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Nitrogen excretion by the surf zone bivalves *Donax serra* and *D. sordidus*

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ABSTRACT: Nitrogen excretion by 2 surf zone bivalves, *Donax serra* and *D. sordidus*, was determined under laboratory and field conditions. Comparison of the forms of nitrogen excreted revealed only slight differences between species, with ammonia and amino acids constituting 70 to 78 % and 21 to 30 % of total dissolved nitrogen (TDN) respectively. During exposure at low tide, ammonia accumulated in *D. serra* mantle cavity fluid at 1 to 10 % of the immersed excretion rates. On re-immersion, an initial uptake of ammonia was recorded with subsequent recovery to peak excretion rates within 2 h. Mass significantly influenced rate of ammonia excretion in both species. The effect of temperature on ammonia excretion rates is reflected in Q_{10} values of 2.2 *(D. serra)* and 2.3 *(D. sordidus)* for starved sand-mussels over the temperature range 15 to 25 °C. Mass-adjusted mean ammonia excretion rates of fed sand-mussels were significantly higher than 'starved' excretion rates in both species. *D. serra* and *D. sordidus* recycle a total of 307 g N per m strip of surf zone per year which constitutes 2.3 % of total phytoplankton nitrogen requirements in the surf zone.

INTRODUCTION

Bivalves of the genus *Donax* are widespread on tropical and temperate exposed beaches (Ansell 1983). *Donax serra* Röding, the largest species in this genus, occurs on the west and south coasts of southern Africa (Kilburn & Rippey 1982) and constitutes the largest proportion (> 90 %) of total macrofaunal biomass on beaches in the southeast (McLachlan et al. 1981). Here *D. serra* undergo a semilunar migration pattern with the bulk of the population occupying a position just above the mean tide level during spring tides and lower down the shore during neaps (McLachlan et al. 1979). The smaller and less abundant *D. sordidus* Hanley undergo marked tidal migrations with the population centre of gravity showing a significant correlation with the position of the swash line (McLachlan et al. 1979).

The abundance of these bivalves indicates their importance not only in surf zone food chains (McLachlan et al. 1980) but also in their regeneration of nutrients. Bivalve populations have been shown to be important in nutrient regeneration in various ecosystems including estuaries (Kuenzler 1961, Jordan & Valiela 1982), the Baltic Sea (Kautsky & Wallentinus 1980, Kautskty & Evans 1987) and beaches (Lewin et al. 1979, Prosch & McLachlan 1984).

This study investigates the forms of nitrogen excreted by *Donax serra* and *D. sordidus*, the effects of body size, temperature, feeding and exposure to air (tidal state) on excretion rates, and the contribution of recycled nitrogen to total phytoplankton nitrogen requirements in a high energy surf zone ecosystem.

MATERIALS AND METHODS

Mussels for laboratory and field experiments were collected from Sundays River beach situated on the northern shore of Algoa Bay (25°40'E; 34°00'S), South Africa, during 1986 and 1987. Field experiments were conducted to determine the nitrogen excretion rates of *Donax serra* at various stages of the tidal cycle. During these field experiments the state of tide was monitored and the duration of *D. serra* inundation and exposure to air recorded. Surf and intertidal sand temperatures and the position of the groundwater table were also noted throughout the course of the experiments.

Ten adult *Donax serra* (40 to > 60 mm total length) were carefully removed from the sediment at measured time intervals from first exposure during ebb tide. Mantle cavity fluid expelled on contraction of the foot into the shell was collected in a glass container. Total shell length of each individual was measured, the pH and

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volume of the mantle cavity fluid recorded, and the samples frozen for later analysis. Mantle cavity fluid was filtered (0.45 µm) before chemical analysis.

To determine the effect of re-immersion on excretion rates, sand-mussels were removed from the intertidal after various times of aerial exposure and individually placed into 500 ml experimental containers holding 250 to 300 ml filtered (0.45 µm) seawater. Water samples, which were frozen for later analysis, were removed at 0.5 h intervals. Fresh filtered seawater was used for each 0.5 h incubation. To determine the excretion rates of sand-mussels during complete immersion, specimens were removed from the surf around high tide and a similar experimental procedure followed. Excretion rates during late ebb tide, when the number and duration of swashes covering the *Donax* zone decreased, were determined by removing specimens from the intertidal at 0.5 h intervals and following the above experimental procedure. The 0.5 h incubation times of the experiments were reduced to 0.25 h as swash coverage decreased.

Due to lower abundance and the lack of clear periods of aerial exposure/inundation in the swash zone, the excretion rates of *Donax sordidus* were only determined during inundation.

To evaluate the effects of starvation on excretion rates, *Donax serra* were removed from the intertidal after 4 to 6 h aerial exposure and placed in a 60 l plastic container supplied with sand, filtered seawater (4 µm) and aeration. After 8 h the water was removed and the sand-mussels exposed to air for a further 6 h before being individually introduced into experimental containers. This procedure ensured that the *D. serra* were without food for 18 to 20 h before experimentation. *D. sordidus* were starved for 18 h in a 60 l container supplied with filtered seawater (4 µm) before experimentation. Excretion rates of fed sand-mussels of both species were determined on individuals removed from the surf zone at high tide when visible phytoplankton accumulations were present. The field experiments on fed individuals were conducted at 15, 20 and 25 (± 1 °C) while laboratory experiments on starved individuals of both species were conducted at 15, 20 and 25 (± 0.5 °C). Experiments lasted for 4 h with water samples (15 ml) removed every hour and frozen for later analysis. Dry mass was calculated from McLachlan (1979) and McLachlan & Hanekom (1979). Water samples were analysed for ammonia, nitrate, nitrite urea, amino acids and total dissolved nitrogen (TDN) as described in Cockcroft & McLachlan (1987).

RESULTS

Donax serra

Ammonia constituted 70 % and 77 % of total dissolved nitrogen and amino acids 21 % and 30 % of TDN excreted by starved and fed *Donax serra* respectively (Table 1). Small amounts of urea (< 2 % of TDN) were detected in both instances.

Volume, pH and ammonia excretion rates in mantle cavity water collected at various times of exposure are summarised in Table 2. Mantle cavity water volume ranged from 0.5 to 5.5 ml ind^{-1} depending on the size range of sand-mussels used in the experiments. No pattern of mantle cavity water volume decrease was noted with time. The pH of mantle cavity water was always less than that of the surf water and decreased with time of exposure in all experiments. During exposure, mantle cavity pH ranged from 8.05 to 8.28 with surf water pH ranging from 8.30 to 8.58. Ammonia levels in mantle cavity fluid showed an initial increase in concentration but then remained at a relatively constant level which is reflected in the decreasing ammonia excretion rate with time of exposure. No increase in urea concentration was detected in mantle cavity fluid during exposure although an increase in amino acid concentration was found.

The ammonia excretion rates measured during periods of immersion, exposure to air and re-immersion at various states of the tide (Fig. 1A to G) showed consistent trends despite differences in temperature and season. Excretion rates during complete immersion around high tide remained fairly constant whereas a sharp decrease in excretion rate was found at late ebb

Table 1 *Donax serra* and *D. sordidus*. Forms of nitrogen excreted as a percentage of total dissolved nitrogen for starved and fed sand-mussels. Mean values given with range in parentheses

Species	Diet	Ammonia	Nitrate	Nitrite	Urea	Amino acids
D. serra						
	Starved	70 (55–91)	< 1	–	< 1	30 (15–38)
	Fed	77 (65–96)	< 1	–	2 (0–4)	21 (12–30)
D. sordidus						
	Starved	73 (62–95)	< 1	–	< 1	27 (16–36)
	Fed	78 (68–97)	< 1	–	< 1	22 (10–35)

Table 2. *Donax serra*. Summary of mantle cavity fluid volume, pH and ammonia excretion rates during exposure to air

Date Tidal phase	High water (h)	Low water (h)	Surf temp. (°C)	Sediment temp. (°C)	Time of exposure (h)	Mean mantle cavity water vol. (ml ind.$^{-1}$)	pH mantle cavity water	pH seawater	Mean NH_4^+ excretion rate (µg ind.$^{-1}$ h^{-1})
9 Mar 1986 Spring	03:21	09:26	22	17	0.5	3.2	8.14	8.32	3.20
					1.0	2.9	8.12	8.35	1.06
					2.0	3.0	8.11	8.35	0.77
					3.0	2.6	8.11	8.43	0.31
					4.0	3.0	8.05	8.42	0.29
17 Apr 1986 Neap	08:00	14:22	18		1.0	3.3	8.23	8.41	2.80
					2.0	3.6	8.22	8.40	1.00
					3.0	2.8	8.21	8.41	0.63
					4.0	3.0	8.21	8.41	0.61
27 May 1986 Spring/neap	05:51	12:05	20	18	2.0	2.5	8.17	8.38	4.10
					3.0	3.1	8.15	8.38	1.04
					4.0	3.0	8.16	8.35	1.01
					5.0	2.5	8.14	8.33	0.68
6 Aug 1986 Spring	04:06	10:09	15	14	2.0	3.1	8.24	8.31	2.10
					3.0	3.0	8.22	8.32	1.40
					4.0	2.6	8.22	8.31	0.85
					5.0	2.8	8.21	8.30	0.31
16 Nov 1986 Spring	03:06	09:08	21	18	1.0	3.2	8.24	8.52	2.25
					2.0	3.4	8.21	8.50	2.00
					3.0	3.1	8.22	8.50	0.88
					5.0	2.8	8.20	8.51	0.88
7 Dec 1986 Neap	08:12	14:36	25	19	1.0	4.1	8.15	8.34	1.98
					2.0	4.5	8.15	8.34	1.08
					3.0	3.3	8.13	8.35	0.44
					3.5	4.0	8.13	8.34	0.38
19 Mar 1987 Spring/neap	05:41	11:50	19	17	1.0	3.1	8.22	8.29	1.48
					2.0	3.0	8.22	8.30	1.40
					3.0	3.3	8.18	8.31	1.01
					4.0	2.8	8.18	8.31	0.44
30 Jul 1987 Spring/neap	05:59	11:59	16	15	1.0	4.3	8.29	8.54	2.56
					2.0	4.0	8.29	8.58	1.24
					3.0	5.2	8.28	8.50	0.98
					4.0	4.5	8.28	8.54	0.55
2 Aug 1987 Neap	07:56	13:49	17	16	1.0	5.4	8.15	8.38	5.20
					2.0	5.2	8.12	8.38	3.94
					3.0	4.4	8.07	8.39	3.61
					4.0	5.3	8.02	8.38	2.02
3 Aug 1987 Neap	08:59	02:45	15	15	1.0	5.0	8.19	8.38	3.55
					3.0	4.7	8.15	8.38	2.56
					4.0	4.5	8.15	8.38	1.25

tide during decreasing swash events. During exposure ammonia accumulated in the mantle cavity fluid. Excretion rates decreased with exposure time and ranged from 1 to 10 % of immersed excretion rates. On re-immersion, an initial uptake of ammonia was recorded with subsequent recovery to peak immersed excretion rates within 2 h. *Donax serra* exposed to air for various time periods consistently showed an initial ammonia uptake before complete recovery within 2 h. *D. serra* removed from the surf during decreasing swash events and placed in experimental chambers showed an initial decrease in excretion rate but then recovered to peak levels within 1 h, indicating that physical or chemical stimuli and not an endogenous rhythm was responsible for these responses. A generalised scheme of *D. serra* ammonia excretion over a full tidal cycle is presented in Fig. 1H. By integrating these results over a full tidal cycle, it is apparent that intertidal *D. serra* excrete only 49 % of the ammonia they would have if subtidal. During exposure to air the buried *D. serra* were always 15 to 20 cm above the groundwater table and no evidence of sand-mussels utilizing groundwater for replacement of mantle cavity fluid was noted.

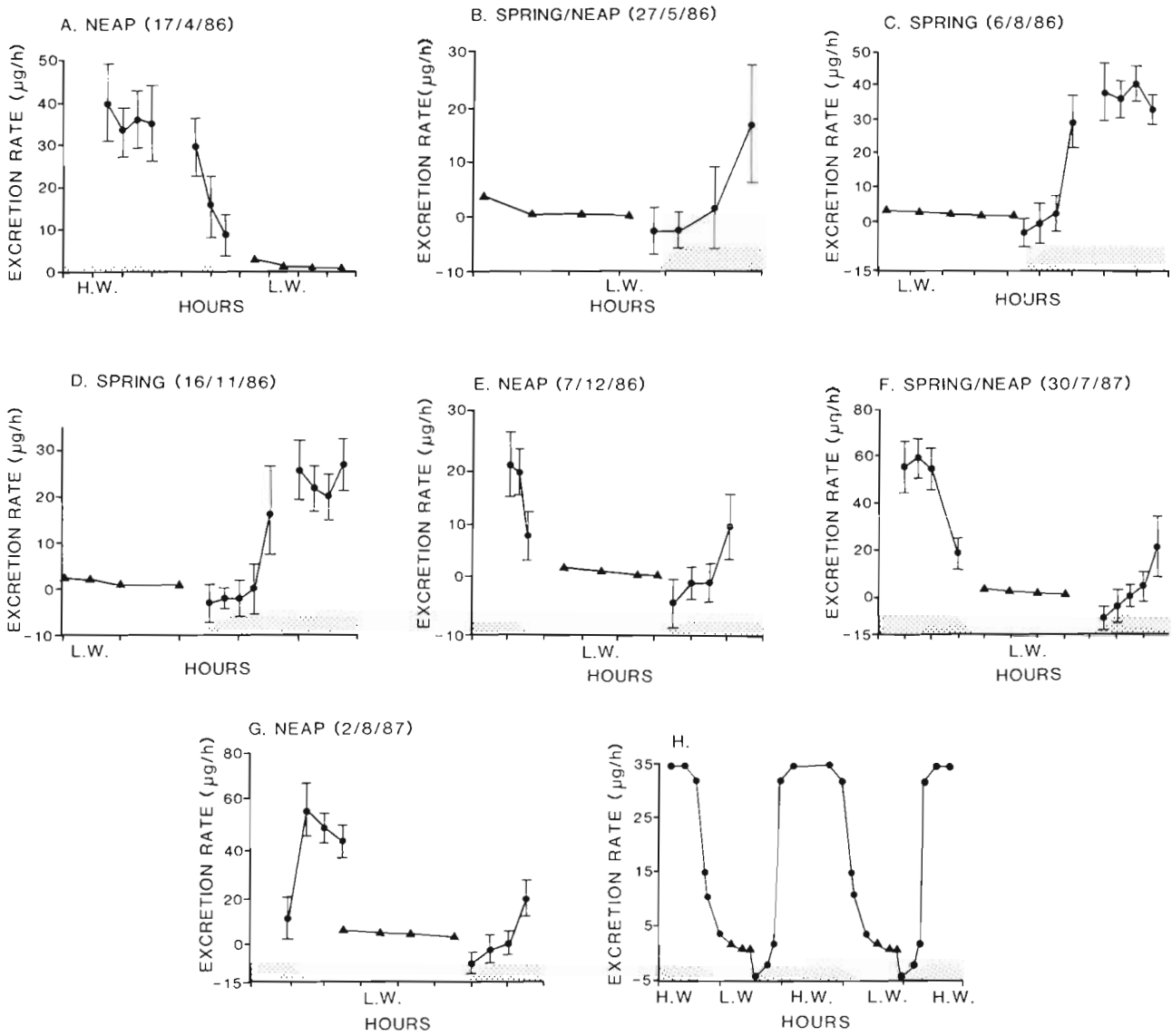

Fig. 1. (A to H). *Donax serra*. Ammonia excretion rates (± SE) at various states of the tide. (▲–▲) Excretion into mantle cavity water during exposure; (●–●) excretion rate while immersed. Negative values = uptake. Shaded areas represent inundation period

The regression equations for starved *Donax serra* at 3 experimental temperatures (Table 3) showed no significant differences in slope ($p > 0.05$, common b = 0.595) but significant differences in elevations ($p < 0.05$). Similarly no significant differences in slopes ($p > 0.05$, common b = 0.526) were obtained in the comparison of regression equations for fed *D. serra* at the experimental temperatures although the intercepts differed significantly ($p < 0.05$). Comparison of regression equations for starved and fed individuals at each experimental temperature indicated no significant differences in slopes ($p > 0.05$) but significant differences in elevations. The effects of temperature on excretion rates are reflected in Q_{10} values. A Q_{10} value of 2.20 was obtained for starved *D. serra* over the experimental temperature range 15 to 25°C.

Table 4 compares mean ammonia excretion rates (µg NH_4 mg^{-1} h^{-1}) of starved and fed sand-mussels at each experimental temperature by analysis of covariance. Mass-adjusted mean ammonia excretion rates for fed *Donax serra* were significantly higher than rates for starved sand-mussels at 15 and 20°C ($p > 0.05$) but not at 25°C ($p < 0.05$). The mass-adjusted mean ammonia excretion rate of sand-mussels starved at 15°C was significantly lower than at 20 and 25°C ($p > 0.05$), whereas no significant differences were detected between mean adjusted starved rates at 20 and 25°C ($p < 0.05$). The mass-adjusted excretion rates of sand-

Table 3. *Donax serra*. Regression statistics describing the relationship between ammonia excretion (μg NH_4^+ h^{-1}) and dry mass (mg) for starved and fed sand-mussels at 3 experimental temperatures

Temp. (°C)	Diet	Log a (± SE)	b (± SE)	r	n	p
15	Starved	−0.787 (±0.358)	0.597 (±0.116)	0.799	17	<0.01
	Fed	−0.428 (±0.249)	0.522 (±0.087)	0.776	26	<0.01
20	Starved	−0.634 (±0.453)	0.607 (±0.153)	0.814	10	<0.01
	Fed	−0.322 (±0.273)	0.566 (±0.096)	0.872	13	<0.01
25	Starved	−0.444 (±0.565)	0.581 (±0.178)	0.719	12	<0.01
	Fed	−0.094 (±0.416)	0.490 (±0.140)	0.636	20	<0.01

Table 4. *Donax serra*. Results of analysis of covariance comparing mass-adjusted rates of ammonia excretion (μg NH_4-N mg^{-1} h^{-1}) for starved and fed sand-mussels at 3 experimental temperatures

Temp. (°C)	Diet	n	Mean dry mass (mg)	Mean excretion rate	Adjusted mean excretion rate (± SE)
15	Starved	17	1478.8	0.010	0.012 ± 0.002
	Fed	26	1066.1	0.020	0.019 ± 0.002
20	Starved	10	1189.0	0.018	0.020 ± 0.004
	Fed	13	1027.4	0.032	0.031 ± 0.003
25	Starved	12	1687.3	0.018	0.026 ± 0.014
	Fed	20	1259.8	0.043	0.039 ± 0.011

mussels fed at 25 °C were significantly higher than at those 15 °C ($p > 0.05$), but no significant differences were detected between 15 and 20 °C or between 25 and 20 °C ($p < 0.05$).

Donax sordidus

Ammonia constituted 73 % and 78 % of TDN excreted by starved and fed *Donax sordidus* respectively (Table 1). Amino acids constituted 27 % and 22 % of TDN excreted by starved and fed sand-mussels respectively, with insignificant amounts of urea detected in both cases.

The regression equations for starved *Donax sordidus* at the 3 experimental temperatures (Table 5) showed no significant differences in slopes ($p > 0.05$; common slope b = 0.843) but significant differences in elevations ($p < 0.05$). Similar results were obtained in the comparison of regression equations for fed *D. sordidus* ($p > 0.05$; common slope b = 0.77). Comparison of regression equations for starved and fed individuals at each experimental temperature indicated no significant differences in slopes ($p > 0.05$) but significant differences in intercepts. The effect of temperature on ammonia excretion rate is reflected in the Q_{10} value of 2.29 obtained for starved *D. sordidus* over the temperature range 15 to 25 °C.

Mass-adjusted mean ammonia excretion rates for fed sand-mussels were significantly higher ($p > 0.05$) than starved rates at all experimental temperatures (Table 6). The adjusted mean excretion rate of *Donax sordidus* starved at 15 °C was significantly lower ($p > 0.05$) than the adjusted excretion rate at 25 °C, whereas no significant differences were found between rates at 15 and

Table 5. *Donax sordidus*. Regression statistics describing the relationship between ammonia excretion (μg NH_4^+ h^{-1}) and dry mass (mg) for starved and fed sand-mussels at 3 experimental temperatures

Temp. (°C)	Diet	Log a (± SE)	b (± SE)	r	n	p
15	Starved	−1.542 (±0.494)	0.901 (±0.287)	0.480	35	<0.01
	Fed	−1.214 (±0.354)	0.819 (±0.198)	0.794	12	<0.01
20	Starved	−1.434 (±0.604)	0.839 (±0.342)	0.523	18	<0.05
	Fed	−1.072 (±0.274)	0.802 (±0.148)	0.854	13	<0.01
25	Starved	−1.184 (±0.326)	0.788 (±0.172)	0.743	19	<0.01
	Fed	−0.855 (±0.418)	0.688 (±0.243)	0.618	15	<0.05

Table 6. *Donax sordidus*. Results of analysis of covariance comparing mass-adjusted rates of ammonia excretion (μg NH_4-N mg^{-1} h^{-1}) for starved and fed sand-mussels at 3 experimental temperatures

Temp. (°C)	Diet	n	Mean dry mass (mg)	Mean excretion rate	Adjusted mean excretion rate (± SE)
15	Starved	35	52.7	0.020	0.020 ± 0.001
	Fed	12	66.2	0.031	0.032 ± 0.003
20	Starved	18	62.6	0.022	0.021 ± 0.003
	Fed	13	82.3	0.040	0.040 ± 0.003
25	Starved	19	83.4	0.027	0.029 ± 0.003
	Fed	15	55.3	0.044	0.042 ± 0.004

20 °C or 20 and 25 °C ($p < 0.05$). Similar results were obtained when comparing the mass-adjusted ammonia excretion rates of fed individuals.

Comparison of *Donax serra* and *D. sordidus*

Comparison of the regression equations for starved *Donax serra* and *D. sordidus* showed no significant differences in slopes ($p > 0.05$) but significant differences in elevations ($p < 0.05$). Similar results were obtained in the comparison of regression equations for fed *D. serra* and *D. sordidus*. Although the intercepts of the regression equations describing the effect of mass on excretion rate of *D. sordidus* were significantly lower than those of *D. serra*, the mean mass-specific excretion rates (μg NH_4-N mg^{-1} h^{-1}) of starved *D. sordidus* were significantly higher (Student's t-test, $p > 0.05$) than those of starved *D. serra* at 15 and 25 °C but not at 20 °C. The mean mass-specific excretion rates of fed *D. sordidus* were only significantly higher than those of *D. serra* at 15 °C. The large mass difference between the species, and the fact that excretion rates of *D. serra* used in the above comparisons are those for the period of immersion only, did not allow a meaningful comparison of mass-adjusted mean excretion rates. Comparison of the amount of ammonia excreted by a 50 mg (dry mass) sand-mussel of each species over a full tidal cycle using the regression equations in Tables 3 and 5 indicated that sand-mussels of equal mass excreted comparable amounts of ammonia over a tidal cycle despite the periods of exposure experienced by the intertidal *D. serra*. If the same procedure is used for a 1000 mg sand-mussel (hypothetical in the case of *D. sordidus*), *D. serra* would excrete considerably less NH_4 per tidal cycle than *D. sordidus*.

DISCUSSION

During exposure to air at low tide *Donax serra* remains buried 20 to 35 cm below the sediment surface with siphons retracted, valves closed and the foot extending downwards into the sand. Despite the many other studies on this species on Eastern Cape beaches (Dye 1979, McLachlan & Hanekom 1979, Ansell & McLachlan 1980, Ansell 1981, McLachlan & Young 1982), no information on the metabolism of these animals during exposure is available. Many bivalve species have been shown to withstand periods of shell closure and the resultant lack of oxygen by utilization of anaerobic metabolism. The switch from aerobic to anaerobic respiration in bivalves normally occurs when the oxygen tension of the mantle cavity fluid falls to low levels after valve closure (Akberali & Trueman 1985). Measurements of the oxygen in extrapallial fluid of the clam *Mercenaria* (Crenshaw 1972) revealed that it became completely anaerobic within 25 min of shell closure.

In bivalve molluscs some tissues may be adapted to function anaerobically while others, which are near sites of gas exchange, may be primarily aerobic (Booth & Mangum 1978). Some epifaunal bivalve species have been shown to utilize the oxygen diffusing into the mantle cavity fluid through the shell gape during periods of exposure to air (Lent 1968, Moon & Pritchard 1970, Coleman & Trueman 1971, Boyden 1972a, b, Bayne et al. 1976a, Widdows et al. 1979) while infaunal species have not been reported to utilize atmospheric oxygen at such times (Boyden 1972a). Although no direct evidence of anaerobic metabolism is available for *D. serra*, the fact that these animals are buried in sediment surrounded by reduced pO_2 (although not anaerobic) and that the shell valves are tightly closed for up to 8 h indicate that this species is likely to operate anaerobically during exposure.

During exposure *Donax serra* mantle cavity fluid volume remains relatively constant while pH decreases with exposure time. The accumulation of end products of aerobic metabolism which are usually alanine and succinate (Stokes & Awapara 1968, Hammen 1969, De Zwaan & Zandee 1972, De Zwaan & van Marrewijk 1973), and the increase in CO_2 levels, are considered the cause of the pH decrease in mantle cavity or extra-

pallial fluid found in some bivalve species during valve closure (Crenshaw 1972, Wijsman 1975, Abkerali & Trueman 1985).

The accumulation of ammonia in the mantle cavity of *Donax serra* during exposure occurs at 1 to 10 % of the rate of ammonia excretion during immersion. Similar results were obtained for *Mytilus californianus* (Bayne et al. 1976a) which accumulated ammonia in mantle cavity fluid at 5 % of immersed excretion rates. No accumulation of ammonia during exposure at low tide was found in *Geukensia demissa* (Jordan & Valiela 1982). The difference between exposed and immersed ammonia excretion rates may be due to an increase in glycolysis relative to protein degradation (Bayne et al. 1976b) or the conversion of ammonia to less toxic end products via a variety of metabolic sequences. The conversion of ammonia to urea was suggested as a possible pathway for the detoxification of ammonia during exposure (Andrews & Reid 1972) while the fixing of ammonia into alanine (using alanine dehydrogenase) was proposed by De Zwaan & van Marrewijk (1973) for the same purpose. No increase in urea concentration was noted in *D. serra* mantle cavity fluid during exposure although accumulation may have occurred in the tissues and blood. An increased production of amino nitrogen has been proposed as a mechanism for the detoxification of ammonia under certain circumstances (Bayne et al. 1976b) and the increase in amino acid concentration found in *D. serra* mantle cavity fluid during exposure may serve this purpose. Hammen (1968) suggested that the large concentration difference between tissue and medium amino acid concentration in bivalves caused a leakage of amino acids across the body membranes. Lange (1970, 1972) suggested that the loss of amino acids may be a process of active excretion since certain amino acids may be formed as end products of energy metabolism.

The uptake of ammonia during the initial period of immersion after exposure in *Donax serra* may possibly be due to increased amino acid synthesis to replace lost amino acids. Hammen (1968) suggested that bivalves have very active amino transferase enzymes in order to replace amino acid loss. He recognised that for such replacement to occur, transamination must be coupled with a fixing of ammonia, which is traditionally viewed as the role of the enzyme glutamate dehydrogenase (GDH). Widdows & Shick (1985) recorded no overshoot in ammonia excretion of *Mytilus edulis* during recovery after 5 h exposure to air, rather a conservation or fixation of ammonia at a time of year (winter) when the rate of ammonia excretion was at a seasonal minimum. Experiments on this species in summer (Widdows in Widdows & Shick 1985) showed a distinct overshoot in ammonia excretion after re-immersion. De Vooys & De Zwaan (1978) reported a similar overshoot in ammonia excretion by *Mytilus edulis* which was proportional to exposure time.

The decrease in ammonia excretion rates in *Donax serra* exposed to decreasing swash cover is considered purely a response to environmental conditions rather than part of an endogenous rhythm of excretion. Individuals removed during late ebb tide and re-immersed showed a rapid recovery of excretion rate to immersed levels after an initial decrease. Hodgson & Fielden (1984) identified 2 ciliated sensory receptor types on the siphon and mantle cavity edge in *D. serra* and 3 types in *D. sordidus*. Estimates of abundance show that the receptors are most numerous on the tips of the siphon tentacles and they suggested that these operate as chemoreceptors.

Ammonia constituted 70 to 78 % of TDN and amino acids 21 to 30 % of TDN excreted by these species. Although ammonia is the dominant form of nitrogen excreted in most bivalves, amino acids constitute a considerable portion of total nitrogen excreted (Lum & Hammen 1964, Hammen 1968, Allen & Garret 1971, Bayne 1973). The proportions of excreted forms have been demonstrated to change with stress. Bayne (1973) reported increased amino-nitrogen excretion relative to ammonia nitrogen during stress from temperature and starvation in *Mytilus edulis*. Urea was not an important component of the nitrogen excreted in *Donax serra* or *D. sordidus*, although small but significant amounts have been recorded in other bivalves (Lum & Hammen 1964, Allen & Garret 1971, Bayne 1973).

Body mass significantly affected the excretion rates of both species. In this study no significant differences in regression coefficients (b in the expression ammonia excretion rate = a.body size^b) were found between 'starved' and 'fed' experiments or between species. The mean b values for *Donax serra* (b = 0.561) and *D. sordidus* (b = 0.806) are similar to those obtained for *D. vittatus* (b = 0.639) (Ansell & Sivadas 1973).

The effect of temperature on ammonia excretion rates is reflected in the Q_{10} values of 2.2 *(Donax serra)* and 2.3 *(D. sordidus)* for starved sand-mussels over the temperature range 15 to 25 °C. A mean Q_{10} of 2.07 was found for ammonia excretion by *D. vittatus* between 10 and 20 °C (Ansell & Sivadas 1973). In both species studied, 'fed' excretion rates were significantly higher than 'starved' excretion rates at all temperatures with one exception *(D. serra,* 25 °C).

Intertidal adult *Donax serra* exposed for 4 h excrete 51 % less ammonia than they would have excreted if inundated for the full tidal cycle. Widdows & Shick (1985) showed a net energy saving and improved scope for growth in intertidally acclimated *Mytilus edulis* and *Cardium edule* compared to intermittently fed subtidal individuals. The intertidal habitat and concomitant

periods of exposure and anaerobic metabolism may mean a significant energy saving for *Donax serra* and could be a possible reason for the obvious success of this species on the South African south coast. Further work is clearly required on the anaerobic metabolism of this species during exposure and the role of various enzymes (especially GDH) before final conclusions can be drawn.

Having determined the forms of nitrogen excreted and the effects of temperature, feeding, starvation, and tidal state on excretion rates of these species, the contribution of their recycled nitrogen to total phytoplankton requirements can be estimated. Using the biomass values from McLachlan & Bate (1984), the innundation periods for the major *Donax serra* zone (Donn et al. 1986) and the excretion rates from this study, *D. serra* is calculated to recycle 185 g NH_4-N per meter strip of surf zone per year or 264 g N m^{-1} yr^{-1}. Similarly, *D. sordidus* is calculated to recycle 30 g NH_4-N m^{-1} yr^{-1} or 43 g N m^{-1} yr^{-1}. These species therefore cycle 307 g N m^{-1} yr^{-1} which constitutes 2.3 % of total phytoplankton nitrogen requirements in the surf zone (Cockcroft 1988).

Although these values are low compared to the amounts of nitrogen recycled by surf zone penaeid prawns (Cockcroft & McLachlan 1987) and mysids (Crockcroft et al. 1988) (12 % and 10 % total phytoplankton nitrogen requirements, respectively), the time scale of nutrient release may be of importance. The pulse of nutrients entering the surf zone water column ca 2 h after inundation of the *Donax* zone may play an important role in the dynamics of phytoplankton nutrient uptake.

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