Burrowing Times of *Donax serra* from the South and West Coasts of South Africa

by

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Abstract. Burrowing times of winter acclimated populations of *Donax serra* from the west and south coasts of South Africa were compared at three experimental temperatures in an effort to explain observed zonation patterns. The west coast population burrowed slower than the south coast population at 10°C and 15°C, but at the same rate at 20°C. Burrowing time decreased at increased temperatures. The burrowing rate index ranged from 5 to 14, indicating that *D. serra* is among the most rapidly burrowing bivalves examined to date. The results indicate no physiological adaptation of burrowing rate to temperature between populations.

INTRODUCTION

Members of the bivalve genus *Donax* are common inhabitants of open coastal sandy beaches throughout the warmtemperate and tropical regions of the world (ANSELL, 1983). In response to the dynamic nature of these environments, most species are tidal migrants, burrowing rapidly into the sediments of the beach face between wave swashes. STANLEY (1970) considers members of the genus *Donax* to be among the most rapidly burrowing bivalves.

Of the nine species of Donax inhabiting the southern African region (KILBURN & RIPPEY, 1982), Donax serra Röding is the best studied (BROWN et al., 1989). Its distribution extends from the Kunene River at the northern border of Namibia into western Transkei, South Africa (Figure 1). Throughout this range, it is capable of maintaining large populations with biomasses of up to 7000-9000 g (dry wt.)/m (McLachlan, 1977; HUTCHINGS et al., 1983). Temperature regimes along the west and south coasts of southern Africa are markedly different, the west coast being dominated by the cold waters of the Benguela upwelling region, while the south coast is influenced by the warm waters of the Agulhas current. Differences in zonation pattern between populations inhabiting the two coasts have also been reported. Donax serra is found in low intertidal and shallow subtidal zones along the west coast (HUTCHINGS et al., 1983), while along the south coast it is found in the mid-intertidal zone (McLACHLAN et al., 1979; DONN et al., 1986).

Members of the genus *Donax* rely on their ability to burrow rapidly in order to maintain their position on highly dynamic beaches (TRUEMAN, 1971). The burrowing mechanisms used by *D. serra* have been described in detail by TRUEMAN & BROWN (1985). MCLACHLAN & YOUNG (1982) have shown that reduced temperatures negatively affect burrowing rate in a south coast population. One would expect a population inhabiting colder waters to have evolved mechanisms to compensate for lower temperatures. Burrowing time is an easily measured parameter relating directly to the bivalve's response to its environment and is important in maintaining zonation patterns. The objective of this study was to compare the burrowing times of south and west coast populations of *D. serra* and to assess any temperature adaptation between the two populations.

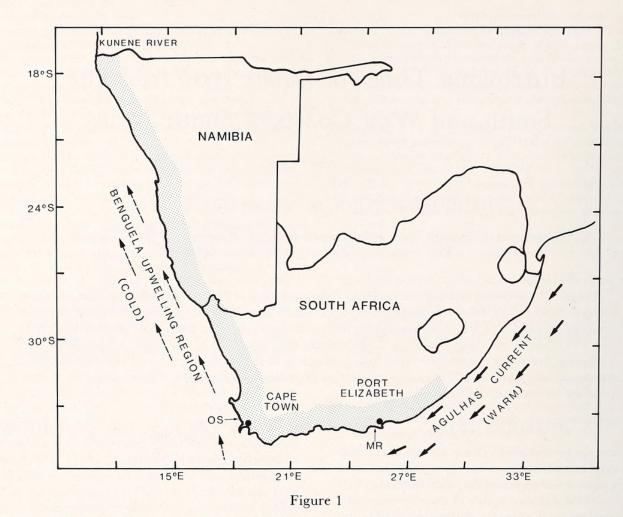
MATERIALS AND METHODS

Individuals of *Donax serra* were collected from Maitlands River beach near Port Elizabeth (hereafter referred to as the south coast population) and from Ou Skip north of Cape Town (west coast population) during May–June 1989 (Figure 1). Average expected sea surface temperatures at this time were 17°C for Port Elizabeth and 14°C for Cape Town (CHRISTENSEN, 1980). Annual temperature range for Port Elizabeth is 15–21°C, and 12–15°C at Cape Town (CHRISTENSEN, 1980). Individuals ranged in length from 15 to 75 mm. In the laboratory, bivalves were allowed to burrow into natural Maitlands River beach sediments covered by aerated, flowing seawater and acclimated at 15°C for 36 H prior to initiating the experiment.

Three experimental temperatures, 10, 15 and 20°C, were used, covering the range of temperatures experienced by

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Map of Southern Africa showing distribution of *Donax serra* (shading) and location of sampling sites at Ou Skip (OS) and Maitlands River (MR). Also included are the positions of the Agulhas Current and the Benguela upwelling region.

the species in nature. Animals were transferred directly from the holding tank and placed into experimental chambers. Burrowing time was defined as the time from initiation of digging by the foot until complete burial or until all burrowing activity stopped (MCLACHLAN & YOUNG, 1982). Each animal was allowed to burrow three times and the mean burrowing time determined. At least 30 animals covering the full range of sizes from each site were tested at each temperature.

After having burrowed three times, each individual of *Donax serra* was measured to the nearest 0.1 mm in anterior-posterior length and blotted wet weight determined to 0.01 g. The burrowing rate index (BRI), defined as the cube root of wet weight (g) divided by the burrowing time (s) multiplied by 100 (STANLEY, 1970), was calculated.

RESULTS

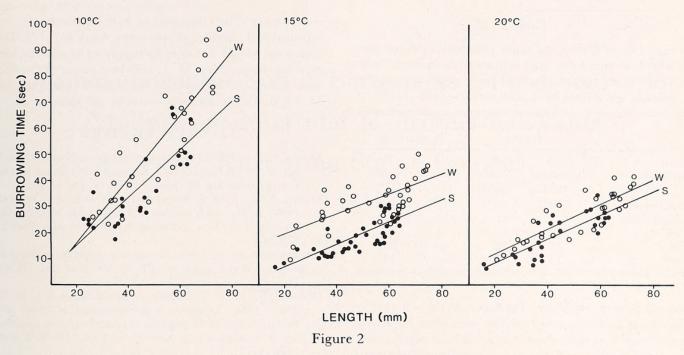
Most animals burrowed completely. Only a few of the largest west coast individuals of *Donax serra* remained partially ($\leq 10\%$) exposed when burrowing activity ceased.

Linear regressions of mean burrowing time against length were determined for each population at the three temperatures (Figure 2) and compared between sites using the dummy-variable regression approach (KLEINBAUM & KUPPER, 1978) (Table 1). Significant differences were detected between the population regression lines at 10 and 15°C, but not at 20°C. Burrowing time decreased with increasing temperatures for the west coast population, *i.e.*, burrowing rate increased. The south coast population showed a decrease in burrowing time between 10 and 15°C, but not between 15 and 20°C.

Analysis of the burrowing rate index (STANLEY, 1970) yielded similar results. BRI was independent of *Donax* serra length at all temperatures. A one-way analysis of variance on BRI for *D. serra* at each temperature (Table 2) indicated significant differences between populations. BRI increased with temperature in the west coast population. In the south coast population, BRI increased markedly between 10 and 15°C, but decreased slightly between 15 and 20°C.

DISCUSSION

STANLEY (1970) determined the BRI at ambient environmental temperatures for over 60 western Atlantic bivalve



Mean individual burrowing time (sec) versus length (mm) for west (W) and south (S) coast populations of *Donax* serra at three experimental temperatures. O west coast; \bullet south coast.

species including two species of *Donax*. BRI for these species ranged from 0.01 to 20; species with a BRI greater than two were classified as rapid burrowers and greater than six as very rapid burrowers. *Donax denticulatus* and *D. variabilis* scored 17 and 7, respectively, on this scale. Recently, TRUEMAN & BROWN (1989) have given a BRI for west coast *D. serra* of 6.9. This corresponds well with the BRIs determined in this study, which span the range determined for the other two *Donax* species, indicating that *D. serra* is one of the most rapid burrowers of all species of bivalve examined to date. Furthermore, we have shown that the BRI is influenced by temperature. When comparing BRIs, care must be taken to state whether the measurements were done at ambient environmental tem-

Table 1

Comparison of burrowing time vs. length regressions for south and west coast populations of *Donax serra* at three test temperatures. * P < 0.05.

	Intercept	Slope	r^2	n
$T = 10^{\circ}C$			3315	1
South coast	-2.312	0.904*	0.683	32
West coast	$-8.791^{n.s.}$	1.234	0.790	30
$T = 15^{\circ}C$				
South coast	-1.672*	0.428	0.643	50
West coast	11.512	0.387 ^{n.s.}	0.497	36
$T = 20^{\circ}C$				
South coast	-0.926	0.459	0.697	33
West coast	$2.490^{n.s.}$	$0.474^{n.s.}$	0.707	29

peratures (ecological differences) or at constant experimental temperatures (physiological differences).

McLACHLAN & YOUNG (1982) found that summer acclimated *Donax serra* burrowed more slowly at 10°C than winter acclimated animals, indicating seasonal acclimation in south coast populations. In light of this we expected that either both populations would burrow at the same rate, *i.e.*, no adaptation, or that the west coast population would have adapted to the colder temperatures and burrowed more rapidly. Our results show that west coast populations burrow more slowly than south coast populations when acclimated to the same temperature.

One possible explanation for differences in burrowing time may be differences in shell morphology. Both shell obesity (width-to-height ratio) (TRUEMAN *et al.*, 1966) and shell elongation (STANLEY, 1970) have been shown to affect the rate at which bivalves burrow. Preliminary results indicate differences in shell morphology between south and west coast populations of *Donax serra*. These differences and their effect on behavior will be investigated in sub-

Table 2

Comparison of burrowing rate index (BRI) of south and west coast populations of *Donax serra* at three temperatures. * P < 0.05; ** P < 0.01; *** P < 0.001.

Temperature	South coast	West coast	Significance level	
10°C	6.35	5.22	**	
15°C	13.85	8.97	***	
20°C	12.52	10.42	**	

Table 3

Comparison of burrowing times (seconds) for three size classes of summer and winter acclimated *Donax serra* from the south and west coasts. Data for summer acclimated animals taken from McLachlan & Young (1982).

Coast Acclimation	McLachlan & Young (1982)		Present study	
	S summer (21°C)	S winter (16°C)	S winter (15°C)	W winter (15°C)
Test temperature Length (mm)	20°C	10°C	10°C	10°C
15	9	16	11	10
25	13	23	20	22
50	23	35	43	53

sequent papers. Similarly, TRUEMAN & BROWN (1989) found that *Bullia digitalis* from the west coast burrowed more slowly than individuals from south coast populations, but ascribed this to differences in physiological condition.

Water temperatures along the west coast are considerably colder than along the south coast (CHRISTENSEN, 1980). In addition, west coast populations of Donax serra burrow more slowly than south coast populations at the same temperatures. Therefore, in their natural habitats, the two populations will differ markedly in burrowing rate (Table 3). As both coasts experience similar wave climates (Rossouw, 1984), swash periods and frequencies should be similar. McLACHLAN & YOUNG (1982) estimated that burial times must be less than 48 sec to prevent D. serra from being dislodged by subsequent swashes. Clearly, south coast populations can burrow sufficiently fast to maintain their position on the beach face, whereas the west coast populations would not have sufficient time to burrow at the peak of the swash before being carried down the beach by the backwash. This is indeed the pattern reflected in their observed field distributions; D. serra in the south coast inhabit the intertidal zone (McLACHLAN et al., 1979; DONN et al., 1986), while on the west coast they are found at or below spring low water (HUTCHINGS et al., 1983).

We conclude that there is little evidence for physiological adaptation of burrowing time to temperature between south and west coast populations of *Donax serra* and suggest that the lower than expected burrowing rates of the west coast population may be a result of morphological differences between the two. Furthermore, the combination of slower burrowing rates and lower environmental temperatures may be responsible for differences in zonal differences on the shore.

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