozoon during spermiogenesis, this protein moiety does not contain tyrosine (negative M reaction). It does, however, contain other types of non-ionized polar amino acids in common with the accessory droplet, i.e. amino acids bearing -SS- and -SH functional groups (TFF, DDD and TDDD tests all positive).

Carbohydrates

The early germ-cells do not contain any periodate reactive carbohydrates, as indicated by the negative PAS reaction (Fig. 2B). Carbohydrates that are present consist of acid mucopolysaccharides (AB 2.5 test and appropriate control; Fig. 2C) and the ribose of RNA (AB 2.5; RNAase-AB 2.5).

Nucleic acids

The early stages of spermatogenesis contain DNA (green MG reaction and RNA control; Fig. 2D). The preliminary indication that RNA is also present in these germ-cells (see above) could not be confirmed by the nucleic acid test. It seems likely that this resulted from the preponderance of DNA in these cells.

In summary, the early stages of spermatogenesis contain a) a protein moiety which differs both quantitatively (in being less concentrated) and qualitatively (in containing no tyrosine) from the protein subsequently accumulated by the accessory droplet during spermiogenesis; b) a carbohydrate moiety which includes

Table 3. Histochemistry of early stages of spermatogenesis

TEST	RESULT	INTERPRETATION
GENERAL ORIENTATION		
H/E	+++/-	nuclear material present
PROTEINS		
BB	+	some protein present ($-NH_2$ groups)
M	-	no tyrosine present
TFF	+	few SS groups present
DDD	+	few SH groups present
TDDD	+	few SS and SH groups present
CARBOHYDRATES		
PAS	-	periodate unreactive
acetylation-PAS	(see text)	-
MH	+	some mucus present
AB 2.5	++	acid mucus present
RNAase-AB 2.5	+	positive reaction due partly to RNA
NUCLEIC ACIDS		
MG	+++ (green)	DNA present (RNA not visible)
RNAase-MG	++ (green)	DNA and some RNA present

+, ++, +++: intensity of positive staining
-: negative staining
Abbreviations of tests: see Table 1.

acid mucopolysaccharides but, contrary to the accessory droplet, no periodate reactive material; and c) DNA and possibly RNA.

Discussion

Structure

The testis of T. serrata contains germ-cells only. Observation by light microscopy revealed no evidence of nutritive phagocytes associated with the developing germarium. These non-germinal elements are known to store materials destined for utilisation during spermatogenesis and to ingest spermatozoa during non-reproductive periods in some marine invertebrates (Czihak, 1975; Bernard, 1977).

The main ultrastructural features of the spermatozoon in T. serrata resemble those observed in other barnacles. It was not the purpose of this study to investigate this aspect in any detail. The reader is referred to the work of Munn and Barnes (1970) for further information and a schematic representation of the ultrastructure of the spermatozoon. It seems likely that, in analogy to other barnacles, certain structural entities that were not observed in the present study also exist in T. serrata (e.g. an elongated mitochondrium).

The accessory droplet of barnacles is either spheroidal or ovoidal in the testicular spermatozoa and may become reduced or nearly absent in the vesicular spermatozoa (Barnes et al., 1971; this study). It has been suggested that morphological differentiation of the spermatozoon affects its motility and may be related to the capacity for self-fertilization in certain species (Barnes and Crisp, 1956). However, it is as yet not clear whether the form of the droplet itself is relevant in this context. For a start, the presence of the droplet does not seem to affect the potential motility of the male gametes which are activated by the secretion of the oviducal glands (Walley et al., 1971; Lewis, 1975) and/or by their passage through the penis (Barnes et al., 1971). Significantly, the activation of the gametes occurs irrespective of whether the droplet is present or not. The force required to expel the semen is presumably supplied by the muscular wall of the seminal vesicle (Barnes et al., 1977). Furthermore, existing information on the morphological differentiation of the droplet is too scant to reveal any relation between the size of the droplet and, amongst other factors, the amount of time spent in the adult prior to cross-fertilization as opposed to self-fertilization. It seems therefore that this aspect has yet to be investigated.

The spermatozoon loses its droplet by the time it passes through the pores of the oviducal sac. The diameter of these 'pores' is, in fact, not adequate for the passage of gametes which still possess droplets (Walker, 1977; Klepal et al., 1977). From this Klepal et al. (1977) concluded that the role of the droplet is completed prior to fertilization.

Histochemistry

Bocquet-Védrine and Pochon-Masson (1969) reported a loss of osmophilic (lipoproteinaceous?) material from the accessory droplet of Balanus perforatus during its sojourn in the seminal vesicle. On the basis of this observation, Barnes et al. (1977) suggested that the droplet might contain metabolic substrates and/or enzymes. Specific staining of frozen sections and specific extractions coupled with thin-layer chromatography indicated negligible amounts of neutral lipids in the spermatozoon of T. serrata (Delafontaine, pers. obs.). On the other hand, the present study has shown that specific proteins and carbohydrates accumulate in the droplet during spermiogenesis, i.e. they seem to be associated with the requirements of the spermatozoon.

The mere accumulation of organic compounds in a specialized region of the male gamete is in itself no formal proof of their utilization. However, it is generally accepted that the spermatozoon of animals contains an endogenous nutrient supply.

Storage is often in the mitochondrial or axonemal compartments. Thus, animal spermatozoa "possess the physiological capacity for maintaining the energy demands for metabolism and motility" (Anderson and Personne, 1970). For example, phospholipids and/or glycerides are utilized as endogenous metabolic substrates by the spermatozoa of mammals, especially if there is no supply of exogenous glycolysable sugar, such as the fructose of the seminal plasma (White et al., 1976). In man, this endogenous respiratory activity is capable of supporting motility for a few hours only. Human spermatozoa, therefore, have an absolute requirement for exogenous hexose to drive glycolysis (Peterson and Freund, 1976). Localized storage of organic nutrients is relatively poorly documented in invertebrates. In the oyster Crassostrea virginica, for example, the subacrosomal region (axial body) contains numerous vesicles (Daniels et al., 1971) that conceivably enclose as yet unidentified nutrients. Possible sources of nutrients seem varied in invertebrates and include the accessory cells and ductus deferens of the marine calanoid copepod Labidocera aestiva (Blades-Eckelbarger and Youngbluth, 1982) and the prostate gland of the oligochaete Tubifex tubifex (Fleming, 1981). Nutrient types have been identified in some species. For example, the spermatozoa of some seastars contain phospholipids as well as neutral lipids (Nimitz, 1976), whereas energy for movement is provided by phospholipids in the male gamete of sea-urchins (Brachet, 1960; Schmekel, 1975).

In view of the fact that spermatozoon activity in animals depends at least partially on endogenous nutrients, it is suggested that the accumulation of organic compounds in the accessory droplet of T. serrata is relevant for the spermatozoon's survival. In order to establish the exact nature and roles of the major nutrients, these compounds would have to be investigated in far greater detail than was possible in this study. It is as yet uncertain when these nutrients would be needed. Klepal et al. (1977), for example, have suggested that once the spermatozoa of barnacles are expelled into the mantle-cavity of a functional female, the energy expended to reach the oocytes would be 'trivial'. Some metabolically derived energy would be utilized during the spermatozoon's sojourn in the cavity prior to fertilization, but egg-laying commences just one hour after the first insemination in Semibalanus balanoides, during which time several subsequent inseminations occur (Barnes et al., 1977; Walker, 1977). This implies that the nutrients are needed before copulation - an implication which is strengthened by the knowledge that, in T. serrata at least, the spermatozoa remain in the vesicles throughout the prolonged, non-breeding period.

To summarize, it is suggested that the proteins and carbohydrates which accumulate during spermiogenesis in the accessory droplet of T. serrata are necessary for the survival of the spermatozoon in the seminal vesicle prior to copulation. If this is so, and on condition that there is no uptake of exogenous nutrients by the vesicular spermatozoa, then the amount of nutrients in the droplet should reflect the length of time spent in the seminal vesicle. More information is needed on this subject, especially with regard to the presence of RNA in the droplet and to a possible exogenous nutrient supply. Electron micrographs of the seminal vesicle revealed a complex ultrastructure of the wall, including a prominent endoplasmic reticulum and ribosomes (Delafontaine, pers. obs.). Significantly, the seminal vesicles are the source of fructose in the seminal plasma of man (Hudson et al., 1980).

Finally, it remains to be shown why T. serrata maintains apparently self-sufficient male gametes in the seminal vesicles during the non-breeding period. In view of parallel evidence for the female gonad (Section 3C), a possible link with variable timing of reproduction (Section 3A) seems indicated.

Figure 2. Histochemistry of the testis and seminal vesicle (light micrographs; cf. Tables 2 and 3). A: general proteins. B: general carbohydrates. C: acid mucopolysaccharides. D: nucleic acids. Abbreviations: AB: Alcian blue; BB: mercury-bromphenol blue; MG: methyl green-pyronin Y; PAS: periodic acid-Schiff; SC: spermatocyte; SG: spermatogonium; ST: spermatid; SV: seminal vesicle; SZ: spermatozoon. Scale bar in μm.

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SECTION 3C

Ovarian maturation during the extended non-breeding season of the intertidal barnacle *Tetraclita serrata* Darwin

Abstract

Ovarian structure and histochemistry were investigated in the intertidal barnacle Tetraclita serrata Darwin at Dalebrook (False Bay, South Africa). Gonadal structure was essentially similar to that previously reported in other barnacles. Contrary to expectations, however, the ovary showed no clear signs of spawning activity during the brooding season. In addition, developing and mature oocytes persisted in the female gonad during the non-breeding season, although ovarian mass was much reduced during this time.

Histochemical analyses showed no obvious differences in gross biochemical composition between oocytes at different stages of the annual reproductive cycle. The pre-hatched nauplius inherited yolk of similar gross composition to that present in the mature oocyte.

It is concluded that T. serrata maintains apparently viable developing and mature oocytes in the ovary, albeit in small quantities, even when the adult is not breeding. The commonly held view that so-called 'acyclic' gametogenesis is automatically associated with continuous spawning is thus refuted.

Introduction

The reproductive patterns of marine invertebrates are easily investigated in situ, although detailed observations of reproductive events are often not feasible in environments such as the deep sea which afford irregular and infrequent sampling opportunities. This has caused considerable difficulty in determining, amongst other things, the unequivocal occurrence of spawning by observing the spawning products themselves as soon as they appear.

A procedure commonly used to overcome these problems consists of associating observed variations in the size-frequency distribution of the oocytes with periodic spawning (e.g. Webber and Giese, 1969; Nimitz, 1971, 1976). By analogy, the lack of such cycles has been considered to indicate continuous spawning (e.g. Rokop, 1979; Tyler et al., 1985). However, recent studies (Sections 3A, 3B) suggest that the relationship between oocyte size-frequency distributions and spawning frequency warrants further investigation.

In sessile intertidal barnacles, the unequivocal occurrence of spawning is easily determined because the brooding adult is readily accessible. Tetraclita serrata Darwin spawns during a few months each year along the southern African coast. The brooding period shifts from spring/early summer in the temperate coastal region, to winter in the subtropical zone (Section 3A). In the warm temperate environment of False Bay, where the present study was carried out, gonadal mass also varies seasonally, especially that of the ovary which decreases sharply at the onset of spawning in spring (Section 3A).

A first attempt to correlate these reproductive events with gametogenesis focused on the histochemistry of the male genital system. In contrast with other barnacles which breed periodically, the seminal vesicles of T. serrata are filled with spermatozoa throughout the year. Furthermore, it seems that the mature male gamete is to some extent metabolically self-sufficient and therefore capable of surviving an extended period in the seminal vesicle prior to fertilization (Sections 3A, 3B).

These results prompted a similar investigation of the female gonad. The first aim here was to investigate whether the ovary maintains developing and mature oocytes during the interim period separating annual spawning events. If so, it would mean that 'acyclic' gametogenesis is not necessarily associated with continuous spawning. In anticipation of this, the second aim was to investigate whether, as far as could be ascertained by histochemical techniques, these oocytes are potentially functional. Finally, some information concerning relevant aspects of naupliar histochemistry is included.

Study area

The sampling site was situated on a rocky, intertidal platform at Dalebrook (False Bay, South Africa; see General Introduction, Fig. 1). A detailed description of the topography and animal distribution in this locality has been provided in a separate study (Section 1A). Specimens of varying shell length were collected at the upper and lower distribution limits of the population during various phases of the predetermined reproductive cycle (Section 3A). The cycle is summarized in Fig. 1 for ease of reference.

Materials and Methods

Fresh samples were processed within a few hours of collection. The ovary was removed with fine forceps and fixed immediately in Bouin's fluid for 12 hours (Culling, 1974). Standard preparations for sectioning and viewing by light microscopy have been described elsewhere (Section 3B). Standard histochemical tests used for general observation and to identify proteins, carbohydrates and nucleic acids are also described in the above study. The tests have been listed in Table 1.

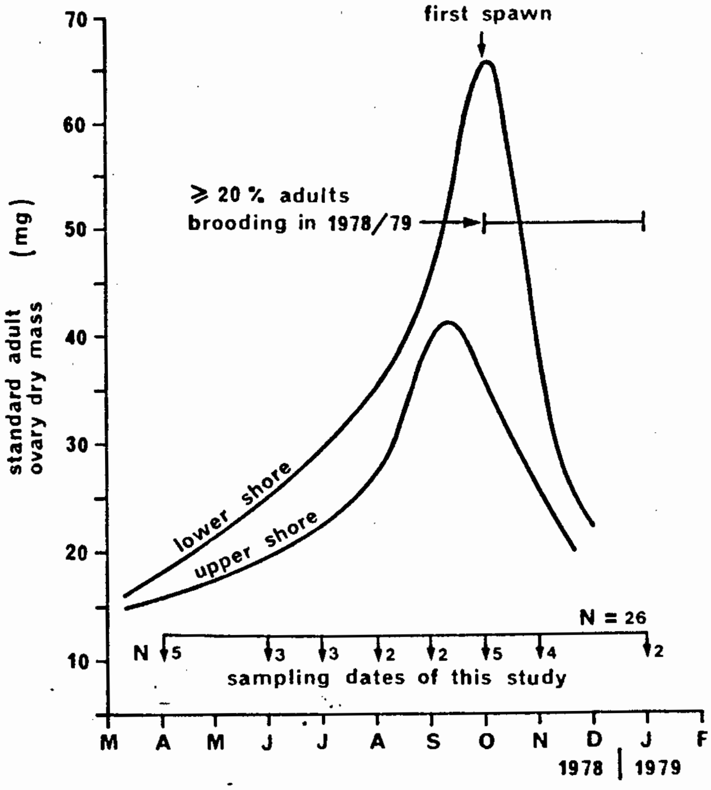


Figure 1. The reproductive cycle of *T. serrata* at Dalebrook during the 1978/79 sampling period (Sections 3A, 3B). A 'standard' adult is one in which the valves weigh 100 mg when dry.

Terminology

- spawning: release of ova into mantle cavity; since in barnacles fertilization follows very shortly after the ova enter the mantle cavity, a spawning event is reliably indicated by the presence of immature eggs in the brooding adult.

- periodic spawning: spawning of the population confined to specific period or periods of the year.
- continuous spawning: spawning of the population throughout the year.
- yolk: any recognizable globule (not only protein) in the cytoplasm of the oocyte (Brachet, 1960).

Results

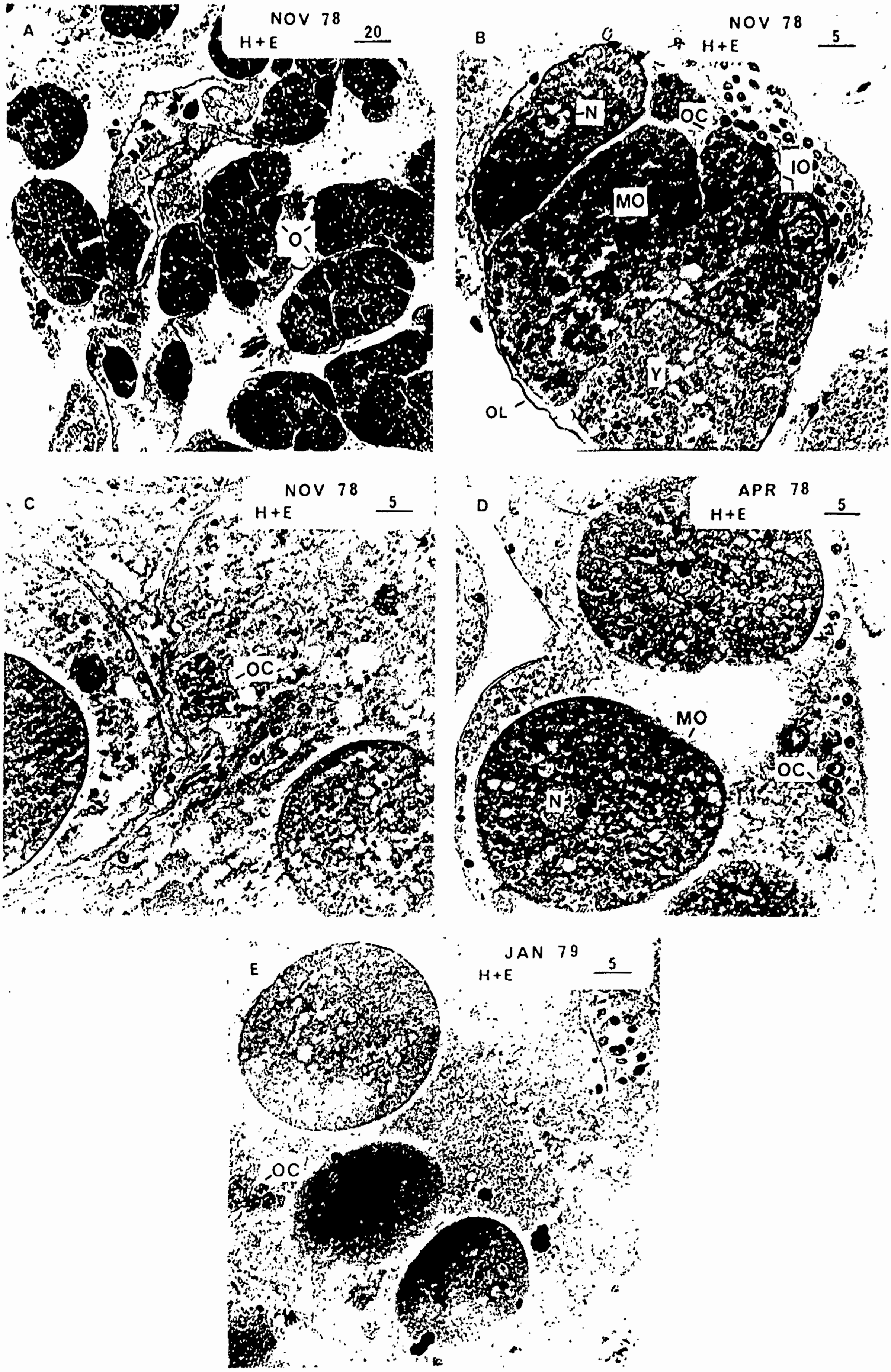
Ovarian structure

The female gonad consists of numerous tubules (ovarioles) which are separated by loose connective tissue (Fig. 2A). The ovariole is delimited by a thin membrane (oolema) which encloses the germarium (oogonia) and the vitellarium (gametocytes). The oogonia occur generally in isolated groups or clusters throughout the vitellarium (Fig. 2 B-E). They exhibit various stages of mitosis which were not further identified. The gametocytes comprise oocytes of varying maturity. Small, immature (previtellogenic) oocytes are found frequently at the periphery of the ovariole (Fig. 2B). Meiotic configurations are not visible in the large nuclei of these oocytes. Larger, mature oocytes generally occupy most of the ovariole (Fig. 2 A-B). Their cytoplasm becomes progressively granular as yolk droplets accumulate.

The structure of the ovary does not differ between barnacles from the upper and lower distribution limits of the population. Oogonia and developing oocytes are observable throughout the year in all specimens (Fig. 2 B-E). It is not possible to distinguish the ovarioles which must have shed at least some

Figure 2: next page (caption overleaf).

Figure 2. Structure of the ovary during various phases of the reproductive cycle. A: general view during the brooding period. B, C: detail of the ovariole during the brooding period. D: detail of the ovariole before the brooding period. E: detail of the ovariole after the brooding period. Abbreviations: H+E: haematoxylin and eosin stain; MO: mature oocyte; N: nucleus; IO: immature oocyte; O: ovariole; OC: oogonial cluster; OL: oolema; Y: yolk. Scale bar is in μm.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oocytes during the spawning season. The oolema sometimes encloses a loose, relatively amorphous tissue in which proliferating oogonia are clearly visible. This does not seem to be related to spawning, because it is observed throughout the year (Fig. 2 C-E). In addition, there are no clear signs of resorption processes. In other words, it would seem that mature oocytes which are not spawned during the non-breeding period are not resorbed but continue to persist in the ovary.

Ovarian histochemistry

Histochemical reactions of the extranuclear region of immature and mature oocytes are shown in Tables 1 and 2 respectively and are discussed below. These reactions were similar during all phases of the reproductive cycle. Comparative data for Balanus amphitrite and Balanus eburneus (Fyhn and Costlow, 1977) are also shown and will be discussed further on.

Proteins

Protein accumulates as the oocyte develops (strong BB reaction in mature oocyte; Fig. 3C), and contains tyrosine and SS/SH functional groups (M, TFF, DDD and TDDD tests positive).

Carbohydrates

The 1,2 glycol groups are most evident in the mature oocyte (PAS and appropriate control; Fig. 3A). The periodate-reactive carbohydrates include some mucins (MH test). The positive reaction for acid mucopolysaccharides, evident especially in the immature oocyte, is apparently due to the presence of RNA (AB 2.5 and appropriate control). Some RNA seems to be associated also with the yolk of the mature oocyte (Fig. 3D).

Table 1. Histochemistry of the immature oocyte (cytoplasm)

TEST	RESULT Balanus (*)	 Tetraclita (this study)	INTERPRETATION (this study)
PROTEINS			
BB	-	+	some protein present ($-NH_2$ groups)
M	-	+	some tyrosine present
TFF	-	+	SS groups present
DDD	-	+	SH groups present
TDDD	-	+	SS and SH groups present
CARBOHYDRATES			
PAS	++	+	periodate reactive material present (1,2 glycol)
acetylation-PAS	-	-	reactive groups blocked by esterification
MH	+	++	mucus present
AB 2.5	++ (pH?)	++	acid mucus present
RNAase-AB 2.5	-	-	positive reaction due to RNA
NUCLEIC ACIDS			
MG	+++	+++ (pink)	RNA present
RNAase-MG	-	-	positive reaction blocked

+, ++, +++: intensity of positive staining
-: negative staining
* study of Balanus amphitrite and Balanus eburneus (Fyhn et al., 1977)

Abbreviations of histochemical tests: AB 2.5: Alcian blue pH 2.5; BB: mercury bromphenol blue (Bonhag); DDD: 2,2'-dihydroxy-6,6'-dinaphthyl disulphide; M: Million's (Baker); MG: methyl green-pyronin Y; MH: mucihematein; PAS: periodic acid-Schiff; TDDD: thioglycollate reduction/DDD; TFF: thioglycollate-ferric ferricyanide. Controls for tests: RNAase for AB 2.5 and MG; acetylation for PAS.

Table 2. Histochemistry of the mature oocyte (yolk)

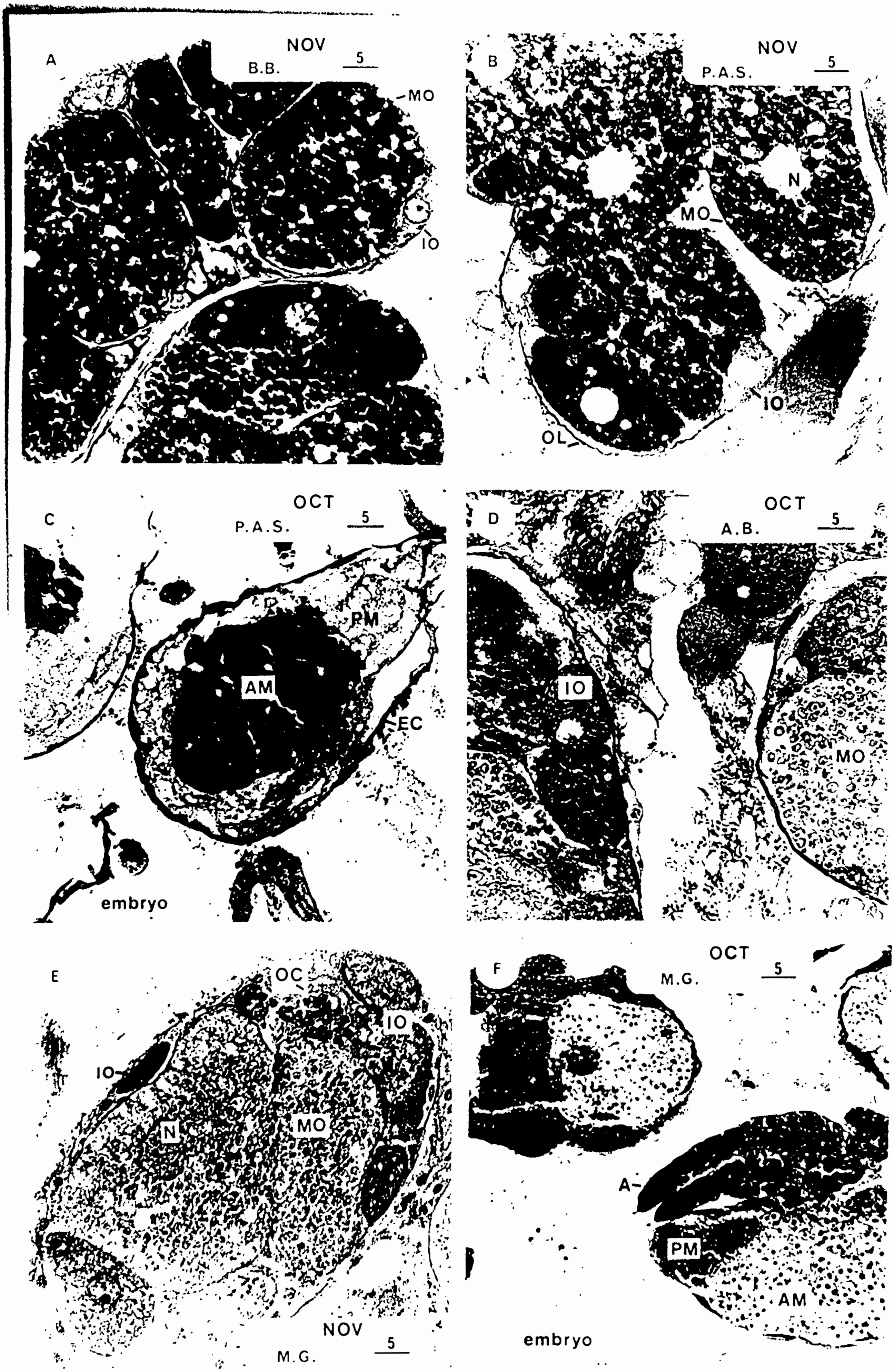
TEST	RESULT Balanus (*)	 Tetraclita (this study)	INTERPRETATION (this study)
PROTEINS			
BB	+++	+++	protein present (-NH_2 groups)
M	+	++	tyrosine present
TFF	+++	++	SS groups present
DDD	++	++	SH groups present
TDDD	+++	++	SS and SH groups present
CARBOHYDRATES			
PAS	+	+++	periodic reactive material present (1,2 glycol)
acetylation-PAS	-	-	reactive groups blocked by esterification
MH	-	+	mucus present
AB 2.5	-	+	acid mucopolysaccharides present
RNAase-AB 2.5	-	-	positive reaction due to RNA
NUCLEIC ACIDS			
MG	-	+ (pink)	RNA present
RNAase-MG	-	-	positive reaction blocked

+, ++, +++: intensity of positive staining
-: negative staining
* study of _Balanus amphitrite_ and _Balanus eburneus_ (Fyhn et al., 1977)

Abbreviations of histochemical tests: see Table 1.

Figure 3: next page (caption overleaf).

Figure 3. Histochemistry of the ovary and pre-hatched nauplius. A: 1,2 glycol groups of carbohydrates (PAS test) in the ovary. B: nauplius stained as for A. C: general proteins (BB test) in the ovary. D: acid mucopolysaccharides (AB test) in the ovary. E: nucleic acids (MG test) in the ovary. F: nauplius stained as for E: Abbreviations: A: naupliar appendages; AM: anterior midgut rudiment; EC: egg-case; PM: posterior midgut rudiment; others, including histochemical tests: see Fig. 2 and Table 1. Scale bar in μm.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Nucleic acids

Preliminary indications of the presence of RNA in the oocytes (see above) are supported by a positive MG reaction and appropriate control. The reaction is strongest in the young oocyte (Fig. 3E). The efficiency of the control is indicated by the strong reaction for DNA in the oogonial clusters.

In summary, the following extranuclear compounds accumulate as the oocyte develops: a protein moiety which includes amino acids with non-ionized, polar substituents such as -OH (tyrosine), -SH (e.g. cysteine) and -SS- (e.g. cystine); a carbohydrate moiety which consists of periodate-reactive material incorporating some mucins; and RNA which is most evident in the cytoplasm of the immature oocyte and becomes 'diluted' as the oocyte develops (Brachet, 1960).

Naupliar structure and histochemistry

The morphology of the pre-hatched nauplius of T. serrata is typical of barnacles in general. Reference may be made to the work of Rainbow and Walker (1977) for further details.

Results of the histochemical tests for the anterior and posterior midgut rudiments (AM and PM respectively) are shown in Table 3 and are discussed below. Comparative data for Semibalanus balanoides (Rainbow and Walker, 1977) are also shown and will be discussed further on.

Proteins

Protein is accumulated in the AM (strong BB reaction) and is negligible in the PM and the limbs. It contains tyrosine and SS/SH functional groups (M, TFF, DDD and TDDD tests positive).

Table 3. Histochemistry of the pre-hatched nauplius (anterior and posterior midgut rudiments)

TEST	RESULT			INTERPRETATION (this study)
	AM		PM	
	Semibal. (*)	Tetraclita (this study)	Tetraclita (this study)	
PROTEINS				
BB	+++	+++	+	protein (-NH_2 groups) in AM > PM
M (Diazo*)	+++	++	+	tyrosine present
TFF	+	++	+	SS groups present
DDD	++	++	+	SH groups present
TDDD	+++	++	+	SS and SH groups present
CARBOHYDRATES				
PAS	+++	+++	+	periodate reactive material present (1,2 glycol)
acetylation-PAS		-	-	reactive groups blocked by esterification
MH	-	+	+++	mucus in PM > AM
AB 2.5	-	+	+++	acid mucopolysaccharides in PM > AM
RNAase-AB 2.5		-	-	positive reaction due to RNA
NUCLEIC ACIDS				
MG		+	+++	nucleic acids in PM > AM
RNAase-MG		-	-	positive reaction due to RNA

+, ++, +++: intensity of positive staining
-: negative staining
* study of Semibalanus balanoides (Rainbow and Walker, 1977)

Abbreviations: histochemical tests: see Table 1; AM: anterior midgut rudiment: PM: posterior midgut rudiment.

Carbohydrates

1,2 glycol groups are indicated by the positive PAS reaction and appropriate control. The periodate-reactive material is concentrated in the AM (Fig. 3B) and includes some mucins (MH test). The strong positive reaction for acid mucopolysaccharides in the PM and limbs is due to the presence of RNA (AB 2.5 and appropriate control).

Nucleic acids

Preliminary indications that RNA is present in the PM and limbs (see above) are supported by the results of the nucleic acids test and appropriate control (MG test; Fig. 3F).

In summary, components which are concentrated in specialized regions of the pre-hatched nauplius include: protein and carbohydrate moieties in the AM, the composition of which is similar to that of the yolk in the mature oocyte; and RNA which is more concentrated in the PM and limbs.

Discussion

Naupliar structure and histochemistry

Barnacle larvae enter the plankton as free-swimming, non-feeding nauplii (naupliar stage I) (Barnes et al., 1977). The ability to feed is soon acquired in some species and hatching of the egg often coincides with maximal food availability (Barnes, 1957). The transition to the feeding nauplius (naupliar stage II) depends, amongst other factors, on the presence of adequate endogenous reserves, i.e. on the remnants of the egg-yolk (Barnes and Barnes, 1958; Rainbow and Walker, 1977; Klepal and Barnes, 1978).

Segregation of a yolky anterior midgut rudiment (AM) from a yolk-free posterior midgut rudiment (PM) (Rainbow and Walker, 1977; this study) is considered to be an adaptation which temporarily localizes the storage and release of the remaining egg-yolk in a specialized region of the midgut (Anderson, 1969). Supporting evidence for this includes a) the disappearance of the yolk from the AM by the time the nauplius starts feeding (Rainbow and Walker, 1977); b) the biochemical similarity of the yolk in the egg and in the AM of the larva (Rainbow and Walker, 1977; this study); c) the absorptive, as opposed to secretory, character of the AM and PM respectively (Rainbow and Walker, 1977). Significantly, the present study showed that RNA is especially evident in the PM.

In conclusion, the pre-hatched nauplius of T. serrata isolates the remaining egg-yolk in the anterior midgut of the rudimentary alimentary canal, thus conforming to the pattern generally observed in cirripedes. These reserves include carbohydrates and proteins, as in the case of the larvae of other barnacles (Rainbow and Walker, 1977; cf. Table 3) and other marine invertebrates (e.g. Loeb and Walker, 1977; Holland, 1978). During its development in the mantle-cavity of the adult, the embryo also accumulates certain lipids (Delafontaine, unpub. data). Thus, as has been reported for various marine invertebrates (e.g. Pieters et al., 1979), the young nauplius of T. serrata inherits specific organic compounds which tide it over the non-feeding stage of its planktonic existence.

Ovarian structure and histochemistry

Generally speaking, little information is available on the structure and histochemistry of the ovary in barnacles, but the results of this study are similar to those of Fyhn and Costlow (1977), and Fyhn et al. (1977) (see Tables 1 and 2).

The ovariole contains germ-cells only. There was no evidence of accessory cells associated with the developing oocyte, nor of a 'follicular' (nutritive) function of the oolema (Czihak, 1975). It is concluded that the oocyte of T. serrata develops autonomously (Norrevang, 1968).

T. serrata resembles some other marine invertebrates, such as sea urchins, in that the oogonia and primary oocytes tend to occur in isolated clusters scattered throughout the ovariole, rather than in a peripheral layer (Chatlynne, 1969; Gonor, 1973a). Mitotic activity was easily discernible within the oogonia, but the nuclei of the oocytes showed no sign of meiotic configurations. The question therefore remains at what stage of maturation meiosis is initiated in barnacles (cf. Czihak, 1975; Barnes et al., 1977). In some species the oocytes are in the prophase of the first meiotic division when the secretion of the oviducal sac is completed (Walley et al., 1971). Possibly, meiosis is initiated in T. serrata shortly before the eggs descend into the mantle-cavity.

The present study has shown that the developing oocyte accumulates carbohydrates and proteins. Both the ovary and the newly spawned egg also contain triacylglycerols as the major neutral lipid (Delafontaine, unpub. data). The yolk of T. serrata therefore resembles the 'glycolipovitellin' of various marine invertebrates including other barnacles (see Tables 1 and 2) (Holland, 1978). In contrast with previous studies, it was additionally found here that some RNA is associated with the yolk of the mature oocyte (Table 2). In fact, it is generally accepted that the yolk of the animal oocyte is not a mere 'reserve' but that it incorporates specific species of RNA (e.g. maternal mRNA) which play an active role in embryogenesis (Brachet, 1960; Norrevang, 1968; Czihak, 1975).

Contrary to common expectations, there were no visible signs here that ovarian structure and histochemistry varied during the periodic reproductive cycle. For example, the size-frequency distribution of the oocytes, which was assessed qualitatively, was clearly similar throughout the year. In addition, there was little evidence of degenerated yolk droplets, i.e. of the gonad (vitellogenesis)-inhibiting action imputed to ecdysterone in barnacles (Fyhn et al., 1977). Because these data clearly provide no indication of the rate of spawning, it follows that the gonad maturation index - a related measure which is commonly used to predict spawning frequency - is also meaningless in this instance.

Table 4 is a selective review which shows that 'acyclic' gametogenesis has often simply been equated with continuous spawning (points 1 - 5 in Table 4). The present study suggests that this is unjustified. In effect, if spawning frequency had not been established unequivocally in T. serrata by observing the spawning products as soon as they appeared (Section 3A), it would have been impossible, on the basis of ovarian structure alone, to predict spawning frequency. The gonad mass index and the monitoring of juveniles have sometimes been considered useful in this respect (Table 4, points 6 and 7). However, other workers have had difficulty in interpreting such indirect evidence of spawning (e.g. Denys and McWhinnie, 1982), while related events such as the pattern of activity in the accessory cells do not seem relevant here. There is clearly a need for future research on this topic. Conversely, it may be easier to estimate spawning frequency if the gonad maturation index or the size-frequency distribution of the oocytes vary with time. At least the maximum possible duration of major spawning periods is then evident (Table 4, points 8-23) (e.g. Bowmer, 1982; Lowe et al., 1982).

To summarize, this study has shown that, in analogy to the male genital system (Sections 3A, 3B), T. serrata maintains elements of both the germarium and the vitellarium in the female gonad during the interim period separating observed spawning seasons. As far as could be ascertained by histochemical tests, these elements seem potentially functional during this period. Any future research should attempt to establish why T. serrata maintains mature gametes throughout the year although it has a limited spawning season. Alternatively, why does this species limit breeding and spawning to a specific time of the year in spite of the fact that it maintains mature gametes all year round? It is known that the onset and duration of the annual spawning period vary from year to year in False Bay (Section 3A). Possibly, the continued presence of developing and mature oocytes during the non-breeding season enables T. serrata to

Table 4. Selected literature survey of direct and indirect evidence of spawning frequency in marine organisms.

SPECIES	GONAD MATURATION$ 0: acyclic +: cyclic		OVARY MASS INDEX 0: constant +: variation	ACCESSORY CELLS 0: absent +: present		SPAWNING SEASON P: periodic C: continuous		REFERENCE
	female	male		female	male	predicted	observed#	
Ophiuroidea								
1	0					C		Tyler and Gage, 1979
Bivalvia								
2	0*	0				C		Rokop, 1979
3	0*	0				C		Rokop, 1979
4	0*	0				C		Rokop, 1979
Gastropoda								
5	0*	0				C		Rex et al., 1979
Asteroidea								
6	0	0	0	++	0	C		Tyler et al., 1982
Ascidiacea								
7	0*	0	+ suspected				C (1 main)?	Svane and Lundälv, 1981
Cirripedia								
8	0	0?	+++	0			P	This study, Section 3B
Teleostei								
9			0					Gordon, 1979
10			+++				P	Gordon, 1979
Echinoidea								
11	+++		++	+++		P		Masuda and Dan, 1977
12	+++		++	+++		P		Masuda and Dan, 1977
13	+++		+++	+++		P		Holland and Giese, 1965; Gonor, 1973b; Rokop, 1979
14	+++	+++	++	+++	+++	P		Bernard, 1977
15	++(2 y^{-1})		++	+++		C (2 y^{-1})		Ernest and Blake, 1981

Table 4 (cont.)

Bivalvia								
16	++(3 y^{-1})	++(3 y^{-1})		+++	+++	C (3 y^{-1})		Braley, 1982
Ophiuroidea								
17	++					P		Tyler and Gage, 1979
18	+++	+++	+++				P	Tyler, 1977
19	+++	+++	++(?)				P	Tyler, 1977
Ascidiacea								
20	+++*	+++*					P	Svane and Lundälv, 1982
Polychaeta								
21	+++*	+++*					P	Christie, 1982
22	+++*	+++*					P	Christie, 1982
Asteroidea								
23	++*	+	++	+		P		Nimitz, 1971, 1976
24	++*	+	++	+		P		Nimitz, 1971, 1976
Gastropoda								
25	++	0	+++			P		Webber and Giese, 1969

Species: 1: Ophiomusium lymani; 2: Nuculana pontonia; 3: Nucula darella; 4: Bathycarca sp.; 5: Benthonella tenella; 6: Bathybiaster vexillifer; 7: Ascidia mentula; 8: Tetraclita serrata; 9: Coryphaenoides rupestris; 10: Nezumia aequalis; 11: Anthocidaris crassispina; 12: Hemicentrotus pulcherimus; 13: Strongylocentrotus purpuratus; 14: Strongylocentrotus franciscanus; 15: Lytechinus variegatus; 16: Saccostrea cucullata; 17: Ophiura ljungmani; 18: Ophiura albida; 19: Ophiura texturata; 20: Pyura tessellata; 21: Pholoe minuta; 22: Pholoe cf. anoculata; 23: Pisaster ochraceus; 24: Patiria miniata; 25: Haliotis cracheroidii.

Abbreviations and symbols: $: description of gonad maturation based on staging or analysis of the size-frequency distribution of the gametocytes (*); #: direct evidence of spawning in the form of eggs or larvae (i.e. spawning season observed), indirect evidence of spawning based on gonad maturation index, ovary mass index and/or activity of accessory cells (i.e. spawning season predicted); (?) personal interpretation with reservations; ?: respective author's interpretation with reservations; +, ++, +++: increasing degree of cyclicity; N y^{-1}: number of cycles per year.

respond to any short-term fluctuations of those conditions which enhance reproductive success.

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Section 4 PRODUCTION

SECTION 4

The role of muscle reserves and production costs in the life-history of the intertidal barnacle *Tetraclita serrata* Darwin

Abstract

The life-history of the intertidal barnacle Tetraclita serrata Darwin was examined at Dalebrook, False Bay (South Africa). Ovarian growth is assured by pre-accumulated muscle reserves. This suggests that reproductive success is thus facilitated in the event of any unpredictable fluctuations in, amongst other things, food supply.

Barnacles low on the shore have faster rates of somatic production than their high shore counterparts, and their reproductive outputs also increase more rapidly with age. However, they live much shorter on average (their mean adult age is 3 years as compared to 8 years for animals higher up the shore). As a result, cumulative production at mean age is of a similar order of magnitude irrespective of tidal elevation. Production costs, therefore, are possibly of fundamental importance in explaining life-expectancy. In this context, somatic growth could play as significant a role as reproduction (at mean age, more energy had invariably been devoted to the former than to the latter). Because developmental influences violate an assumption implicit in demographic models, it is suggested that life-history variability of T. serrata at different shore levels does not constitute evidence of diverging life-history tactics.

Up to mean adult age, shell production invariably forms the single most important expenditure of energy. This is especially so in animals which are submerged for longer periods low on the shore, where rapid growth to large size may procure protection against excessive wave impact. However, these barnacles produced relatively few young compared with individuals higher up the shore, so that a trade-off possibly exists between somatic growth and reproduction. It is suggested that the emergence/submergence regime and wave impact, via their effects on shell growth, may thus be of fundamental importance in explaining the life-history of intertidal barnacles.

Introduction

The major processes occurring during the life of an organism are growth, reproduction and senescence (Calow, 1978). The former two processes are both considered to affect longevity. However, 'costs' of reproduction alone are incorporated into current demographic models (Stearns, 1976). Indeed, growth is not a demographic variable and one assumption implicit in such models is that life-history 'traits' co-evolve independently of developmental influences (Stearns, 1980).

The intertidal barnacle Tetraclita serrata Darwin has a seasonal breeding cycle (Section 3A). However, its sexual organs remain active (albeit at a reduced level) throughout the year, possibly enabling this species to counteract unpredictable variations in factors affecting reproduction, notably food supply (Section 3B, C).

For most members of local populations of T. serrata, the annual reproductive output appears to be limited by shell internal volume (Section 3A). Because shell accretion rates vary depending on shore position, topography, etc. (Section 2A), it is to be expected that reproduction rates will differ correspondingly between local subpopulations. One exception may be the oldest barnacles low on the shore, which have reduced annual reproductive outputs despite internal volumes being sufficiently large. This is possibly a sign of ageing (Section 3A).

On the basis of the findings described above (see Sections 2A and 3), the present study examines two aspects relevant to the life-history of T. serrata. One concerns the possible role of somatic reserves in facilitating reproductive success in the event of any unpredictable variations in food, the other the possible influence of production costs on longevity.

The somatic components which are enclosed by the shell and can potentially act as storage organs in barnacles are the prosoma and the muscles. The prosoma of T. serrata maintains an essentially constant mass during the year (Section 2B). It therefore seems unlikely that prosomal reserves are drawn upon during the marked increase in ovarian mass observed prior to spawning (Section 3A). This leaves muscle reserves as the only alternative.

Furthermore, it is anticipated that costs incurred during the growth and reproduction of T. serrata accumulate at variable rates depending on tidal position. In terms of current ageing theory (Calow, 1978), therefore, mean age should vary within local populations.

Study area

The work was carried out at Dalebrook (False Bay, South Africa; see General Introduction, Fig. 1). The topography and population distribution at this site have been described in a separate study (Section 1A).

T. serrata was found to be symmetrically distributed along the tidal gradient on a gently sloping rock platform. Two corridors parallel to the shore were chosen for this study, the lower one at the seaward limit of species occurrence, the upper one at the landward limit (Fig. 1).

Materials and Methods

The body components considered in this study are listed below and, where necessary, defined. In each case, the sources of data are identified.

Body components:
a) the shell (Section 2B);
b) the opercular valves (Section 2B);
c) the 'structural' ovary: i.e. the residual mass of ovarian
   tissue persisting during the non-breeding period

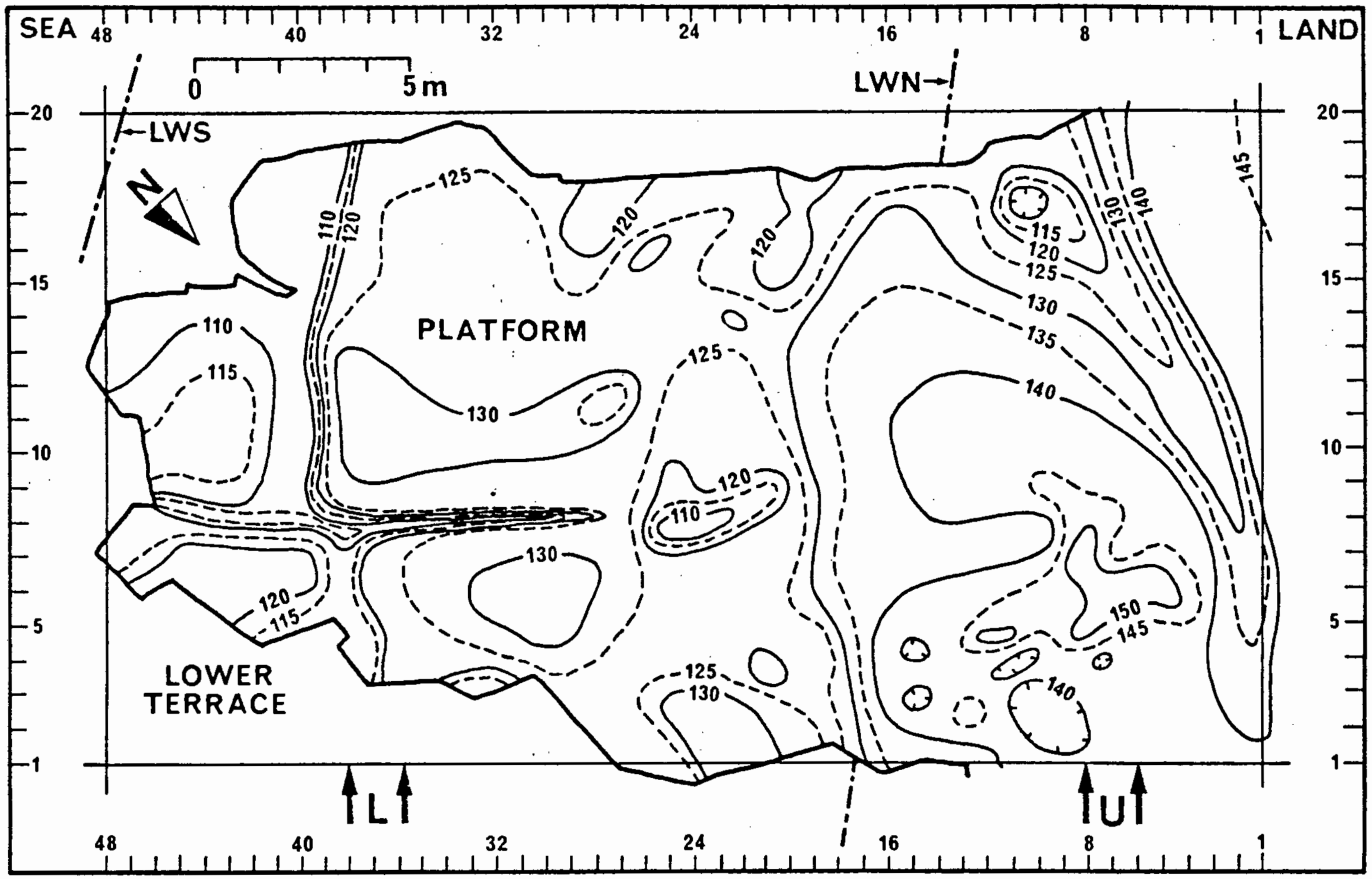

Figure 1. Elevation map of rock platform at Dalebrook showing major topographical features and the positions of the two corridors parallel to the shore (U: upper corridor; L: lower corridor; LWN: low water neaps; LWS: low water springs; elevations in cm above chart datum, extracted from Section 1A).

(Section 3A);

d) the 'reserve' ovary: i.e. the difference between the annual maximum in ovarian mass reached prior to spawning and the mass of the structural ovary (Section 3A);

e) the newly spawned eggs (Section 3A);

f) the semen: i.e. the mass of the seminal vesicles (Section 3A);

g) the prosoma: i.e. the cirri, the mouth, the stomach, the intestine, the penis and the paired testis and seminal vesicle (Section 2B);

h) the 'structural' muscle: i.e. the annual minimum in muscle mass (this study; see Sections 2 and 3 for the preparation of samples);

i) the 'reserve' muscle: i.e. the difference between the annual maximum in muscle mass and the mass of the structural muscle (this study).

Energy equivalents of freeze-dried masses were determined for animals of various sizes collected at different times of the year (Table 1). Analyses were carried out either with a Gallentkamp ballistic bomb (components a and b) or with a Phillipson microbomb (components c to i; Holme and McIntyre, 1971).

Results

Somatic and ovarian reserves

Monthly variations in the masses of body components enclosed by the shell of a 'standard' animal (100 mg valve dry mass) are shown in Fig. 2. Additional data from which the results on muscle mass were derived are listed in Table 2.

Prosomal masses of 'standard' animals remained similar throughout the year. On the other hand, the masses of other components varied. Muscles decreased in mass during the time of ovarian growth in autumn and winter (April to September), suggesting that muscle reserves were utilized as an energy source during

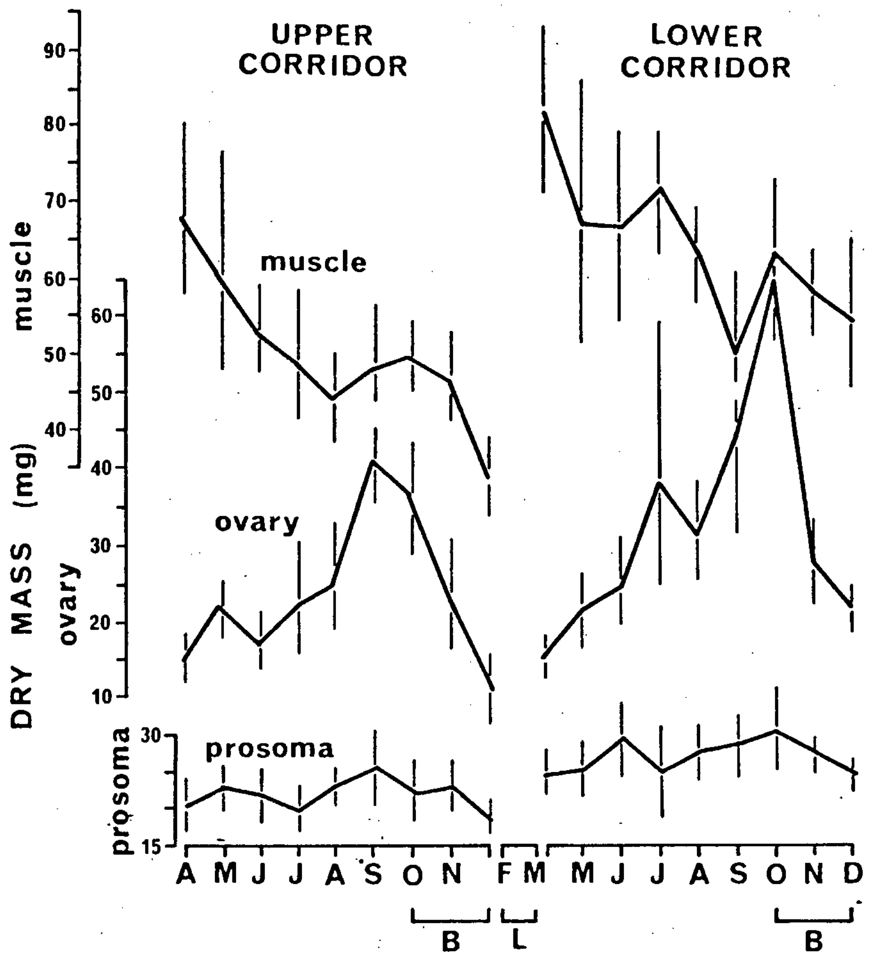

Figure 2. Monthly variations in muscle, ovary and prosomal masses in 'standard' sized animals (100 mg valve dry mass) from the upper and lower corridors (95 % confidence limits are indicated by vertical bars; see Table 2 for data on muscle masses and see text for other data sources). Abbreviations: B: period during which at least 20 % of each subpopulation contained broods; L: onset of larval settlement.

Table 1. Energy equivalents of various body components (data for the upper and lower corridors were combined).

body component	number of analyses	average energy equivalent ±standard deviation (kJ g-1 dry mass)	
shell	5	0.8693	0.3270
prosoma	5	12.9422	0.7494
structural muscle	5	12.5525	0.4828
reserve muscle	5	15.0225	0.5001
structural ovary	5	11.0201	1.3900
reserve ovary	5	11.6792	1.4566
eggs	5	14.0460	0.4933
semen	5	16.6751	0.3064

Table 2. Equations relating muscle dry mass to animal size at different times of the year (animal size was represented by the dry mass of valves; M: muscle mass (mg); V: valve mass (mg); CL: confidence limits; r: correlation coefficient; N: sample size).

month	upper corridor	±95 % CL	r	N
1978				
Apr	log M = 0.250 + 0.793 log V	0.126	0.9566	31
May	log M = 0.483 + 0.650 log V	0.154	0.9072	37
Jun	M = 4.260 + 0.490 V	9.510	0.9044	25
Jul	log M = 0.031 + 0.833 log V	0.124	0.9370	33
Aug	M = 9.370 + 0.355 V	10.600	0.8414	25
Sep	M = 9.190 + 0.395 V	11.500	0.7804	25
Oct	M = 5.610 + 0.446 V	7.110	0.9623	25
Nov	M = 13.100 + 0.330 V	7.080	0.9225	25
Dec	log M = 0.161 + 0.690 log V	0.101	0.9418	25
	lower corridor			
1978				
Apr	log M = 0.221 + 0.851 log V	0.090	0.9788	28
May	log M = 0.545 + 0.641 log V	0.155	0.8521	25
Jun	M = 4.880 + 0.620 V	8.570	0.8649	26
Jul	M = 4.240 + 0.680 V	5.800	0.9524	25
Aug	log M = 0.211 + 0.796 log V	0.074	0.9623	25
Sep	M =-40.500 + 45.300 log V	14.200	0.6253	25
Oct	M = 6.350 + 0.576 V	14.600	0.8643	25
Nov	M = 16.000 + 0.431 V	10.300	0.9225	25
Dec	log M = -0.019 + 0.880 log V	0.140	0.8983	25

N.B.: for each monthly data set, the best fit equation (highest r value) is listed.

reproduction. Muscle masses remained at low levels during the ensuing brooding period in early summer (October to December).

From the above, it is inferred that muscles accumulate reserves sometime between late summer (December) and autumn (April), i.e. after the larvae are released from the mantle-cavity and before the onset of ovarian maturation.

Ontogenetic production

Accretion rates of body components were computed by means of von Bertalanffy equations for linear shell growth (Section 2A, B). The equations for the lower and upper corridors are respectively:

$L_t = 2.900\ (1-e^{-0.3869(t+0.7863)})$, $r = 0.9672$
and
$L_t = 3.0784\ (1-e^{-0.1252(t+1.3701)})$, $r = 0.9974$

(where L_t = shell length (cm) at time t). Note that animals could be aged only up to the point at which the maximum shell length observed in vivo was reached. This was at approximately 11 and 18 years of age in the lower and upper corridors respectively.

Shell length, shell volume and shell mass all increased with age (Figs. 3, 4). The masses of various components enclosed by the shell increased likewise, though with one exception: in the lower corridor, annual egg production increased up to a certain age (11 years) only, after which it decreased (Fig. 4B).

Length, volume and mass accretion rates were invariably faster in the lower corridor. Significantly, in the upper corridor, masses of reserve muscles increased more rapidly with age than masses of reserve ovaries, the reverse being the case in the lower corridor.

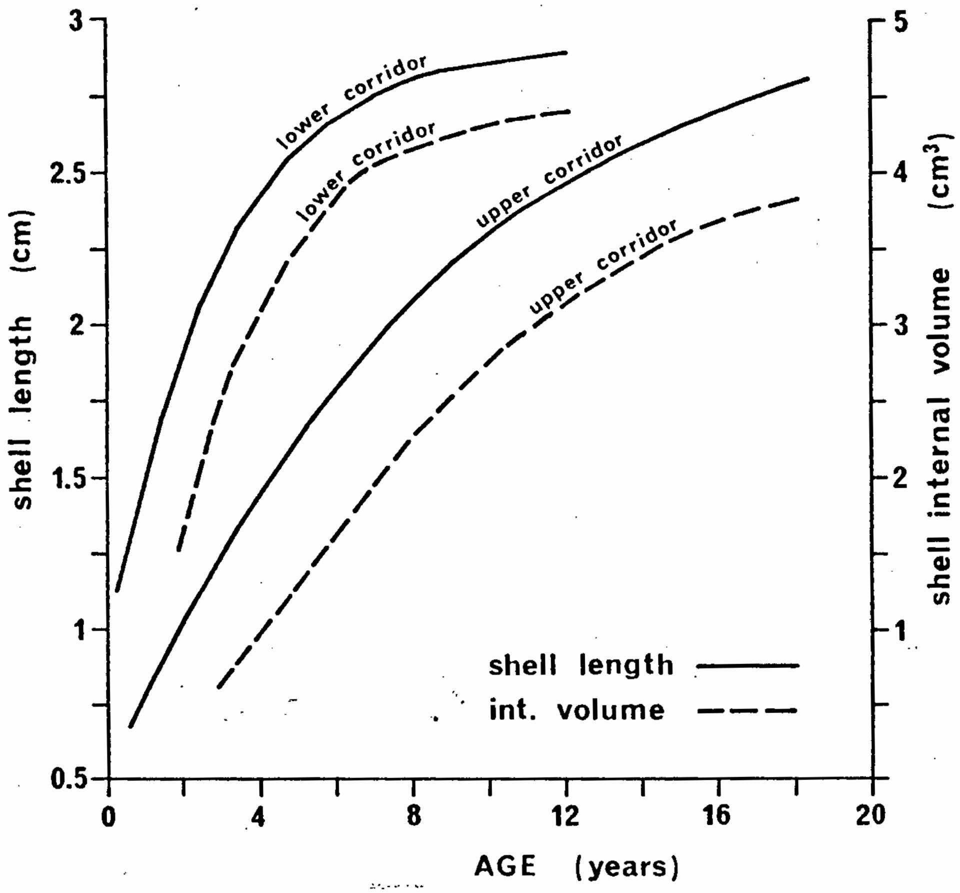

Figure 3. Linear and volumetric shell accretion rates for individual barnacles from the upper and lower corridors (extracted from Sections 2A and 3A; see text for von Bertalanffy equations describing linear shell growth).

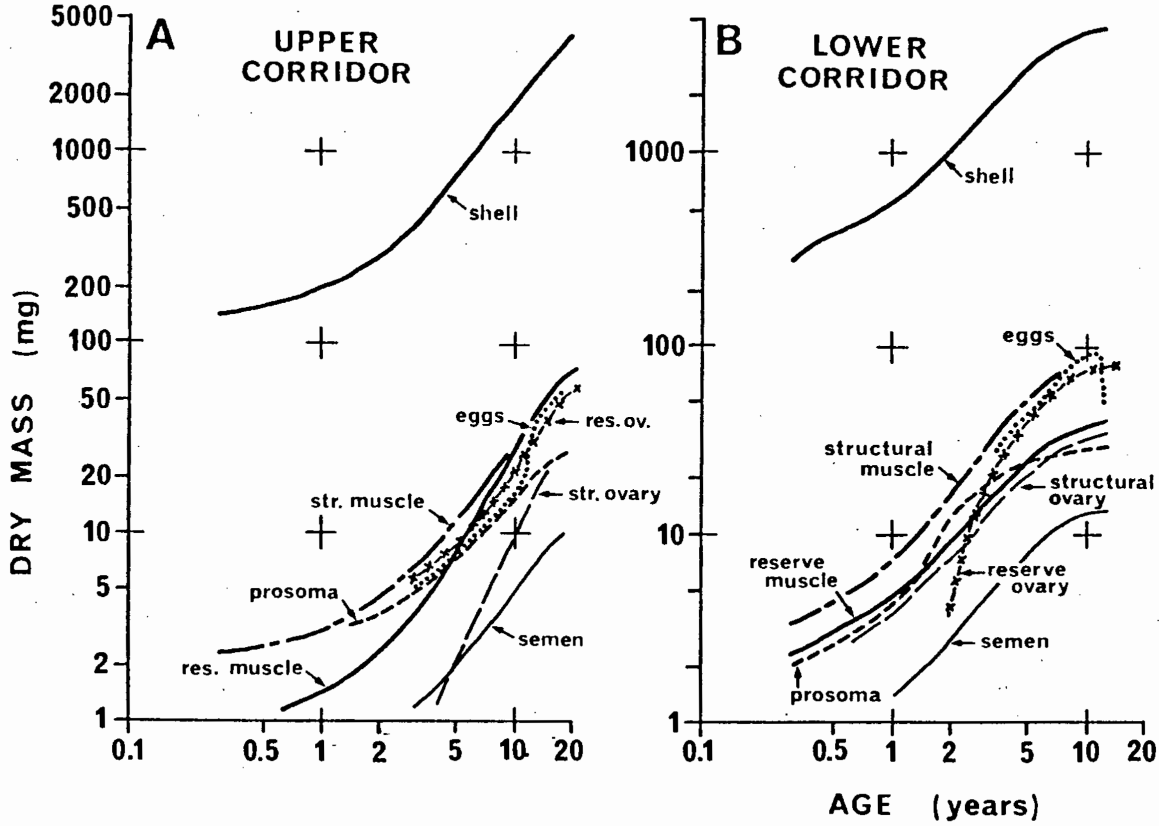

Figure 4. Mass accretion rates of major body components for individual barnacles (reserves, eggs and semen: annual biomass). A: upper corridor. B: lower corridor.

At all ages, shell growth invariably formed the single most important item of energy expenditure in somatic production (if the term 'somatic production' excludes the accumulation of somatic reserves in the muscles; Fig. 5). Shell production tended to be evenly distributed throughout ontogeny in the upper corridor but there was a pronounced peak early in life in the lower corridor.

In both corridors, with increasing age, progressively more energy was expended on gamete production (eggs and semen) and on the accumulation of reserves (in the ovaries and muscles) than on somatic production (Fig. 5). In the upper corridor, energy input into reserve muscles also increased more rapidly with age than input into reserve ovaries, the reverse once again being the case in the lower corridor.

Ontogenetic production vs mean adult age

Age-frequency distributions were extracted from a separate study (Section 2A). The data (Fig. 6A, B) show that, in the upper corridor, very young barnacles were rare and the majority of the adults (reproductive individuals) were 5 to 10 years old. In the lower corridor, on the other hand, young barnacles were more abundant and most adults were between 2 and 4 years old. Correspondingly, the mean age of adult barnacles in the upper corridor was approximately 8 years and that in the lower corridor approximately 3 years. In the following, 'mean age' shall always refer to mean adult age.

In both corridors, the annual amount of energy devoted per individual to somatic production (P_S) increased approximately up to the mean age of each subpopulation (Fig. 6C, D), shell growth (P_{sh}) evidently being the dominant contributor in each case (Fig. 5). Thereafter, input into P_S decreased. Annual gamete production (P_R), on the other hand, continued to increase with age, surpassing P_S approximately 2 years after the barnacles reached their respective mean ages. As a result, reproductive 'efforts' (RE, the ratio of annual gamete production to annual

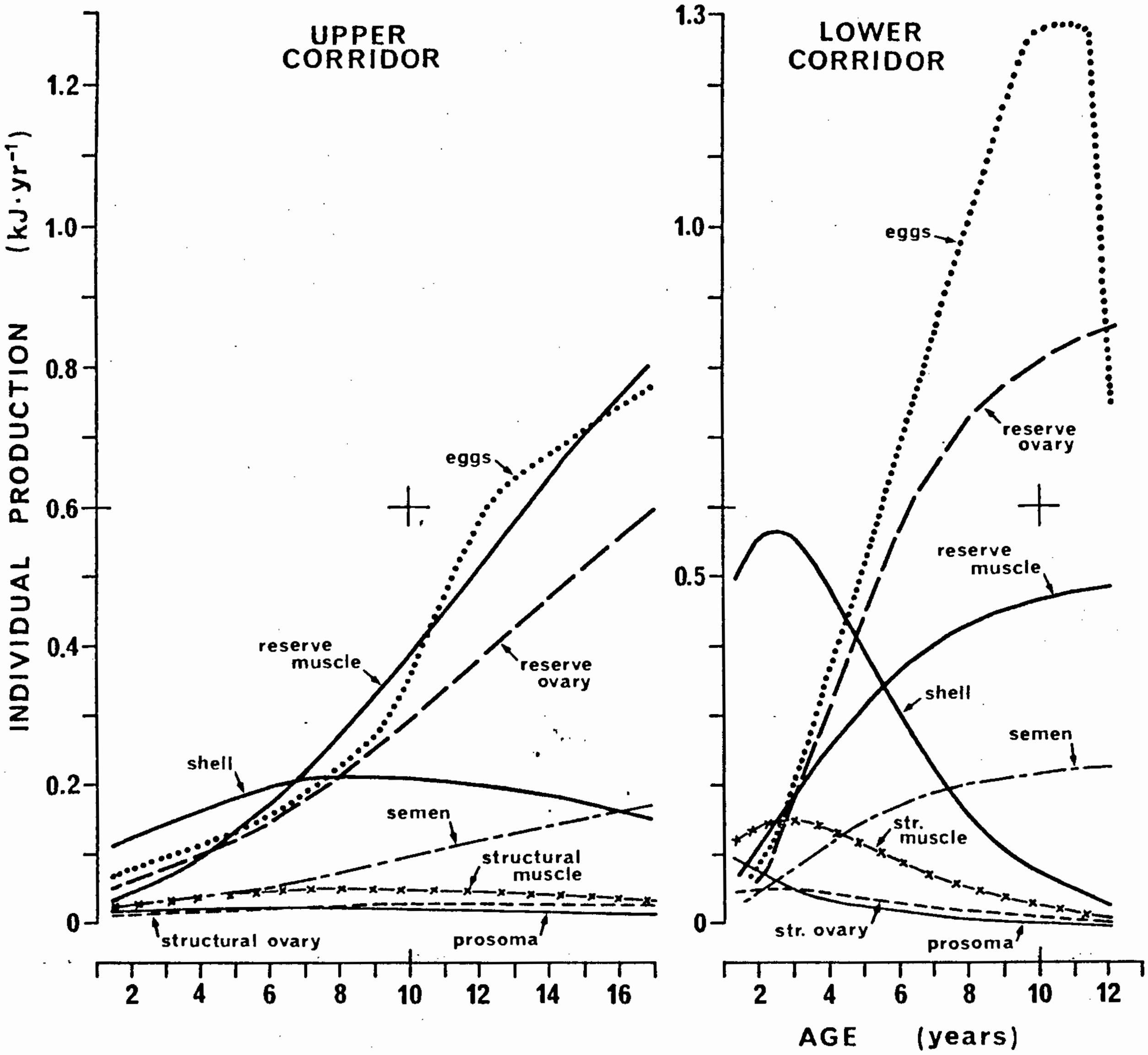

Figure 5. Annual production (energy equivalents) of major body components for individual barnacles of various ages from the upper and lower corridors.

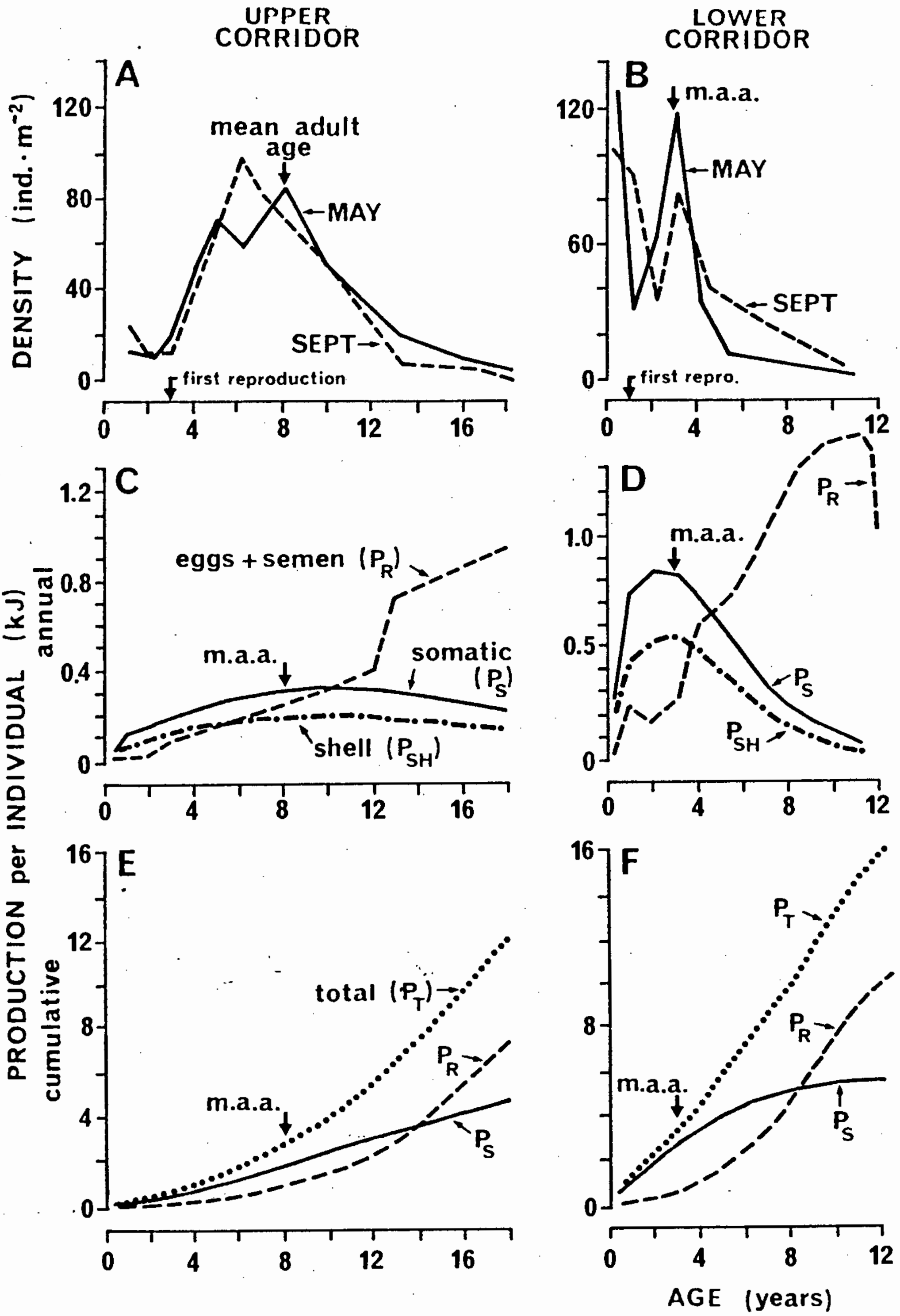

Figure 6. Age-frequency histograms and production (energy equivalents) of somatic vs reproductive components for individual barnacles of various ages. A: age-frequency histograms for the upper corridor either 3 or 7 months after the onset of larval settlement in February (i.e. May and September respectively). B: idem A for the lower corridor. C, D: annual production for the upper and lower corridors respectively. E, F: cumulative production for the upper and lower corridors respectively. Abbreviations: m.a.a.: mean adult age; P_S: somatic production (shell, valves, prosoma, structural muscle, structural ovary); P_{sh}: shell production; P_R: production of eggs and semen; P_T: total production (P_S+P_R).

total production = P_R / P_R + P_S) increased in animals older than the mean age of each subpopulation (Fig. 7A). Because P_R increased more rapidly to reach higher values in the lower corridor, RE showed corresponding trends.

In contrast to annual production, cumulative P_R surpassed cumulative P_S as much as 5 to 6 years after the respective mean ages of the barnacles in each corridor (Fig. 6E, F). At mean age, cumulative P_S exceeded cumulative P_R by a factor of 4.11 in the lower corridor, but by much less (1.85) in the upper corridor.

At their mean ages, the barnacles in each corridor had expended comparable amounts of energy in cumulative total production, with a marginally higher value being recorded in the lower corridor (3.49 kJ) than in the upper corridor (2.85 kJ), a ratio of 1.22 (Fig. 6E, F). On the other hand, cumulative P_S was measurably greater in the lower corridor (2.80 kJ) compared with the upper corridor (1.85 kJ; ratio 1.51), while the reverse was the case for cumulative P_R (lower corridor/upper corridor = 0.68/ 1.00 kJ = 0.68). As a result, smaller mean ages in the lower corridor were associated with smaller cumulative reproductive efforts at mean age (lower corridor/upper corridor = 0.68/2.59 = 0.26; Fig. 7B).

Population production

In both corridors, all age-groups showed comparable levels of expenditure in P_R (Fig. 8A, B).

On the other hand, P_S was similar to P_R for all age-groups in the upper corridor only. In the lower corridor, P_S was markedly higher in younger age-groups. In fact, the maximum level of somatic production observed in the lower corridor was the highest recorded in the study, coinciding with the mean adult age-group of the subpopulation. The cumulative total production (cumulative P_T) was correspondingly higher in the lower corridor (lower corridor/upper corridor = 361/219 kJ m^{-2} yr^{-1} = 1.65; Fig. 8C, D). As evident from Figs. 5 and 6, cumulative shell

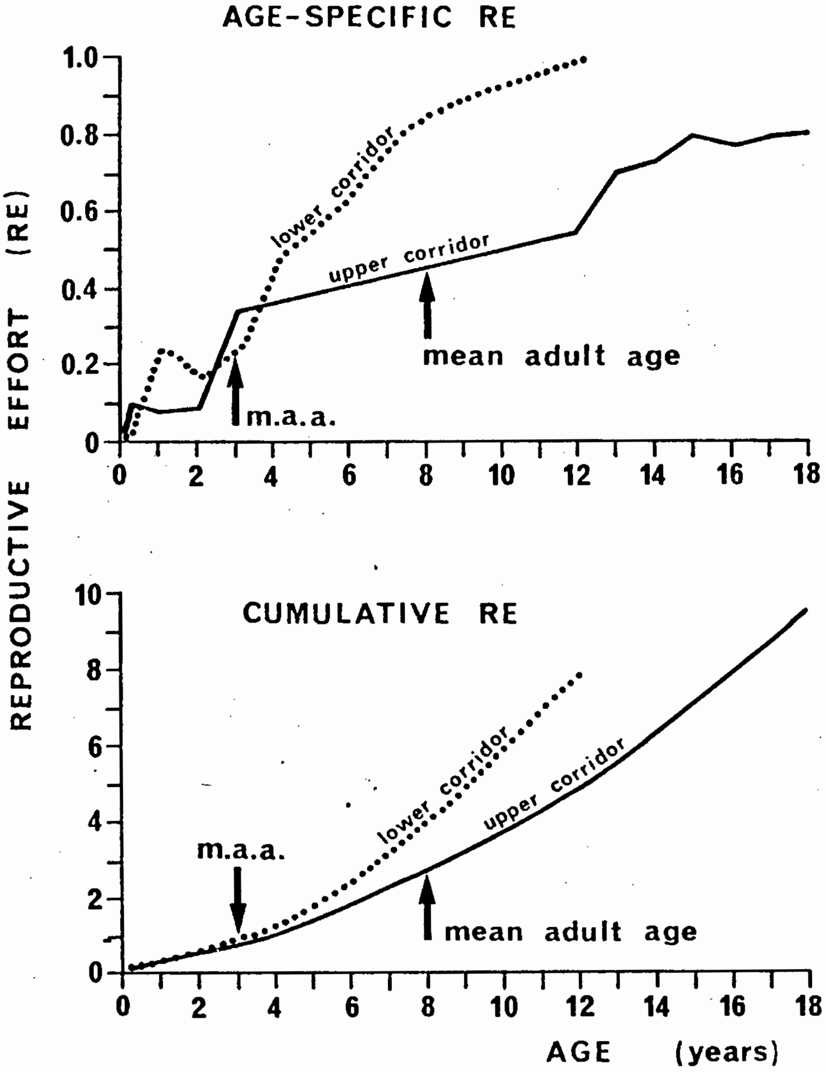

Figure 7. Accretion rates of reproductive effort for individual barnacles from the upper and lower corridors (reproductive effort: annual gamete production (eggs + semen) / annual total production).

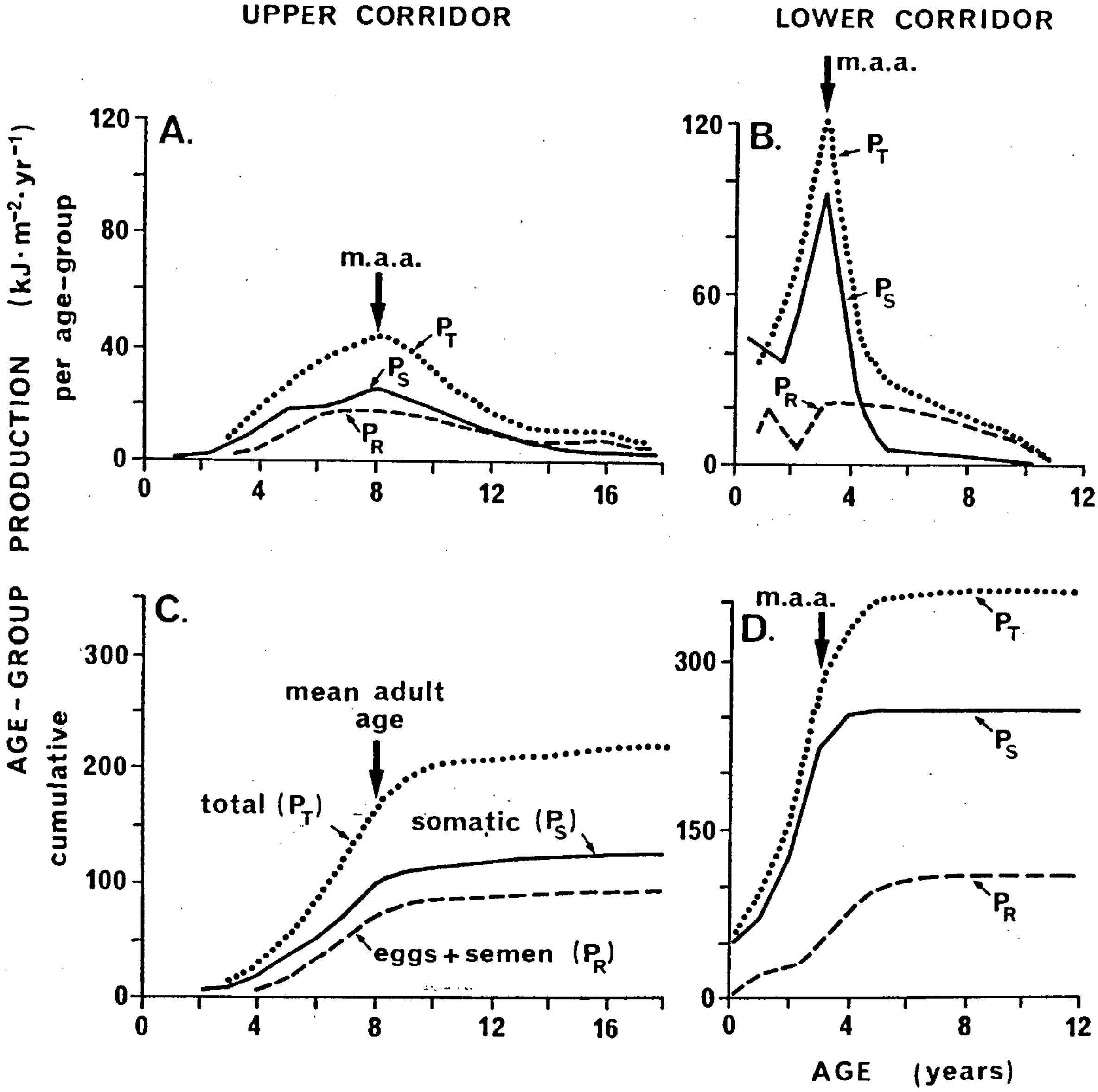

Figure 8. Population production (energy equivalents) per unit area for barnacles of given ages (age-groups) A, B: annual production for specific age-groups from the upper and lower corridors respectively. C, D: cumulative annual production for age-groups from the upper and lower corridors respectively. Abbreviations: see Fig. 6.

production formed the single most important item in energy expenditure in both corridors (cumulative P_{sh}/cumulative P_T = 0.47 and 0.38 for the lower and upper corridors respectively).

Discussion

The results of this study show that, up to mean adult ages within T. serrata populations, shell production formed the single most important expenditure of energy, even outweighing the combined production of eggs and semen (Fig. 6). Dead shell material therefore forms a significant energy sink, an aspect thus far little considered in energy flow studies of barnacles - and of many other organisms producing calcareous skeletons, for that matter (cf. Wu and Levings, 1979; Rhoads and Lutz, 1980). Since barnacles contribute over 60 % to local bioclastic sediments in the study area (Flemming, 1976), it would be of interest to investigate the trophic role of this material, particularly the degree to which the organic shell matrix is utilized by primary consumers and other organisms.

Similarly, the utilization of muscle reserves has also not been formerly investigated in barnacles. Whereas muscles have been shown to store energy in a variety of organisms including fish (e.g. Henderson et al., 1984), lobsters (e.g. Dall, 1981), slugs (e.g. Catalan et al., 1977) and scallops (e.g. Barber and Blake, 1981), the role of muscles in barnacles has thus far been viewed only in terms of anti-predatory defenses (Anderson, 1981).

In the present study, indirect evidence of muscle reserves accumulating outside the breeding period is consistent with previous findings that space availability within the shell is limited during the breeding period (Section 3A). Furthermore, the fact that these reserves were utilized during this period implies that reproduction was correspondingly less dependent on exogenous energy sources and therefore, less affected by any unpredictable variations in food supply. Indeed, reproductive success is known to depend on muscle reserves in various marine animals including scallops and fish (e.g. Barber and Blake, 1981 and Henderson et al., 1984 respectively). Significantly, reproduction apparently became more dependent on such reserves in regions of the shore where feeding time was diminished in the present study. In the upper corridor where T. serrata was submerged for shorter periods than lower down the shore, reserve muscles had faster rates of mass and energy accretion than reserve ovaries, the reverse being the case in the lower corridor.

An interesting comparison may be made here with one of the most extensively studied barnacles, Semibalanus balanoides. This species may experience severe food limitation at certain times of the year. In contrast to T. serrata, the ovary re-accumulates reserves immediately after the annual spawning season when diatom blooms are frequent (Barnes et al., 1963). If S. balanoides also utilizes muscle reserves, these are evidently not sufficient to satisfy reproductive demands when food is very scarce.

The need to determine whether somatic reserves provide energy during reproduction is highlighted by current views of reproductive 'costs'. Although this concept has been under considerable debate (e.g. Thompson, 1984; Trillmich, 1986; see also review concerning marine invertebrates by Grahame and Branch, 1985) since it was initially proposed by Williams over 20 years ago (1966a, b), assessments based on energy budgets are today considered superior to those based on size-related reproductive output (Calow, 1978; cf. Parry, 1982). In the case of energy budgets, however, somatic reserves destined for use during reproduction must be taken into account. Surprisingly, this aspect has to date been ignored in barnacles (Wu et al., 1977; Wu and Levings, 1978, 1979; cf. Barber and Blake, 1986).

The notion that costs incurred during somatic growth and reproduction inversely affect lifespan forms the basis of current ageing theory (Calow, 1978). In the present study, production rate may indeed have adversely affected longevity because, in different subpopulations of T. serrata, barnacles had reached similar levels of cumulative production at mean adult age, irrespective of their average lifespans.

It cannot, however, be assumed that production as such is an adequate measure of all costs incurred in growth and reproduction. Differential tapping of muscle reserves, for instance, may also be important in determining such costs. On the other hand, production rate may mediate the effects of extrinsic factors affecting longevity (viz. disease, predation, etc.). For example, fast growth of _T. serrata_ low on the shore could result in an early encounter with predators selectively eliminating large barnacles, thereby indirectly shortening lifespan. In view of these considerations, further investigations of all possible causes of mortality are necessary to establish how _important_ (_sensu_ Welden and Slauson, 1986) intrinsic causes such as production costs are in determining mean adult age within _T. serrata_ populations.

Life-history parameters of _T. serrata_ at different shore levels at Dalebrook show classical associations consistent with both 'r-k' and 'bet-hedging' demographic theories (Stearns, 1976; Calow, 1978). Barnacles in the lower corridor reached sexual maturity slightly earlier than animals in the upper corridor (2 _vs_ 3 years of age; Section 3A), their reproductive outputs increased more rapidly with age to reach higher reproductive 'efforts' (i.e. higher proportions of somatic biomass (Section 3A) and of total production) and they had lower mean adult ages (3 _vs_ 8 years).

Similar correlations of life-history parameters have been observed in studies comparing various barnacle species (Table 3; see also Barnes and Barnes, 1968; Klepal and Barnes, 1975; Barnes and Achituv, 1976; Littler et al., 1983; Dungan 1985). It is as yet unknown whether such interspecific differences are consistent with assumptions implicit in demographic models, in particular that life-history 'traits' co-evolve independently of developmental constraints (Stearns, 1980). On the other hand,

Table 3. Life-histories of selected barnacles.

species		sexual maturity (months)	mean adult life (months)	reproductive effort	reference
ACORN BARNACLES					
Chthamalus fissus					
California	I	3	8	11.49	Hines (1979)
	cs	0.7	-	25.80	Page (1984)
Balanus glandula					
California	I	9	26	9.48	Hines (1979)
British Columbia	I	4	-	-	Wu & Levings (1978)
Balanus pacificus					
California	S	2	-	-	Hurley (1973)
Balanus porcatus					
Irish Sea	S	24	42	-	Crisp (1954)
Tetraclita squamosa rubescens					
California	I	22	44	3.63	Hines (1979)
Tetraclita serrata					
South Africa	I				This study, Section 3A
high shore		36	96	2.1 2.4*	
low shore		24	36	3.1 3.5*	
STALKED BARNACLES					
Pollicipes polymerus					
California	cs	3	-	2.31	Page (1984)

Abbreviations: I: intertidal; S: subtidal; cs: continuous submergence (experimental).
Reproductive effort: the relationship between annual reproductive biomass and somatic biomass. Note that in all species except *T. serrata*, efforts are expressed in terms of regression slopes. In *T. serrata*, efforts are expressed as ratios (highest values being listed) because correlations are not linear in all cases (see Section 3A).
Reproductive biomass: eggs (*: eggs and semen, *T. serrata*).
Somatic biomass: acorn barnacles: prosoma; stalked barnacles: prosoma and stalk.

this assumption seems to be violated at the intraspecific level, at least in the case of T. serrata.

In one such instance, differences in reproductive 'efforts' (the ratio of reproductive to somatic biomasses) between barnacles from the lower and upper corridors may be explained by corresponding variations in shell internal volume (Section 3A), suggesting that reproduction may be influenced by space availability within the shell. Whereas the positive correlation between the rate of volumetric shell accretion and the rate of reproduction observed in the present study is compatible with the above physical constraints, such constraints are incompatible with life-history theory (see above).

The other instance of life-history parameters possibly interacting more with developmental processes than amongst themselves (thus violating assumptions implicit in demographic models) concerns production 'costs'. If energy expended in production influences life-expectancy in T. serrata, then costs incurred in somatic growth (particularly in shell growth) are probably at least as important as those associated with reproduction. By their mean adult age, the barnacles had invariably devoted more energy to cumulative somatic production than to cumulative reproduction, especially in the lower corridor where energy input into shell production was high.

The above considerations suggest that variations in the life-history of T. serrata at different shore levels at Dalebrook do not constitute evidence of diverging life-history tactics (Stearns, 1980). Indeed, recent reappraisals of life-history evolution indicate that tactics are more likely to exist above the intraspecific level (Stearns, 1980). According to Stearns (1980), these may in fact become apparent well above the species level only, if they exist at all (e.g. Fletcher, 1984a, b; Dobson and Murie, 1987). In the case of intertidal barnacles, and evidently also of other organisms producing calcareous skeletons (Hemleben et al., 1979; Palmer, 1981, 1983), developmental influences (both physical and energetic) associated with variable shell growth may thus be of primary importance in explaining life-history divergence within species.

In terms of such divergence, environmental demands to which shell growth may be responding have not been considered so far. It is probable that increased time for feeding and calcification enables barnacles low on the shore to grow faster (Section 2A). Nevertheless, independent evidence (the production of thick shells by small T. serrata at low shore levels) suggests that rapid attainment of large size may procure protection against excessive wave impact in the low shore (Section 2A). Indeed, the present study demonstrates that, at mean adult age, low-shore barnacles not only had invested more energy into shell production than their high-shore counterparts, they also had larger shells (Fig. 3). On the other hand, they had produced fewer young. It is possible, therefore, that a trade-off in fitness exists between the advantages of growth and reproduction (cf. Clarke, 1987). This complies with conditions necessary for the maintenance of polymorphisms or variability in animal populations and has recently been linked to anti-predatory defenses in barnacles (Lively, 1986).

In view of the preceeding discussion, it appears that both wave impact and the emergence/submergence regime affect shell growth and that this possibly plays a fundamental role in determining the reproductive capacity of T. serrata. Furthermore, it has been found that the same factors also influence zonation by controlling larval settlement (Section 1B). In conclusion, therefore, it is suggested that species-specific requirements for conditions of wave impact and emergence/submergence may be of primary importance, not only to the life-history, but also to the general biology of intertidal barnacles.

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SUMMARIZING DISCUSSION

In this final discussion, key findings of the study are integrated within the broad framework of the biology and evolution of sessile barnacles. Major conflicts with some current concepts are once more highlighted.

Biotic interactions have to date been considered of overriding importance in this field. For instance, the evolutionary decline of one superfamily, the Chthamaloidea, has been attributed to competititve interference with other barnacles (Stanley and Newman, 1980; see Section 1B). Indeed, in some temperate intertidal communities, competition is at present still a major factor determining zonation, with physical disturbance and predation playing additional roles (Paine, 1981).

Arising from the afore-mentioned notions concerning zonation are current interpretations of life-history patterns. For example, species which are likely to loose out in competition as a result of slow growth and/or small body size often have longer breeding periods, larger reproductive 'efforts' (ratios of reproductive to somatic biomasses) and they also have shorter lives than large, fast-growing barnacles (see Hines, 1979). It is thought that these 'opportunistic' characteristics a) facilitate survival under harsher abiotic conditions in 'refuges' from competition; b) promote competitive superiority by increasing population density; and c) also promote rapid recolonisation of physically disturbed habitats (Hines, 1979; Paine, 1981; Dungan, 1985). Evidently, selective pressures associated with competition are considered of major significance in the field of life-history theory.

In contrast, the findings presented in this thesis argue against the general importance of biotic interactions (notably competition) and physical disturbance in the biology of several intertidal barnacles in southern Africa. Indeed, a conceptual model of community structure for the coronuloid *Tetraclita serrata* Darwin and the chthamaloids *Chthamalus dentatus* Krauss and

Octomeris angulosa Sowerby suggests that each species occurs under a specific set of physical conditions defined by two major intertidal factors, namely emergence/ submergence regime in combination with wave impact (Section 1B). Conditions vary on the shore, depending on topography, regional setting, etc. This explains the large diversity in distribution patterns displayed by these species, notably vertical zonation on evenly sloping rock surfaces, horizontal zonation in gullies and patchy distributions on rugged shorelines. Over the limited range of conditions under which species-specific habitats overlap, no evidence for interspecific competition was found. One possible explanation for this is low population density under conditions of species overlap. Indeed, at least one of the three barnacles, namely T. serrata, is symmetrically distributed along the emergence/submergence gradient (Section 1A).

The tendency for T. serrata to be symmetrically distributed along the emergence/submergence gradient was revealed only when topographically-induced variability in abundance was averaged at small height increments (2 cm), irrespective of position on the shore and over a relatively large area (in this instance, over 63,000 barnacles were counted in an area of 325 m^2). This is in sharp contrast to distribution patterns observed when relating abundance to mean slope gradient as is common practice. Since factors such as wave action, coupled with topographic variability, obscure the relationship between predicted and actual submergence regimes, this procedure pre-empts the recognition of topographic effects and thereby impairs the interpretation of distribution patterns. The same difficulty arises in computing abundance at irregular and relatively large height intervals. The new method employed here, with its finer resolution, evidently provides a solution to this problem, facilitating interpretation of distribution trends, notably zonation.

Circumstantial evidence presented in Section 1B suggests that the emergence/submergence regime in combination with wave impact affect larval settlement and thereby set clear distribution limits. In addition, both factors are evidently important in the biology of post-settled animals.

Barnacles feed and calcify only when they are submerged. Indeed, production rates of various body components of T. serrata were generally faster in animals which were submerged for longer periods (Sections 2 and 4). Notably, shell growth invariably formed the single most important expenditure of energy up to the mean ages of high- and low-shore subpopulations. The emergence/submergence regime may thus be important in regulating a significant energy sink (i.e. barnacle shells) whose trophic role remains to be investigated.

In addition to growth rate, the form of the shell may also be influenced by the abiotic milieu. For example, it was found that young barnacles produced thicker shells low on the shore (Section 2A). This may be a response to excessive wave impact, in which case fast growth to a large size would be an obvious advantage.

Fast growth, however, appears to be maintained at the expense of fecundity (Section 4). Thus, lifelong total production per individual was of a similar order of magnitude for different subpopulations, irrespective of the average lifespans of the barnacles. It is possible, therefore, that production rate is a major determinant of longevity in T. serrata, with shell growth playing the single most important role.

These findings violate one assumption implicit in demographic models, namely that life-history traits co-evolve independently of developmental constraints. In addition, differences in reproductive 'efforts' (ratios of reproductive to somatic biomasses) between subpopulations may be explained by corresponding variations in shell internal volume, suggesting that reproductive output may be limited by physical constraints (Section 3A). It is doubtful therefore, that intraspecific life-history variability in local populations of T. serrata constitutes evidence for the evolution of diverging life-history tactics.

From the above discussion, it is evident that species-specific requirements with respect to two major physical factors - emergence/submergence regime in combination with wave impact - may be of fundamental importance in the biology of intertidal barnacles, notably in connection with zonation and intraspecific life-history divergence.

Processes leading to zonation have generally been vital to the interpretation of interspecific life-history divergence. However, this approach may be inappropriate because it ignores the evolutionary baggage of present-day barnacles. For instance, it is noteworthy that chthamaloids, some of which today breed throughout much of the year, first appeared in the Cretaceous Epoch (Newman and Stanley, 1981) when climatic conditions were warmer and much more stable than today. Coronuloids and balanoids, on the other hand, appeared later in earth history as conditions became progressively colder and more unstable (Newman and Stanley, 1981). Significantly, these barnacles generally show marked seasonality in their breeding habits. As shown in Section 3A, the coronuloid *T. serrata* conforms to this pattern. In addition, acyclic gonadal activity (Sections 3B and 3C) and the utilization of substantial muscle reserves during reproduction (Section 4) may enable this species to counteract unpredictable variations in factors affecting reproduction, notably food supply. While the importance of past events cannot be ignored, this aspect may never be satisfactorily explored in barnacles because they have left a poor fossil record (see Dungan, 1985).

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