# THE REGENERATION OF SURF-ZONE NUTRIENTS BY THE SAND MUSSEL, *DONAX SERRA* Röding

R. M. PROSCH[1]

and

A. McLACHLAN

*Zoology Department, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth, South Africa 6000*

**Abstract:** This paper estimated the significance of ammonia excretion by *Donax serra* Röding in the regeneration of nitrogen for the surf-zone adjacent to a high energy beach. The migrations of *D. serra* over a tidal cycle were quantified in order to calculate inundation periods for each size class on an exposed beach. The rôle of this animal in surf-zone nitrogen regeneration was then estimated by measuring ammonia excretion rates of individual animals and then calculating $NH_4$-N excretion for the whole population along the shoreline investigated. This gave an estimate of $\approx 300$ g $NH_4$-N per m of shoreline per yr using a biomass of 7000 g per m. This quantity is probably sufficient to regenerate the total nitrogen pool of the surf-zone every month.

## INTRODUCTION

The phenomenon of phytoplankton blooms associated with beach generation of nutrients has recently been suggested (McLachlan *et al.*, 1981). Lewin *et al.* (1975) monitored populations of surf diatoms at Copalis Beach, Washington, over a 2-yr period and found that during those times when nitrate was absent the nitrogen source for algal growth was apparently supplied by ammonia, which was always present in appreciably high concentrations in surf samples. Subsequently, Lewin *et al.* (1979) showed that the surf clam, *Siliqua patula*, regenerated significant quantities of ammonia in these surf-zones. Eppley *et al.* (1979) found that 35% of the nitrogen assimilated by the phytoplankton in the euphotic zone in southern Californian coastal waters was provided by ammonia which was generated by the metabolic activities of animals, sewage and refinery outfalls, advection and aerial fallout.

McLachlan *et al.* (1981) studied open sandy beach ecosystems along the southeastern coast of South Africa and noted that the surf-zones in this area were the sites of intensive phytoplankton growth and dense blooms of surf diatoms were common. They concluded that a broad, shallow surf-zone best develops circulation cells that allow a build-up of phytoplankton blooms. As a result of these circulation cells the residence times of beach generated nutrients are prolonged in the surf-zone, thereby stimulating

---

[1] Present address: Sea Fisheries Research Institute, Private Bag X2, Roggebay, South Africa 8012.

phytoplankton growth. Furthermore, they suggested that abundant filter-feeding popula-
tions will generally only develop on beaches where surf-zone circulation patterns are
such that nutrients, produced by beach mineralization of organic matter, can be trapped
long enough to allow the development of phytoplankton blooms. They suggested that
on the beaches studied the macrofauna may contribute as much as 37% and the
interstitial fauna 63% of the total inorganic nitrogen compounds generated by the
mineralization of organic material in the beach. Subsequently, some accurate attempts
have been made to estimate the rôle of the interstitial fauna in this generation of
inorganic nitrogen (McLachlan, 1982). This paper attempts to quantify the rôle of the
macrofauna.

Ammonia–nitrogen excretion rates and the ways in which environmental factors may
influence different end-products have been investigated by a number of workers, notably
Hammen (1968) and Ansell & Sivadas (1973) for *Donax*, Bayne *et al.* (1976) for *Mytilus*,
and Lewin *et al.* (1979) for *Siliqua*. No such work, however, has been undertaken on
the sandy beaches of the eastern Cape where vast macrofaunal populations have been
recorded. The bivalve *Donax serra* comprises 96.8% of the macrofaunal biomass on
sandy beaches in this area (McLachlan *et al.*, 1981) and this study attempted to
establish the importance of this species in the regeneration of inorganic nitrogen
compounds on these exposed beaches.

## AREA STUDIED

Maitland River beach is a high energy, south-facing beach which is situated 20 km
west of the city of Port Elizabeth, South Africa, and is $\approx 25$ km long (Fig. 1). The
intertidal slope is gentle, averaging 1/30 and the sand consists of very well sorted
medium quartz grains with medium diameters of $\approx 300 \, \mu$m. The extreme spring tidal
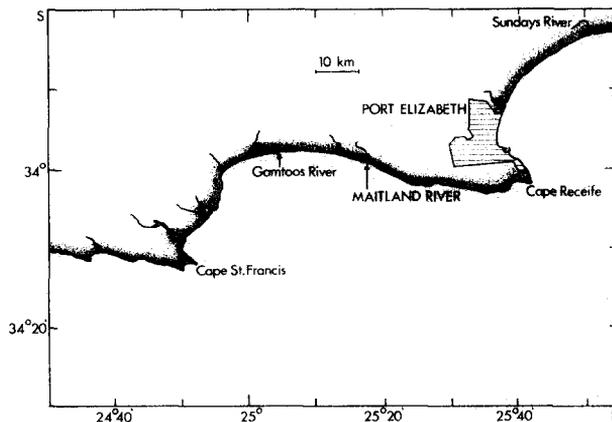


Fig. 1. Map of the area studied – Maitland River beach; $\approx 20$ km from the city of Port Elizabeth.

range is 2.1 m and maximum temperature range 10–25 °C (McLachlan *et al.*, 1979). The macrofauna is dominated by the white sand mussel, *D. serra*, which can exceed 7 kg ash-free dry biomass per m of shoreline (McLachlan, 1977).

## METHODS

As *D. serra* Röding can only excrete ammonia when covered by the tide it was first necessary to estimate the inundation times for this intertidal species. This was complicated by the occurrence of tidal migrations and the vertical segregation of size classes. Following this, attempts were made to measure individual excretion rates of different size classes in situ.

### INUNDATION TIMES AND TIDAL MIGRATIONS

Four stakes were placed 25 m apart, on a line parallel to the shore and above the high water drift line. This was undertaken on the first day of a circa-semi-lunar sampling sequence to monitor population distribution and movements over a full spring–neap tidal cycle. These poles remained fixed reference points for the duration of the experiment. Sampling was started during spring tide when the drift line was approximately 1 m below these reference points, and subsequent drift lines occurred below this. At the start of each sampling period, transect lines of stakes were set up at 10-m horizontal intervals from these fixed reference points down to just below the low tide swash zone. This was usually a distance of 80–90 m. Sampling was undertaken every few days over a 16-day period and the slope of each transect was measured using graduated poles. The low water swash zone and the drift line were determined in relation to the reference points for each transect during each sampling period.

Quadrats measuring 0.25 m$^2$ were taken adjacent to each stake, starting from the bottom of the shore in the swash zone up to a point where no *D. serra* were encountered. All mussels were removed using a 2-mm mesh sieve and measured with sliding callipers. A chi-squared test of homogeneity revealed that each sample was representative of an area up to a point halfway between itself and the neighbouring sample.

Inundation time over a 14-day period of tidal cycles was calculated assuming the vertical rise and fall of the tides to be sinusoidal. By reference to the beach profile (the change of which was insignificant), the high tide drift line and the low water swash for each sampling day, a computer model was constructed to give the average inundation time for each size class based on its daily positions.

### AMMONIA–NITROGEN EXCRETION RATES

Ammonia–nitrogen excretion rates were measured in plastic containers in situ in three series of experiments. Earlier analysis had failed to show production of measurable amounts of nitrogenous waste products other than ammonia. The first series followed

ammonia generation by different size classes of *D. serra* over full tidal cycles while the second series looked at short term generation rates.

In the first series of experiments the size classes selected were: 0–20 mm, 21–30 mm, 31–40 mm, 41–50 mm and 51 + mm (maximum shell length equals 63 mm). On each day a single size class was sampled, starting early in the morning regardless of the state of the tide. Sampling continued for 12 h, a fresh sample of animals being taken every hour. Each sample consisted of duplicate sets of five animals from a single size class placed into two plastic buckets containing between 250 ml and 1 litre of unfiltered sea water, the volume depending on the size class. Before the animals were introduced a control was taken from each container. Every 2 h a 50-ml sample was taken from each bucket for the determination of ammonia–nitrogen. Two controls of sea water were taken from the swash zone. In all the samples from this experiment, ammonia–nitrogen was determined by the phenol-hypochlorite method (Strickland & Parsons, 1972). The first step in this method, the addition of phenol, was undertaken in the field in order to reduce atmospheric contamination and bacterial utilization of the ammonia (Degobbis, 1973).

As the excretion values obtained from these field experiments were much lower than those determined by other workers and, because these values in all cases appeared to decrease dramatically after a few hours, a trial experiment was run to determine whether the time interval of sampling as well as the absence or presence of sand and filtered or unfiltered water had any effect. In this case, duplicate sets of five animals of 55-mm shell length were placed in buckets containing 2 l of sea water with and without sea sand and samples taken every 30 min for 3 h. A rapid drop in ammonia excretion rate was confirmed, presumably due to uptake of ammonia compounds by bacteria on the shells and sand. Consequently, it was decided to repeat the field experiment using the shortest practical time interval namely, 30 min. The final experiment was again conducted in the field and consisted of a series of measurements of ammonia excretion for all size classes over 30-min periods on three different days and covering all states of tide. In each case five animals of the same size class were placed in a bucket containing 0.1–1.0 l of 0.45-$\mu$m filtered sea water and samples taken at the beginning and end of a 30-min period. These samples were immediately frozen and taken back to the laboratory for $NH_4$-N analysis using a Technikon auto-analyser. Only the results of this final experiment were used in subsequent estimates of ammonia excretion rates by the *D. serra* population on Maitland River beach.

## RESULTS

### INUNDATION TIMES

Results from the survey of inundation times and tidal migrations over a 16-day period are given in Table I and illustrated in Fig. 2. The population has been grouped into two size classes, namely 0–30 mm and 30–63 mm because of the different migration

Numbers of *Donax serra* per quadrant

- ▨ 0 - 10
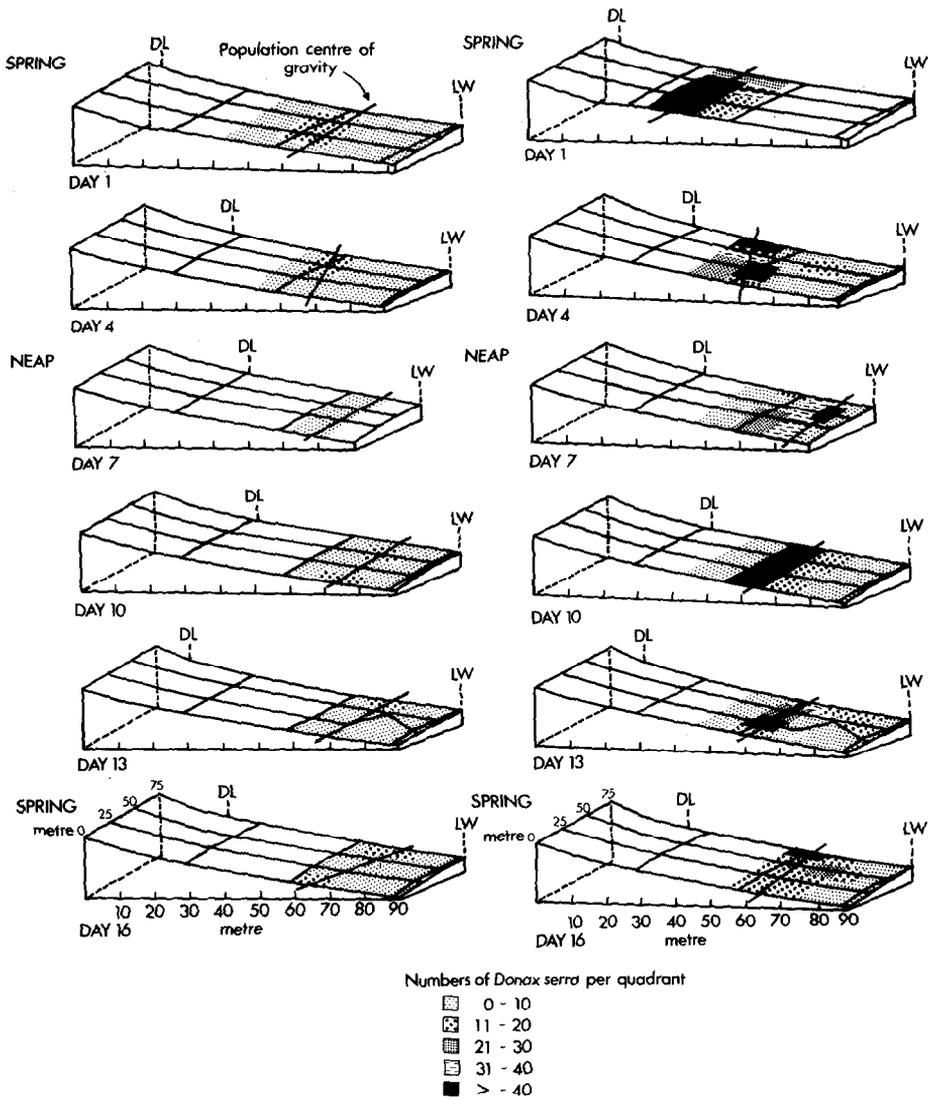- ▨ 11 - 20
- ▦ 21 - 30
- ▤ 31 - 40
- ■ > - 40

Fig. 2. The horizontal movement of *Donax serra* on a sandy beach: left, size 0–30 mm; right, size > 30 mm; the spring and neap tides as well as the high water drift line and low water are indicated; the centre of gravity of the population is indicated to facilitate interpretation; the horizontal lines represent contour lines; LW, low water; DL, drift line.

patterns for large and small mussels. In all cases the population, particularly the larger size class, exhibited patchy distribution. The larger animals appear to occupy a higher intertidal position during spring tides and a lower position during neap tides than the smaller group of animals. Despite these apparent differences, integration of inundation times over a full spring–neap tidal cycle reveal relatively small differences between the

TABLE 1

Biomass values and inundation times for different size classes of *Donax serra* on Maitland River beach.

| Size class (mm) | Dry biomass ($g \cdot m^{-1}$) | % of total biomass | Inundation ($h \cdot tidal\ cycle^{-1}$) | % of time inundated |
|---|---|---|---|---|
| 0–20 | 98 | 1.4 | 8.1 | 71.7 |
| 21–30 | 224 | 3.2 | 8.0 | 66.9 |
| 31–40 | 238 | 3.4 | 8.4 | 69.7 |
| 41–50 | 420 | 6.0 | 8.0 | 66.7 |
| 51+ | 6020 | 86.0 | 7.7 | 63.9 |
| Total | 7000 | 100.0 | Mean 8.1 | 67.8 |

different size classes (Table I). Only the 0–20-mm size class show a significantly higher inundation time than the other size classes, being covered by water for $\approx 72\%$ of the time during a 14-day spring–neap cycle. The other classes exhibited inundation times between 63 and 70%. Table I also summarizes the relative contribution to total population biomass of the different size classes on Maitland River beach based on McLachlan & Hanekom (1979).

AMMONIA EXCRETION

Fig. 3 illustrates ammonia–nitrogen excretion rates and surf-zone ammonia–nitrogen concentrations for the series of 12-h field experiments conducted for five size classes of *D. serra*. For all five size classes excretion rates appear to show a cyclical trend. Maximum values occurred mostly before the tide was at its highest. The most significant aspect of these results is that in all cases the periods of maximum excretion rate are followed within 1–3 h by high surf levels of $NH_4$-N. Furthermore, in all cases $NH_4$-N concentrations in the experimental containers dropped severely during the duration of the experiment. While these experiments clearly show the importance of $NH_4$-N excretion by the *D. serra* population, the apparent removal of $NH_4$-N from the experimental containers results in an under-estimate so that these values cannot be used to calculate absolute excretion rates for the population.

Table II summarizes the results of the experiment designed to evaluate the effects of filtered and unfiltered sea water, the presence or absence of sea sand and time on measured ammonia excretion rates of 55-mm size mussels. There were small differences in excretion rates between treatments, although in all treatments the excretion rate decreased significantly with time, fastest rates always being recorded within the first hour. As the solutions in which the animals were kept were not changed during the course of this experiment, this clearly suggests $NH_4$-N removal. For accurate estimation of $NH_4$-N excretion rate in this species, it therefore appears necessary to keep experiments as short as possible, ideally not > 30 min, and to introduce some correction for the $NH_4$-N removed. The final experiment attempted to meet these requirements.
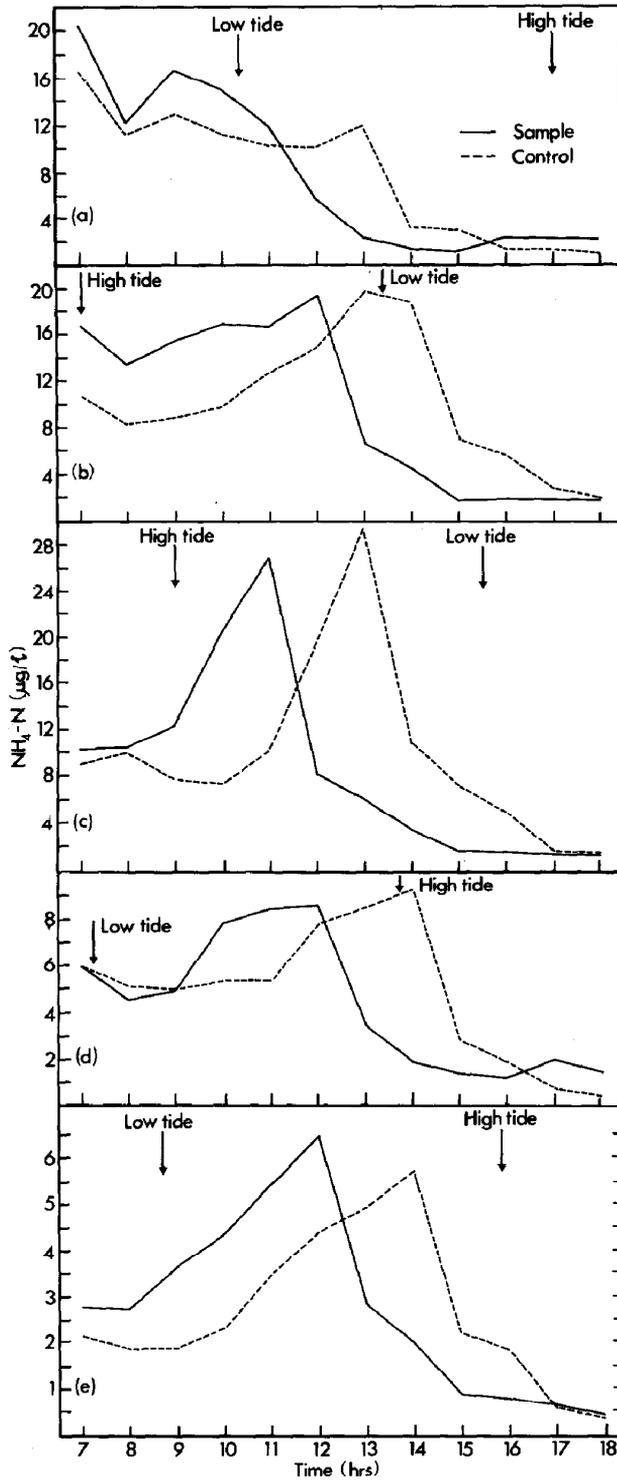
Fig. 3. Ammonia–nitrogen excretion for different size groups of *Donax serra* and surf-water NH$_4$-N levels over 12 h: the respective times of low and high tides are indicated; (a) 50 mm; (b) 41–50 mm; (c) 31–40 mm; (d) 21–30 mm; (e) 0–20 mm.

R.M. PROSCH AND A. McLACHLAN

Excretion of $NH_4$-H by *Donax serra* in different media.

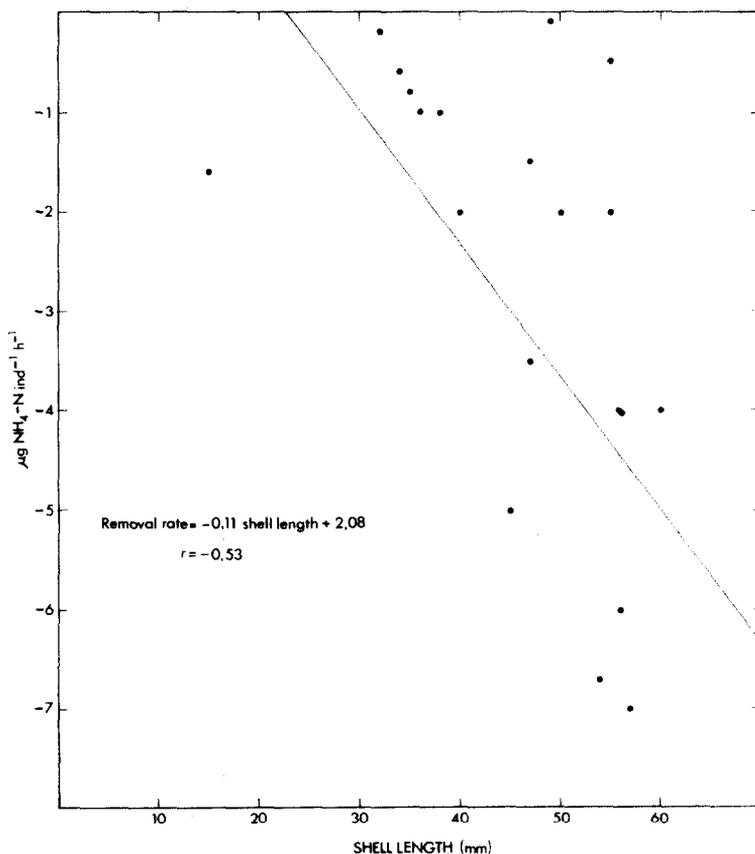| Time (h) | Excretion ($\mu$g/mussel during each time interval) | | | | |
|---|---|---|---|---|---|
| | Two l unfiltered sea water + two l sand | One l unfiltered sea water + one l sand | One l unfiltered sea water | One l filtered sea water + one l sand | One l filtered sea water |
| 0 | 0 | 0 | 0 | 0 | 0 |
| 0.5 | -- | 5.0 | 4.0 | 4.0 | 7.0 |
| 1 | 8.6 | 3.0 | 4.0 | 3.0 | 7.0 |
| 1.5 | -- | 2.3 | 2.0 | 1.0 | 5.6 |
| 2 | 5.6 | Removal | Removal | Removal | Removal |
| 3 | 2.8 | Removal | Removal | Removal | Removal |



Fig. 4. $NH_4$-N removed plotted against shell length of *Donax serra*.

In this experiment a large number of $NH_4$-N excretion rates for different size classes were measured for 30-min periods. In several cases negative values, i.e. $NH_4$-N removal, were recorded. All these cases of $NH_4$-N removal are plotted in Fig. 4 and a regression line fitted to the data. Consequently, these values give some estimate of $NH_4$-N removal as a function of size. Values from this regression line were used to correct $NH_4$-N excretion rates for each size and these corrected values are plotted in Fig. 5.
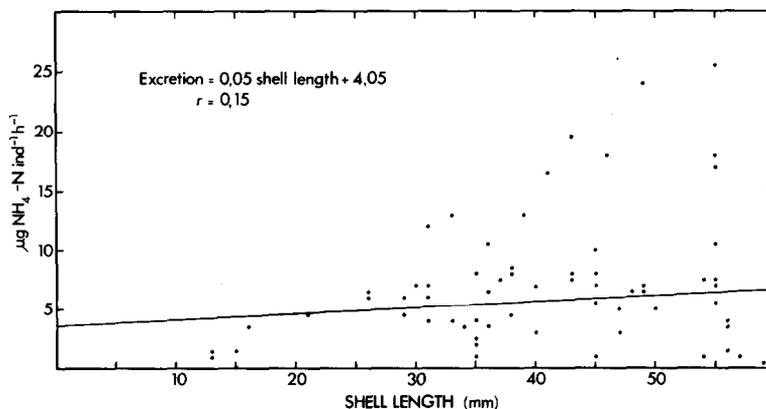


Fig. 5. Corrected $NH_4$-N excretion rates for individual *Donax serra*.

Despite considerable scatter, there is a clear increase in $NH_4$-N excretion rate with increasing shell length, from values $<3$ $\mu$g $NH_4$-N per individual per h for 10-mm *D. serra* to values $>8$ $\mu$g $NH_4$-N per individual per h for the largest specimens $>60$ mm. Using this excretion rate, and the inundation times and biomass values in Table I, $NH_4$-N regeneration by the total *D. serra* population on Maitlands River beach can be calculated. These results are summarized in Table III. This clearly shows significant amounts of $NH_4$-N regenerated by the *D. serra* population with the 51-mm + size class accounting for most of the excretion. The total amount excreted is $\approx 300$ g $NH_4$-N per m shoreline per year.

It was not possible in this work to demonstrate effects of temperature on $NH_4$-N excretion rates. No measurable excretion could be obtained from animals in the laboratory and the excretion values in Fig. 5, obtained on three different occasions when temperatures ranged between 16 and 21 °C, exhibited no significant differences.

## Discussion

The distribution of different sizes of *D. serra* on the shore corresponds to the description of McLachlan & Hanekom (1979) and the description of tidal migrations

TABLE III

Ammonia–nitrogen excretion by the *Donax serra* population on Maitland River beach.

| Size class (mm) | | Mean dry mass (mg) | Dry biomass ($g \cdot m^{-1}$) | Mean excretion rate ($\mu g\ NH_4\text{-}N \cdot ind.^{-1} \cdot h^{-1}$) | Inundation time ($h \cdot day^{-1}$) | Total excretion ($g\ NH_4\text{-}N \cdot m^{-1} \cdot yr^{-1}$) |
|---|---|---|---|---|---|---|
| Range | Mean | | | | | |
| 0–20 | 15 | 32 | 98 | 3.7 | 17.2 | 71.1 |
| 21–30 | 25 | 155 | 224 | 5.0 | 16.1 | 42.4 |
| 31–40 | 35 | 437 | 238 | 6.3 | 16.7 | 27.8 |
| 41–50 | 45 | 944 | 420 | 7.4 | 16.0 | 19.3 |
| 50 + | 55 | 1749 | 6020 | 8.5 | 15.3 | 163.6 |
| | | | | | Total | 324.2 |

by McLachlan *et al.* (1979). The bulk of the population occupies a position near the middle of the shore during spring tides and lower down the shore during neaps. This is presumably to prevent the animals ever being covered by > 1 m depth of water at high tide, thereby limiting their accessibility to marine predators. Despite the apparent segregation of size classes there were, however, little differences between their inundation times. The largest animals, which move highest up the beach during springs, have a total inundation time only 8% less than the smallest animals.

It is now well documented that $NH_4$-N is not the only form of excretory nitrogen loss in bivalves. Hammen (1968) found that $NH_4$-N made up 50–75% and amino acids 21–34% of excretory nitrogen in a variety of bivalves. Other reported values for amino-N excretion range from 0 to 63% (Lum & Hammen, 1964; Hammen *et al.*, 1966; Bayne, 1973; Bayne & Scullard, 1977). This varies with season and habitat and has been suggested to be an active process of amino-N excretion and not passive leakage (Hammen, 1968; Bayne & Scullard, 1977). Urea excretion is generally negligible (Lum & Hammen, 1964; Hammen, 1968; Allen & Garrett, 1971). It is therefore likely that there is amino-N loss in *D. serra* and that this would add to its contribution to surf nitrogen. The fact that preliminary experiments, however, failed to show measurable amounts of nitrogenous waste products other than $NH_4$-N, suggests that this would be considerably less important than $NH_4$-N.

Rates of $NH_4$-N production are related to a variety of factors including temperature, nutritional status, exposure time and reproductive condition (Ansell & Sivadas, 1973; Bayne & Scullard, 1977; De Vooys & De Zwaan, 1978). The influence of these factors has not been specifically investigated in this study. Although the importance of all these factors is acknowledged, the aim here was to obtain a general estimate of $NH_4$-N production by a whole population rather than to undertake a physiological investigation of $NH_4$-N excretion in *D. serra*. While seasonal temperature changes are relatively small and surf-zone phytoplankton in reasonably constant supply in the area studied, the effects of exposure and reproductive condition on $NH_4$-N excretion in *D. serra* warrant further study.

The impact of $NH_4$-N excretion by the population on $NH_4$-N concentrations in the surf-zone can be seen from Fig. 3, with dramatic increases in the latter following closely on each peak of excretion. Clearly these mussel populations have the ability to boost significantly inorganic nitrogen levels in the surf-zone. The final calculations of excretion rates give a figure of ≈ 300 g $NH_4$-N per m of shoreline per yr on this beach which is enough to generate the total inorganic nitrogen pool of this surf-zone ≈ 15 times every year. These estimates are conservative as they do not include amino-N and are based on corrected excretion values to take into account the removal of $NH_4$-N, possibly by bacteria. In the field this problem may not be so severe as the excretory products do not come into contact with the shell as water expelled from the siphons mixes immediately with the overlying surf-zone water.

Estimates given by McLachlan (1982) suggest that the interstitial fauna will generate about twice as much inorganic nitrogen as the *D. serra* populations. Unfortunately we

do not yet have estimates of the nitrogen requirements of surf-zone phytoplankton. Ammonia excretion by bivalve populations has also been shown to be quantitatively important in nitrogen regeneration in Pacific surf-zones (Lewin *et al.*, 1979), the Baltic (Kantsky & Wallentinus, 1980), and an estuary (Jordan & Valiela, 1982).

A significant finding of this study was the dramatic drop in surf-zone $NH_4$-N following elevated values resulting from peaks in excretion by the *D. serra* population. This fast decrease is indicative of a rapid turnover of nutrients within the surf-zone presumably as a result of uptake by phytoplankton. Rich surf phytoplankton blooms of *Anaulus birostratus* are common in these surf-zones and have been described by McLachlan & Lewin (1981). This and other species in the surf together with micro-organisms in the water are presumably capable of extremely rapid removal of inorganic nitrogen. *A. birostratus* blooms are normally positioned over rip currents in the surf during daylight hours. In this position they would be situated so as to receive rapidly any nutrient excreted into the surf. Their maintenance of position over rip currents therefore seems significant in allowing them to tap a constant supply of inorganic nutrient generated not only by the macrofauna of the beach, but also by the mineralizing activities of the interstitial fauna acting on large volumes of water filtered through the sand.

## ACKNOWLEDGEMENTS

## REFERENCES

ALLEN, J. A. & M. R. GARRETT, 1971. The excretion of ammonia and urea by *Mya arenaria* L. (Mollusca: Bivalvia). *Comp. Biochem. Physiol.*, Vol. 39A, pp. 633–642.

ANSELL, A. D. & P. SIVADAS, 1973. Some effects of temperature and starvation on the bivalve *Donax vittatus* (da Costa) in experimental laboratory populations. *J. Exp. Mar. Biol. Ecol.*, Vol. 13, pp. 229–262.

BAYNE, B. L., 1973. Aspects of the metabolism of *Mytilus edulis* during starvation. *Neth. J. Sea Res.*, Vol. 7, pp. 399–410.

BAYNE, B. L., C. J. BAYNE, T. C. CAREFOOT & R. J. THOMPSON, 1976. The physiological ecology of *Mytilus californianus* Conrad. I. Metabolism and energy balance. *Oecologia (Berlin)*, Vol. 22, pp. 211–228.

BAYNE, B. L. & C. SCULLARD, 1977. Rates of nitrogen excretion by species of *Mytilus* (Bivalvia: Mollusca). *J. Mar. Biol. Assoc. U.K.*, Vol. 57, pp. 355–369.

DEGOBBIS, P., 1973. On the storage of seawater samples for ammonia determination. *Limnol. Oceanogr.*, Vol. 18, pp. 146–150.

DE VOOYS, C. G. N. & A. DE ZWAAN, 1978. The rate of oxygen consumption and ammonia excretion by *Mytilus edulis* after various periods of exposure to air. *Comp. Biochem. Physiol.*, Vol. 60A, pp. 343–347.

EPPLEY, R. W., E. H. RENGER, W. G. HARRISON & J. J. CULLEN, 1979. Ammonium distribution in Southern California coastal waters and its role in the growth of phytoplankton. *Limnol. Oceanogr.*, Vol. 24, pp. 495–509.

HAMMEN, C. S., 1968. Aminotransferase activities and amino acid excretion of bivalve molluscs and brachiopods. *Comp. Biochem. Physiol.*, Vol. 26A, pp. 697–705.

HAMMEN, C.S., H.F. MILLER & W.H. GEER, 1966. Nitrogen excretion of *Crassostrea virginica*. *Comp. Biochem. Physiol.*, Vol. 17A, pp. 1199–1200.

JORDAN, T.E. & F. VALIELA, 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen-flow in a New England salt marsh. *Limnol. Oceanogr.*, Vol. 27, pp. 75–90.

KANTSKY, N. & J. WALLENTINUS, 1980. Nutrient release from a Baltic *Mytilus* red algal community and its rôle in benthic and pelagic productivity. *Ophelia*, Suppl. 1, pp. 17–30.

LEWIN, J., T. HRUBY & D. MACKAS, 1975. Blooms of surf zone diatoms along the coast of the Olympic Peninsula, Washington. *Estuarine Coastal Mar. Sci.*, Vol. 3, pp. 229–241.

LEWIN, J., J.E. ECKMAN & J.N. WARE, 1979. Blooms of surf zone diatoms along the coast of the Olympic Peninsula, Washington. XI. Regeneration of ammonium in the surf environment by the Pacific Razor clam, *Siliqua patula*. *Mar. Biol.*, Vol. 52, pp. 1–9.

LUM, S. & C.S. HAMMEN, 1964. Ammonia excretion of *Lingula*. *Comp. Biochem. Physiol.*, Vol. 12A, pp. 185–190.

MCLACHLAN, A., 1977. Composition, distribution, abundance and biomass of the macrofauna and meiofauna of four sandy beaches. *Zool. Afr.*, Vol. 12, pp. 279–306.

MCLACHLAN, A., 1982. A model for the estimation of water filtration and nutrient regeneration by exposed sandy beaches. *Mar. Environ. Res.*, Vol. 6, pp. 37–47.

MCLACHLAN, A. & N. HANEKOM, 1979. Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of *Donax serra* in the Eastern Cape. *S. Afr. J. Zool.*, Vol. 14, pp. 183–193.

MCLACHLAN, A. & J. LEWIN, 1981. Observations on surf phytoplankton blooms along the coast of South Africa. *Bot. Mar.*, Vol. 24, pp. 553–557.

MCLACHLAN, A., A.H. DYE & P. VAN DER RYST, 1979. Vertical gradients in the fauna and oxidation of two exposed beaches. *S. Afr. J. Zool.*, Vol. 14, pp. 43–47.

MCLACHLAN, A., T. ERASMUS, A.H. DYE, T. WOOLDRIGE, G. VAN DER HORST, G. ROSSOUW, T.A. LASIAK & L. MCGWYNNE, 1981. Sand beach energetics; an ecosystem approach towards an energy interface. *Estuarine Coastal Shelf Sci.*, Vol. 13, pp. 11–25.

STRICKLAND, J.D.H. & T.R. PARSONS, 1972. A practical handbook of sea water analysis. *Bull. Fish. Res. Board Can.*, No. 167, 311 pp.