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ADAPTATIONS OF TWO INTERTIDAL ISOPODS

II. COMPARISON BETWEEN *CAMPECOPEA HIRSUTA* AND *NAESA BIDENTATA* (SPHAEROMATIDAE)

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(Text-figs. 1–5)

In the first report (Wieser, 1962*a*) the respiratory and feeding activities of *Naesa bidentata* (Adams) were discussed. In this paper some biological parameters of a related but ecologically different species, *Campecopea hirsuta* (Mont.), will be analysed and compared with those of *N. bidentata*. A few words will also be said about the respiration of the bivalve *Lasaea rubra* (Mont.), the adaptations of which were studied by Morton, Boney & Corner (1957).

C. hirsuta occurs in the middle part of the shore where it can be found within empty shells of *Chthamalus*. Its preferred habitat, however, is the lichen *Lichina pygmaea* the vertical distribution of which extends from OD to MHWS. Colman (1940) in his investigation of the Wembury rocks found this plant to support populations of up to 3800 specimens of *C. hirsuta* per 100 g of damp weed. In the present investigation lichens scraped off rocks below the Plymouth laboratory, at Cellar Beach in the mouth of the river Yealm, and at Wembury, were found to harbour a fair number of specimens but certainly not more than one-tenth of the figures given by Colman. Particularly the upper portion of the *Lichina* belt seemed to be almost devoid of the isopod and most of the specimens used in the experiments described below came from around EHWN where the percentage of exposure is about 60% or 50% if corrected for splash (Colman, 1933; Morton *et al.*, 1957). The reasons for this change in population density between 1930 (when Colman conducted his research) and 1961 are unknown. In the present investigation no attempt was made to distinguish between populations from different tidal levels or from the three localities mentioned above.

The respiration rate of freshly collected *C. hirsuta* was measured at 20° C in Scholander's volumetric respirometers as described before (Wieser 1962*a*, *b*). This time, however, a larger number of specimens had to be used in order to obtain significant changes in gas pressure (see below). The animals respired either in a shallow layer of water or in air. In the latter case the animals rested either on a piece of damp filter paper or on the glass bottom of the respirometer vessel itself, the damp

filter paper having been pushed higher up in order to keep the air in the vessel saturated with moisture.

The loss of water in *C. hirsuta* and in *N. bidentata* was determined by putting either single specimens or batches of animals in a small cup made of wire mesh and suspending it through a split cork into a desiccator charged with concentrated H_2SO_4 and $CaCl_2$. A torsion balance was used for recording the changes in weight. The experiments were carried out at room temperature, which was approximately 18° C at the time.

For histological purposes specimens were fixed in the following fluid (kindly suggested and supplied to me by Dr J. S. Alexandrowicz):

2% picric acid in 80% alcohol	75 c.c.,
formaldehyde	20 c.c.,
acetic acid	5 c.c.,
trichloroacetic acid	4 c.c.,

preserved in 96% alcohol and stained with Mallory's triple stain.

My thanks are due again to the staff of the Plymouth Laboratory, and particularly to Dr A. D. Boney for a number of helpful suggestions in connexion with the work on *C. hirsuta*. Miss Maria Wimmer made the drawings of the isopods with her usual skill.

RESULTS

RESPIRATION

The effect of the number of animals used in one experiment

Specimens of *C. hirsuta* in water tend to aggregate. This affects the measurable gas exchange as has also been found for *Lasaea rubra* by Morton *et al.* (1957). However, with up to about 40 specimens per vessel the effect of clumping was slight, due to the continued activity of the animals. The respiration rate of one specimen in water can be estimated to be about 500 mm^3 $O_2/g/h$ by extrapolating the regression line based on batches of from 10 to 40 specimens (Fig. 1). One experiment with 60 specimens per vessel resulted in a Q_{O_2} of almost half that of the determinations with 40 specimens, from which it may be concluded that in groups of that size the activity of the animals is drastically cut down and (or) the free gas exchange is seriously impaired by the effect of crowding. Since females outnumbered males by about 10:1, the Q_{O_2}-values given in Fig. 1 indicate predominantly the respiratory activity of the former sex.

Respiration in water and in air

In water the animals can be seen to aggregate, but at the same time they move about very energetically, crawling all over each other, swimming away for short stretches and returning to the group. Thus the Q_{O_2}'s shown in the left upper part of Fig. 1 are considered to represent the average activity metabolism of groups of *C. hirsuta* under experimental conditions.

In air the animals stay separated, each rolling up into a more or less perfect ball (see Fig. 5 C) and remaining motionless. This is reflected in their low Q_{O_2}'s (lower left group of values in Fig. 1). However, if placed on damp filter paper the animals have a somewhat higher and more variable Q_{O_2} (108 ± 30 mm^3/g/h; $n = 7$) than if put directly on the glass bottom of the vessel (87 ± 14 mm^3/g/h; $n = 8$). This can be interpreted to indicate the degree to which the tight closing mechanism of the body has been relaxed. The experiments to be described below suggest that in dry air the gas exchange of *C. hirsuta* must be minimal. In moist air, but on a dry substrate (as on the glass bottom of the respirometer vessel), the body unrolls slightly, permitting measurable gas exchange. On a moist substrate (as on damp filter paper) the body relaxes even more and the average oxygen consumption increases again. The gradual relaxation of the body can also be observed under a dissecting microscope by

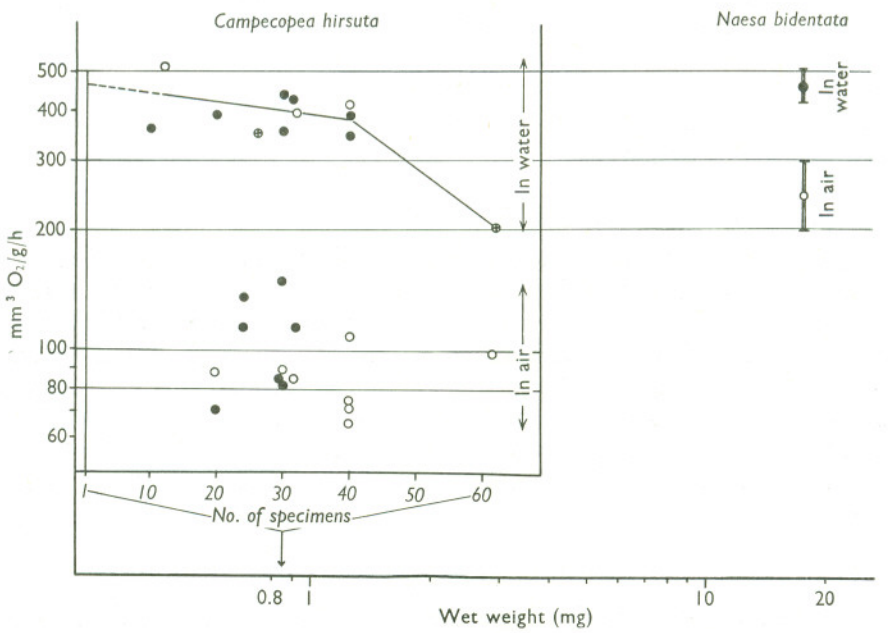

Fig. 1. Double logarithmic plot to show the relationship between respiration rate and wet weight for the two sphaeromids, *C. hirsuta* and *N. bidentata*. Respiration in air is distinguished from respiration in water, both of which are represented by the individual experimental values in *C. hirsuta*, by means and standard deviations in *N. bidentata*. The data for *C. hirsuta* are presented in form of an inset in order to provide additional information on the relationship between respiration rate and number of specimens per experiment. Furthermore, the following distinctions were used in the case of *C. hirsuta*—Respiration in air: ○, animals resting on glass bottom of respirometer vessels; ●, animals resting on damp filter paper. Respiration in water: ○, experiments conducted around low water; ●, experiments conducted around high water; ⊕, experiments at ill-defined tidal hours. The regression line is eye-fitted and extrapolated in order to give the approximate respiration rate in water of one specimen of *C. hirsuta*.

putting specimens of *C. hirsuta* on a dry piece of filter paper and soaking it slowly with water.

In comparing the oxygen consumption of *C. hirsuta* with that of the lower intertidal species *N. bidentata* (Wieser, 1962*a*) it must be remembered that due to the tidal rhythmicity of its activity, sexual differences and the effect of starvation on respiration, it is very difficult to assign an average Q_{O_2} in water to the latter species. On the other hand, the respiration rate in *air* of freshly collected *N. bidentata* is more easily defined and can be calculated from Table 3 of the earlier paper as 247 ± 50 mm³/g/h. Now the Q_{O_2} in water of freshly collected ♀ and ♂ (the former outnumbering the latter about 3:1), measured at the same tidal hours as with the animals for which the Q_{O_2} in air was determined, is 467 ± 36 mm³/g/h. Furthermore, the mean of *all* the measurements made on freshly collected females is 490 mm³ O_2/g/h. Thus a range of 430–510 mm³ O_2/g/h can safely be taken as representing the average Q_{O_2} in water of freshly collected—predominantly female—specimens of *N. bidentata*.

It follows that the average respiration rate in water of single specimens of *N. bidentata* is about the same as that assumed for single specimens of *C. hirsuta*, whereas the respiration rate in air of *N. bidentata* exceeds that of *C. hirsuta* by nearly 250%.

The question of tidal rhythmicity in C. hirsuta

While in freshly collected specimens of *N. bidentata* the respiration rate quite clearly followed a tidal rhythm, the hourly values of respiration rate in batches of *C. hirsuta* remained more or less the same, irrespective of the tidal situation. This allowed the calculation of a single value of Q_{O_2} for an experiment lasting about 6 h and the variation of this value in different experiments showed no correlation with the state of the tide. This is apparent from Fig. 1 in which the values of experiments which started a few hours before *high* water cannot be distinguished from those which started a few hours before *low* water.

Relationship between respiration rate and weight

The wet weight of individual specimens of *C. hirsuta* (after brief rinsing in distilled water) varied from 0·54 to 0·91 mg, with a mean value of 0·85 mg, whereas specimens of *N. bidentata* weighed between 11·0 and 25·0 mg, with an average of 18·5 mg. If the Q_{O_2} values of these two species of sphaeromatids are plotted against their weights on a logarithmic scale (Fig. 1) it becomes obvious that contrary to what is known in other crustaceans (see Wolvekamp & Waterman, 1960) the smaller species has just about the same Q_{O} in water as the larger species and by far the lower Q_{O_2} in air.

Respiration of the bivalve Lasaea rubra

The mats of *Lichina pygmaea* in the Plymouth neighbourhood are populated mainly by two species of animals, the isopod *C. hirsuta* and the bivalve *Lasaea rubra* (see Colman, 1940). Ecologically these two species resemble each other at least in so far as both depend on the presence of water for their feeding activity and both can survive periods of desiccation by effectively shutting themselves off from the environment. The data presented so far seem to show that in moist air the isopod relaxes its protective position and shows a measurable resting metabolism which corresponds to about one-fourth to one-fifth of its activity metabolism in water. On the other hand, the data presented by Morton *et al.* (1957) seem to suggest that *L. rubra* behaves differently in this respect since no oxygen consumption (measured by the Warburg technique) could be detected in moist air nor even when the animals were covered by a thin film of water. This unexpected finding was commented on by Morton *et al.* as follows:

'There seems a need to explain why no respiration could be detected when animals are covered by a thin layer of water, though in this state filtering may be taking place. However, absence of measurable respiration need not imply absence of feeding, because collection of solid particles by the gill—although a ciliary process—must be relatively much faster than gaseous exchange.'

Since the present author had difficulty in understanding this statement a few determinations of respiration rate of batches of *L. rubra* (30–60 specimens) were made with volumetric respirometers. The animals were at first put on damp filter paper and their respiration rate was measured. After a few hours the respirometer was opened, a few drops of sea water were pipetted on to the filter paper, the respirometer was closed again and after some time of equilibration the readings were resumed. The data for the most significant experiment are set out in Fig. 2 in which hourly oxygen consumption (in mm^3 per g wet weight) is plotted against time. It is quite obvious that there is a measurable oxygen consumption even in moist air which, however, decreases as the experiment continues. After adding a few drops of water so that the animals are covered by a thin film oxygen consumption rises again. In this one experiment maximum oxygen consumption was about 70 mm^3/g wet weight/h and minimum 30 mm^3. In another experiment the Q_{O_2} on damp filter paper stayed at 40 mm^3 for 3 h and after addition of a few drops of sea water rose to 74 mm.[3] In a third experiment in which no water was added the respiration rate remained at 29 mm^3 O_2/g/h for three hours. It thus seems as if *L. rubra*—just as *C. hirsuta*—relaxes its closing mechanism if its surrounding is sufficiently damp, and under such conditions displays a measurable oxygen consumption. The divergent findings of Morton *et al.* might be due to lower sensitivity of their method or to an adverse effect of the shaking of the Warburg apparatus on the animals.

In order to compare the oxygen consumptions of the isopod and the bivalve account has to be taken of the possibility that the contents of calcium carbonate and of water in these two species might be very different. Therefore a number of weighings were carried out on *L. rubra*, *C. hirsuta* and also on *N. bidentata*. The animals (batches in the former two species, individuals in *N. bidentata*) were rinsed briefly in distilled water, dried on filter paper and weighed; then they were dried for 12 h at 104° C for the determination of

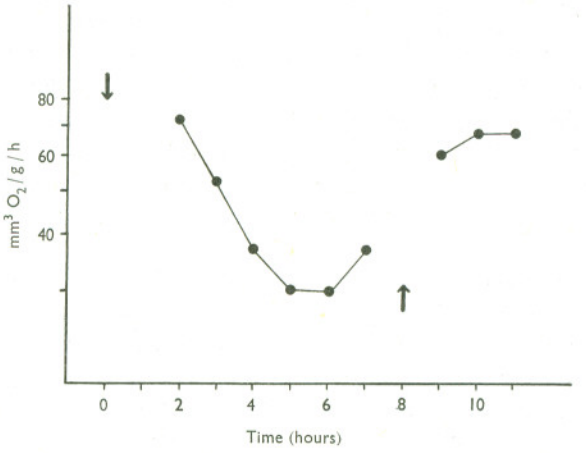

Fig. 2. Hourly respiration rate at 20° C of 60 specimens of *L. rubra* collected the day before at Cellar Beach. At the beginning of the experiment (downward pointing arrow) the animals were put on damp filter paper; after 8 h (upward pointing arrow) the experiment was interrupted and a few drops of sea water were added, sufficient to moisten the animals with a film.

their oven-dried weight. Finally, they were treated with strongly acidified (HCl) alcohol for 24 h, rinsed, dried again and weighed. The results are set out in Table 1.

It is apparent that in *L. rubra* the water content is considerably lower, the calcium carbonate content, however, considerably higher than in the two isopods, while in *N. bidentata* both the water and the mineral content are slightly lower than in *C. hirsuta*.

The Q_{O_2}'s referred to decalcified rather than wet weight are given in Table 2.

The Q_{O_2}'s of *L. rubra* in a film of water as determined with the volumetric respirometer are in good agreement with Morton's data for submerged animals from the same tidal level (HN) measured with the Warburg apparatus. From this I conclude that the filtering activity and thus the respiratory rate of *L. rubra* is essentially the same in submerged specimens and in those just covered by a thin film of water—a conclusion which seems to make sense ecologically since other data by Morton *et al.* (1957, p. 390) show that the animals become fully active immediately after being wetted by wave splash.

If this assumption is correct, Morton's deviating results on the respiration of *L. rubra* in films of water would have to be explained by the effect of shaking on animals not fully submerged.

TABLE 1. RELATIVE AND ABSOLUTE WEIGHTS OF SPECIMENS OF ONE BIVALVE AND TWO ISOPODS

	Weight of oven-dried specimens (% wet weight)	Weight of decalcified specimens (% wet weight and dry weight in parentheses)	Average decalcified weight of one specimen (mg)
L. rubra			
Batch no. 1	59	6·2 (10·6)	0·135
Batch no. 2	—	4·8	0·067
Batch no. 3	52·5	8·1 (14·1)	0·16
Batch no. 4	60·2	7·3 (12·0)	0·135
Morton's specimens	—	~ 8·3	~ 0·1
C. hirsuta			
Batch no. 1	—	(30·3)	—
Batch no. 2	36·4	11·8 (32·5)	0·1
Batch no. 3	36·0	11·5 (32·0)	0·105
N. bidentata			
Means of 4 ♂	42·5	15·7 (36·7)	3·44
Means of 6 ♀	38·0	16·3 (43·4)	2·32

TABLE 2. AVERAGE RESPIRATION RATE OF ONE BIVALVE AND TWO ISOPODS AT 20° C

	$mm^3O_2/h/g$ decalcified tissue weight	Average decalcified weight of one specimen (mg)	
L. rubra			
Submerged (calculated from Morton's data)			
Wembury HS	1250	0·1	
Plymouth HN	1050		
Plymouth LN	650		
With film of water	970	0·124	Own data, Plymouth, HN
On damp filter paper (minimum)	455		
C. hirsuta			
In water	~ 3650	0·1	
In air			
On damp filter paper	930		
On glass	750		
N. bidentata			
In water	~ 3000	2·5	
In air	~ 1550		

STRUCTURE OF GILLS

In most sphaeromatids the last two pairs of pleopods are completely transformed into gills. The shape of the gills may be very different in different genera, which fact was used by Hansen (1906) to establish three groups within thesubfamily Sphaeromatinae, i.e.: Hemibranchiatae, Eubranchiatae, and Platybrancheatae

Naesa bidentata belongs to the Eubranchiatae in which both rami of the last two pleopod pairs are deeply folded, whereas *C. hirsuta* belongs to the Platybranchiatae in which the rami are without any folds (Fig. 3). Since these structural differences might have some bearing on the ecological differences between the two species, an attempt was made to measure the surface area of the gills. These organs are plate-like and nearly oblong in outline. Their respective areas can be established by cutting sagittal sections and measuring

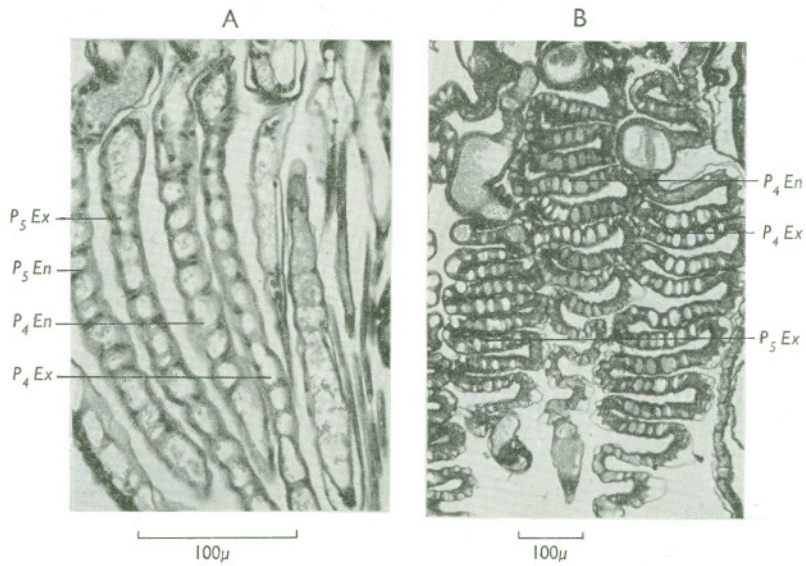

Fig. 3. Sagittal, off-median section through abdomen of *C. hirsuta* (3 A) and *N. bidentata* (3 B), presenting a sagittal, median section of the gills, that is, the two posteriormost pleopods (P_4, P_5), each consisting of endopodite (*En*) and expodite (*Ex*). Photograph by Dr H. Adam, Vienna.

on some of them the true length of the gill epithelium by means of a planimeter. In this way an average length of contour was found for the longitudinal section of each gill which was then multiplied by the average width of the ramus. Completing such measurements on one representative of each of the two isopod species the following values and relations were established:

	N. bidentata	*C. hirsuta*
Area of gills in mm²	11·70	0·49
Wet weight of animal in mg	18·0	0·85
Ratio $\frac{\text{gill area}}{\text{wet body weight}}$	0·65	0·62

The conclusion from this set of measurements is that in the two species of sphaeromatids investigated the gill area varies with the weight of the animals. Since the same holds for their respiration rate in water (see Fig. 1) there is a

strong possibility that in these two species one of the factors controlling the rate of activity metabolism in water is the area of the gills and thus the diffusion of oxygen through their epithelia.

RESISTANCE TO DESICCATION

The method by which the loss of water in the two isopod species was measured is the one used by Morton *et al.* (1957) in their investigation of *L. rubra* and has been outlined above (p. 98). Batches of *C. hirsuta* and single specimens of *N. bidentata* were used to establish the data which are summarized in Fig. 4. Included are Morton's data for *L. rubra* and for *Lichina pygmaea*. In all cases a weight of 100% refers to the weight reached after 1 h in the desiccator.

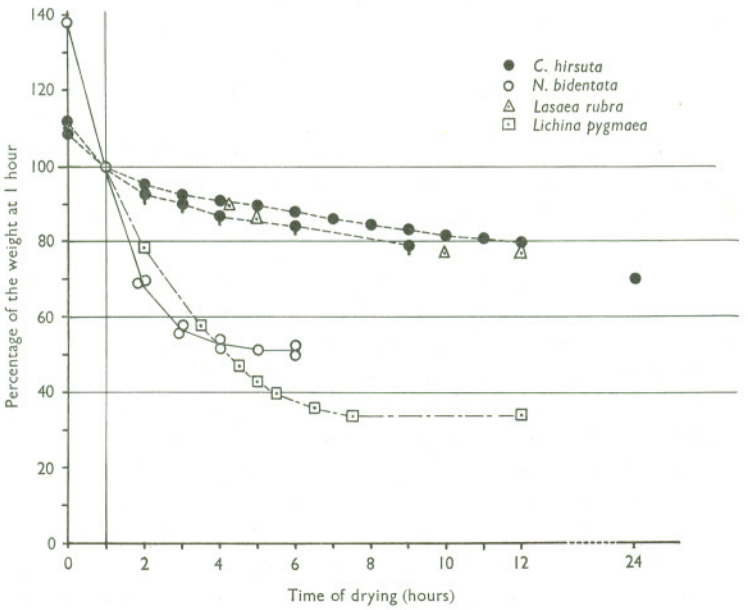

Fig. 4. Loss of weight (after blotting) of two isopods (*C. hirsuta* and *N. bidentata*), one bivalve (*L. rubra*) and the lichen *Lichina pygmaea* in dry air at room temperature (approximately 18° C). Data for *L. rubra* and the lichen from Morton *et al.* (1957). All the data are referred to the weight of the organisms after 1 h of drying = 100 %. Each convention represents one measurement. *C. hirsuta* is represented by two sets of measurement, one of which refers to specimens lifted directly out of sea water, the other (full circle with dash) to specimens briefly rinsed in distilled water before drying.

The results show very clearly two things, namely, the great difference in resistance to desiccation between the two isopod species, and the very close similarity in this respect between the isopod *C. hirsuta* and the bivalve *L. rubra*.

Of 35 specimens of *C. hirsuta* left in dry air for 23 h and then re-immersed in sea water, 18 survived. Of 22 specimens five were still alive after a period of 3 days in the desiccator. *Naesa bidentata*, however, would not survive more

than 3 h under such conditions—in which period it had lost more than 40% of its initial weight, whereas in the same period *C. hirsuta* would lose not more than 10% of its initial weight.

FEEDING BEHAVIOUR

No records of the food and the feeding behaviour of *C. hirsuta* has come to the author's attention. However, if specimens of this isopod are put into a dish with sea water together with the lichen *L. pygmaea* the animals can be observed feeding on the plant, and faecal pellets of bluish green colour will soon accumulate at the bottom of the dish near the lichen. Animals may be kept for several days in such a dish and do not seem to suffer from the long period of submergence (although no detailed analysis has been made of this particular point). After a few days the effect of feeding activity of the isopod on the lichen can be detected. The animals seem to browse along the branches of the plant, eating away the gonidal layer of blue-green algae that surrounds the inner core of fungal mycelium. This mycelium is of a pinkish colour, so that the appearance of pink spots indicates the disappearance of the algal layer. In fact, looking over a mat of *L. pygmaea* in nature one can very often, even with the naked eye, see small pink patches standing out against the bluish black of the healthy lichen. It may thus be surmised that even in nature these patches are caused by the feeding activity of *C. hirsuta*.

If the feeding behaviour of *C. hirsuta* in the laboratory is observed over longer periods of time it soon becomes apparent that this species does not feed continuously but in bursts. The animals might remain motionless for several hours, coiled round a branch of the lichen or rolled up in the fork of two branches. The hourly faecal production reflects this rhythmicity in feeding—at least of specimens that had not been starved for too long before the experiment. This is suggested by Table 3 in which the hourly faecal production of 15 single specimens after various periods of starvation is summarized. After up to 17 h starvation each specimen—both on the first and on the second day of the experiment—fed in bursts, whereas after longer periods of starvation some specimens (experiments nos. 11 and 15) fed continuously for the better part of the first day, but showed signs of returning to discontinuous feeding on the second day.

This mode of feeding might be taken as reflecting the particular way of life of this species which can feed only when its habitat is wet—that is, under normal conditions, for about 50% of the time. *N. bidentata*, as might be recalled (see Wieser, 1962*a*), will feed more or less continuously if only a sufficient amount of oxygen is assured.

There does not, however, seem to be a relationship between the time of day at which the feeding bursts take place and the tidal phase, since experiments nos. 3–8 were all carried out on the same day and obviously show little

synchrony in the hourly faeces production. Rather it might be conjectured that the intervals between feeding periods permit better digestion of the food, and that the timing of the bursts of activity is determined not only by environmental factors (such as sufficient moisture) but also by the state of nutrition of a given individual.

TABLE 3. HOURLY OUTPUT OF FAECAL PELLETS OF *C. HIRSUTA*

Single specimens kept at room temperature (approximately 18° C) in covered dishes with pieces of *Lichina*. For the night-time hours an average figure of faeces production is given.

		After 24 h of feeding		After 17 h starvation								After 2 days starvation		After 4–5 days starvation		
No. of exp. ...		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Hour															
1st day	8–9	Start														
	9–10	1	—													
	10–11	6	1				Start					Start		Start		
	11–12	2	—	6	—	5	8	1	1	—	—	9	—	11	9	10
	12–13	—	—	8	—	6	6	—	4	—	11	14	11	5	17	15
	13–14	1	1	4	—	—	7	7	—	—	11	12	9	3	17	13
	14–15	3	3	5	7	—	1	7	—	—	10	15	12	5	13	11
	15–16	7	11	—	6	—	9	5	—	—	10	13	10	—	9	3
	16–17	7	11	2	9	—	1	4	—	—	6	12	13	—	7	18
	17–18	—	—	10	1	—	—	8	—	—	4	5	7	—	—	10
	18–19	—	4	7	—	—	—	—	—			10	1			
	19–20	—	11	4	—	—	—	—	—			7	—			
	.															
	.		0·4	3	2·5	3	—	+	2	+	2	1	+	1	2	+
	9–10															
2nd day	10–11			—	5	3	—	—	—	—	—					
	11–12			—	5	7	—	—	—	—	8	10	—	—	9	—
	12–13			—	6	7	—	—	—	—	3	7	—	—	17	—
	13–14			1	4	—	—	1	—	—	9	5	—	—	12	6
	14–15			—	7	—	—	—	—	—	11	6	—	—	—	10
	15–16			—	—	—	—	—	—	1	—	5	—	—	8	9
	16–17			—	—	—	—	—	—	7	2	3	6	—	5	1
	17–18			—	—	—	—	—	—	3	7	—	6	—	8	15
	18–19			—	—	—	4	—	—	4	9	—	11	—	—	12
	19–20			—	—	—	1	—	—							

DISCUSSION

The adaptation of marine animals to terrestrial life has led to the evolution of forms that can maintain their feeding activity in air and to others that still have to be submerged in order to be able to feed. The former case requires adequate protection against desiccation, but at the same time metabolism in air will be equal to—or even higher than—metabolism in water of species of comparable basic activity. This is well documented by the series of crabs studied by Pearse (1929), Vernberg (1956), Gray (1957) and others, in which, with increasing terrestrial habit, gill area decreases, but the Q_{O_2} of both gill tissue and whole organisms increases. In this way the loss of exchange-active area is more than compensated for by the gain in respiratory activity.

The other avenue to terrestrial life requires perhaps a less sophisticated means of protection against desiccation since activity stops during exposure to air and the animal may become completely encased by shell or cuticle. Metabolism, however, will have to adjust itself to this periodic mode of life and this can be done in two ways: either by a relative increase in activity during the periods of submergence, or by a relative decrease in basic metabolism during the periods of exposure. The former possibility is illustrated by the populations of *L. rubra* from different tidal levels as studied by Morton *et al.* In that species the higher the position of a population on the shore and therefore the shorter the time available for feeding, the more intense is the respiration and filtering rate during submergence. The latter possibility is illustrated by *C. hirsuta* as discussed in this paper, and also by *Chthamalus* sp. which, according to Barnes & Barnes (1959), has a lower respiration than other cirripede species from low intertidal habitats.

The low metabolism of *C. hirsuta* as compared with that of *N. bidentata* is most obvious in moist air in which that of the latter exceeds that of the former by about 250%, although *N. bidentata* weighs about 20 times as much as *C. hirsuta* (Fig. 1). In most crustaceans metabolism is proportional to body surface or to some intermediate between the latter and body weight. Thus in the equation

$$y = a.W^b$$

where y = oxygen consumption, W = weight and a, b are constants, the exponent b usually assumes values between 0·65 and 0·8 (see Table 4 in Wolvekamp & Waterman, 1960, p. 45). If this range of values were to hold for *C. hirsuta* and *N. bidentata*, and if the metabolism of the latter species were given, then *C. hirsuta* ought to have a Q_{O_2} in water between 600 and 800 mm^3 $O_2/g/h$ and in air between 300 and 400 mm^3; instead it has Q_{O_2}'s of about 500 and 100 mm^3 $O_2/g/h$ respectively.

Compared with *N. bidentata*, the 'resting metabolism' (that is, oxygen consumption in moist air) of *C. hirsuta* is much more reduced than its 'activity metabolism' (that is, oxygen consumption in water). This would be of ecological significance if it indicated that plenty of food can be gathered during the bursts of high activity in water, whereas the demands on the food supply during rest are disproportionally low. The low oxygen consumption in air of *C. hirsuta* as compared with that of *N. bidentata* is very likely correlated with the simple leaf-shaped structure of its gills which can be put together and tucked away under the anterior three pairs of pleopods, thereby reducing greatly the size of exposed gill area. In *N. bidentata* the extensive folds of the gills should make such manoeuvres more difficult. Furthermore, the greater ability of *C. hirsuta* to roll up into a ball ought to give better protection to all sensitive epithelia and therefore reduce even further the exchange of gases between environment and organism. In moist air specimens of *C. hirsuta* will immediately roll into a ball, leaving a small gap between head

and telson through which gas exchange can take place while water loss should be reduced to a minimum. Physiologically the same mechanism is used by intertidal barnacles which, according to Monterosso (1928) and others, keep their opercula gaping a bit in moist air so as to provide for the access of atmospheric oxygen to the gills. In dry air, however, barnacles close their opercula completely. Similarly, specimens of *C. hirsuta* in dry air curl up so well that water loss is kept to the rate shown in Fig. 4. *N. bidentata*, on the other hand, neither in moist nor in dry air will roll its body into a perfect ball.

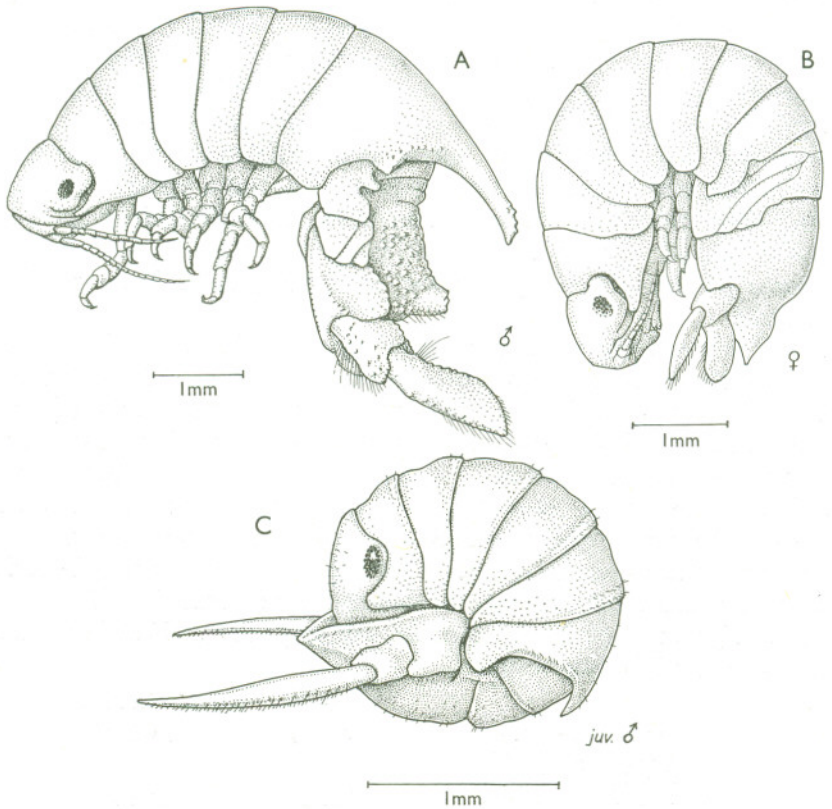

Fig. 5. Drawings (by Miss Maria Wimmer, Vienna) to show the positions occupied by *N. bidentata* (A, male, B, female) and *C. hirsuta* (C, juv. male) when exposed to dry air.

In moist air it will cling to the substratum, in dry air it will curl up, but cannot do much better than is indicated by Fig. 5 A, B—which may be compared with the perfectly constructed ball into which *C. hirsuta* is able to change (5 C). How much oxygen is consumed, if any, by *C. hirsuta* in dry air, cannot be determined by volumetric respirometry. The slow rate of water loss under such conditions indicates that gas exchange must be very small indeed.

If the findings of Bursell (1955) on transpiration in terrestrial isopods may be applied to marine isopods, then it is likely that *C. hirsuta* hardly loses any body water at all, but that most of the loss of weight apparent from Fig. 4 is due to water lost from the cuticle, since lipoids impregnating the endocuticle will effectively prevent further diffusion of body water. Sections through the cuticle of the two isopods failed to reveal any histological differences between them. Thus it may be assumed that the striking differences in their tolerance of desiccation are entirely due to the better protection which *C. hirsuta* is able to give to its more sensitive ventral body surfaces.

The periodicity of submergence and exposure is bound to affect the mode of life of *C. hirsuta* in many ways. Thus the whole metabolism should be profoundly influenced by the steep fluctuations of activity and oxygen consumption in this species. The burst-like mode of defaecation shown in Table 3 is very likely a reflection of this influence, pointing towards an endogenous factor which even under constant conditions imposes a certain rhythmicity on the whole process of feeding and digestion. This rhythmicity apparently is not correlated with the tidal phases, but seems to be the expression of a rhythmic pattern of activity and rest underlying the behaviour of each individual.

In *N. bidentata* the apparent rhythmicity in feeding which is noticeable under certain conditions was shown to be the result of exogenous factors, that is, of daily fluctuations in the oxygen content of the medium (Wieser, 1962*a*). If provided with sufficient oxygen *N. bidentata* feeds round the clock. It could be conjectured that in *C. hirsuta* the pauses between feeding bursts are either a reflection of the relatively low resting metabolism of this species, or an adaptive characteristic assuring better digestion of the foodstuffs.

Whatever the causes might be of the differences in feeding behaviour between the two species of isopods, they did not express themselves in the relative weights of their faeces, since the weighing of several batches of faecal pellets gave the following results:

	C. hirsuta	*N. bidentata*
No. faecal pellets (from Table 3 this paper and Table 4, Wieser 1962*a*)	$6{\cdot}0 \pm 2{\cdot}4$	$13{\cdot}6 \pm 4{\cdot}8$
Average dry weight of one pellet	$0{\cdot}5\ \mu g$	$5{\cdot}0\ \mu g$
Average dry weight of faecal pellets/h	$3\ \mu g$	$65\ \mu g$
Average dry weight of pellets/mg body wt/h	$3{\cdot}5\ \mu g$	$3{\cdot}8\ \mu g$

It follows that just like gill area and respiratory rate in water, the average rate of faeces production in *C. hirsuta* and *N. bidentata* is proportional to the weight of the animals. The meaning of this relationship cannot be understood without studying in a more analytical way the whole nutritional physiology of the two species in question.

SUMMARY

In the investigation described in this paper, respiration, resistance to desiccation and feeding behaviour of the mid- to upper-tidal isopod *Campecopea hirsuta* was studied and compared with the analogous parameters of behaviour in the lower intertidal species *Naesa bidentata*.

Respiration rate in water of *C. hirsuta* depends on the number of specimens used, the Q_{O_2} of one specimen having been estimated to amount to about 500 mm^3 $O_2/g/h$ at 20° C. In moist air the respiration rate is 108 ± 30 and 87 ± 14 $mm^3/g/h$ at 20° C according to whether the animals were put on damp filter paper or directly on the glass bottom of the respirometer vessel.

The respiration rate in water of single specimens of *C. hirsuta* thus equals that of the 20-times heavier species *N. bidentata*, whereas the respiration rate in air of the latter species exceeds that of the former by nearly 250%.

No tidal rhythmicity could be detected in the respiration of *C. hirsuta*.

The respiration of the bivalve *Lasaea rubra*, studied by Morton *et al.* (1957), was reinvestigated and it was found that on moist filter paper this species possesses a low, albeit measurable, oxygen consumption which increases by about 2·5 times if a few drops of water are added so that the animals are covered by a thin film.

In the two isopod species studied the ratio gill area/wet body weight is approximately constant.

C. hirsuta displays amazing powers of resistance to desiccation. After 12 h in dry air at approximately 18° C it has lost not more than 20% of its initial weight and can thus be compared to the bivalve *L. rubra*, whereas *N. bidentata* within 6 h has lost about 50% of its initial weight. The efficiency of *C. hirsuta* in this respect is ascribed to its ability to roll its body into a tightly closed ball, thereby protecting all of the sensitive ventral surface against loss of water.

Campecopea hirsuta feeds on the blue-green algae that make up the outer layer of the lichen *L. pygmaea*. When continuously submerged the isopod feeds in bursts, the timing of which is different in different specimens. This mode of feeding under experimental conditions is taken as reflecting the rhythmic way of life of this species in its natural environment but it seems to be controlled by endogenous factors. *Naesa bidentata*, on the other hand, does not display such endogenous rhythms in its feeding behaviour.

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