



Adaptations of bivalves to different beach types

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Abstract

Burrowing ability, shape and density of 12 bivalve species from a wide range of beach types were compared as part of a general investigation of the adaptations of bivalves to the swash climates experienced on exposed sandy beaches. The genera used were *Donax*, *Mesodesma*, *Tivela*, *Siliqua*, *Atactodea*, *Paphies* and *Donacilla*. Burrowing rates varied widely and burrowing ability showed no relation to beach type along the reflective/dissipative beach gradient, i.e. from beaches with low wave energy and coarse sand to beaches with high wave energy and fine sand. Burrowing rate indices (BRI's) ranged from 2 to 17 (rapid to very rapid) and tended to be higher for juveniles of most species. Bivalve species from dissipative beaches varied in shape from almost blade-shaped to almost spherical, whereas those from reflective beaches were more uniform generally wedge-shaped. Species with the most flattened shapes and (greatest height/width ratios) tended to burrow fastest. Striking interspecific differences were found in densities of whole intact bivalves, these ranging from $1.04 \text{ g} \cdot \text{cm}^{-3}$ to $2.10 \text{ g} \cdot \text{cm}^{-3}$. The highest densities were recorded in bivalves from reflective beaches and the lowest in bivalves from dissipative beaches. Bivalve species typical of intermediate and reflective beaches were successfully separated from those typical of dissipative beaches on the basis of their density, morphology and BRI, particularly their size and density, using discriminant analysis. It is concluded that small species with high density and streamlined shape are best adapted to the dynamic swash conditions that characterise reflective beaches.

Keywords: Beach; Bivalve; Burrowing; Density; Sand

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1. Introduction

Exposed sandy beaches support intertidal macrofaunas well adapted to the physical rigours of these dynamic environments. These communities may be described by the autecological hypothesis (Noy-Meir, 1979) which states that in physically controlled environments populations have little influence on each other and communities are structured by each species responding independently to the physical environment rather than through biological interactions. Since sandy beaches are simple environments defined primarily by two parameters, wave energy and sand particle size, it should be elementary to identify the factors controlling individual species and, by summing their responses, the community as a whole.

Microtidal beaches occur in a continuum from reflective, through intermediate to dissipative types, with the former resulting from the interaction between low wave energy and coarse sand and the latter with high wave energy and fine sand, the resultant states being steep without a surf zone and flat with an extensive surf zone respectively (Short & Wright, 1983). Beach state can be quantified using a dimensionless index (Ω) based on wave energy (wave height/wave period) divided by sand particle size (as fall velocity), where values < 2 signify reflective beaches and values > 5 indicate dissipative beaches. Recent comparative studies of beaches of different morphodynamic types and from different biogeographic provinces have shown a clear and predictable response in species richness to beach type in at least four continents: species richness decreases linearly from dissipative to reflective beaches (McLachlan, 1990; Defeo et al., 1992; McLachlan et al., 1993). The loss in species from dissipative to reflective beach types could be due to increasing particle size, decreasing wave energy or some combination of them. It has recently been shown that there is a better correlation between species richness and an overall index of beach state than with sand grain size or any other single factor (McLachlan, 1990; McLachlan et al., 1993; Jaramillo & McLachlan, 1993).

A limited amount of evidence suggests that most sandy beach animals are fairly catholic in their particle size preferences (Brown, 1983), implying that variation in wave action is important for intertidal macrofauna. However, in the intertidal regions of most beaches wave action is experienced as swash which varies as a function of beach type (McArdle & McLachlan, 1991, 1992). Consequently, the *swash exclusion hypothesis*, which states that swash climate is the key variable controlling intertidal sandy beach macrofauna, has been proposed. Swash climate is considered most benign on dissipative beaches; it becomes harsher and more species are excluded towards reflective conditions until, in the extreme reflective situation, no intertidal species occur and only supralittoral forms, which live “outside” the swash, remain (McLachlan et al., 1993).

Although direct testing of the swash exclusion hypothesis is difficult, this hypothesis does allow formulation of a variety of predictions that can be tested. One of these predictions is that the more demanding swash climate on reflective beaches would require high density, streamlined shape and rapid burrowing ability to cope with short swash periods and high turbulence. On dissipative beaches it is expected that animals with a much wider range of adaptations would occur, including slow burrowers and

forms unable to cope with great turbulence. In this paper we examine this prediction by comparing the adaptations of 12 bivalves from a range of sandy beaches around the world.

2. Methods

The species studied were drawn from four continents and a full range of beach types, including reflective and dissipative conditions. The beach state on which each species was collected is listed in Table 1, but it should be noted that several species occur over a range of beach states. Three species are from Australia, two from South Africa, three from South America, two from North America and two from New Zealand and all but *Atactodea*, *Siliqua* and *Tivela* are donacids (*Donax*), or mesodesmatids (*Mesodesma*, *Paphies*, *Donacilla*).

In each case a series of measurements were undertaken on a full size range of individuals. Numbers used ranged from 12 to 50 in different cases depending on availability. Field observations included recording the range of beach states on which the species occurred and recording burrowing time in situ with a stopwatch. Burial time was the time in seconds for the posterior edge of an animal's shell to become flush with the sand surface from the point when vertical probing of the sand by the foot was initiated. In each case in situ temperature was recorded. Although temperature effects

Table 1
Characteristics of the beaches where bivalves were studied

Species	Location	Temp °C	Beach type	Zonation
<i>Donax faba</i> (Gmelin)	Western Australia	17°C	Reflective	Intertidal
<i>Donacilla angusta</i> (Reeve)	Western Australia	17°C	Reflective	Intertidal
<i>Donax serra</i> (Röding)	South Africa	20°C	Dissipative/ intermediate	Intertidal
<i>Donax sordidus</i> (Hanley)	South Africa	20°C	Intermediate	Intertidal/surf zone
<i>Mesodesma mactroides</i> (Deshayes)	Uruguay	22°C	Dissipative	Intertidal/surf zone
<i>Mesodesma donacium</i> (Lamarck)	Chile	15°C	Dissipative	Surf zone/ subtidal
<i>Donax hanleyanus</i> (Phillipi)	Uruguay	22°C	Dissipative	Intertidal
<i>Tivela stultorum</i> (Mawe)	California, USA	18.5°C	Dissipative	Intertidal/ subtidal
<i>Siliqua patula</i> (Dixon)	Oregon, USA	12°C	Dissipative	Surf zone
<i>Atactodea striata</i> (Gmelin)	Queensland Australia	20°C	Reflective	Intertidal
<i>Paphies subtriangulata</i> (Wood)	New Zealand	20°C	Dissipative	Intertidal/ surf zone
<i>Paphies donacina</i> (Spengler)	New Zealand	15°C	Dissipative	Surf zone

on burrowing are well known (Ansell, 1983), no attempt was made to modify temperature because the response of the animal under natural conditions was of relevance and not its response to temperature.

On a size range of each species, shell length, height and width of the valves were measured to 0.1 mm with vernier callipers, mass was determined to 0.001 g and density of whole animals was measured with a picnometer (Donn, 1990). Regressions were fitted to the relationships between these variables. Burrowing rate was also expressed as a Burrowing Rate Index (Stanley, 1970) which is considered fairly independent of size and is given by:

$$\text{BRI} = \text{mass}^{0.33} (\text{g}) / \text{burrowing time}(\text{s}) \times 100$$

Size differentiation into adults and juveniles for BRI calculations was based on a length 80% of maximum for adults and 10 mm in small species and 25 mm in large species for juveniles.

Shell shapes were compared by plotting height/width against length/height ratios as

Table 2
Morphometric characteristics of 12 bivalve species from sandy beaches

Species	Max L (mm)	L × H	L × W	L × M	n
<i>Donax faba</i>	24	H = 0.63L + 0.68 r = 0.97	W = 0.37L × 0.54 r = 0.99	M = 0.22L ^{2.89} r = 0.99	13
<i>Donacilla angusta</i>	23	H = 0.59L - 0.76 r = 0.99	W = 0.37L - 0.94 r = 0.98	M = 0.07L ^{3.24} r = 0.98	22
<i>Donax serra</i>	66	H = 0.68L - 3.08 r = 0.97	W = 0.42L - 3.48 r = 0.99	M = 0.03L ^{3.37} r = 0.99	30
<i>Donax sordidus</i>	22	H = 0.62L + 1.89 r = 0.87	W = 0.41L - 0.34 r = 0.94	M = 0.23L ^{2.93} r = 0.98	30
<i>Mesodesma mactroides</i>	76	H = 0.52L + 1.05 r = 0.98	W = 0.26L + 0.26 r = 0.98	M = -0.11L ^{2.85} r = 0.99	51
<i>Mesodesma donacium</i>	61	H = 0.52L - 0.27 r = 0.99	W = 0.26L + 0.87 r = 0.98	M = 0.10L ^{2.97} r = 0.99	31
<i>Donax hanleyanus</i>	24	H = 0.63L + 0.26 r = 0.99	W = 0.48L - 0.24 r = 0.97	M = 0.11L ^{3.09} r = 0.99	47
<i>Tivela stultorum</i>	113	H = 0.73L + 0.4 r = 0.99	W = 0.44L - 0.1 r = 0.99	M = 0.19L ^{3.05} r = 1.00	25
<i>Siliqua patula</i>	145	H = 0.52L - 12.5 r = 0.98	W = 0.28L - 10.8 r = 0.97	M = 0.02L ^{3.27} r = 0.99	14
<i>Atactodea striata</i>	36	H = 0.76L + 0.05 r = 0.99	W = 0.53L - 1.23 r = 0.99	M = 0.14L ^{3.20} r = 0.99	12
<i>Paphies subtriangulata</i>	30*	H = 0.63L - 0.2 r = 1.00	W = 0.34L - 0.4 r = 0.99	M = 0.10L ^{3.12} r = 1.00	24
<i>Paphies donacina</i>	32*	H = 0.71L - 0.5 r = 1.00	W = 0.32L + 0.93 r = 0.99	M = 0.18L ^{2.98} r = 1.00	18

Max L = maximum length collected and used in this study, L = shell length (mm), H = height (mm), W = width (mm), M = mass (mg). * In the cases of *P. subtriangulata* and *P. donacina* only juveniles < 32 mm shell length were obtained, but adults exceed 100 mm. All regressions are significant ($p < 0.01$).

outlined by Stanley (1970). Ordination of the 12 species was undertaken by Principal Components Analysis (PCA) using the standardised variables maximum length, density, BRI (for juveniles, since we did not have values for adults of all species) and height/width ratio. For maximum length a value of 100 mm was used for the two *Paphies* species (Cranfield et al., 1994). A Multiple Discriminant Analysis (MDA) was also undertaken with the same variables to classify the bivalve species into three a priori groups, using beach type as the classification factor, i.e. the species were classified as having adult populations extending to dissipative, intermediate or reflective beaches. Linear combinations of the four descriptors (standardised) were used to determine discriminant functions that could maximise differences between the three beach types, since no single factor could clearly and completely separate the groups.

3. Results

Morphometric characteristics of the 12 species (Table 2) indicate that they tend to fall into two groups: small forms (<40 mm) from reflective beaches and larger (>60 mm) forms from more dissipative beaches. The former mostly belong to the genus *Donax* and are generally wedge-shaped, whereas the latter span several genera and vary

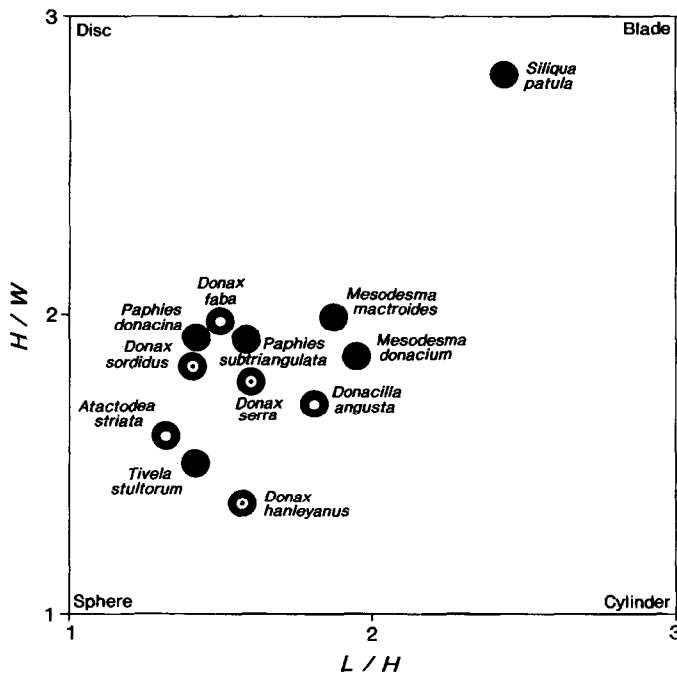


Fig. 1. Shell shapes of 12 bivalves based on length/height (L/H) and height/width (H/W) ratios. Solid circles denote bivalves from dissipative beaches, open circles, species establishing adult populations on reflective beaches and "target" symbols species establishing adult populations on intermediate beaches.

in shape (Fig. 1). This confirms that those species from reflective beaches have similar shapes (a wedge shape intermediate between a disc and a sphere), whereas those from more dissipative beaches vary between almost spherical (*Tivela stultorum*) and almost blade-shaped (*Siliqua patula*).

Linear regressions of burrowing rate against shell length were significant in all cases (Fig. 2, Table 3), with small individuals burying faster than large ones. These regressions hold only for the size ranges measured: maximum lengths used for each species are listed in Table 2 and minimum lengths were 5–10 mm in all cases. The fastest burrowers are *Donax hanleyanus* which occurs over a range from almost reflective to dissipative beaches in Uruguay, and *Siliqua patula* from dissipative beaches in Oregon. The slowest is *Atactodea striata* from reflective beaches in Australia. All species typi-

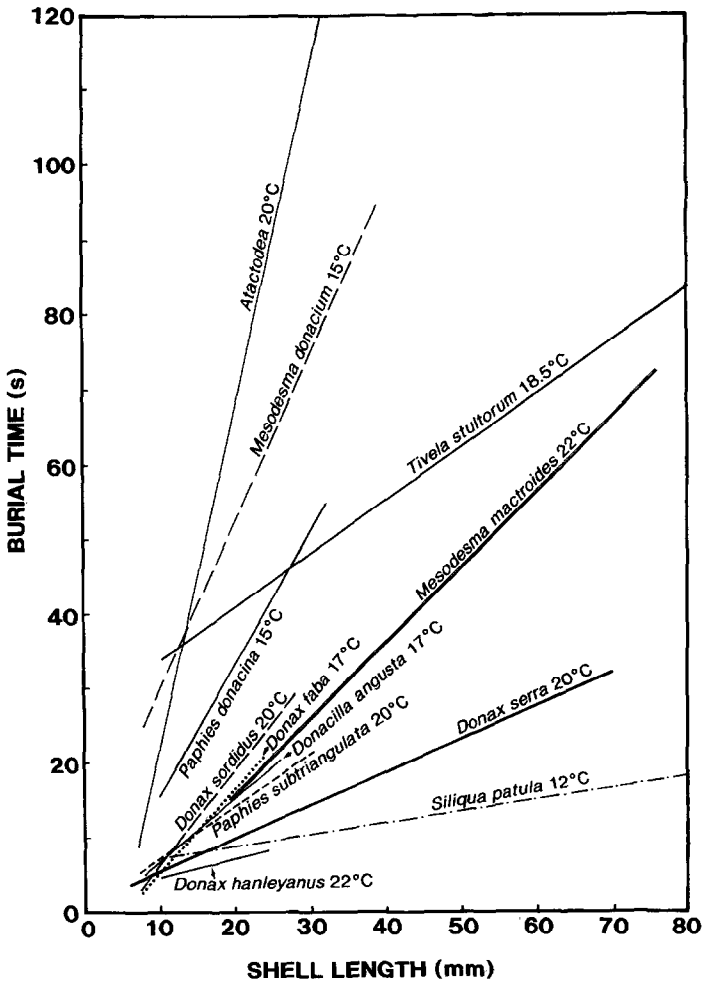


Fig. 2. Burial times as a function of shell length for 12 sandy beach bivalves.

Table 3
Burrowing rates of 12 sandy beach bivalves

Species	BR × L	r	n
<i>Donax faba</i>	BR = 1.15L - 6.21	0.82	13
<i>Donacilla angusta</i>	BR = 0.86L - 2.03	0.75	36
<i>Donax serra</i>	BR = 0.44L + 1.35	0.86	50
<i>Donax sordidus</i>	BR = 1.27L - 6.31	0.51	20
<i>Mesodesma mactroides</i>	BR = 1.03L - 5.30	0.74	53
<i>Mesodesma donacium</i>	BR = 2.20L + 8.10	0.73	39
<i>Donax hanleyanus</i>	BR = 0.24L + 2.24	0.60	48
<i>Tivela stultorum</i>	BR = 0.71L + 26.89	0.67	25
<i>Siliqua patula</i>	BR = 0.16L + 5.42	0.49	25
<i>Atactodea striata</i>	BR = 4.69L - 25.10	0.40	37
<i>Paphies subtriangulata</i>	BR = 0.69L + 0.40	0.66	30
<i>Paphies donacina</i>	BR = 1.78L - 2.53	0.64	30

BR = burrowing rate expressed as burial time (s), L = length (mm). All regressions are significant ($p < 0.05$).

cal of reflective beaches could burrow completely as adults in < 30 s, except *Atactodea striata*. Burial times for species from dissipative beaches ranged from 10 to > 1000 s.

A general comparison of the key features of the 12 species is summarised in Table 4. Density is primarily a function of shell thickness, thin-shelled species (*Mesodesma* spp., *Siliqua patula*) having low densities and thick shelled species (*Atactodea striata*) having high densities. Density varied widely between species but little within species and only four length/density regressions were significant: *Donacilla angusta* ($D = 2.70 - 0.04 L$, $r = -0.83$, $n = 19$), *Donax sordidus* ($D = 0.47 + 0.06 L$, $r = 0.66$, $n = 20$), *Tivela stultorum* ($D = 1.57 + 0.003 L$, $r = 0.87$, $n = 25$) and *Donax faba*

Table 4
Key attributes of 12 bivalves from sandy beaches

Species	Max L (mm)	D (g · cm ⁻³)	BRI		Shape
			J	A	
<i>Donax faba</i>	24	2.00	9	7	Wedge
<i>Donacilla angusta</i>	23	1.96	7	6	Elongate wedge
<i>Donax serra</i>	66	1.68	10	11	Wedge
<i>Donax sordidus</i>	22	1.47	7	6	Wedge
<i>Mesodesma mactroides</i>	76	1.04	6	4	Elongate wedge
<i>Mesodesma donacium</i>	61	1.33	2	2	Elongate wedge
<i>Donax hanleyanus</i>	24	1.24	11	15	Globose wedge
<i>Tivela stultorum</i>	113	1.72	4	6	Globose
<i>Siliqua patula</i>	145	1.18	10	17	Blade
<i>Atactodea striata</i>	36	2.10	2	2	Globose
<i>Paphies subtriangulata</i>	30*	1.65	7	-	Wedge
<i>Paphies donacina</i>	32*	1.82	3	-	Wedge

Max L = maximum length collected, D = density, BRI = Burrowing Rate Index with J = juveniles and A = adults. *Only juveniles were obtained.

($D = 2.51 - 0.03 L$, $r = -0.66$, $n = 9$). Density tended to be constant or decrease with size in all species except *Donax sordidus* and *Tivela stultorum*, where it increased. This may be an adaptation to add stability to small individuals.

There appears to be a good relationship between density and beach type inhabited, density increasing in species inhabiting more reflective beaches (Fig. 3). We have not fitted a regression to this relationship since we have not surveyed all beaches in the range of each species and cannot precisely define the lowest beach state in which it occurs. The estimates of beach type in Fig. 3 are based on Defeo et al. (1992) for *Mesodesma mactroides* and *Donax hanleyanus* and collections for this study for the other species.

In most species BRI (Table 4) decreased with increasing size, smaller individuals burrowing faster than large ones. Exceptions are *Siliqua patula*, *Tivela stultorum*, *Donax serra* and *Donax hanleyanus*, where BRI increased with size. BRI values for clams from reflective beaches range from 2 to 15 and for those from dissipative beaches from 2 to 17, indicating that a wide range of burrowing abilities typifies the clam communities of all beach types. There was thus no clear relationship between BRI and the beach types on which the species occurred. There was also no correlation between BRI and density.

In the PCA the first two components explained 74% of the variance and a biplot (Fig. 4) shows size (max L) and height/width (H/W) ratio to have the greatest influence, although separation of the species into groups related to beach type was not particularly clear. Those species from dissipative beaches separated into a group char-

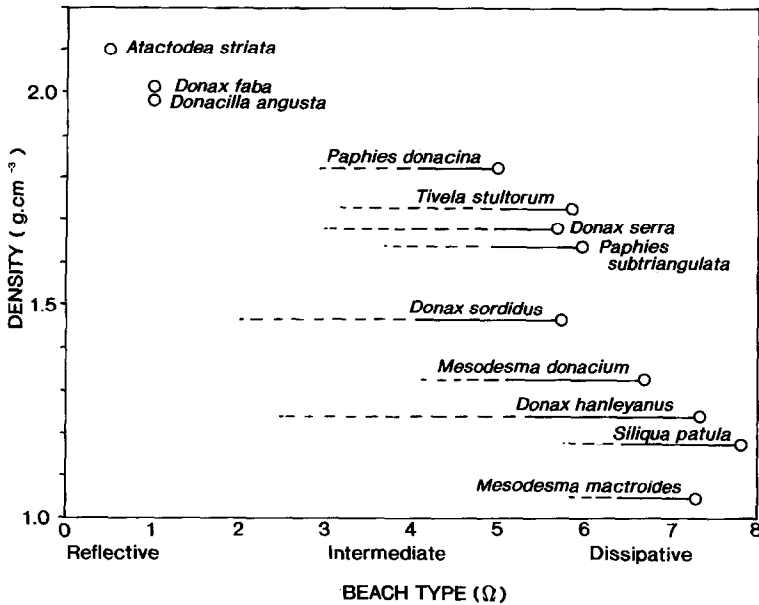


Fig. 3. Density of 12 bivalve species in relation to beach type: ○, the beach type from which specimens were obtained for this study and horizontal lines indicate the range of less dissipative beaches on which each species is known to maintain adult populations. For beach type = $H_b/W_s \cdot T$ where H_b is breaker height (cm), W_s is sand fall velocity ($\text{cm} \cdot \text{s}^{-1}$) and T is wave period in seconds.

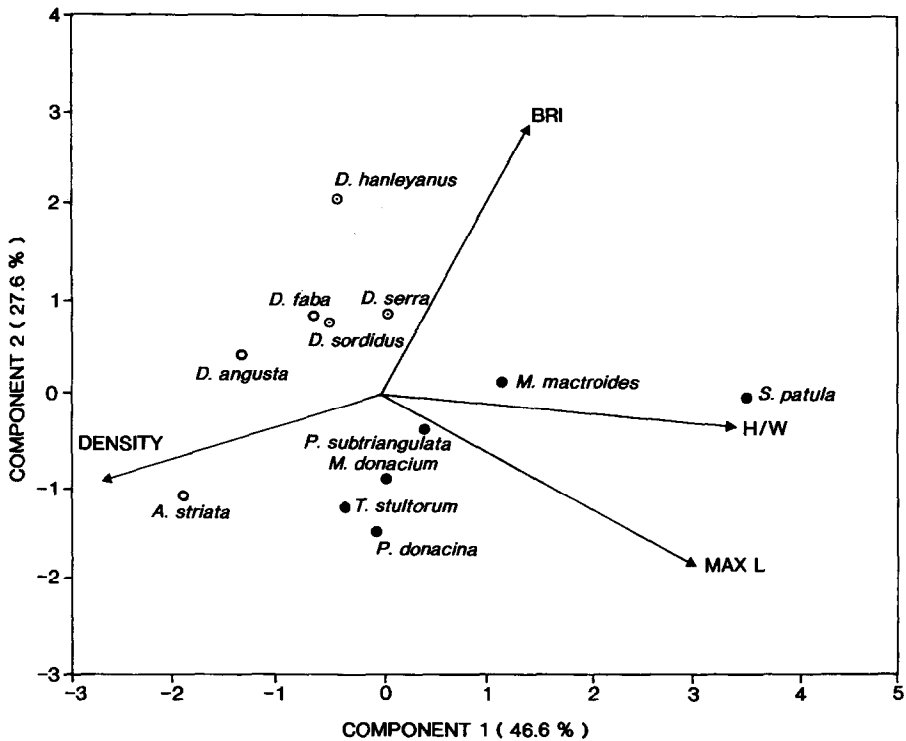


Fig. 4. Ordination biplot for PCA of 12 bivalves based on shell length, height/width ratio, density and BRI. Symbols as in Fig 1.

acterised by large size and medium to low density, whereas species from intermediate and reflective beaches, characterised by smaller size and higher density, were not well separated from each other. *Donax sordidus* has been listed as occurring on intermediate beaches, but in the PCA falls closer to the species from reflective beaches than the other two species from intermediate states. This species may be capable of inhabiting reflective beaches.

Discriminant analysis produced a significant separation of the species into three groups based on the least dissipative beach type colonised by adult populations (Fig. 5). The first discriminant function was significant as measured by the chi-square statistic ($\chi^2_{0.05,8} = 23.9$, $p = 0.002$) and accounted for 89.6% of the variance (Table 5). This function clearly separated Group D (bivalves from dissipative beaches) from Groups R (reflective) and I (intermediate). Although the second discriminant function was not significant ($\chi^2_{0.05,3} = 5.8$, $p = 0.12$) and only accounted for 10.5% of the variance, it appeared to separate Group I from the rest. The discriminant functions achieved an exceptionally high degree of classification accuracy (hit ratio of 100%), well in excess of the highest probability of 50% as described by the maximum chance criterion. However, this may be aided by the small sample size.

Univariate F ratios and standardised discriminant coefficients indicate that maxi-

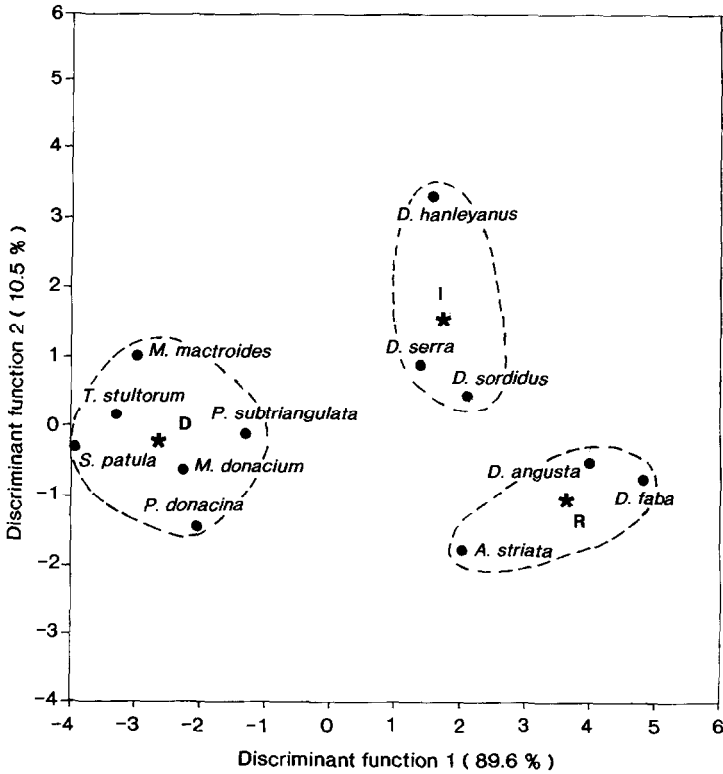


Fig. 5. Discriminant analysis separating 12 bivalves into those typical of dissipative beaches (D), those successfully establishing adult populations on intermediate beaches (I) and those with adult populations on reflective beaches (R). Centroids of each group are indicated by stars.

Table 5

Results of multiple discriminant analysis using descriptors of 12 bivalves

Discriminant functions								
Function	Eigen value	% of variance	Canonical correlation	Derived function	Wilks Lambda	$\chi^2_{0.05}$	df	<i>p</i>
1	10.06	89.6	0.954	0	0.041	23.9	8	0.002
2	1.17	10.5	0.735	1	0.459	5.8	3	0.12
Standardised discriminant function coefficients								
Descriptor	Function 1	Function 2	Univariate <i>F</i> ratio*	Significance <i>p</i>				
Maximum length	-1.382	0.070	10.78	0.004				
Density	1.111	-0.659	5.06	0.034				
BRI	0.880	0.803	1.90	0.204				
Height/width	0.358	-0.926	1.90	0.204				

* $F_{0.05(1)2,9}$

imum length and density contributed most to the discriminating power of the functions and can therefore be considered the most important variables. Thus *Atactodea striata*, *Donax faba* and *Donacilla angusta*, all small forms with high densities, were classified accurately as occurring on reflective beaches. *Donax serra*, *Donax sordidus* and *Donax hanleyanus*, also small but with lower densities, distinguished intermediate beaches and the remaining species, mostly larger and with lowest densities distinguished dissipative beaches.

4. Discussion

All the species investigated in this study were collected from open ocean beaches and display high degrees of mobility, vigorous burrowing ability and some tendency to move in the swash. As a measure of their mobility their BRI values ranged from 2 to 17. Stanley (1970) considered BRI values 2–5 indicative of fast burrowers and values > 6 indicative of extremely fast burrowers. His highest value was 20. Clearly, all beach clams burrow fast and most very fast, especially the *Donax* species and *Siliqua*. Burrowing rate or burial time is known to be affected by temperature (Ansell, 1983). McLachlan & Young (1982) examined the effects of temperature on burial times in four sandy beach molluscs including *Donax serra* and *Donax sordidus* and Donn & Els (1990) compared burial times in *Donax serra* from the west and east coasts of South Africa, both these studies showing the retarding effects of low temperatures on burial rates. Since this study was not an investigation of temperature effects, but examined adaptation to a range of beach morphodynamic states, *in situ* temperatures were used in order to obtain an estimate of burrowing under conditions actually experienced.

Sand penetrability and particle size also influence burrowing and sand particle size has been shown to strongly affect burial times (Alexander et al., 1993). Trueman et al. (1966) suggested that penetration was easier in coarse sands but *Donax vittatus* could burrow more easily in finer sands. Alexander et al. (1993) have shown that particle size strongly affects burrowing rate in two species of *Donax* which they considered to be substrate sensitive species. Brown & Trueman (1991) showed that penetrability increases with acute burrowing angles but resistance increases with depth.

Tivela and *Atactodea*, the slowest burrowers, are both characterised by rounded shapes, whereas *Siliqua*, the fastest burrower, has the most flattened shape. It is well known that shell shape and ornamentation affect burrowing ability in bivalves (Trueman et al., 1966; Stanley, 1970), streamlined shape and thin shells without ornamentation aiding rapid burying. None of the species investigated here had strong shell ornamentation.

Since morphology, temperature and sand particle size all influence burrowing rate in bivalves, no tests were performed to compare burrowing rates between species. The purpose of this investigation was not to confirm the obvious but to see whether differences between species could explain their varying abilities to colonise beaches of different types. All species investigated came from exposed sandy beaches subject to continuous wave action, with the exception of *Atactodea* from Heron Island on the Great Barrier Reef, where the beach is protected from most wave action by the reef.

On the whole, burrowing abilities of the 12 species, as indicated by BRI values, showed little clear pattern in relation to beach type, contrary to the predictions of the swash exclusion hypothesis. Rather, density and morphology exhibited the strongest trends: species from more reflective beaches had the highest densities and tended to be small, with wedge shapes. However, our analysis of burrowing abilities had limitations since we did not control for temperature or particle size.

The species studied differed greatly in burrowing rate as measured by burial time or BRI. Besides interspecific differences and size effects, seasonal acclimation to different temperatures and particle size differences will also influence burrowing rates (Ansell, 1983; Alexander et al., 1993). It would be profitable to investigate these factors separately by comparing burrowing performance between populations from different beach types and over a range of particle sizes within some of these species. The extent of seasonal shifts in BRI should also be investigated. A compilation of the foregoing information would allow a more complex and controlled analysis of the relationship between BRI and beach type. Such analysis might reveal clearer trends in burrowing ability than we have been able to decipher by this preliminary analysis.

Our results indicate that density may be a better predictor of the beach type a bivalve species can colonise and represents a more real adaptation to swash climate than burrowing ability as measured by BRI. Furthermore, BRI may be confounded by interspecific differences in densities of clams; although BRI and density are not correlated, density does affect the calculation of BRI. Other investigators have also suggested that density could be important to the zonation and stability of beach bivalve species. Donn (1990) found that intertidal populations of *Donax serra* had greater densities than subtidal populations, a feature which he considered an adaptation to aid stability in the turbulent conditions of the intertidal. Donn & Els (1990) found that west coast specimens of *Donax serra*, which had lower densities than east coast specimens, burrowed more slowly at low temperatures than east coast forms adapted to higher temperatures, again supporting the contention that high density aids burial under turbulent intertidal conditions. Ellers (1987) similarly concluded that a high density aided stability in *Donax variabilis* and was an important adaptation for tidal migrants.

The small size of bivalve species from reflective beaches and the larger sizes reached by species from intermediate and dissipative beaches (Tables 1 and 2) is in contrast to the prediction that the mean individual size in macrofauna communities increases from dissipative to reflective beaches (McLachlan, 1990). This may be related to greater longevity and survival of bivalves in the more benign conditions of dissipative beaches: lifespans of 5–20 years are typical of species from dissipative beaches, whereas those from reflective beaches mostly have 1–2 yr lifespans (McLachlan et al., in prep.). Under conditions of high life expectancy large size would be favoured. Consequently, in species occurring over a range of beaches, increased size may occur on more dissipative beaches (Dugan et al., 1994). Furthermore, growth rates may be higher on dissipative beaches because of the prevalence of surf diatom blooms (Lewin & Schaefer, 1983).

Other selection pressures changing across the gradient of beach types could include predation. Predation may be more intense on dissipative beaches and large size may provide a refuge from predation. On the other hand, since burial time usually increases with size, large clams will experience longer exposure to predators when exhumed by

the waves. Thus, on reflective beaches where harsh swash conditions often expose clams, small species, by virtue of their capacity for rapid reburial, will be able to spend more time in the sediment and thus reduce exposure to predation. Predation pressures may therefore select for large sizes on dissipative beaches and small sizes on reflective beaches.

This study has found bivalves from reflective beaches to be uniformly small, medium to fast burrowing, wedge-shaped and of high density, whereas those from more dissipative beaches vary widely in all these characteristics. Multiple Discriminant Analysis indicated that bivalves characteristic of different beach types could indeed be discriminated effectively, primarily on the basis of size and density. We conclude therefore that although there is no single feature that characterises sandy beach bivalves or equips them to cope with harsh swash conditions, small size and high density appear the key adaptations common to those species able to colonise the harshest beaches, i.e. beaches with turbulent swash and coarse sand. In addition, wedge shape appears important, whereas burrowing ability is less critical. We found no clear separation between the intertidal and subtidal species, or with respect to species that migrate tidally, in the bivalves investigated here. However, the smallest species with highest densities were intertidal forms and most displayed tidal migrations.

The question then remains as to whether this convergence in bivalve density and shape from reflective beaches indicates selection by and adaptation to harsh swash conditions? Both water movement (as swash) and sand particle size parameters influence beach bivalves directly and must play a role in selection. However, we suggest that high density and wedge shape are primarily adaptations to aid stability and control to animals moving in the swash on the beach face.

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