Mar. Behav. Physiol. 1973, Vol. 2, pp. 21–32
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Printed in Great Britain

The Energy Cost of Migration of the Bivalve *Donax* on Tropical Sandy Beaches

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(*Received January* 12, 1973)

1. The energy cost involved in tidal migration on tropical sandy beaches by the bivalves *Donax incarnatus* Gmelin and *D. denticulatus* L. is estimated from observations and recordings of the burrowing movements involved.

2. The maintenance of position between migratory movements requires expenditure of more energy than does emergence and re-burial during migration. Together these two components of activity require in an animal of 2 cm shell length, 6 cal/day for *D. denticulatus* and 6.6 cal/day for *D. incarnatus*.

3. In *D. incarnatus* the daily oxygen consumption of an animal of this size is 0.25 mg O_2/animal which is equivalent to a maintenance requirement of 20.4 cal/day, so that migration may add about one-third to the daily maintenance requirement.

4. For the mole crab, *Emerita holthuisi* Sankolli from the same beach as *D. incarnatus*, comparable figures for the energy requirements of migration and maintenance are 1.14 cal/day and 27.2 cal/day.

INTRODUCTION

Many members of the genus *Donax*, which occur as dominant members of the macrofauna on tropical and sub-tropical sandy beaches, exhibit a characteristic tidal migratory cycle in which the incoming surf is used to carry the animal up the beach during the flood tide and conversely the backwash during the ebb

for movement down the beach. This behaviour is essentially the same in all those species of *Donax* which have so far been observed (Mori, 1938; 1950; Turner and Belding, 1957; Wade, 1967; Ansell and Trevallion, 1969) and largely depends on the co-ordination of the responses of rapid burrowing with the ability to emerge actively from the sand. The processes of burrowing into and emergence from sand are normally characteristic of all sand dwelling bivalves. Progress in the required direction results from responses to the changing physical conditions prevailing at different locations on the beach relative to the surf zone. These responses, and the movements involved in burrowing and emergence from the sand have recently been described in detail for two species, *D. incarnatus* Gmelin from Indian beaches (Ansell and Trevallion, 1969) and *D. denticulatus* L. from West Indian beaches (Trueman, 1971).

The significance of tidal migration in the life of these species can only be conjectured. Migration retains the animal within a narrowly defined zone of the beach but unlike the static zones occupied by many temperate species, migratory species exhibit a dynamic zonation defined by the moving tide line. The animal is thus subjected to more constant conditions, since it is not subject for example, to alternating periods of exposure to air and sublittoral submergence. Advantages of this ability to maintain position relative to the tide line may include, (1) that within this zone organic material suspended in water may be expected to be maximal, hence presenting the animal with maximal food; and (2) the disturbed wash zone may provide some protection from predation from three groups of predators which are important in the ecology of tropical beaches, namely decapod crustaceans such as *Ocypode* which move down onto the beach exposed at low tide, other sublittoral decapods which move inshore to feed in areas covered by the tide, and wading birds. Against these possible advantages may be set the disturbance to feeding associated with wave action in this zone which is, however, offset by the extremely rapid responses exhibited by tropical *Donax* sp. which are able to re-establish feeding activity immediately after a disturbance (Ansell and Trevallion, 1969) and the energy cost of the locomotory movements involved in maintaining migration. This paper is an attempt to assess the magnitude of the energy cost to the animal of maintaining migration.

MATERIALS AND METHODS

The calculations of energy cost, which are necessarily somewhat empiric, are based on observations on the burrowing activity of *D. denticulatus* from Jamaica and *D. incarnatus* from S. India made in the laboratory and on the beach, and from recordings of the burrowing movements of these two species made either at the marine laboratory of the University of the West Indies at

Port Royal Jamaica, or at the Biological Oceanography Division of the National Institute of Oceanography, Cochin, S. India. *D. denticulatus* were collected from sandy beaches including Green Bay at Port Henderson in Kingston Harbour, Jamaica (Trueman, 1971) and *D. incarnatus* from a sandy beach at Shertallai, S. India (Ansell and Trevallion, 1969; Trevallion *et al.*, 1971). The techniques of recording the activity during burrowing have been described by Trueman (1971) and Ansell and Trevallion (1969).

OBSERVATIONS

The beach environment

The beach at Green Bay on which *D. denticulatus* migrates has been described by Wade (1967). It has a slope of 1 in 10 and the tidal range is little more than 0.5 m so that the intertidal zone is narrow. Wade recognized three zones, namely the surf zone with turbulent water, the wash zone, and the spray zone above the area covered by the uprush of waves (Figure 1). In the wash zone waves run up the slope as a fairly smooth film of water saturating the sand.

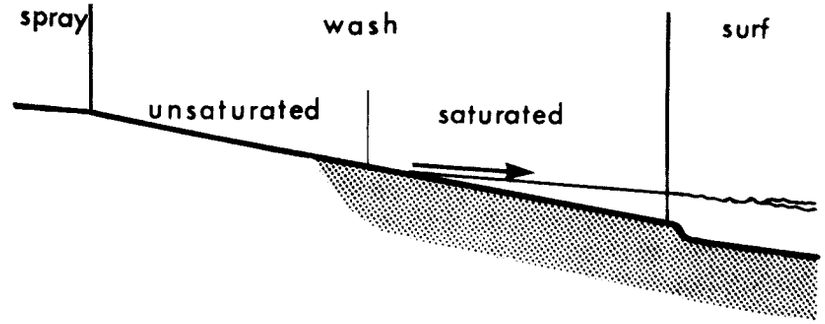

FIGURE 1 Profile of a sandy tropical beach with spray, wash and surf zones indicated, water runs down (arrow) the wash zone leaving unsaturated sand above and a saturated zone below: the saturated area (stippled) follows the receding wave.

The upper part, termed the unsaturated zone, is completely drained between uprushes while in the lower saturated zone drainage is not complete between waves. This stable characteristic pattern moves up and down the beach with the tide and provides the important physical conditions controlling the

migratory activity of *Donax* (Trueman, 1971) as well as that of other migratory macrofauna such as the mole crab *Emerita* (Cubit, 1969; Trueman, 1970). The distance travelled during each flood tide by a *D. denticulatus* may be estimated at about 5 m.

The beach at Shertallai from which *D. incarnatus* was collected was described by Trevallion *et al.* (1970). The beach has a much shallower slope than that at Green Bay, so that although the maximum tidal range was 0.9 m the intertidal zone was much wider, approaching 40 m at its maximum. The dynamic zonation of Green Bay also exists at Shertalli at all states of the tide, and the changing physical conditions act in a lesser manner to control migration of two species of *Donax*, namely *D. incarnatus* and *D. spiculum*, as well as of a mole crab *Emerita holthuisi* Sankolli and a gastropod *Bullia melanoides* (Deshayes). The maximum distance travelled during each flood tide by *D. incarnatus* may be considered to be approximately 40 m.

The movements included in migration

Migratory cycles are made by *Donax* by a repeated series of locomotory events each of which we may refer to as a migratory movement (Figure 2). During each shoreward migration the bivalve actively emerges from the sand into the incoming wave with the shell gaping and the foot and siphons fully extended. In this condition the animal is lifted by the wave and carried shorewards. As the force of the wave is expended the bivalve drops onto the sand surface and the new position is secured by the animal burrowing into the sand by the normal bivalve sequence of digging cycles each of which comprises a burrowing period. All these events make up a single migratory movement. At both Green Bay and Shertallai wave frequency is approximately one per 7 seconds and the time interval between the settlement of the transported *Donax* on the sand and the arrival of the next wave is sufficient to allow burial, but only in one specific zone of the beach (Trueman, 1971).

On the falling tide the bivalve emerges from the sand into the backwash, is carried down the beach until dropped as the force of the backwash is expended, and again maintains the new position by rapid burrowing. On the rising tide, emergence occurs as a response to the increasing fluidity and instability of the sand-water mixture as the buried *Donax* are overtaken by the surf zone. On the falling tide, buried *Donax* are overtaken by conditions in the unsaturated zone and emergence here is a response to immersion after drying of the sand. Following emergence, movement is caused by the water currents and is a process over which the bivalve has little control although the use of the foot and siphons as fins and/or brakes has been suggested. The limits on the beach within which *Donax* will burrow are set by the duration of saturation and the wave frequency. *Donax* cannot burrow into unsaturated sand and are

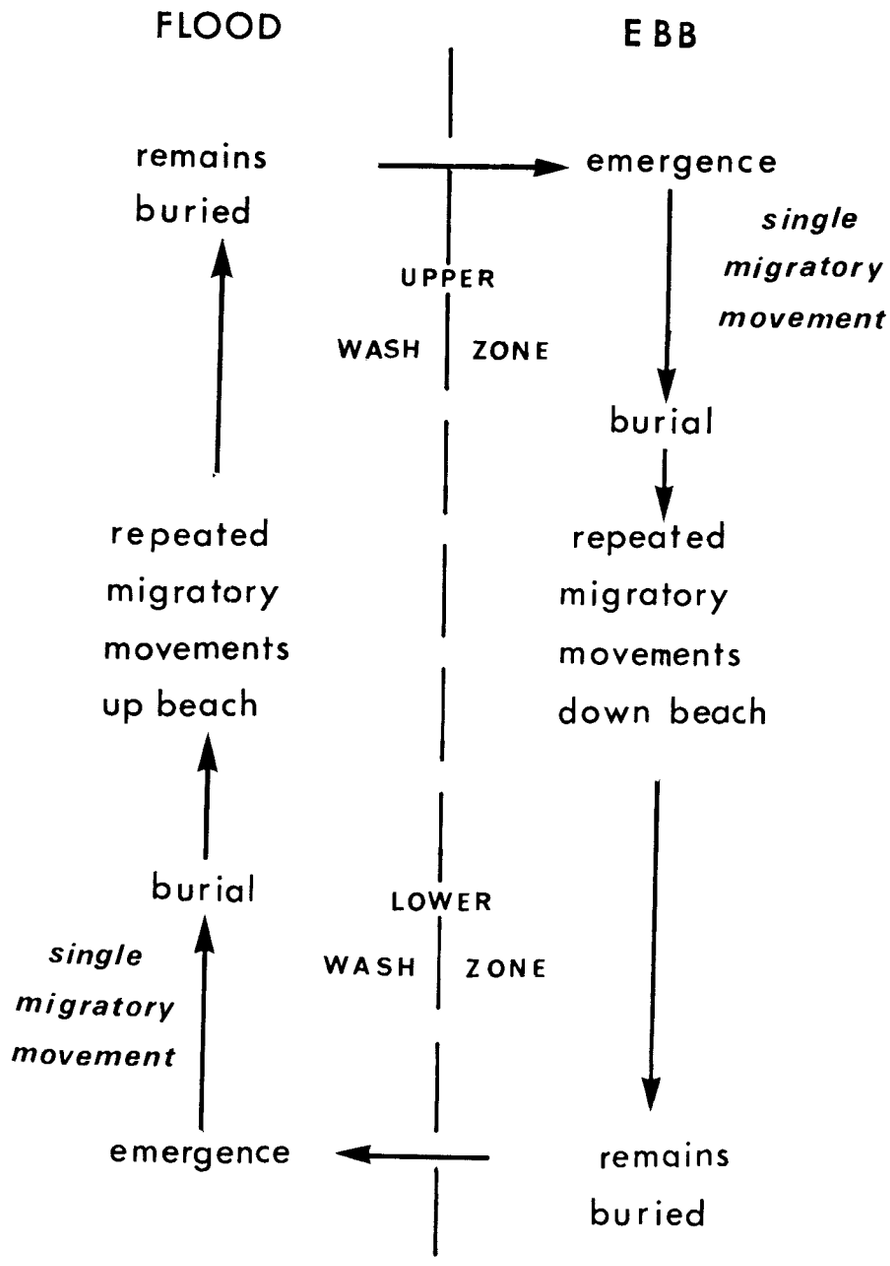

FIGURE 2 Diagram of the principal events of a migratory cycle: broken line represents the change from flood to ebb conditions.

secure against the drag of the waves only when some two-thirds of the shell is buried. Thus, at each stage of the tidal cycle, the limit of the zone in which burial occurs is set by wave frequency, slope of the wash zone, and speed of burrowing. A wave frequency of one per 7–8 seconds appears to be a characteristic feature of surf-washed beaches, and the stability of the environment in this respect together with high-water temperatures allowing the development of uniquely rapid burrowing movements must have been an important contributing factor in the evolution of the habit of tidal migration in the Donacidae. On steeply sloping beaches such as Green Bay, a period of no more than 4 seconds is available for reburial on the beach, and *D. denticulatus* shows a speed of burial in keeping with this. On the more shallow beaches at Shertallei, a slightly greater time is available and the burrowing period of *D. incarnatus* occupies a slightly longer time than that of *D. denticulatus*.

For each individual therefore, a migratory cycle involves a series of migratory movements probably at somewhat irregular intervals through the tidal cycle. Each migratory movement on the rising tide, will carry the individual from a point near the surf zone to a point in the saturated area of the wash zone, or on the ebb tide from a point in the unsaturated area of the wash zone to a point in the lower saturated zone. We may assume that the horizontal distance travelled on ebb and flood tides is approximately the same so that the number of migrations occurring will also be approximately the same, and equal in number to the horizontal extent of the intertidal zone divided by the average horizontal distance travelled during each migratory movement. Each involves expenditure of energy principally in emergence and reburial, since movement up or down the beach is effected by waves and does not require locomotory activity by the bivalve.

When buried in the wash zone *Donax* is subjected to the disturbance of each breaking wave, involving erosion and deposition of sand and it is necessary for the animal to maintain its position by burrowing relative to the surface of the sand in the intervals between waves in order to feed in the backwash, with a further expenditure of energy.

The movements of burrowing

In common with other bivalves, *D. denticulatus* and *D. incarnatus* burrow by means of a series of repeated movements, digging cycles, which together constitute a burrowing period (Trueman and Ansell, 1969) (Figure 3a). Each step represents the part of the digging cycle when contraction of the pedal retractor muscles pulls the shell into the sand. Between the steps extension of the foot takes place by means of cycles of probing. From records of this type the time for complete burial may be estimated. Some characteristics of the burrowing cycle of the two species are given in Table I.

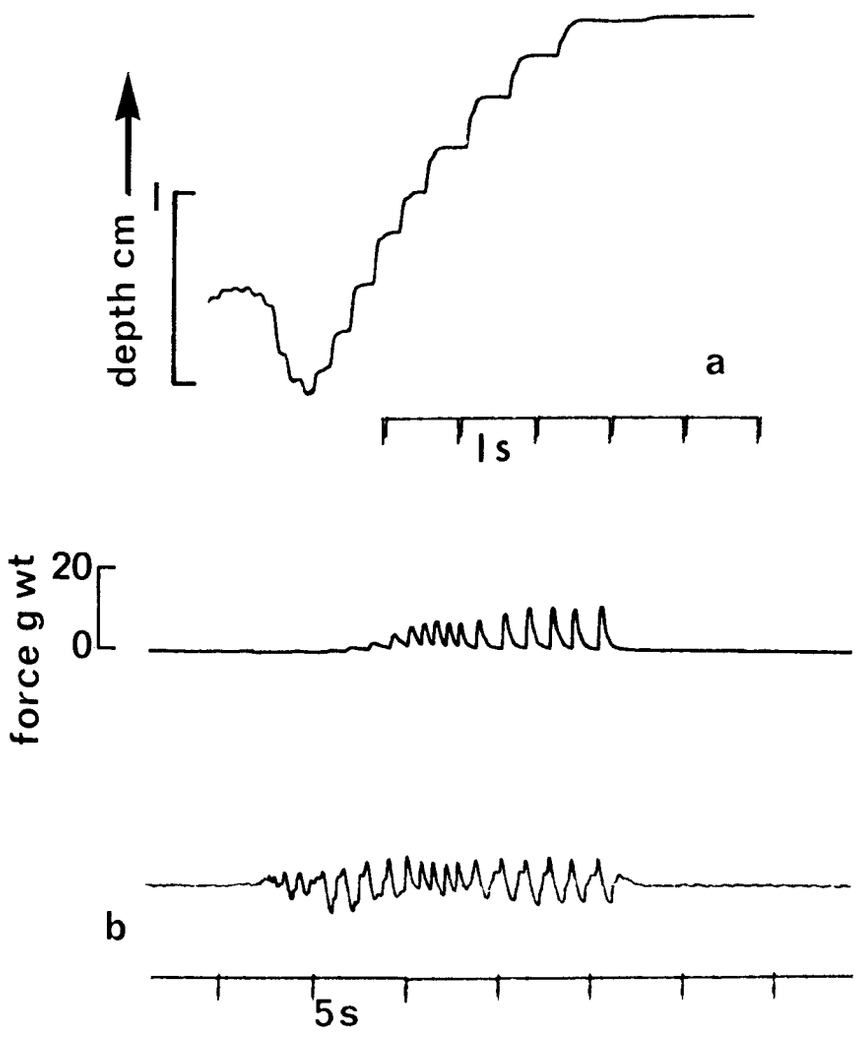

FIGURE 3 Recordings from the digging period of *Donax* (a) using movement and (b) force transducers. a, shows complete burrow period of *D. denticulatus*, each step representing a digging cycle; and b, extract from a series of digging cycles of *D. incarnatus* when restrained by a thread attached to a force transducer showing a maximum force development in pedal retraction. The lower trace is a record of the pressure in the sand adjacent to the animal to show the full duration of the group of digging cycles, which take place more slowly than in unrestrained animals.

The cost of tidal migration

The elements involved in estimating the energy expended over 24 hours in the movements involved in life in the wash zone may now be summarized. They include, (1) emergence from the sand for each migration; (2) complete burial at the termination of each migration; and (3) burrowing in response to each wave while maintaining station in the wash zone.

TABLE I

Summary of the factors involved in the estimation of the energy cost of migration in *D. denticulatus*, *D. incarnatus* and the mole crab *E. holthuisi*.

	Green Bay *D. denticulatus*	Shertallai *D. incarnatus*	Shertallai *E. holthuisi*
Intertidal width of beach (m)	5	40	40
Tidal height (m)	0.5	0.9	0.9
Approx. distance travelled each migratory movement (m)	1	4	4
No. migratory movements/day	20	40	40
Wave frequency	1/7 sec	1/7 sec	1/7 sec
Digging cycles/day (1 cycle/wave)	12350	12350	12350
Burrowing speed (cm/sec)	0.5	0.3	1
Force when restrained (D g wt)	10	12	2
Power required (DU) J sec -1)	5×10^{-4}	3.6×10^{-4}	2×10^{-4}
Time to complete burial (sec)	4	6	1.5
Total energy requirement for burial (J)	2×10^{-3}	2.2×10^{-3}	3×10^{-4}
Energy requirement for burial (cal)	0.48×10^{-3}	0.52×10^{-3}	0.72×10^{-4}
No. burrowing cycles involved	5	5	8
Energy/cycle (cal)	0.096×10^{-3}	0.104×10^{-3}	0.09×10^{-4}
Assumed efficiency	0.2	0.2	0.2
Energy/day migration (cal)	9.6×10^{-2}	20.8×10^{-2}	2.88×10^{-2}
Energy/day maintaining position (cal)	5.9	6.4	1.11
Total energy used in movement/day (cal)	6	6.6	1.14
Maintenance requirement (from O_2 consumption) (cal)	—	20.4	27.2

The power required for movement of an animal may be expressed as the drag multiplied by velocity (DU) (Alexander, 1968), and has previously been determined for the burrowing of the mole crab *Emerita* (Trueman, 1970). Drag cannot be measured directly, but the maximum force exerted by a burrowing animal whilst restrained by a thread attached to a force transducer may be determined (Figure 3b). This is the maximum locomotory force that the animal can exert during burrowing and must normally overcome drag forces: this force may be assumed to represent a maximal value of drag. *D. denticulatus* of 2 cm shell length developed a maximum force of 10 g wt and for the purpose of these calculations this is taken to represent drag. For a bivalve of this length the mean velocity of burrowing was 0.5 cm/sec and the power required accordingly 5×10^{-4} J/sec (= watts). In *D. denticulatus* complete burial takes 4 seconds with a total energy requirement of 2×10^{-3} J equivalent to 0.48×10^{-3} cals. Since 5 digging cycles are normally involved for complete burial we may estimate the energy requirement of a single cycle as 0.096×10^{-3} cal.

For *D. denticulatus* the individual animal migrating up and down the beach over one tidal cycle moves approximately 10 m. From observations on the beach an average distance of 1 m for each migration seems a reasonable estimate, so that 10 complete burials would be involved in each tidal cycle, i.e. moving both up and down the beach. Emergence from the sand takes place at approximately the same velocity as burial and the drag may be assumed to be similar so that we may estimate the total energy requirement involved for migration over one tidal cycle as $0.48 \times 10^{-3} \times 10 \times 2 = 9.6 \times 10^{-3}$ cal, or approximately 19.2×10^{-3} cal/day assuming two tides a day, which is not always the case in Jamaica. For *D. incarnatus* of 2 cm shell length the maximum force recorded during burrowing was 12 g wt. The mean velocity of burrowing was 0.3 cm/sec and the power required therefore 3.6×10^{-4} J/sec (= watts). Complete burial took 6 seconds with a total energy requirement of 2.2×10^{-3} J or 0.52×10^{-3} cal. Since 5 digging cycles again were required for complete burial the energy requirement of a single cycle may be estimated as 0.104×10^{-3} cal.

In migrating up shore the individual *D. incarnatus* moves approximately 40 m. However, on the shallower beach the average distance travelled during each migratory movement is greater, say 4 m, so that about 20 complete burials would be involved in each tidal cycle. In this species, therefore, we may estimate the total energy requirement involved for migration over one tidal cycle as $2 \times 20 \times 0.52 \times 10^{-3} = 20.8 \times 10^{-3}$ cal, or approximately 41.6×10^{-3} cal/day, again assuming two tides a day, which is also not always the case at Shertallai where the tides are of mixed type.

For the periods between migration we may estimate the energy expenditure for maintaining position relative to the sand surface if we assume an average response to each wave produces 1 cycle of digging movements and that the waves occur at 7 second intervals. The total energy expenditure for *D. denticulatus* is then

$$24 \times 3600/7 \times 0.096 \times 10^{-3} = 1.18 \text{ cal/day}$$

and for *D. incarnatus*,

$$24 \times 3600/7 \times 0.104 \times 10^{-3} = 1.28 \text{ cal/day}.$$

These estimates take no account, however, of the efficiency of propulsion of the animal in the sand (Trueman, 1970). Since this efficiency (i.e. the energy used to overcome drag/total energy used in locomotion) is by analogy with *Emerita* likely to be about 0.2, we may revise the estimates accordingly (Table I beneath entry for assumed efficiency). The total energy used in all movements

in the wash zone over 24 hours is then 6 cals/day for *D. denticulatus* and 6.6 cal/day for *D. incarnatus*.

DISCUSSION

The migratory habit of the species of *Donax* which inhabit the wash zone of tropical beaches involves additional energy expenditure when compared with other species living in more static conditions. This energy consists of two components, (a) movement in or out of the sand to perform a migration; and (b) repeated burrowing movements necessary for maintenance of position in response to erosion and deposition of sand by wave action. It is clear from Table I that the latter represents by far the greatest part of the additional energy required.

Dr. Ann Trevallion and one of us (A.D.A.) (unpubl.) have measured the oxygen consumption of *D. incarnatus* at 29–30°C (the temperature of the surf for much of the year) and it is interesting to compare the energy requirement for maintenance estimated from the oxygen consumption with that derived here for migration. The measurements were made using adult *D. incarnatus* suspended by a thread attached to the shell in seawater which was stirred by a magnetic stirrer. Depletion of oxygen in the water, the surface of which was sealed with a thick layer of liquid paraffin, was measured using an oxygen electrode. For an animal of 2 cm body length (dry tissue weight c 100 mg) the oxygen consumption is 0.25 mg oxygen/animal/h. This is equivalent to 20.4 cal/day, assuming a calorific equivalent of 3.4 cal/mg (Winberg, 1971). The animals suspended in water in the experimental vessels extended the siphons and foot and were clearly producing feeding currents throughout the period of observation; from time to time series of probing movements of the foot were seen, but these did not lead to the full movements of the burrowing cycle, probably because in this situation the stimulus for completion of the burrowing cycle, i.e. contact with sand (Trueman, 1971), is missing. Nonetheless, these movements, although in no way equivalent in frequency to those we have taken as present during migration on the beach, must have contributed to the observed consumption of oxygen. If the assumptions we have made in the calculations concerning the energetics of migration are correct, then activity on a surf-washed beach may add about one-third to the daily maintenance requirement of the species. Unfortunately we have no comparable data for the oxygen requirements of *D. denticulatus* nor any other tropical species, but for the European species *D. vittatus* (da Costa) Ansell (in preparation), has measured the oxygen consumption at different temperatures. A 20°C an individual of this species has an oxygen consumption of c 0.12 mg O_2/animal/h, that is, approximately half that of *D. incarnatus*. This suggests

that there is in this group no temperature compensation as between tropical and temperate species and it is probable that *D. denticulatus* shows a similar maintenance requirement to that of *D. incarnatus*.

Similar calculations to those for *Donax* may be made for the mole crab *Emerita portoricensis* Schmidt for which Trueman (1971) has shown that the power requirement for burrowing is 2×10^{-4} J/sec. Since only 1.5 seconds are needed for complete burial in this species the energy requirement would be 3×10^{-4} J, or 0.72×10^{-4} cal. If we assume a similar figure applies to *Emerita holthuisi*, and allowing an efficiency factor of 0.2, this species would have an estimated total energy requirement of 2.88×10^{-2} cal/day for burrowing and emerging during each migratory movement, and 1.11 cals/day for maintaining position assuming an average of two burrowing cycles in response to each wave (orientation of the body in *Emerita* is more critical than in *Donax* since the plumose antennae must be extended accurately in the backwash of the wave to collect food, Efford, 1966). This gives an estimate of 1.14 cals/day for the energy requirement for migratory and burrowing movement (Table I).

Measurements of the oxygen consumption for *E. holthuisi* made by Dr. Ann Trevallion and one of us (A.D.A.) suggest a daily maintenance requirement for an animal of similar size of 8 mg O_2/animal, equivalent to 27.2 cal/day. In this case therefore the proportion of the total maintenance energy requirement used in migration would appear to be much lower than in *Donax*.

These estimates of the energy requirement of *Donax* in the wash zone of tropical beaches are only approximate but it is clear that migration uses little energy. In this environment *Donax* exhibits adaptations of the behavioural responses of burrowing common to most infaunal bivalves, to respond to different physical conditions and so can migrate. This considerably prolongs the time when *Donax* is able to feed and on this basis migration must be economical: however, irrespective of migration, survival in the wash zone adds a considerable energy requirement, but with adaptions of behaviour and feeding mechanisms *Donax* is outstandingly successful since the very instability of the environment tends towards the exclusion of competitors.

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