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Morphometrics of *Donax serra* Röding (Bivalvia: Donacidae) Populations With Contrasting Zonation Patterns

Theodore E. Donn, Jr.[†]

Department of Zoology and
Institute for Coastal Research
University of Port Elizabeth
Post Office Box 1600
Port Elizabeth 6000, South Africa

ABSTRACT

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Ten morphometric variables were measured on samples of the sandy-beach bivalve *Donax serra* Röding from six populations displaying two contrasting zonation patterns. The data were examined using cluster, discriminant and factor analysis, with covariance. The first canonical variable of the discriminant analysis accounted for 48% of the variation in the data for large (> 45 mm) animals and clearly separated the populations into two groups with different zonation patterns. Factor analysis yielded three factors, weight, surface area and elongation, which explained 36.4%, 23.0% and 12.9%, respectively, of the variance present in the data for large animals. These results indicate that high intertidal populations had thicker, heavier valves resulting in a greater density, whereas low intertidal/subtidal populations exhibited flatter, more rounded valves. Increased density yields increased stability in the shifting sediments of the intertidal. Reduced burrowing rate and less efficient swash-riding morphology in west coast as compared to south coast *D. serra* populations result in the observed change in zonation pattern.

ADDITIONAL INDEX WORDS: *Donax, sandy beach, intertidal, zonation, swash.*

INTRODUCTION

Donax serra Röding is the largest member of the genus and one of the most abundant macrofaunal organisms inhabiting southern African sandy beaches. It is capable of reaching biomass values in excess of 8500 gm m^{-1} (HUTCHINGS *et al.*, 1983; DONN, 1987). In a previous paper the change in zonation pattern of *D. serra* along its geographic range was described (Donn, 1990). This change is probably an effect of the local water temperature regime on burrowing rate. Two types of zonation pattern were described depending on the location of the adults. Adults occupied the high intertidal on the south coast of South Africa and in northern Namibia but occurred in the low intertidal/subtidal along the west coast of southern Africa. The question which then arises is, if these populations show different zonation patterns, are there corresponding morphometric differences between them which are related to their respective environments?

In addition to zonation pattern, several other parameters also vary between the south and west coast populations. DE VILLIERS (1975) reported a maximum size of 80 mm on the west coast, while the largest size recorded from the south coast was 73 mm (DONN and McLACHLAN, submitted). DONN and ELS (in press) have noted differences in the color of the foot and siphons between west and south coast populations. However, VAN DER HORST *et al.* (1986) were unable to detect any differences in sperm morphology in populations from the two coasts. In addition, VAN DER HORST (*pers. comm.*) has succeeded in culturing larvae from crosses between populations from the west and south coasts to the same stage as larvae collected from the same population. These results support the contention that these populations belong to the same species.

Differences in morphology between populations or species are usually not the result of a

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[†] Present address: 219 French St., Bristol, CT 06010, U.S.A.

change in a single variable, but are rather the result of several interacting variables (MISRA and CARSCADDEN, 1987; BOWERING, 1988; GIANNICO and NAGORSEN, 1989). Various multivariate techniques, including principle components analysis (DILLON, 1984; WEINBERG and STARCZAK, 1988; DILLON and MANZI, 1989), multivariate analysis of covariance (MISRA and CARSCADDEN, 1987; BOWERING, 1988), and discriminant analysis (MISRA and NI, 1983; KRISTENSEN and CHRISTENSEN, 1989; GIANNICO and NAGORSEN, 1989), have been employed to identify and isolate key variables. In this paper, the morphometrics of six *D. serra* populations are examined using discriminant function analysis, with covariance, and factor analysis to determine: 1) whether there are morphological differences between populations, in particular between high and low intertidal populations, and 2) what these differences are and how they relate to the zonation patterns observed.

METHODS

Donax serra was collected from six locations throughout its range: Angra Fria (AF) (18.26°S, 11.96°E), 117 km from the northern border of Namibia; Langstrand (LS) (22.07°S, 14.17°E), 10 km north of Walvis Bay; 2 km south of the Olifants River (OR); at Silwerstroomstrand (SSS) in the western Cape Province; 10 km east of the Sundays River (SR); and at Cintza (CZ) in the eastern Cape Province (see DONN, submitted). Between 80 and 100 individuals in as wide a range of sizes as possible were collected at each site, with the exception of Cintza, where only 60 individuals could be collected. The samples were preserved immediately in 5% formalin in seawater.

In the laboratory, the formalin was poured off and the animals rinsed in tap water. A total of 10 morphometric variables were measured. Anterior-posterior length (LEN), shell height (HGT) and width (WTH) (STANLEY, 1970) (Figure 1) were measured to the nearest 0.1 mm with vernier calipers. Wet weight (WWT) was measured to 0.01 gm on a top loading balance. Density (mass per unit volume) (DEN) was determined using a picnometer (DANA and FORD, 1949). The left valve was then removed, all tissue scraped off and then dried at 60°C for 24 h and subsequently weighed (VWT). Valve surface area (VSA) was determined by carefully wrapping the external surface of the valve with aluminum foil and trimming the excess, weighing the foil, and converting to area based on weights of foil of known area. Cross-sectional area (CXA) was determined, similarly, by photocopying the valve, cutting out and weighing the paper. Two additional variables were measured from the photocopies, namely anterior length (AL) and dorsal height (DH) (Figure 1). A line was drawn along the greatest anterior-posterior axis and a perpendicular to this was then drawn through the umbo. Anterior length was defined as the distance from the intersection of these lines to the anterior margin of the valve. Similarly, dorsal height was defined as the distance from the intersection to the outer point of the umbo. These two variables were chosen to provide some indication of the position of the umbo and hence the shape of the shell.

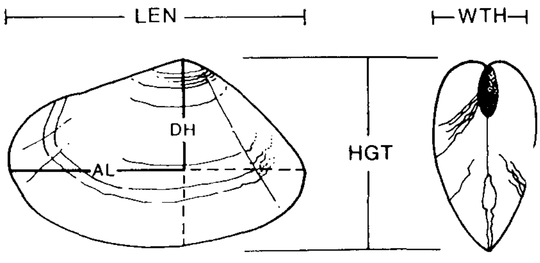

Figure 1. Diagram of *Donax serra* showing five of the morphometric variables measured. LEN, length; HGT, height; WTH, width; AL, anterior length; DH, dorsal height.

For the purposes of these analyses, the morphometric data were grouped by site and zonation pattern. Morphometric variables tend to be highly intercorrelated, especially those related to size. Differences in the size frequency distributions between sites can also confound the results: sites with predominantly small individuals cannot be directly compared to sites composed of mostly large specimens. In an effort to remove these effects, all data were natural log transformed and regressed against ln (length). The deviations from the common regression line (residuals) were then used as the new morphometric variables. Removal of the effect of the covariate, length (size), from the data also had the effect of improving multivariate normality and reducing within-site variability, thusly improving the validity of the analyses (MISRA and NI, 1983). Since differences in morphology between populations are not usually attributable to a single variable, but rather to a combination of variables acting in concert (MISRA and CARSCADDEN, 1987; BOWERING, 1988; GIANNICO and NAGORSEN, 1989), multivariate analyses were used to distinguish between populations. All statistical analyses were run using the BMDP statistical package (DIXON, 1981).

The analysis was approached in the following manner. Prior to looking for differences in morphology between populations, it was first necessary to show that these differences existed. This was accomplished using a pairwise multivariate comparison of variable vectors (BMDP3D) between zonation patterns and sites. This analysis also yielded the Mahalonbis D^2 distance measure which was used to cluster the sites to determine if any pattern was evident. Sites and zonation patterns were then analyzed using stepwise discriminant analysis (BMDP7M) and factor analysis (BMDP4M, extraction of principle components of the correlation matrix followed by orthogonal rotation) to identify variables which were important in separating the groups.

RESULTS

The means and ranges for each of the 10 morphometric variables at each site are presented in Table 1. There is a high degree of overlap between groups for all variables. All variables were highly intercorrelated ($0.65 < r < 0.995$). After removal of the effect of the covariate, length, correlations between the variables were substantially reduced ($-0.35 < r < 0.83$) indicating the effectiveness of this transformation. The multivariate F test (BMDP3D) yielded significant ($p << 0.001$) between group differences between all pairs of sites and between popula-

Table 1. *Means and ranges for the ten morphometric variables at the six sites.*

Site N	Angra Fria 84	Langstrand 52	Olifants River 91	Silwerstroom strand 86	Sundays River 76	Cintza 59
Length	63.3	66.5	56.9	43.1	54.4	45.2
(LEN)	12.7–79.5	44.0–78.9	18.4–81.3	15.2–75.3	26.5–66.3	16.8–57.0
Height	42.5	46.0	38.7	28.5	35.8	29.8
(HGT)	7.5–47.7	29.7–56.3	11.4–57.7	9.0–53.2	16.4–44.1	9.7–39.2
Width	22.6	23.6	20.0	14.8	20.1	16.5
(WTH)	3.3–27.2	15.3–30.8	5.2–30.3	4.1–29.5	8.1–26.0	4.0–22.3
Wet weight	42.2	46.4	36.2	21.2	26.1	16.6
(WWT)	0.19–58.1	11.9–88.6	0.62–80.8	0.31–73.8	2.08–45.5	0.35–30.2
Density	1.60	1.50	1.41	1.34	1.50	1.45
(DEN)	1.24–1.76	1.38–1.61	1.15–1.68	1.11–1.66	1.30–1.65	1.10–1.36
Valve weight	12.5	11.9	10.0	5.9	6.7	4.5
(VWT)	0.04–18.1	2.5–24.9	0.13–24.5	0.06–22.6	0.44–12.7	0.07–9.0
Valve surface area	28.1	30.9	26.9	17.1	20.7	16.2
(VSA)	1.1–35.1	12.9–46.6	2.7–50.5	1.6–44.7	4.7–30.5	1.6–27.1
Dorsal height	25.2	29.1	22.7	17.3	21.6	17.8
(DH)	4.1–29.5	18.0–36.0	6.5–32.8	5.4–33.7	10.0–26.5	4.8–24.0
Anterior length	36.9	37.7	33.0	25.7	29.5	25.2
(AL)	8.0–43.5	25.0–44.0	111.6–48.0	9.0–45.7	17.0–36.5	10.5–33.4
Cross-sectional area	20.5	22.3	18.8	11.2	15.0	10.4
(CXA)	0.74–25.0	9.8–32.7	1.6–36.7	1.0–27.9	3.3–21.7	1.1–15.6

Linear measurements in mm, weights in g, and areas in cm.^{2}

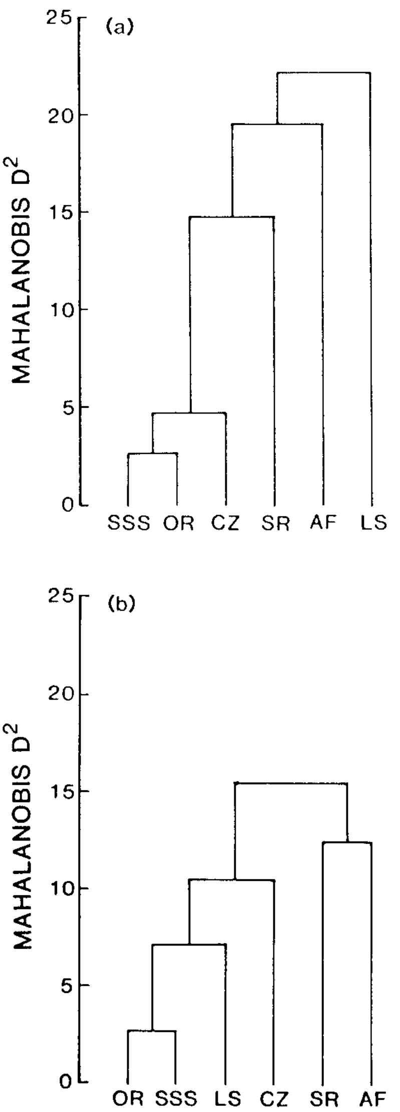

Figure 2. Cluster dendograms of sampling sites based on group average clustering of Mahalanobis D^2 distance metric of morphometric variables for raw (a) and residual (b) data.

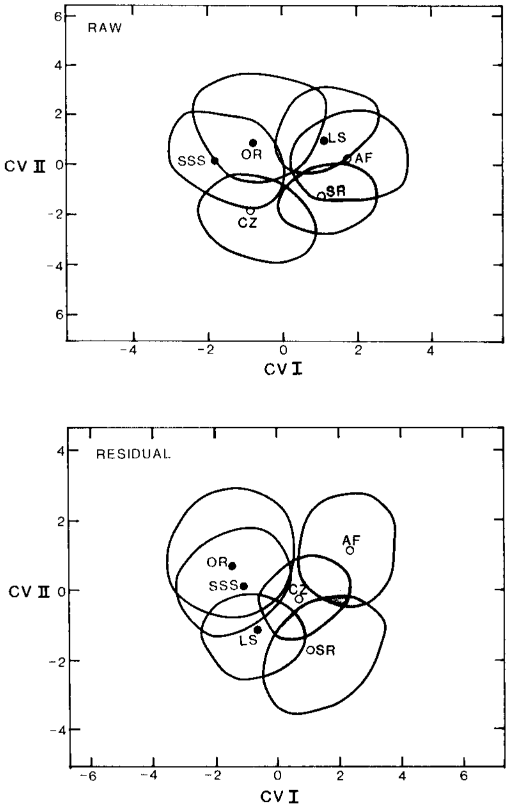

Figure 3. Plots of first two canonical variables from discriminant analysis of raw and residual data for the entire population. Dots represent centroids of distribution; high intertidal populations are shaded.

tions pooled into two groups based on zonation pattern for both raw and residual data. This analysis also yielded the Mahalonbis D^2 distance metric which was used to cluster sites as a preliminary means of identifying groups (Figure 2). Both the raw and residual data showed a close association between OR and SSS, two sites within 300 km of each other. From that point, the raw data clustered to form a gradient related to increasing mean body size. The residual data grouped the three low intertidal sites (LS, OR, and SSS) and two high intertidal sites (AF and SR). The remaining site, CZ, showed closer links to the low intertidal sites than to AF and SR.

Stepwise discriminant analysis (BMDP7M) was run on both the raw and residual data (Figure 3). Based on the raw data, the high and low intertidal sites did not separate along either of the first two canonical variables. A gradient running from the lower left to upper right of the plot is associated with the mean size of the sampled populations; CZ and SSS have the smallest mean lengths (45 mm and 43 mm) and LS and AF, the largest (66 mm and 63 mm). The residual data yielded a clear separation along canonical variable (CV) I; the high intertidal populations were associated with positive values and the low intertidal populations with negative values.

Based on the results of a previous study (DONN, submitted), the morphometric data were divided into two size groups, < 45 mm and > 45 mm in length, to test whether the differences were more distinct in the adult populations. Table 2 presents a summary of the jackknifed classifications (% observations correctly classified) for all the discriminant analyses run. Separations between sites and between zonation patterns are more distinct for the large animals than for the entire population or small individuals. The number of variables included in each analysis is greater for the residual data than for the raw data, and greater for the large animals than for the small. This is a result of the reduction of intercorrelations between variables, with the ultimate result that each variable adds new information to the discriminant function. Although classification based on the raw data is often as good as that based on the residual data, the interpretive value is less due to the confounding effect of size.

The results from the discriminant analysis of the residual data for large animals are plotted in Figure 4, and the standardized coefficients for the first three canonical variables given in Table 3. Canonical variable I explains 48% of the variance, and separates the low and high intertidal populations. Variables positively associated with CV I relate to the width and weight of the animals, indicating that high intertidal populations had thicker, heavier valves. Variables negatively associated with CV I relate to the surface area and roundness of the valves, indicating that low intertidal populations have flatter, more circular valves. The effect of CV II is less distinct, but appears to separate AF from the other high intertidal populations based on the degree of shell elongation.

Factor analysis of the raw data yielded a single factor associated with size, which accounted for 92.5% of the variance. Factor analysis of the residual data yielded three factors which accounted for 68.6% of the variance in the entire population and 72.3% of the variance in the large animals. For the large animals, the three factors and variance explained were: 'weight', 36.4%; 'surface area', 23.0%; and 'elongation', 12.9% (Figure 5). When the centroids for the sites are plotted in factor space, it can be seen that Factor 1 clearly distinguishes the high and low intertidal groups based on weight and density. Factor 2 aids in this separation in terms of the greater surface area and roundness of the valves in the low intertidal groups. The third factor measures the degree of elongation of the shell, markedly separating AF from the other high intertidal populations (SR and CZ).

DISCUSSION

The genus *Donax* consists of typically wedge-shaped species which inhabit exposed, open-coastal beaches and migrate up and down the beachface with the tides (ANSELL, 1983). ANSELL and TRUEMAN (1973) have shown that migratory behavior is energetically expensive, comprising up to 30% of the daily metabolic costs of tidal migratory species. *D. serra* does not undergo tidal migrations, possibly as a result of its large size. However, previous studies (McLACHLAN *et al.*, 1979; PROSCH and McLACHLAN, 1984; DONN *et al.*, 1986) have shown that populations on the south coast undergo migrations associated with the spring-neap tidal cycle. In these populations, individuals are found in the mid to upper intertidal at

Table 2. *Summary of jacknifed classifications (percent correct) of discriminant analysis on raw and residual data for entire population, small (< 45mm) and large (> 45mm) individuals only, grouped by site and zonation pattern.*

Site		Raw (10)	Residual (9)
Total population	n = 448	74.1 (6)	76.3 (8)
< 45mm	n = 105	48.6 (3)	42.9 (2)
> 45mm	n = 343	93.6 (10)	93.9 (9)
Zonation Pattern		Raw (10)	Residual (9)
Total population	n = 448	91.5 (6)	88.6 (7)
< 45mm	n = 105	78.1 (2)	69.5 (4)
> 45mm	n = 343	98.0 (9)	96.5 (9)

The number of variables included in each analysis is given in parentheses.

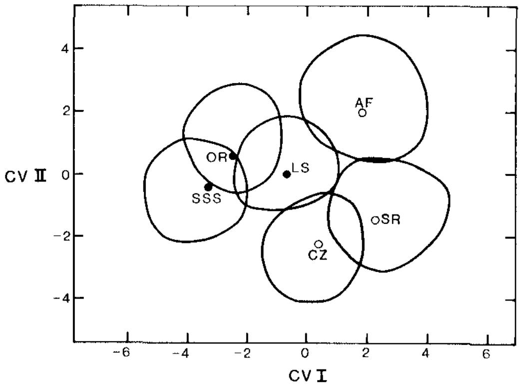

Figure 4. Plots of first two canonical variables from discriminant analysis of residual data for large (> 45 mm) individuals only. Shading as in Figure 4.

spring tides, and move towards the lower intertidal at neap tides. Along the south-west coast of southern Africa, adult *D. serra* inhabit the low intertidal/subtidal, often extending to considerable depths offshore (HUTCHINGS *et al.*, 1983; BRANCH and GRIFFITHS, 1988; DONN, submitted). The adults in these populations presumably do not show any migratory behavior.

Shell morphology affects both burrowing rate and orientation in flow. STANLEY (1970) related differences in morphology between bivalve genera to differences in their burrowing rates. He showed that most rapid burrowing bivalves tend to have thinner, lighter shells than slow burrowers as heavy shells tend to impede burrowing. The notable exceptions to this rule were two species of *Donax* which had thick, robust shells. Heavy shells also occur in the families Mesodesmatidae and other Donacidae, which contain species inhabiting unstable, shifting substrata. Thick, heavy shells, he argued, provided increased stability for maintaining position within the sediments in dynamic environments. Additionally, *Donax* species exhibit a high degree of shell elongation, with the umbo being located very near the posterior margin of the shell, a further adaptation to rapid burrowing.

ELLERS (1987) determined four parameters to be important in controlling orientation to swash in *Donax variabilis*; namely, density, weight distribution, shell shape, and water velocity. High density increases the minimum water velocity necessary for orientation, but decreases the tendency of the shell to tumble, an advantage at high swash speeds. A wedge-shaped shell orientates more readily (*i.e.* at

Table 3. *Standardized coefficients for the first three canonical variables (CV) from the discriminant analysis of the residual data for large (> 45 mm) animals grouped by site and the single CV for the data grouped by zonation pattern.*

Between Sites

Variable	CV I	CV II	CV III
WTH	0.323	-0.799	0.245
CXA	0.302	0.593	-0.320
DEN	0.235	-0.210	0.819
VWT	0.191	0.366	1.048
WWT	0.044	-0.043	-1.589
DH	-0.034	-0.211	-0.561
HGT	-0.211	0.006	-0.429
AL	-0.256	0.711	-0.090
VSA	-0.817	-0.482	1.509
% variance explained	48.0	23.7	14.9

Between Zonation Patterns

Variable	CV 1
WTH	0.399
DEN	0.353
VWT	0.299
CXA	0.131
DH	-0.097
WWT	-0.220
HGT	-0.264
AL	-0.266
VSA	-0.408

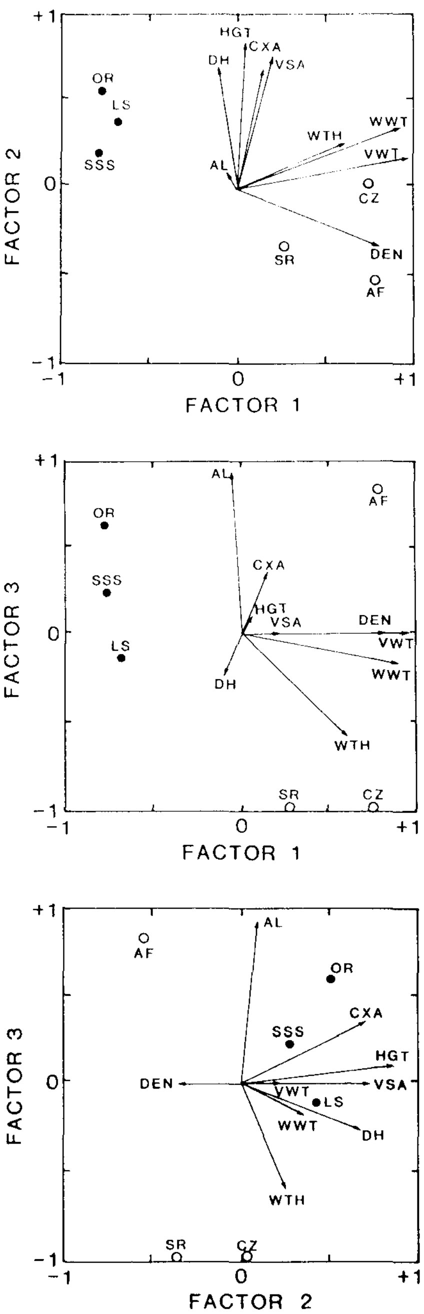

Figure 5. Plots of the three factors extracted from residual data of large individuals. The mean scores for the sites are plotted in the factor space. Open dots are high intertidal and filled dots, low intertidal sites.

lower swash speeds) than flatter shells by shifting the centers of lift and drag posteriorly and the point about which the shell pivots anteriorly. Weight distribution affects orientation through its effect on the location of the pivot point. Therefore, a dense, wedge-shaped shell will orientate easily in a wide range of swash conditions, whilst having a lower tendency to tumble than a less dense, flatter shell.

The present results clearly show that the high and low intertidal populations primarily differ from each other in terms of the factor 'weight': 'weight' being a combination of the variables wet weight, valve weight, density and width. These are precisely the variables which are expected to differ between migratory and non-migratory populations based on Eller's (1987) model. Increased width provides a more wedge-shaped shell allowing more rapid orientation and increased density increases stability in the swash. Both of these effects result from thickening of the valves (STANLEY, 1970).

The observed differences in morphology, zonation patterns and burrowing rates form a complex set of interactions. DONN and ELS (in press) have shown differences between the burrowing rates of south and west coast *D. serra* populations at constant experimental temperatures and suggested that they may be attributable to differences in morphology. West coast *D. serra* have more rounded valves and are flatter, while on the south coast they are more wedge-shaped. These differences are similar to the patterns described by STANLEY (1970); more rounded species tending to burrow more slowly than elongate, wedge-shaped species. In addition, the high intertidal populations are better adapted to riding the swash without tumbling. A combination of reduced burrowing rate due to the lower water temperatures on the west coast of southern Africa and the effect of morphology on burrowing rate and orientation in the swash have resulted in the zonation pattern observed in west coast populations (DONN, 1990).

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□ RÉSUMÉ □

Six populations de bivalve *Donax serra* Röding se répartissent en deux types de zonation contrastés. Elles ont été étudiées selon dix variables morphométriques par analyses hiérarchique, discriminante et factorielle avec covariance. La première variable canonique de l'analyse discriminante rend compte de 48% de la variation des données pour les bivalves dépassant 45mm, et sépare nettement les populations en deux groupes de zonation différente. L'analyse factorielle montre 3 facteurs expliquant respectivement 36,4% 23,0% et 12,9% de la variance des bivalves de taille importante (>45mm). Ces résultats indiquent que les populations du haut estran ont des valves plus épaisses et plus lourdes, donc, de plus grande densité, alors que les populations intertidales et subtidales sont plus plates et ont des valves plus arrondies. L'accroissement de la densité augmente la stabilité des sédiments intertidaux remaniés. Le taux d'enfouissement réduit de *D. serra*, comme la morphologie moins efficiente du haut estran (jet de rive) de la côte Ouest, comparativement à la côte Sud se traduisent par une modification de la zonation observée.—*Catherine Bressolier, Géomorphologie EPHE, Montrouge, France.*

□ ZUSAMMENFASSUNG □

Zehn morphometrische Variable wurden an Exemplaren der in Sandstrand lebenden Muschel *Donax serra* Röding aus sechs Populationen gemessen, die zwei gegensätzliche Zonierungsmuster zeigten. Die Daten wurden mittels Cluster-, Diskriminations- und Faktorenanalyse mit Kovarianz untersucht. Die erste kanonische Variable der Diskriminationsanalyse traf auf 48% der Verteilung bei den Werten für große Tiere (über 45 mm) zu und trennte die Populationen deutlich in zwei Gruppen mit unterschiedlichen Zonierungsmustern. Die Faktorenanalyse ergab die drei Faktoren Gewicht, Oberfläche und Ausdehnung, die 36,4%, 23,0% bzw. 12,9% der Verteilung der Werte für die großen Tiere erklärten. Diese Ergebnisse weisen darauf hin, daß Populationen, die im oberen intertidalen Milieu leben, dickere und schwerere Schalen haben, woraus eine größere Dichte folgt, während Populationen des unteren intertidalen oder subtidalen Milieus flachere und rundere Schalen aufweisen. Eine Zunahme der Dichte bewirkt eine zunehmende Stabilität im Bereich der sich verlagernden Sedimente des Intertidals. Die ruduzierte Eingrabungsrate und die weniger wirksame Morphologie in Bezug auf das Ausnutzen der auflaufenden Welle der Populationen von *D. serra* an der Westküste im Vergleich zu denen der Ostküste führen zu dem beobachteten Wandel in Anordnungsmuster.—*Helmut Brückner, Geographisches Institut, Universität Düsseldorf, F.R.G.*