



ELSEVIER

Journal of Experimental Marine Biology and Ecology,  
201 (1996) 23–35

**JOURNAL OF  
EXPERIMENTAL  
MARINE BIOLOGY  
AND ECOLOGY**

## Spatial and temporal factors affecting sediment turnover by the lugworm *Arenicola marina* (L.)

A.S.W. Retraubun, M. Dawson, S.M. Evans\*

*Department of Marine Sciences and Coastal Management, University of Newcastle upon Tyne, Newcastle upon Tyne, NE1 7RU, UK*

Received 29 March 1995; revised 21 December 1995; accepted 31 January 1996

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### Abstract

There were substantial differences in the amounts of sediment reworked by *Arenicola marina* (lugworms) on different parts of the shore and at different times of the year. The amounts were affected by the density, distribution and movement of worms. Rates of cast production were also important, and they were affected by the nature of the substrate and temperature. The production of casts occurred at regular intervals during periods of high activity.

*Keywords:* Bioturbation; Sediment turnover; Lugworm; *Arenicola marina*

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### 1. Introduction

The lugworm *Arenicola marina* (L.) is a dominant member of the macrobenthos of tidal flats throughout much of its geographic range. Beukema (1976) found that its biomass was higher than that of all other worm species together, accounting for 20% of the total mass of the macrobenthos, in flats of the Dutch Wadden Sea. Worms inhabit characteristically U-shaped burrows and have a substantial impact on sediment by reworking it. Sediment is ingested at the base of the headshaft of the burrow and is deposited as faecal casts on the surface, adjacent to the exit of the tailshaft. Cadée (1976) estimated that *A. marina* at a density of 85 worms per m<sup>2</sup> reworked 400 cm<sup>3</sup> of sediment per annum, equivalent to a layer 40 cm deep. Lugworms also oxygenate sediments by irrigating their burrows in a posterior-anterior direction. Maximum pumping rates were 40 cm<sup>3</sup> of water through the burrow per hour (Baumfalk, 1979).

Not surprisingly, lugworms have a substantial impact on the substrate. Bioturbation by

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\*Corresponding author.

*A. marina* destabilises the sediment, and has negative effects on the abundance of the crustacean *Corophium volutator* (Flach, 1992) and several other macrobenthic species (e.g., Wilson, 1981, Woodin, 1985, Brey, 1991). Sediment turnover is however much lower in winter than in summer (Cadée, 1976) and is also likely to be affected by factors such as changes in the distribution, density and spacing of lugworms on the shore. In the present study, estimates have been made of the amount of sediment turned-over by lugworms at different levels on the shore, at different times of year.

The behaviour of *A. marina* is also of ethological interest. Wells (1950) showed that lugworms kept under constant conditions in the laboratory were spontaneously active. Patterns of irrigation–defecation behaviour (i–d cycles) often occurred at regular intervals of about 40 minutes, for periods of several hours. In performing this behaviour, the worm would crawl backward up the tailshaft of its burrow to defecate, and then undertake a spell of vigorous headward irrigation as it crept back to the horizontal gallery of its burrow. The cycles were driven by pacemaker systems located in the ventral nerve cord. Similarly, patterns of feeding activity were driven by a pacemaker system in the plexus of nerve tissue around the oesophagus. These cycles could be modified by changes in external events, such as the sudden non-availability of oxygenated water. Under these conditions, the cycles continued with the same timing as before, but the intensity and duration of acts changed. These findings are important because they demonstrate that the worms' behaviour is not organised simply as a series of reflex responses. Whole patterns of behaviour can be generated internally and then modified in response to changes in sensory input (Evans, 1970). However, the experimental set-up of Wells (1950) was artificial, and the behaviour he described has not been observed in worms living under natural conditions. There are obvious difficulties in observing the behaviour of burrowing animals but the problem has been overcome in part by recording the deposition of faecal casts in the field. This is part of the i–d cycle and can be recorded without disrupting the animal's normal activities.

## 2. Methods

The study was carried out from 1992 to 1994 inclusive. Field studies were made on a population of *A. marina* inhabiting the shore at Whitley Bay (Tyne and Wear, UK) which is an exposed, medium energy shore. It suffered a severe decline in numbers during the winter of 1992/93 (see below) and was virtually eliminated during the following winter. Worms used in laboratory studies were also collected from this site.

### 2.1. The distribution, density and spacing of *A. marina* on the shore

Five transects were made from about high water of spring tides (the base of the cliffs at the Whitley Bay study site) to approximately low water of spring tides. Quadrat frames, measuring 0.5 m<sup>2</sup> were placed at 10 m intervals along transects and the number of lugworm casts was counted in each of them. The diameters of casts (one per worm) were measured with Vernier callipers. The measurements were repeated in summer (August 1992), autumn (November 1992), winter (February 1993) and spring (May

1993). The relationship between the sizes of casts and the sizes of worms producing them was investigated in August 1992. The diameters of casts of 39 lugworms, which were relatively isolated from other worms were measured before the worms were dug out of the sediment. They were then taken back to the laboratory and weighed (fresh weight).

The distribution of worms on the shore line (i.e., the tendency for them to be spaced evenly, randomly or aggregated) was investigated by recording the position of all casts in 13 0.5-m<sup>2</sup> quadrats in August 1992. The quadrats were at mid-tide level. Nearest neighbour distances were measured, and data were subjected to Nearest Neighbour Analysis (Clark and Evans, 1954). The statistic  $R$  is calculated from it. A value of 1 indicates random distribution,  $< 1$  aggregated distribution, and  $> 1$  even spacing.

Local movements of lugworms (i.e., as indicated by changes in the positions of their faecal mounds) were investigated by recording the positions of faecal casts in five 1-m<sup>2</sup> quadrats, where there were low densities of worms, during low tide at daily intervals for 10 consecutive days. This was done in August 1992. It was assumed that, when there were no casts within 1 cm of a previously marked position for three consecutive days, the lugworm had moved. Its new position was assumed to be the nearest mound of faecal casts which could not be accounted for. The distances between the positions were measured. Worms which moved out of the quadrat during the study period were discounted. Additional measurements were made of worms ( $n = 13$ ) kept individually in plastic aquaria, measuring  $37 \times 30 \times 21$  (high) cm in the laboratory. These contained sediment from the shore to a depth of 18 cm. This was covered by seawater about 2 cm deep. The positions of faecal mounds were recorded at daily intervals for 8 days, and measurements made of distances moved (as above).

## 2.2. Activity patterns

In order to record cast production over periods of several hours in the field, the positions of the exits of tailshafts of burrows were marked by pushing numbered sticks, approximately 10 cm in length, into the adjacent sediment. The mounds of casts were then smoothed over with the index finger. Marked burrows were visited at intervals of 15 min and the recurrence of fresh casts recorded. If a cast had been produced, the surface was smoothed again. Rates of cast production were measured during low tide in groups of worms whose burrows were in sediment which dried out, and those whose burrows were submerged in tidal pools. Recordings were made for periods of 2 h immediately following exposure of the substrate by the outgoing tide. This was done at four times of the year: summer (August 1992), autumn (November 1992), winter (February 1993) and spring (May 1993). The number of worms in groups are shown in Table 1 below. In addition, rates of cast production were recorded in two groups of worms ( $n = 25$  in both cases) throughout the period of low water, and then for 1 h after burrows had been re-submerged by the incoming tide. This was done on a calm day in June 1992 when casts were not destroyed by waves, and they could be seen even when covered by 20 cm or so of water. The timing of cast production was investigated by recording continuously for a period of 6 h from a group of 20 worms, whose burrows were submerged in tidal pools relatively high up the shore. This was for the maximum

Table 1

Defecation rate (mean number of casts produced  $\pm$  standard error  $\text{h}^{-1}$ ) of worms inhabiting sediment which dried out during the period of low water, and of worms which were submerged in tidal pools at low water

Time of year	Dry sediment			Pools		
	Temperature ( $^{\circ}\text{C}$ )	<i>n</i>	Defecation rate	Temperature ( $^{\circ}\text{C}$ )	<i>n</i>	Defecation rate
Summer 1992	13.9 $\pm$ 0.2	106	0.2 $\pm$ 0.1	15.0 $\pm$ 0.1	107	0.6 $\pm$ 0.2
Autumn 1992	7.3 $\pm$ 0.1	38	0	7.5 $\pm$ 0.1	43	0.4 $\pm$ 0.2
Winter 1992	6.0 $\pm$ 0.1	58	0	6.3 $\pm$ 0.2	97	0.2 $\pm$ 0
Spring 1993	9.7 $\pm$ 0.1	132	0.5 $\pm$ 0.2	11.5 $\pm$ 0.4	85	1.3 $\pm$ 0.6

period of exposure during a spring tide in September 1992. Numbers of worms producing different numbers of casts (0, 1, 2, 3, 4, etc.) were compared with those expected if cast deposition was a random process. The latter was calculated from the Poisson distribution.

Cast production was also investigated in the laboratory. Worms were kept individually in plastic buckets, measuring 25 cm in diameter and 22 cm in depth. They were filled with sediment from the worm's habitat to a depth of 20 cm. Seawater covered the surface to a depth of 2 cm above it. After a period of at least four days acclimatization, buckets were transferred to constant temperature rooms. They were left overnight before recordings were made of cast production. The recording procedure was identical to that described above, except that the interval between recordings was 10 min. The rate of cast production was recorded in a group of worms ( $n = 20$ ) kept at 15 $^{\circ}\text{C}$  and observed for three hours. In addition, the effect of temperature on defecation was investigated by recording from worms kept over a range of temperatures. Each individual was observed for a period of two h, and there were 12 of them in each group. Separate groups of worms were subjected to a range of temperatures in summer (August 1992) and winter (January 1993).

The effect of sediment particle size on the rate of cast production was investigated in worms which were kept in plastic buckets (as above) containing: (i) sieved sediment of particles between 500 and 1000  $\mu\text{m}$  diameter ( $n = 7$ ); (ii) sieved sediment of particles < 250  $\mu\text{m}$  in diameter ( $n = 8$ ); and (iii) unsieved sediment ( $n = 8$ ). The sediment in each case had been collected from the worms' natural habitat. The worms were of approximately equal size in each of the groups. They were acclimatised for seven days before recordings were made of cast production during observation sessions lasting for 4 h for each of the next five days. The worms were kept at constant temperature of 14 $^{\circ}\text{C}$  throughout this experiment.

### 2.3. Bioturbation

Estimates were made of the amount of sediment turned over per month by lugworms at different tidal levels on the shore. They are expressed as equivalent to layers of sediment (cm deep). The following information was used (see above) in the calculations: (i) the rate of cast production at different times of the year of worms in tidal pools, and of worms in sediment which dried out during the period of low tide, (ii) the densities

and sizes of worms on different parts of the shore and (iii) the mean volumes of casts produced by worms of different sizes. Volumes were calculated on the assumption that casts were cylinders. It was assumed: (i) that when worms were submerged by seawater at high tide, they produced casts at the same rate as worms in tidal pools during the period of low tide, (ii) that 20% of worms were covered by tidal pools (and therefore continued to be active) when the tide was out and that 80% were in sediment which dried out (and therefore became inactive at this time). Estimates of the lengths of time that different parts of the shore were covered by the tide (or exposed to air) were based on recordings of the position of the tide at hourly intervals throughout one complete cycle of a spring tide and one cycle of a neap tide in August 1992. The mean time each part of the shore was exposed or covered was calculated from these two recordings.

Means are quoted  $\pm$  their standard errors throughout this paper. Unless stated otherwise, the *t*-test has been used to determine levels of significance between means.

### 3. Results

#### 3.1. The distribution, density and spacing of *A. marina* on the shore

*A. marina* casts were distributed from about 40 m below high water spring tides to low water spring tides, with maximum numbers of  $> 200 \text{ m}^{-2}$  at about mid-tide level in summer 1992 (Fig. 1). There was a high correlation between the size of *A. marina* and the diameter of faecal casts produced by them ( $r_s = 0.91$ ;  $P < 0.001$ ), large worms produced larger casts than smaller worms. The range of cast diameters was 1.0–4.5, and 2–11 g. The regression equation was  $\log \text{diameter} = -0.457 + 1.18 \cdot \log \text{weight}$ . It was evident, from the distribution of casts, that individuals high up the shore tended to be smaller than those lower down it (Fig. 1).

There were seasonal differences in the abundance and distribution of *A. marina* on the shore. Densities of casts produced by worms decreased severely during the autumn of 1992. The vertical range occupied by them also decreased during the winter. Lugworm casts were recorded in quadrats at distances of 40 and 50 m from high water in the summer (1992), and were present in the latter (50 m) quadrats at mean densities of more than  $100 \text{ m}^{-2}$ . There were, however, no casts in these quadrats in the winter (1993). The upper shore was recolonised in part in the spring (1993). Casts were recorded at 50 m and, judging from their relatively large diameters, they were produced by small adults from the previous year's population, i.e., they were not juvenile recruits (Fig. 1).

There were considerable differences in the ecological conditions on different parts of the shore inhabited by *A. marina*. Worms at the upper extreme of the range occupied by the species were submerged by the tide for about half of the tidal cycle, whereas those at the lower extreme were permanently submerged by seawater, with the exception of a few hours during low water of spring tides (Fig. 2). Approximately 20% of the shore was covered by tidal pools during the period of low water. These pools were at least semi-permanent in the sense that they were evident from one low tide to the next. However, there is no evidence that populations of worms in areas covered by tidal pools were different from those in dry sand. The density of casts in pools was  $69.7 \pm 10.6 \text{ m}^{-2}$

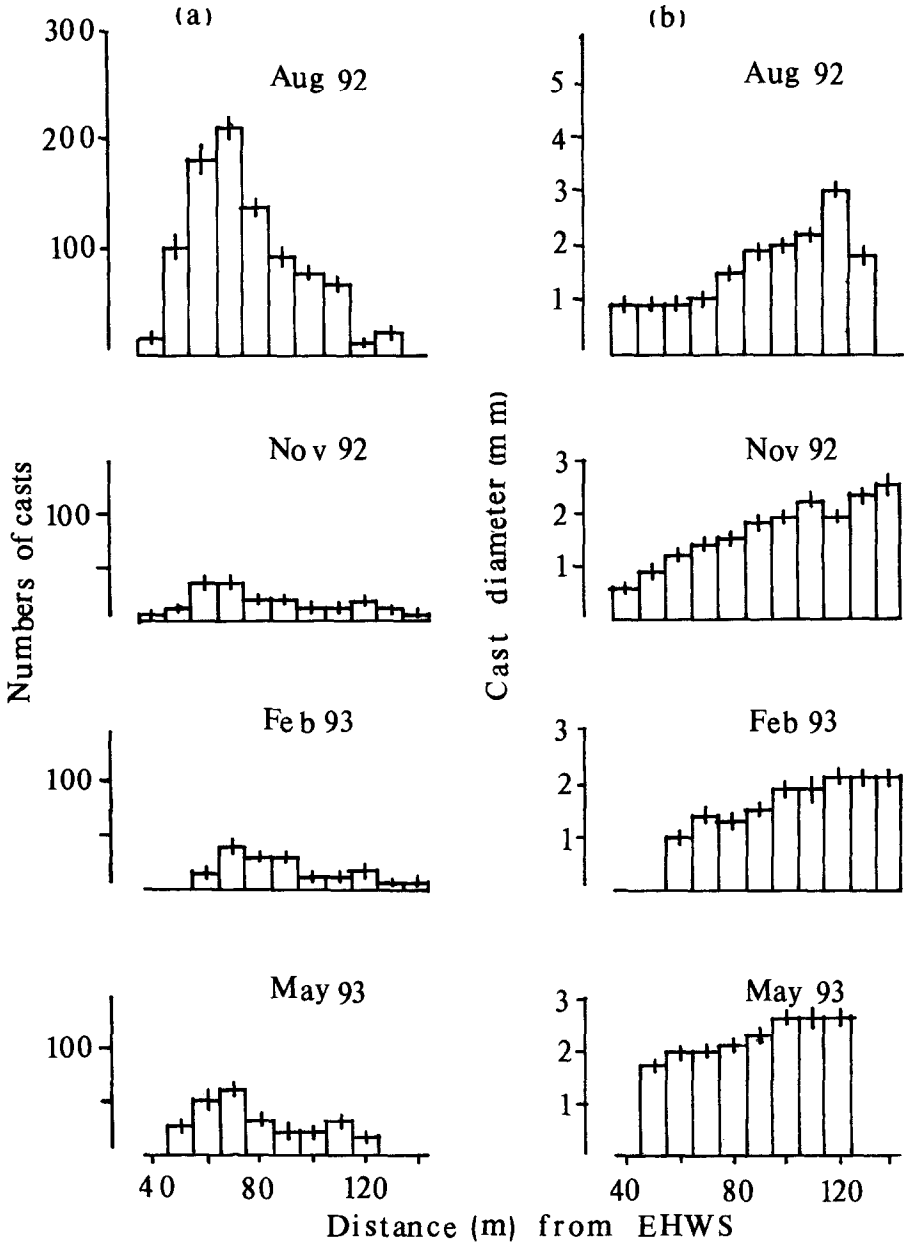


Fig. 1. (a) The distribution of *A. marina* casts in transects down the shore at Whitley Bay, (b) the mean diameters of casts at different tidal levels.

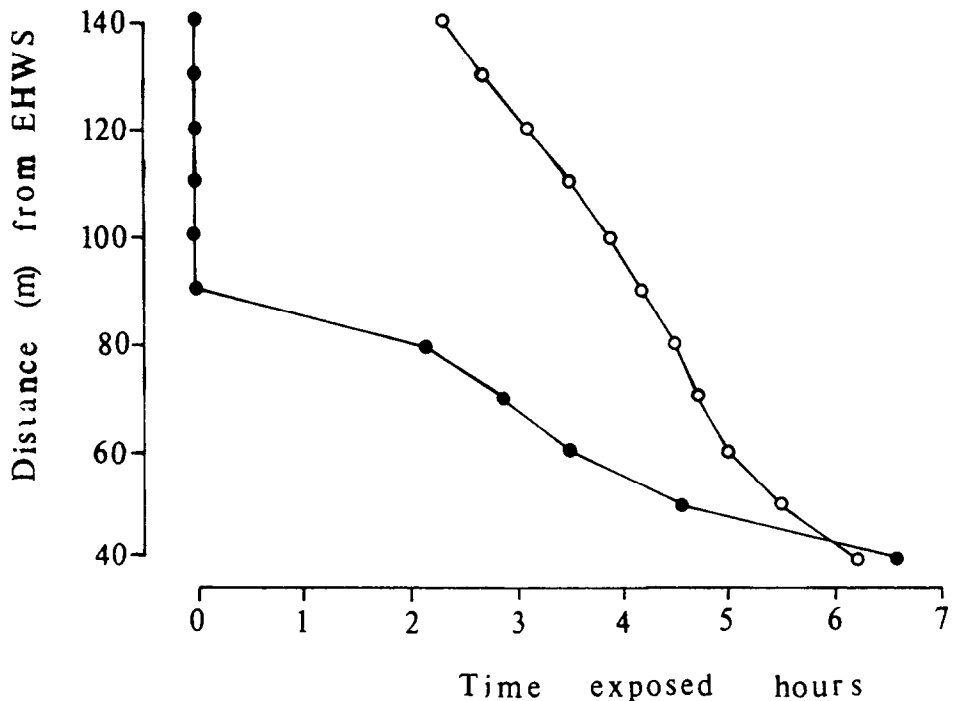


Fig. 2. The length of time that different parts of the shore (indicated by distances from EHWS), inhabited by lugworms, were exposed to air at low tide during a spring (○-○-○) and a neap tide (●-●-●) in August 1992.

compared with  $58.3 \pm 5.2 \text{ m}^{-2}$  in dry substrate (measured in  $1 \text{ m}^2$  quadrats in both cases,  $n = 26$ ,  $P > 0.05$ ). Mean diameters of casts in these two situations were identical:  $0.17 \pm 0.01 \text{ cm}$  ( $n = 10$  in both cases).

Burrows, measured by the positions of faecal casts, were evidently distributed at random. The mean value of  $R$  was  $1.07 \pm 0.004$  (range 0.80 to 1.40) in 13 quadrats each measuring  $1 \text{ m}^2$  (Clark and Evans, 1954). It was not significant in any of them ( $P > 0.05$  in each case). There was often movement of the positions of tailshafts (i.e., faecal mounds) of burrows. In the laboratory, 22.1% of worms ( $n = 13$ ) moved per day; the mean distance moved was  $11.3 \pm 1.4 \text{ cm}$ . Equivalent figures for movements in the field were: 59.6% of worms ( $n = 41$ ) moved per day, and the mean distance moved was  $10.8 \pm 0.8 \text{ cm}$ .

### 3.2. Activity patterns

Lugworms were active when their burrows were submerged during high tide because, at least during calm weather, there were substantial quantities of faecal casts adjacent to burrow exits when the tide receded. Worms on parts of the shore which dried out at low tide were inactive for most of the period when they were exposed to air (Fig. 3). In spring and summer they continued to produce casts for about an hour after being

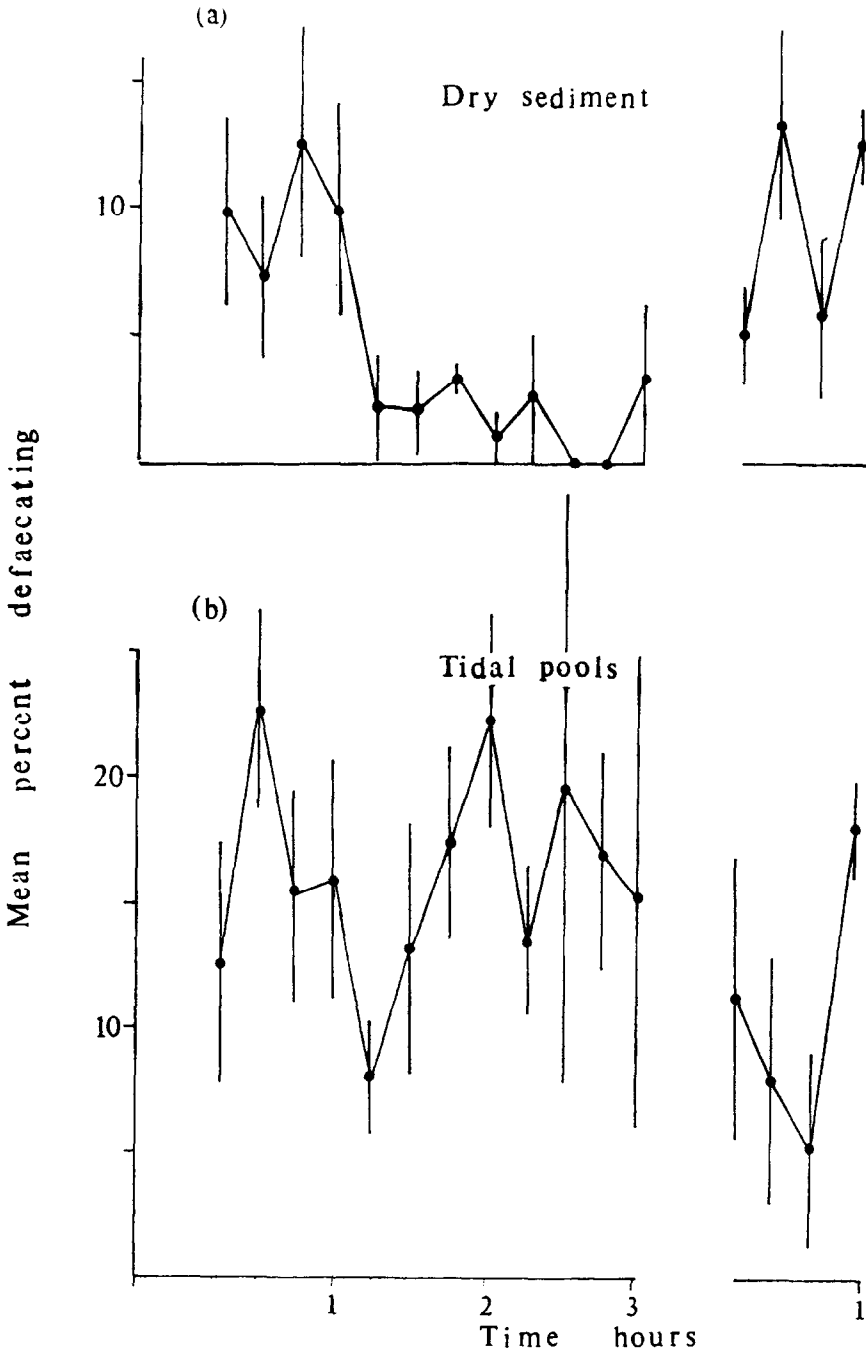


Fig. 3. Percentage cast production by *A. marina* (a) in sediment which dried out during the period of low water and (b) in tidal pools. Observations were made before and after the worms were submerged by the incoming tide.

uncovered but in autumn and winter, they became inactive as soon as this happened (Table 1). Cast production recommenced as soon as worms were resubmerged by the incoming tide (Fig. 3). Worms whose burrows were covered by water in tidal pools produced casts throughout the period of low water.

There were considerable differences in the rates of cast production. Two of the 20 worms in tidal pools which were observed continuously for six hours, were totally inactive (as far as cast production was concerned) and nine of the remaining worms were sporadically active, producing less than six casts within the observation period. However, 9 worms were highly active, producing 9 or more casts. Overall, the numbers of worms producing different numbers of casts (0, 1, 2, 3, 4, etc.) was significantly different from that expected if cast production had been a random process ( $X^2 = 18.02$ ,  $df = 3$ ,  $P < 0.001$ ) (Fig. 4). There is evidence that casts were produced at regular intervals in the highly active individuals. There were significantly more runs of successive recordings in which defecation occurred (or did not occur) than would have been expected by chance in six of them ( $P < 0.05$ , One Sample Runs test). In all other cases, the numbers of runs were not significantly different from chance ( $P > 0.05$ ). The mean interval between successive defecations in these worms was  $35.7 \pm 3.6$  min.

The mean rate of cast production was faster in spring than at other times of the year, and was particularly slow in autumn and winter, when sediment temperatures were low

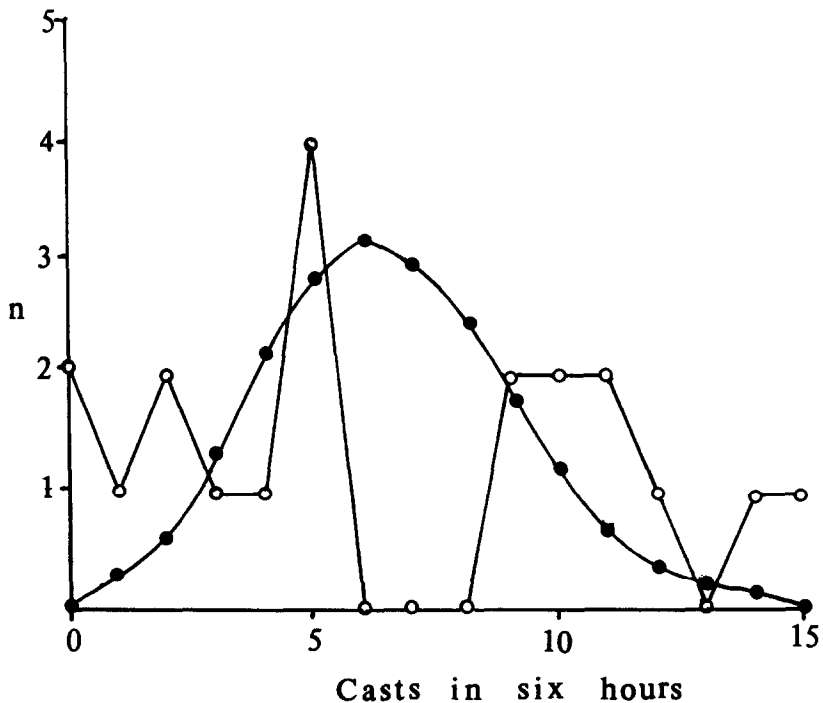


Fig. 4. Numbers of *A. marina* depositing different numbers of casts (○-○-○), plotted with the expected numbers if cast production was random (●-●-●).

(Table 1). The effect of temperature was demonstrated in laboratory tests. The rate of cast production increased with increasing temperatures, up to a maximum of 14–20°C, after which it declined (Fig. 5). Temperature was not the only factor which affected rates of activity, because they were faster in spring than in summer despite lower sediment temperatures at the former time of the year (Table 1). It is noteworthy that rates were faster in worms tested in summer than in winter, throughout the range of temperatures tested (Fig. 5).

Cast production was also affected by the nature of the sediment inhabited by the worms. Rates were significantly faster in worms inhabiting sediment consisting of small particles (diameter < 250  $\mu\text{m}$ ),  $2.74 \pm 0.10 \text{ h}^{-1}$ , or coarser particles (500–1000  $\mu\text{m}$ ),  $2.66 \pm 0.05 \text{ h}^{-1}$ , than in unsieved sediments  $2.30 \pm 0.07 \text{ h}^{-1}$ ,  $P < 0.05$  in both cases.

### 3.3. Bioturbation

There are considerable differences in the amounts of sediment turned over by *A. marina* on different parts of the shore, and at different times of the year. Overall sediment turnover was much higher in the spring and summer, than in autumn and winter (Table 2). It also tended to be higher in the middle part of the tidal range, where

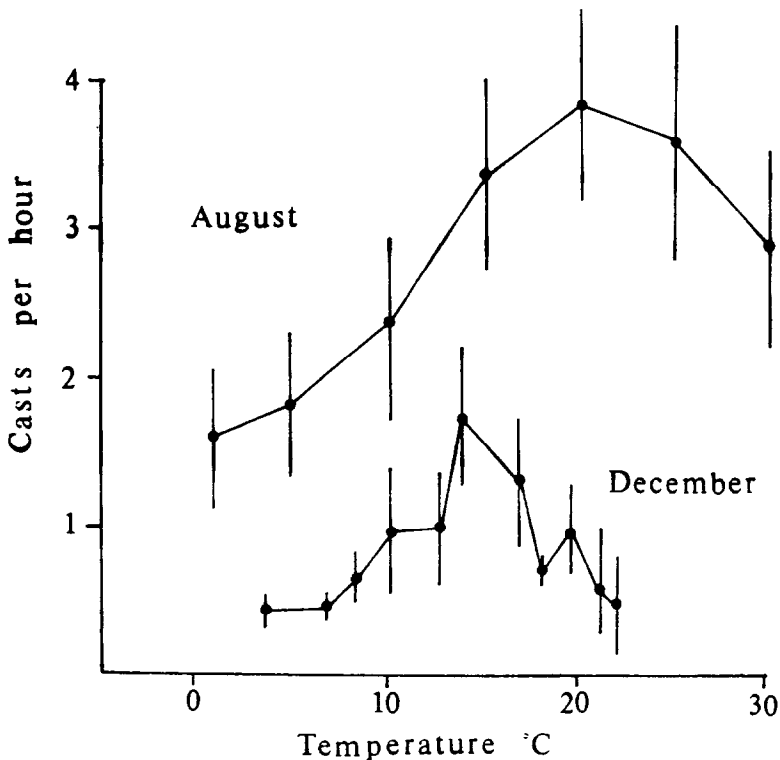


Fig. 5. The effect of temperature on rates of cast production by worms tested in August and December.

Table 2

Sediment turned-over by *A. marina* at various distances from High Water Spring Tides (HWST) and at different times of year, expressed as a depth of sediment (cm)

Distance from HWST (m)	Summer 1992	Autumn 1992	Winter 1993	Spring 1993	Annual total
40	0.13	0.08	0	0	0.21
50	1.02	0.74	0.06	2.26	4.08
60	1.90	0.46	0.37	6.68	9.41
70	2.93	0.70	0.26	9.29	13.18
80	5.32	0.48	0.29	6.06	12.15
90	6.73	0.79	0.18	4.80	12.50
100	6.34	0.54	0.18	6.59	13.65
110	7.05	0.82	0.36	9.59	17.82
120	2.97	0.94	0.12	5.48	9.51
130	1.33	0.92	0.12	0	2.37
140	0	0.09	0	0	0.09
Mean	3.57	0.53	0.20	5.08	9.38

lugworms were most abundant but not necessarily from the largest class sizes, than at the extremes of the range.

#### 4. Discussion

Lugworms rework substantial quantities of sediment during the feeding process. Feeding cannot be observed directly under natural conditions but it was possible to record the deposition of faecal casts on the surface adjacent to the tailshafts of their burrows. Individual differences in rates of cast production suggest that worms may alternate between periods of high feeding activity and low feeding activity (or inactivity). The durations of periods of inactivity were not measured, but they may last for hours or days. Two worms in the present study failed to produce casts during the entire six-hour recording session, even though their burrows were covered by water, and Cadée (1976) found that some worms failed to deposit casts for periods of up to five days. Cast production occurred at regular intervals during periods of high activity and, in this respect, the behaviour of worms was similar to that described by Wells (1950) in his studies of *A. marina* kept under artificial conditions in the laboratory. The mean time between defecations (about 36 min) was similar to that described by Wells (1950); about 40 min. It was also evident, as Wells (1950) had found, that i–d cycles could be modified by external events. For example, it was shown here that cast production was temporarily suspended when the sediment, in which the worm had burrowed, dried out during the period of low water.

There were substantial differences in the amount of sediment reworked on different parts of the shore and at different times of the year. In general, sediment turnover was highest at mid- and mid-low tidal levels, and in spring and summer. The following factors are important.

#### 4.1. Distribution

Maximum densities of worm casts occurred at about mid-tide level, but larger casts, which were presumably produced by larger worms, tended to occur nearer low water. The sizes of casts at different tidal levels changed seasonally, and this can be related to the recruitment of small worms into the population in spring and normal growth processes. There were fewer casts on the shore in winter, presumably due to mortality, migration of worms from the study area (see below) and decreased activity.

#### 4.2. Spacing and movement

Within individual quadrats in the study area, worms were spaced at random. However their distribution probably depends on local factors because Flach and Beukema (1994) described even spacing of *A. marina* inhabiting tidal flats of the Wadden Sea. In either case, the impact of *A. marina* on the shore is likely to be more general than that of the Pacific lugworm *Abarenicola pacifica* which does aggregate and therefore has a patchy impact on the shore (Krüger and Woodin, 1993). There were also dynamic components to the spacing of *A. marina* because individuals frequently moved the positions of their burrows (see also Brey, 1991, Flach and Beukema, 1994). They may also undertake migrations over longer distances. Flach and Beukema (1994) described a seaward migration, which occurred in response to cold weather, and was carried out by worms leaving their burrows and swimming. Changes in the distribution of worms in the study site at Whitley Bay suggest that a downshore migration in autumn is followed by a reverse upshore migration in spring.

#### 4.3. Rates of cast production

Cast production is affected by the nature of sediment in which worms are living. It is also affected by temperature. Consequently, rates of cast production were faster at the warmer times of the year, in spring and summer, than in autumn and winter. However, temperature alone cannot explain differences in rates of cast production. Cadée (1976) found that the summer peak in the rate of cast production occurred earlier than the summer peak in sea temperatures and, similarly, in the present investigation, spring rates, which were recorded when the temperature of the sediment was 11.5°C, were faster than summer rates, when the temperature was 15.0°C. One possibility, suggested by Cadée (1976) is that food availability affects rates of activity, and this may be higher in spring and early summer than later in the year. Another possibility is that differences in rates of activity reflect seasonal differences in metabolic state. It is already known that *A. marina* responds in different ways to sulphide toxification (Völkel and Grieshaber, 1994) and to deoxygenation (Schöttler, 1981) in summer and winter. Similarly, in the present study, rates of cast production were faster in summer than in winter over a range of temperatures. Worms also reacted differently to being uncovered by the receding tide at different times of the year. They continued to be active (i.e., produce casts) for about an hour after being exposed in spring and summer but became immediately inactive on exposure in autumn and winter.

## Acknowledgments

ASWR acknowledges with thanks funding from the Indonesian Government's Marine Sciences Education Project, support from Mr. J.L. Nanere and Mr. J.M. Nanlohy, the former Rector and Dean of Fisheries of Pattimura University (Ambon) respectively, and Dr. M. Huliselan, the present Rector of Pattimura University.

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