

ADAPTATIONS OF TWO INTERTIDAL ISOPODS

I. RESPIRATION AND FEEDING IN *NAESA* *BIDENTATA* (ADAMS) (SPHAEROMATIDAE)

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(Text-figs. 1-5)

The zonation of littoral organisms is well known and can already be described in general terms (see, for example, Southward, 1958). On the other hand, our knowledge of the mechanisms—physiological and ecological—that determine the position of each organism on the shore is much less satisfactory. Investigations like those by Morton, Boney & Corner (1957) are still exceptions.

The present investigation was undertaken to learn something about the adaptations to environmental conditions of two intertidal sphaeromid isopods, *Naesa* (= *Dynamene*) *bidentata* (Adams) and *Campecopea hirsuta* (Montagu). In this paper some findings pertaining to the former species will be discussed while a second paper will deal with the latter species and with comparative aspects.

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MATERIAL AND METHODS

Naesa bidentata (Adams) is common on sea-weeds in the lower half of the shore (Omer-Cooper & Rawson, 1934). The animals used in this investigation were collected from the shore below the Laboratory at Plymouth. Clumps of algae, mainly *Fucus serratus*, taken to the Laboratory and shaken in sea water yielded a sufficient number of specimens.

Oxygen consumption was measured in plastic volumetric respirometers according to Scholander, Claff, Andrews & Wallach (1952) at $20 \pm 0.1^\circ$ C. The respirometers used were sensitive to gas changes of $2 \text{ mm}^3/\text{h}$. Glass tubes with their distal third bent downwards served as experimental vessels (see Wieser, 1962). Respiration was measured in single specimens, most of the time in a shallow layer of filtered sea water which barely covered the animals, but in

some cases the isopods were put on moist filter-paper and the respiration in air was determined. The circulation of the water caused by the activity of the animals and particularly by their pleopod movements was deemed sufficient to ensure rapid diffusion of the gases in the shallow layer of water and the respirometers were therefore not shaken. In *N. bidentata* the stream of water maintained by the beating of the pleopods is particularly forceful because of the jet-like effect of the 'respiratory channel which leads from the pleopods to the extremity of the pleotelson' (Omer-Cooper & Rawson, 1934).

Before measurements the animals were acclimatized for about 1 h in glass dishes with sea water and *Fucus*; they were then transferred to the respirometer vessels which were next placed in the water-bath. After another 40–60 min interval to permit temperature adjustment of the whole system the plugs of the respirometers were put in place and the manometer fluid was levelled. After about 30 min the fluid was levelled again and this reading served as the starting value for the experiment. From then on readings were taken every 30 or 60 min. However, since it was found that the oxygen consumption during the first hour invariably was higher than that during the following hour—irrespective of the course the oxygen consumption might take in the remainder of the experiment—this first hour value was not used in calculating the oxygen consumption of *N. bidentata* during a tidal cycle. Therefore all curves pertaining to the relationship between Q_{O_2} and tidal cycle as presented in this paper begin with the second hour after the respirometers were closed and with the third hour after the beginning of acclimatization to the experimental temperature.

After the experiments the animals were quickly rinsed in distilled water, dried on filter paper and weighed on a torsion balance.

Feeding activity was determined by measuring the rate of production of faecal pellets under various experimental conditions. How this was done will be described in the relevant sections.

RESULTS

RESPIRATION

Tidal rhythms

Since *N. bidentata* is exposed to tidal changes in its habitat, at least some of its activities may be adjusted to the rhythmic pattern of ebb and flood. These rhythms will probably be reflected in the respiration rate of the animals.

The usual procedure for investigating tidal rhythms in animals is to measure changes in a given activity over periods of time sufficiently long that the shift of maxima and minima across the solar day in synchrony with the tidal cycle can be observed (Brown, Bennet & Webb, 1954). However, in order to prove the occurrence of biological rhythms synchronous with the lunar *day* only—that is, disregarding rhythms with longer periods, like the

14·8-day cycle of spring and neap tides—the comparison of two distinct tidal aspects is sufficient.

In the present study the tidal aspect of *high tide occurring around noon and midnight, low tide around 6 p.m.* (Fig. 1 A, B) will be compared with the reverse situation, i.e. *low tide occurring around noon and midnight, high tide around 6 p.m.* (Fig. 1 C, D). In Fig. 1 the data of several days are pooled, referring to a given tidal stage as occurring at 'noon', 'midnight' or '6 p.m.' if it occurred within 2 h of that time of day (see specifications in Table 1). Each set of data begins with the measurement for the hour in which either high or low tide occurred around noon time and from this arbitrary starting point (zero in Fig. 1) the tidal cycle is divided into two periods of 6 h each. This procedure tends to blur all rhythmic changes that might occur in dependence on solar day or on lunar cycles with longer periods, but it is well suited to detecting correlation between changes in biological activity and *daily* tidal cycle.

The changes in respiratory rate observed in the present investigation are assumed to reflect changes in locomotor activity of the animals; it is not known to what extent changes in resting metabolism may also take place.

Fig. 1 A and 1 C are based on animals washed out from algae about 2 h before the start of the experiment, Fig. 1 B and 1 D on animals which had spent 1–2 days in a vessel with running sea water and a piece of *Fucus* (on which they immediately started to feed) in the laboratory at about 18° C.

An inspection of Fig. 1 shows that there is a clear dependence of the respiration rate of freshly collected *N. bidentata* on the tidal cycle, with the maximum occurring at high tide, the minimum at low tide. In the animals that had spent 1–2 days in the laboratory, the tidal rhythmicity is less pronounced; it is highly significant in the tidal aspect of high tide occurring around noon and midnight, low tide around 6 p.m. (Fig. 1 B), but seemingly not significant in the reverse aspect (Fig. 1 D which, however, is based on 2–3 female specimens only).

However, in interpreting measurements of the oxygen consumption of *N. bidentata* the following complication might have to be taken into account:

There probably exists a great number of animals in which the respiration rate depends on the state of nutrition so that an emptying of the gut or a depletion of cellular reserves is immediately accompanied by a reduction of this rate. Reductions of this kind are known to occur in some terrestrial isopods (Wieser, 1962), but the phenomenon has not been studied systematically.

Now if the respiration of such an animal were also to exhibit tidal rhythms, with a maximum at high tide, a minimum at low tide, an experiment lasting for about 6 h would deal with a number of different metabolic situations. In an experiment starting at *high* tide the decrease in activity corresponding to the falling of the tide, and the effect of partial starvation would combine to produce a steep drop in the Q_{O_2} of the animal. In an experiment starting at

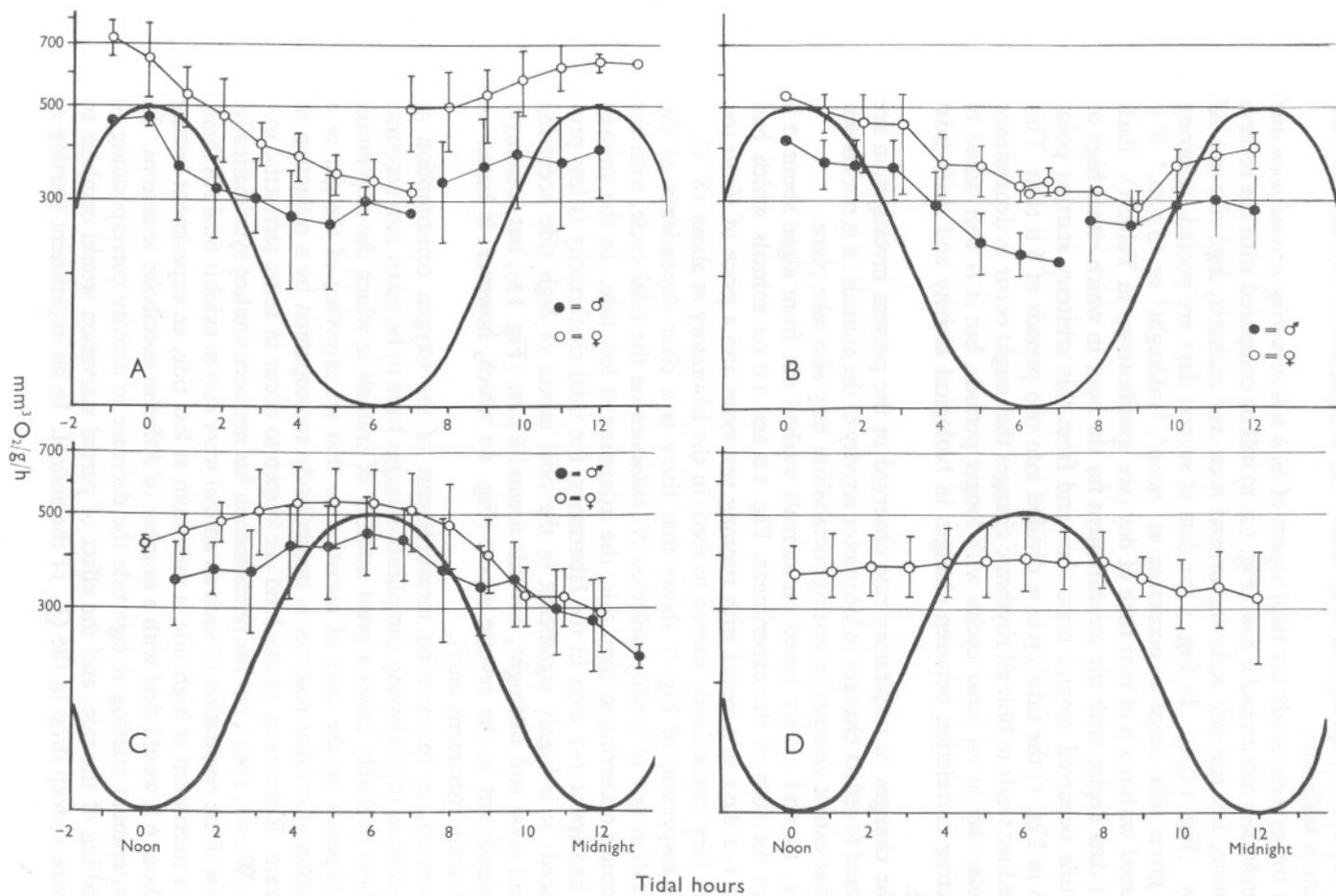


Fig. 1. *Naesa bidentata*. Respiration rate in $\text{mm}^3 \text{O}_2/\text{g}$ fresh weight/h at different tidal hours. Two different tidal stages (A, B: HW-LW-HW; C, D: LW-HW-LW) and two different groups of specimens (A, C: freshly collected; B, D: after 1-2 days in the laboratory) are compared. Means and standard deviations are given, except for tidal hours in which not more than 2 specimens were measured (listed in Table 1) in which case means and ranges are indicated.

low tide, however, the drop in metabolic rate due to starvation would be counteracted by an increase in activity due to the rise of the tide. Thus the combination of these two forces would always result in the slope of activity changes from *high* to *low* water being steeper than that from *low* to *high* water. Fig. 1 shows this to be always the case, from which it is concluded that in *N. bidentata* the rate of metabolism is sensitive to the changes in nutrition which occur in the course of the experiment. Therefore the absence of significant changes in Q_{O_2} during a rising tide might nevertheless be taken as indicating a tidal effect since without such an effect starvation would cause the respiration rate to drop.

Despite the interaction of these two forces it is possible to estimate the magnitude of both the tidal and the starvation effect on respiration by keeping separate sets of determinations of the oxygen consumption which were begun at different tidal hours. The difference in Q_{O_2} at identical tidal hours between animals that had spent different lengths of time in the respirometers can be interpreted as being due to the effect of starvation. Such conditions are represented in Fig. 1A, B. In Fig. 1A at tidal hour no. 7 the females have an average oxygen consumption of 315 or of 500 mm³/g/h according to whether this value was obtained at the end or at the beginning of a set of experiments.

Another way of estimating the tidal effect on respiration is by staggering the beginnings of the experiments whereby average values between 'starved' and 'non-starved' animals for each tidal hour can be obtained (Fig. 1C, D).

It is interesting to note that in the freshly collected specimens (Fig. 1A, C) the Q_{O_2} -values at high tide and at the beginning of the experiments are always higher than in the laboratory specimens (Fig. 1B, D), while the minimum values are approximately the same in all experiments. This could be taken as indicating a higher level of excitement in the freshly collected specimens or—in correspondence with what has been said above—a better state of nutrition which causes their metabolism to start at a higher level.

Sex differences

From Fig. 1 it seems clear that nearly throughout the tidal cycle ♂ have a lower Q_{O_2} than ♀. However, the data for '♂' refer to mature ♂ only, weighing from 19.4 to 28.1 mg, whereas the data for '♀' refer to both juveniles and mature ♀ with a weight range from 10.2 to 22.0 mg (Table 1). Thus differences in weight and developmental stage might be partly responsible for the seemingly clear-cut differences in Q_{O_2} . A comparison of the respiration rate of a few mature specimens with nearly identical weight and measured at identical hours suggests, however, that there is a true difference in metabolism between ♂ and ♀, the former possessing a lower Q_{O_2} than the latter (Table 2).

TABLE 1A. NUMBER OF SPECIMENS MEASURED, WEIGHTS, TIMES OF HIGH OR LOW WATER AND DATES FOR THE Q_{O_2} -DETERMINATIONS SUMMARIZED IN FIG. 1A, B

	Noon											Mid-night				
Tidal stage	HW											LW		HW		
Tidal hour	-1	0	1	2	3	4	5	6	7	8	9	10	11	12	13	
Number of specimens	2	3	5	5	5	5	5	3	2	7	9	10	10	3	1	} juv., ♀♀ Freshly collected
Weights	← 10.2-22.0 mg →											← 10.2-20.7 mg →		3	1	
Number of specimens	1	2	3	3	3	3	3	1	1	2	4	5	5	5	3	} ♂♂
Weights	← 21.1-28.1 mg →											← 21.43-22.20 →		3		
Times of high or low water	11.26-14.08							17.27-19.31				21.43-22.20				
Dates	7 July, 3, 5 Aug.							2, 6, 18, 19 July, 17, 18 Aug.								
Number of specimens	1	3	3	3	4	4	4	2	1	2	3	3	3	2	1	} juv., ♀♀ 1-2 days in laboratory
Weights	← 12.4-20.2 mg →							← 20.7-21.1 mg →				← 23.4-29.9 mg →				
Number of specimens	1	2	2	2	4	4	4	1	1	3	3	3	3	3	2	} ♂♂
Weights	← 22.9-33.6 mg →							← 23.4-29.9 mg →				← 23.4-29.9 mg →				

TABLE 1B. NUMBER OF SPECIMENS MEASURED, WEIGHTS, TIMES OF LOW OR HIGH WATER AND DATES, FOR THE Q_{O_2} -DETERMINATIONS SUMMARIZED IN FIGS. 1C, D.

	Noon						Midnight								
Tidal stage	LW						HW						LW		
Tidal hour	0	1	2	3	4	5	6	7	8	9	10	11	12	13	
Number of specimens	2	7	7	10	10	10	10	7	7	7	4	4	4		} juv., ♀♀ Freshly collected
Weights	← 11.0-19.1 mg →						← 19.4-27.7 mg →						3	2	
Number of specimens		2	2	3	4	4	4	4	5	5	4	3	3	2	} ♂♂
Weights	← 19.4-27.7 mg →						← 22.52-23.50 →						3	2	
Times of low or high water	12.08-12.48						16.15-19.40						22.52-23.50		
Dates	27, 29 June, 10, 11, 25, 26 July, 10, 11, Aug.														
Number of specimens	3	3	3	3	3	3	3	2	2	2	2	2	2		} juv., ♀♀ 1 day in laboratory
Weights	← 13.9-24.4 mg →														

TABLE 2. RESPIRATION RATE (MM³O₂/G/H; INDIVIDUAL VALUES OR MEANS) OF FRESHLY COLLECTED *NAESEA BIDENTATA* OF SIMILAR WEIGHT AT DIFFERENT TIDAL HOURS

		Tidal hour												Mid-night HW	Weight (mg)	n	
		Noon HW	LW										Mid-night HW				
		0	1	2	3	4	5	6	7	8	9	10	11	12			
♀♀	{		550	465	465	370	370	300	300	—	—	—	—	—	—	—	—
										440	440	440	615	615	615	22.0	1
♂♂	{		475	360	320	300	275	265	300	—	—	—	—	—	—	—	—
										215	215	270	270	370	22.6-23.5	3	
															20.7	1	
															20.3	1	
															21.1	1	

Respiration in air

Most intertidal animals are able, at least over shorter periods of time, to respire in air. Whether the respiration rate is higher in water or in air will depend on the biology and ecology of the species, but in most cases the former will be true.

In Table 3 the respiration rate of a few specimens of *N. bidentata* in moist air is set out and compared with the mean rate of animals respiring under water. The available data suggest that (1) the respiration rate in air corresponds to approximately one-half to two-thirds of the mean respiration rate in water and thus to somewhat less than the resting Q_{O_2} of animals in water; (2) no tidal rhythmicity can be detected in animals respiring in air.

These characteristics reflect the near absence of locomotor activity as well as the reduction in amplitude of the pleopod movements of *N. bidentata* in moist air. In more terrestrial crustaceans, like fiddler crabs, the differences in activity displayed in the two media are less conspicuous (Teal, 1959). In barnacles, on the other hand, the cessation of all activity in air causes the respiration rate to drop by 80–97% (Crisp & Southward (1961), comparing their own data with those of Borsuk & Kreps (1929), for *Balanus balanoides*).

FEEDING

Specimens of *N. bidentata* if put into a jar filled with sea water and provided with a piece of *Fucus serratus* can be kept in the laboratory for at least 1 week (as to the viability of *Fucus* under such conditions see Hyde (1938)). The animals immediately start to feed on the alga and within from 10 to 20 min after the beginning of the experiment faecal pellets are being produced. If it is assumed that faeces production and feeding activity are directly correlated the latter can be expressed quantitatively.

In each experiment to be described below the faeces were removed from the experimental vessel after a given period of time, rinsed briefly in distilled water, counted, placed in a drop of distilled water on a coverslip, dried at 104° C, and weighed in batches on an analytical balance.

Weight of faecal pellets

In each experiment dry weight plotted against number of faeces yielded a straight line, the slope of which, however, was different in the different experiments. If the average weight of one faecal pellet is plotted against the weight of the animals (Fig. 2) a linear relationship between the two variables is revealed, the heaviest specimens producing also the heaviest faeces. It cannot be decided whether the increase in weight of faeces is only due to an increase in size or also to an increase in specific weight, but the faecal pellets of mature animals were darker and seemed to be denser of consistency than those of the young specimens.

TABLE 3. RESPIRATION RATE ($\text{MM}^3 \text{O}_2/\text{G}/\text{H}$; INDIVIDUAL VALUES OR MEANS) OF *NAESA BIDENTATA* IN AIR AND IN WATER, AT DIFFERENT TIDAL ASPECTS AND HOURS

	Tidal hour													Weight (mg)	n		
	0	1	2	3	4	5	6	7	8	9	10	11	12			13	
Freshly collected	Noon HW						LW						Mid-night HW				
Q_{O_2} in air	—	—	—	—	—	—	—	—	—	—	340	340	295	295	250	19.5	1
♀	—	—	—	—	—	—	—	—	—	—	280	260	230	230	280	23.4	1
Q_{O_2} in water (means)	—	—	—	—	—	—	—	—	—	—	520	585	625	645	640	—	10
♀	—	—	—	—	—	—	—	—	—	—	365	390	370	400	—	—	3-5
	LW						HW						LW				
Freshly collected	LW						HW						LW				
Q_{O_2} in air	—	—	—	250	240	260	260	220	240	—	—	—	—	—	—	19.0	1
♀+♂	—	265	290	290	290	290	290	240	—	—	—	—	—	—	—	25.0	1
Q_{O_2} in water (means)	—	455	480	510	530	525	530	515	475	—	—	—	—	—	—	—	1-10
♀	—	350	375	390	420	420	450	430	—	—	—	—	—	—	—	—	2-4
1 day in lab.	LW						HW						LW				
Q_{O_2} in air	—	270	270	270	270	215	270	—	—	—	—	—	—	—	—	11.2	1
♀	—	275	215	215	215	275	275	275	—	—	—	—	—	—	—	11.0	1
♂	140	140	140	140	155	180	195	140	—	—	—	—	—	—	—	21.8	1
Q_{O_2} in water (means)	360	370	380	360	390	390	395	395	—	—	—	—	—	—	—	—	3
♀	360	370	380	360	390	390	395	395	—	—	—	—	—	—	—	—	3

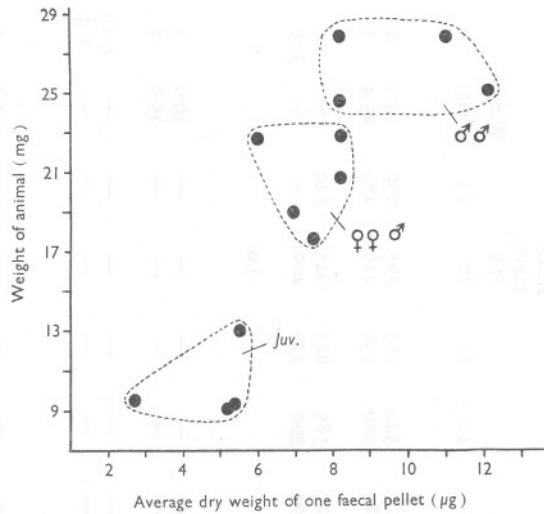


Fig. 2. *Naesa bidentata*: Relationship between average dry weight of one faecal pellet and weight of animal. Each point represents the value obtained for a pair of specimens during one of the experiments described in the text.

Hourly output of faeces

Single females were put into stoppered jars filled with sea water, supplied with a piece of *Fucus*, and kept in a day-lit room. The faeces produced were counted every hour during the day, whereas for the night an average value was calculated. The results of eight experiments on two different days are summarized in Table 4. Feeding seems to begin immediately after the start of the experiment and to continue during the first day without any interruption; during the second day a few breaks in faeces production were observed. The latter rises after the first hour of the experiment, stays high over the middle of the day and falls slowly in the afternoon. During the night the average faeces production is distinctly lower than during the day. There does not seem to be a clear-cut relationship between faeces production and state of tide at the time of the experiment.

One faecal pellet measures about one-tenth the length of the gut. By assuming that the food material is of the same density throughout the gut it can be calculated that in ♀♀ the turnover rate of the gut content during the time of maximum feeding activity is 30 min. That is, under the experimental conditions described above the gut contents will be renewed twice every hour.

Faeces production under different experimental conditions

Since the feeding experiments so far had shown a decline in faeces production at night it was decided to explore more carefully this seeming diurnal rhythmicity.

TABLE 4. HOURLY OUTPUT OF FAECES OF SINGLE FEMALES OF *NAESA BIDENTATA* KEPT IN A DAY-LIT ROOM IN STOPPERED JARS WITH PIECES OF *FUCUS*.

Hours	8 August				15-16 August						State of tide
	Start			State of tide	Start			Start			
8-9	Start										HW
9-10	14	—	8	—	Start						
10-11	21	—	11	LW	6	—	1				—
11-12	25	—	15	—	13	13	10	Start			—
12-13	22	13	14	—	20	21	13	2	1	—	
13-14	21	18	10	—	23	24	9	9	11	—	
14-15	24	23	13	—	26	9	8	8	14	LW	
15-16	20	19	10	—	22	27	12	15	12	—	
16-17	17	13	7	HW	16	21	9	10	6	—	
17-18	19	16	5	—	16	20	12	12	8	—	
18-19	15	14	4	—							—
19-20	14	11	4	—							—
.											—
.											—
.											—
.											—
.											—
9-10	2.2	1.3	0.5		4.5	5.0	2.2	4.2	4.3	HW	
10-11	—	—	—	—	3	13	1	7	10	—	
11-12	—	—	—	—							—
12-13	—	—	—	—	5	19	4	6	12	—	
13-14	—	—	—	—	20	10	4	9	15	—	
14-15	—	—	—	—	16	6	8	11	11	—	
15-16	—	—	—	—	15	—	9	13	15	LW	
16-17	—	—	—	—	11	—	—	13	15	—	
17-18	—	—	—	—	9	—	—	11	16	—	
18-19	—	—	—	—	7	3	7	14	13	—	
19-20	—	—	—	—	—	—	—	9	10	—	

In the following set of experiments two specimens of about equal weight were put into one jar. The piece of *Fucus* used as food was collected from the shore one hour before the start of the experiment. The jars were placed in running water on benches in the aquarium and thereby held at a temperature of $18 \pm 1^\circ \text{C}$. The water in the stoppered jars was either left unchanged between readings ('still-water experiments') or a slow stream of water from the circulation system of the aquarium was sent through the vessel ('running-water experiments'). In the latter case a piece of fine bolting silk prevented contamination of the vessel and escape of faeces. The water used in the 'still-water experiments' came most of the time from the aquarium system too, but since this water differs from Sound water in many respects (Dr Cooper, verbal information) three experiments were run with filtered Sound water (Figs. 3E, 4F, G). It is possible that under these conditions the faeces

production of *N. bidentata* was slightly higher than with aquarium water (Fig. 5), but the qualitative phenomena to be described were unaffected.

Faeces production was counted twice a day, once in the morning and once in the evening. The intervals between counts were not of equal duration.

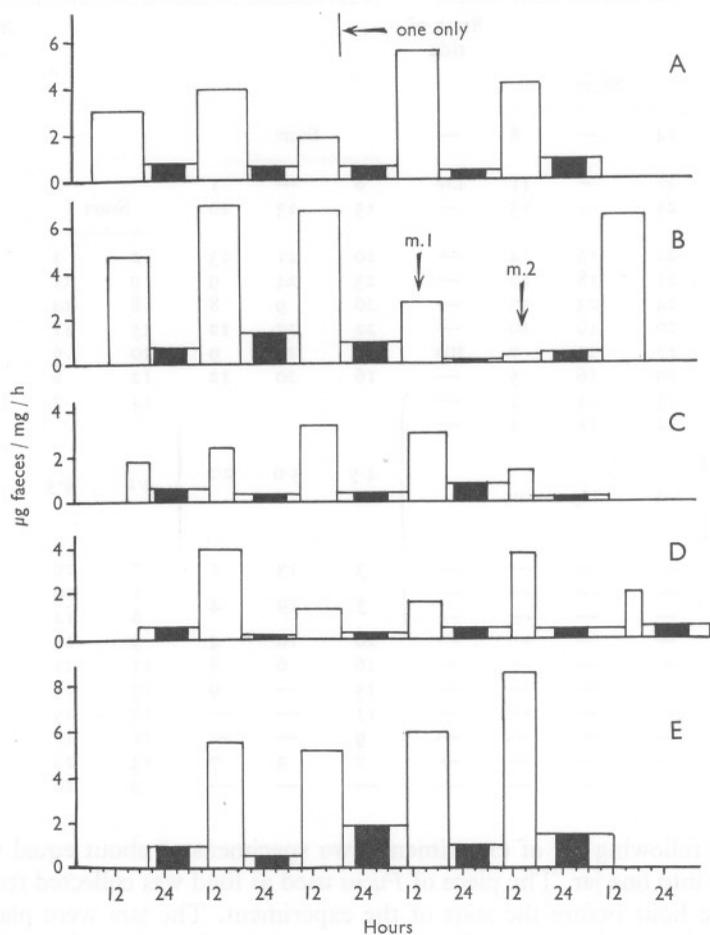


Fig. 3. *Naesa bidentata*. The rate of faeces production (in μg dry weight/mg animal/h) of pairs feeding on *Fucus serratus* in water that remained unchanged between counts. White columns: day-light periods; black columns: night-time hours (10 p.m.-6 a.m.). A: 1-2 juv., mean weight (m.w.) = 13 mg; B: 2 juv., m.w. = 9.1 mg; C: 2 $\delta\delta$, m.w. = 24.5 mg; D: 2 $\delta\delta$, m.w. = 27.7 mg; E: 2 ♀♀ , m.w. = 17.5 mg, in filtered Sound water (other experiments in aquarium water). m. 1, m. 2: first and second moult.

However, as will be shown, the main trend of the argument remains valid despite this deficiency in procedure. Each experiment with one pair of specimens lasted from 5 to 6 days.

The results of the feeding experiments in still water are summarized in

Fig. 3, the height of the columns representing faeces production (in μg dry weight) per hour per mg of live animal. The faeces production—and thus, by inference, the feeding activity—is significantly higher during the day (white columns) than during the night (black columns indicating the hours from 10 p.m. to 6 a.m.). That this seeming rhythmicity is not endogenous but depends on exogenous factors is shown by the experiments summarized in Fig. 4. If the water in the experimental vessels is constantly renewed the rhythmicity is all but obliterated (Fig. 4A, B, C). This is particularly clear in Fig. 4A, where after 3 days the flow of water was stopped and thus the animals subjected to still-water conditions. This resulted in a resumption of the rhythmic mode of faeces production. Even the mishap of having the outflow from the experimental vessel blocked by debris (Fig. 4A, C, E) served to show that the faeces production during the night is about as high as that during the day if there is a constant flow of water through the experimental vessel but that it falls off sharply if the water remains unchanged.

If the still-water experiment is conducted in a darkened vessel (Fig. 4D) the rhythmicity is also nearly obliterated, but this time by reducing the day-time output of faeces instead of by increasing the night-time output (note the different scale in Fig. 4D).

The effect of flowing water conditions on faeces production can be simulated by bubbling compressed air or oxygen through an experimental vessel in which the water is not renewed (Fig. 4F, G).

In summary it can be said that if *N. bidentata* is kept in transparent glass vessels in water that remains unchanged, it will feed much more actively by day than at night. In a darkened vessel the day-time feeding activity is reduced. On the other hand, if the water is continuously renewed or if air or oxygen is bubbled through the otherwise unchanged water the night-time feeding activity rises to about the level of the day-time activity.

All these results can be explained by assuming that the lack of oxygen at night owing to the cessation of photosynthesis by the algae inhibits the feeding activity of *N. bidentata*. If oxygen is supplied either directly or by renewing the water in the experimental vessel this inhibition is released.

Daily faeces production and size of animals

Even under similar experimental conditions there exist large differences between the daily amounts of faecal pellets produced by different specimens. If the average number of faeces produced during 24 hours per mg of animal is plotted against the mean weight of the animals a surprising result comes to light (Fig. 5). The largest specimens, i.e. mature males, produce the same amount of faeces whether they are subjected to still-water (Fig. 3C, D) or to running-water (Fig. 4B, C) conditions, whether their feeding activity displays diurnal periodicity or not. The young animals, however, produce about twice as many faeces in running water (Fig. 4A left and another experiment,

not shown in Fig. 4) as in still water (Figs. 3A, B, 4A right). In other words: if juvenile specimens of *N. bidentata* are forced to feed only during the light hours of the day by depriving them of oxygen at night they do not feed as much as they would if conditions were favourable for 24 h. Mature specimens,

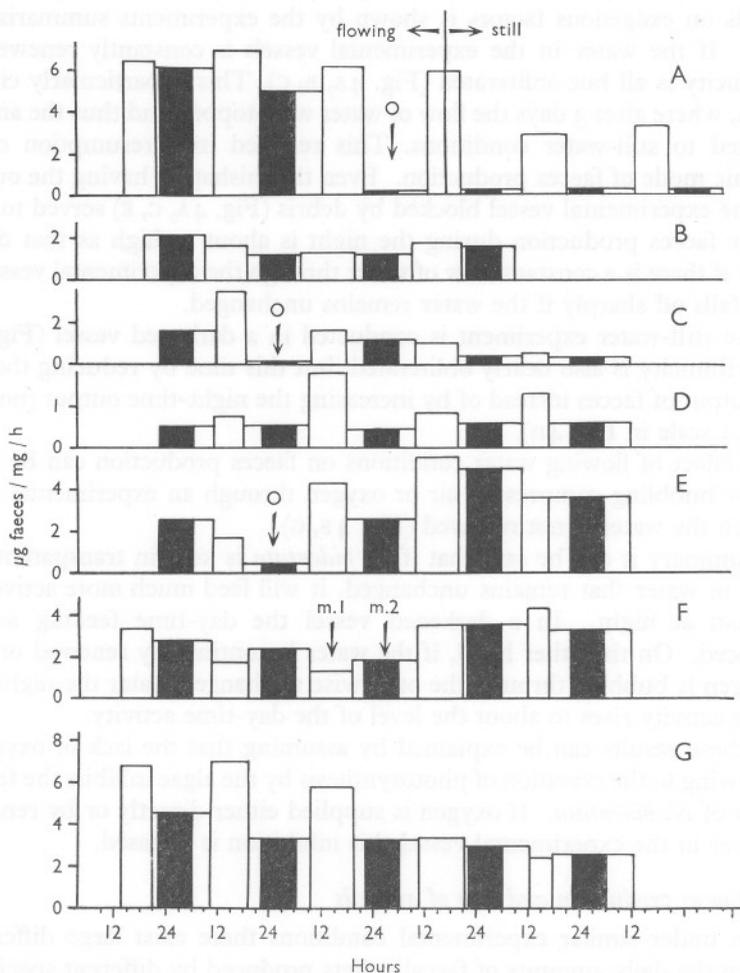


Fig. 4. *Naesa bidentata*. Rate of faeces production as in Fig. 3, but under different experimental conditions. The accidental blocking of the outflow (O) in the running-water experiments and the incidence of moulting (m. 1, m. 2) in one of the experimental animals is indicated. A: 2 juv., m.w. = 9.2 mg; the vertical line indicates the time at which still-water conditions were introduced by stopping the flow of water; B: 2 ♂♂, m.w. = 25.0 mg, running water; C: 2 ♂♂, m.w. = 27.8 mg, running water; D: 2 ♀♀, m.w. = 21.8 mg, still water, darkened vessel (note different scale!); E: 2 ♀♀, m.w. = 20.7 mg, running water, darkened vessel; F: 1 ♀♀ + 1 ♂♂, m.w. = 22.7 mg, still water (filtered Sound water) charged with compressed air; G: 2 ♀♀, m.w. = 19.0 mg, still water (filtered Sound water) charged with oxygen.

however, seem to be able to cover their food demands even when conditions are unfavourable at night: they do not increase average faeces production if they are given the possibility of feeding round the clock.

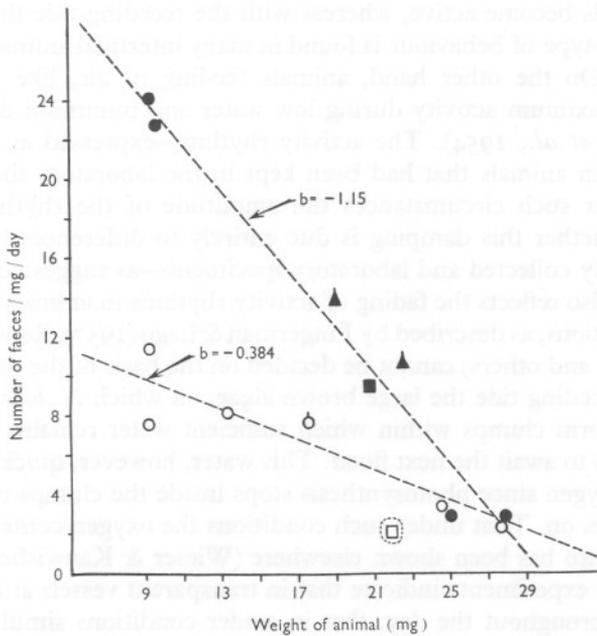


Fig. 5. *Naesa bidentata*. Average number of faeces produced in 24 h/mg of animal, plotted against weight of animals. *Open circles*: experiments with periodic feeding activity (Fig. 3); *open square*: experiment in still water and darkened vessel (Fig. 4D), not used for calculation of regression line; *full symbols*: experiments without periodic feeding activity (*circles*: flowing-water, transparent vessels; *square*: flowing water, darkened vessel; *triangles*: water charged with compressed air or oxygen). A dash on top of the symbol indicates that filtered Sound water was used for the experiment; other experiments in aquarium water; *b* is the regression coefficient (Animals below 17 mg were immature; from 17 to 23 mg both sexes represented, from 25 to 29 mg ♂♂ only).

The experiments in which air or oxygen was bubbled through the water (▲) or the running-water experiment conducted in a darkened vessel (■) yielded values comparable to the running-water experiments in transparent vessels if a linear relationship between weight-specific faeces production and weight of animals is assumed to hold. The regression coefficient of this relationship can be used to characterize the difference in feeding activity between specimens feeding periodically and specimens feeding round the clock ($b = -0.384$ and $b = -1.15$ respectively).

DISCUSSION

The rhythmical fluctuations in respiration rate and locomotor activity as shown in Fig. 1. suggest that when the habitat of *N. bidentata* is flooded by the rising tide the animals become active, whereas with the receding tide their activity subsides. This type of behaviour is found in many intertidal animals that feed under water. On the other hand, animals feeding in air, like the fiddler crabs, show maximum activity during low water and minimum during high water (Brown *et al.*, 1954). The activity rhythm—expressed as changes in Q_{O_2} —persists in animals that had been kept in the laboratory for 1–2 days, although under such circumstances the amplitude of the rhythm appears ‘damped’. Whether this damping is due entirely to differences in nutrition between freshly collected and laboratory specimens—as suggested on p. 669, or whether it also reflects the fading of activity rhythms in animals exposed to constant conditions, as described by Fingerman & Lago (1957), Rensing (1961), Enright (1960) and others, cannot be decided on the basis of the present data.

With the receding tide the large brown algae, on which *N. bidentata* lives, collapse and form clumps within which sufficient water remains trapped to permit animals to await the next flood. This water, however, quickly becomes depleted of oxygen since photosynthesis stops inside the clumps of algae but respiration goes on. That under such conditions the oxygen content of water may drop to zero has been shown elsewhere (Wieser & Kanwisher, 1959).

The feeding experiments indicate that in transparent vessels at night, or in dark vessels throughout the day, that is, under conditions simulating those prevailing inside clumps of algae during low water, faeces production of *N. bidentata* is very much reduced. This agrees with the reduction of the respiration rate at low tide, suggesting that in nature this species forages actively during high water while during low water it moves into the clumps of *Fucus* where feeding activity must become inhibited by the onset of anaerobic conditions. It can be shown quite easily that on the shore collapsed clumps of large brown algae indeed harbour many specimens of *N. bidentata* during low tide. For mature specimens the rhythmicity of feeding at high water, resting at low water seems to be sufficient to satisfy their food demands (Fig. 5). Juvenile specimens, however, if given the chance, feed twice as much under continuously favourable (that is: aerobic) conditions as under the regime of intermittently favourable and unfavourable conditions. The question remains unanswered whether this is an artifact or whether it indicates actual differences in behaviour between adults and juveniles. It may be that in nature young specimens of *N. bidentata* follow the receding tide in order to be able to feed round the clock; such movements with the tides are known to occur in other vagile crustaceans (Wieser, 1952).

The rate of production of faecal pellets is probably linked to energy-expending processes and thus should be subject to the laws which govern the

relationship between size and metabolic processes of that type in poikilotherms. These laws are always of an exponential nature (see, for example, Zeuthen, 1947), whereas the relationship between rate of weight-specific faeces production and weight of animals seems to be—at least within the range investigated—a linear one. Further data are needed to confirm this finding.

SUMMARY

In freshly collected *Naesa bidentata* there exists a clear dependence of respiration rate, measured in sea water, on the tidal cycle, with the maximum occurring at high tide, the minimum at low tide. In specimens that had spent 1–2 days in the laboratory the tidal rhythmicity is less pronounced due to a lowering of the Q_{O_2} -values at high tide and at the beginning of experiments. This is interpreted as reflecting differences in nutrition between freshly collected and laboratory specimens.

Males have a lower Q_{O_2} than females of equal weight.

Respiration in air corresponds to approximately one-half to two-thirds of the mean respiration rate in water and thus to somewhat less than the resting- Q_{O_2} of animals measured in water.

The dry weight of faecal pellets increases in linear proportion with the weight of the animals.

In females the turnover rate of the gut contents during periods of maximum feeding activity is approximately 30 min.

Faeces production in animals feeding on *Fucus serratus* in the laboratory depends on the size of the animals and apparently on the degree to which aerobic conditions are maintained in the experimental vessels. Specimens kept in unchanged water will feed more actively at day than at night. If the water is continuously renewed or if air or oxygen is bubbled through the otherwise unchanged water, the night time feeding activity rises to about the level of the day time activity. These results can be explained by assuming that the lack of oxygen at night owing to the cessation of photosynthesis by the algae inhibits the feeding activity of the isopods.

In the largest specimens the average rate of daily faeces production is the same whether their feeding activity shows diurnal periodicity or not, suggesting that they are able to cover their food demands even when they do not feed continuously. Juvenile specimens, however, produce about twice as many faeces in running water as in still water. This causes the regression of weight-specific rate of faeces production on weight of animals to be steeper in the running-water experiments ($b = -1.15$) than in the still-water experiments ($b = -0.384$).

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