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EFFECTS OF FEEDING AND OF CHEMICAL STIMULATION ON THE OXYGEN UPTAKE OF *NASSARIUS RETICULATUS* (GASTROPODA: PROSOBRANCHIA)

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(Figs. 1–8)

Exposure to food odours causes an increase in oxygen uptake by *Nassarius reticulatus* L. The response is immediate and lasts between $\frac{1}{4}$ and $\frac{1}{2}$ h. When snails have fed, oxygen uptake remains elevated for 2–3 days. The duration of elevated rates of oxygen uptake parallels the duration of the behavioural effects of feeding.

INTRODUCTION

Nassarius reticulatus, like most other members of the Nassariidae and Buccinidae, is a scavenger. It apparently relies on the rapid detection and location of a food supply which is intermittently and unpredictably available. The olfactory reactions of *Nassarius* species are well-adapted for finding dead or damaged animals (Copeland, 1918). Stimuli indicating the presence of food provoke an impressive increase in activity of most starved *Nassarius* (Dimon, 1905; Copeland, 1918). Recently-fed whelks, however, often fail to respond to the same stimuli (Crisp, in preparation).

It is commonplace for oxygen consumption or metabolic rate to increase after feeding. A single meal elevates the oxygen uptake of such diverse animals as cod, crabs and mussels (Saunders, 1963; Wallace, 1963; Thompson & Bayne, 1972). We were therefore interested in finding out whether the behavioural changes of *Nassarius* involved in food detection and resulting from its ingestion were accompanied by changes in the non-nervous physiology, as represented by oxygen uptake.

As preliminaries to a study of the effects of feeding and food stimuli on oxygen consumption it was essential to obtain an idea of the rates of oxygen uptake of starved whelks, and of the factors, other than feeding or the stimuli associated with food, likely to affect oxygen uptake in our experiments. These included the size, sex and reproductive condition of the individuals. The principal external factor bound to change during each experiment was the oxygen tension.

MATERIALS AND METHODS

Collection and maintenance of animals

Most specimens of *Nassarius reticulatus* L. were supplied by the Marine Biological Association of the United Kingdom from Plymouth Sound. A few were collected from the sandy shore at

Rhosneigr, Anglesey. Animals were kept in running sea water (33·5‰) without food for 2 weeks before use. Most were held at 16 °C, but the animals used in experiments to establish the duration of increased respiration after feeding were simply held in the laboratory sea-water supply which fluctuated between 16 and 19 °C.

Respirometric technique

Oxygen consumption of *Nassarius* was measured using a scaled-up version of the oxygen electrode technique described and evaluated by Davenport (1976). Perspex vessels of 35 or 55 ml capacity were used and are illustrated in Fig. 1. The oxygen electrode (Radiometer E 5046) was connected via a Radiometer PHM 71 Mk2 pH meter to a Smith's Servoscribe chart recorder on which oxygen tensions were displayed.

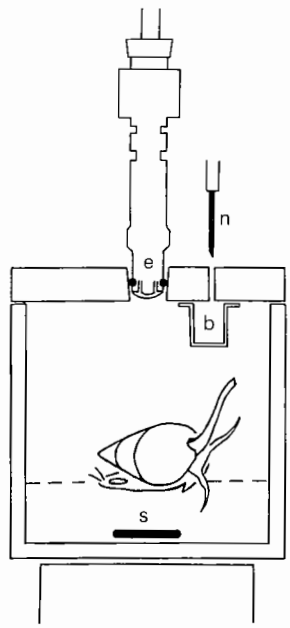

Fig. 1. Respirometer chamber. b, Beaker for food or chemical stimuli; e, electrode; n, hypodermic needle; s, stirrer.

The following experimental protocol was adopted to estimate oxygen consumption of individual *N. reticulatus*. All experiments were done at 16 °C. Zero oxygen tension was calibrated by immersing the electrode in sodium dithionite solution for 20 min. Before each experiment the oxygen electrode was suspended in air-saturated, filtered, u.v.-treated sea water and allowed to equilibrate until a constant oxygen tension was recorded (usually 30–60 min). The trace obtained represented 100 % air-saturated sea water and the apparatus was adjusted so that the range from zero oxygen tension to 100 % air saturation was represented by a near full-scale chart deflexion.

The respiration chamber was then filled with air-saturated, filtered, u.v.-treated sea water and the whelk added. The lid, complete with vial where appropriate (see 3 below), was sealed to the chamber body by a smear of silicone grease. The electrode was gently inserted into the tapered hole in the lid and the assembly placed in a 16 °C bath over an immersible magnetic stirrer.

The slope of the trace produced as the animal reduced the oxygen tension in the chamber was a measure of the rate of oxygen uptake, which was calculated from the relationship:

$$\text{rate of oxygen uptake} = \frac{V\,[O_2]\,S\,(\cot\theta_{exp} - \cot\theta_{contr})}{R},$$

where V = volume of water (ml),
$[O_2]$ = oxygen concentration in air-saturated sea water (ml O_2 per ml s.w. at 760 mmHg total pressure),
θ_{exp} = angle made by trace with the horizontal when chamber contained animal,
θ_{contr} = angle made with the horizontal when chamber did not contain animal,
R = scale deflexion from zero oxygen tension to air saturation (cm),
S = chart speed (cm h^{-1}).

Control experiments showed that the electrode's oxygen consumption was negligible in vessels of the sizes used. However, in some experiments, as noted below, not all the oxygen consumption was attributable to the whelk.

At the end of the experiment the total wet weight of the whelk, the wet weight of the tissue and the dry weight of the tissue after freeze-drying were measured.

Delivery of food or chemical stimuli

In pilot experiments, measurement of the oxygen consumption of *Nassarius* before and after feeding established that an increase in respiration rate occurred after feeding. The method involved repeated handling of the animals, and no information was available about their respiration in the critical period immediately before, during and immediately after feeding. Consequently, a more refined method of delivery of food and other substances to the whelks was devised. The lid of the Perspex respirometer has a fine hole (1 mm diameter, 10 mm long) to one side of the main electrode hole. Control experiments with deoxygenated water in the respirometer showed that oxygen exchange between the temperature bath and the water of the respirometer through this hole was undetectable, even over 2–3 days. In those experiments which involved the delivery of substances to the whelks, a small plastic vial (1·4 ml) with a substantial upper flange was attached by a film of silicone grease to the underside of the lid beneath the fine hole. In feeding experiments the vial contained 0·2 g wet weight of *Carcinus* gonad and was topped up with aerated, filtered sea water. In crab extract experiments, the extract, prepared by grinding whole crabs with a little sea water and then filtering and freezing in aliquots to provide a consistent stimulus, filled the whole vial. When either glycine or sucrose was the stimulus, the vial was filled with a molar solution in distilled water; this resulted in a final concentration of 25 mM in the respirometer chamber.

After the vial had been filled and applied to the underside of the lid, external surfaces were carefully washed and dried so that there was no trace of the vial contents outside. The lid was fitted to the respirometer which contained aerated filtered sea water and a specimen of *Nassarius*. After inserting the electrode the whole assembly was placed in the temperature bath and respiration monitored for 30–45 min to give an estimate of the rate of oxygen uptake of the starved, unstimulated animal. Then a hypodermic needle was gently inserted into the fine hole in the chamber lid and the vial dislodged, thus delivering its contents to the animal. Measurement of oxygen consumption continued for a further period which depended on the purpose of the experiment.

A variety of control experiments was performed. Firstly, with a whelk present, a vial containing sea water only was dislodged. The slight disturbance caused by the falling vial had no discernible effect on oxygen consumption. Secondly, for experiments with crab gonad, crab extract, sucrose and glycine a series of control studies was performed to establish the 'respiration rates' of the substances added. These were negligible for the crab extract, sucrose and glycine, but were appreciable for the crab gonad. In all calculations of *Nassarius* oxygen consumption, these control experiments were taken into consideration, as was the change in effective respirometer water volume caused by the delivery of the vial contents into the chamber.

Behavioural observations

Throughout the period of respirometry the behaviour of each whelk was observed. In those experiments in which substances were added to the respirometer chamber the timing of various activities was noted on the trace. These included onset of movement, proboscis extension and retraction, finding of the food, eating and ceasing to eat. Later, these activities were scored by 5 min periods. Positive responses were noted if the whelk moved or everted the proboscis respectively for more than half the time under consideration. If the response was displayed, but persisted for less than half the time, a partial response was recorded.

Experimental sequences

Using the techniques detailed above, the following experiments were performed:

Effect of oxygen tension upon oxygen uptake

Nine specimens of *Nassarius* were placed, in turn, in the respirometer and allowed to exhaust the available oxygen. Oxygen consumption at various air saturation levels was calculated from the changing slopes of the oxygen tension traces.

Resting oxygen uptake of starved Nassarius

The oxygen uptake of seven male *Nassarius* (ranging from 0·0086 to 0·996 g dry tissue weight) and 13 females (0·0242–0·1859 g dry tissue weight) was measured at 80 % saturation to assess the range of resting oxygen uptake rates and the effects of size and sex on respiration.

Response to food

The period of food detection, eating and return to quiet behaviour. Fifteen whelks were held, in turn, in the respirometer for 30–40 min to establish their initial oxygen consumption rates. Food was added and behaviour and respiration monitored for a further hour. Behaviour after the addition of food was not synchronous since some whelks took much longer than others to locate and eat the food. However, all had finished eating and become quiescent before the end of the experimental period.

Longer term study to establish the duration of elevated rates of oxygen uptake after feeding. Six whelks were placed in turn in the respirometer and treated as for the short-term study above. The rates of oxygen uptake of six others were measured without allowing feeding. All were replaced in running sea water. Rates of oxygen uptake were measured again 1, 2 and 4 days later. Student's t test was used to assess the significance of any changes in oxygen uptake compared with starved levels.

Response to crab extracts

Full strength extract. Six starved *Nassarius* were placed, in turn, in the respirometer and held for 30–40 min to establish the initial respiration rate. The crab extract was then delivered to the animal and respiration and behaviour monitored for a further hour.

Diluted crab extract. To establish a threshold concentration for the respiratory response to the presence of crab extract, a further series of 17 whelks was exposed in the respirometer to dilutions of the stock extract of 1/10th or 1/60th strength.

Response to glycine and sucrose

The response to these two substances was studied as for full strength crab extract.

Effect of feeding on the response to crab extract

Four whelks were fed in the respirometer and returned to the stock tanks. Their rates of oxygen uptake were measured every day for 3 days.

RESULTS

Effects of oxygen tension on oxygen uptake

We obtained 26 complete records of oxygen uptake over the range 0–100 % saturation in the 33·5‰ sea water at 16 °C. Ten of these were repeated observations on one individual and nine on another. The remaining seven were all from different animals. Fig. 2 shows the mean relative oxygen uptake together with 95 % confidence limits at various oxygen tensions for all 26 records. In order to reduce the effect of the wide variation in

initial rates of oxygen uptake, the values of oxygen uptake were calculated as a percentage of the uptake at 80% saturation. There was an approximately linear relationship between average oxygen uptake and oxygen tension over the range 10–90% saturation. Below 10–15% saturation, oxygen uptake was more rapidly reduced with declining oxygen tension. Many of the records, however, showed clearly that oxygen uptake did not decline asymptotically to zero at near zero oxygen tension, but was maintained at 10–20% of the 80% saturation level until virtually all the oxygen was exhausted.

Animals removed from the apparatus after some hours at zero oxygen tension were inactive. When returned to aerated sea water they recovered almost immediately. There were no deaths attributable to anoxia.

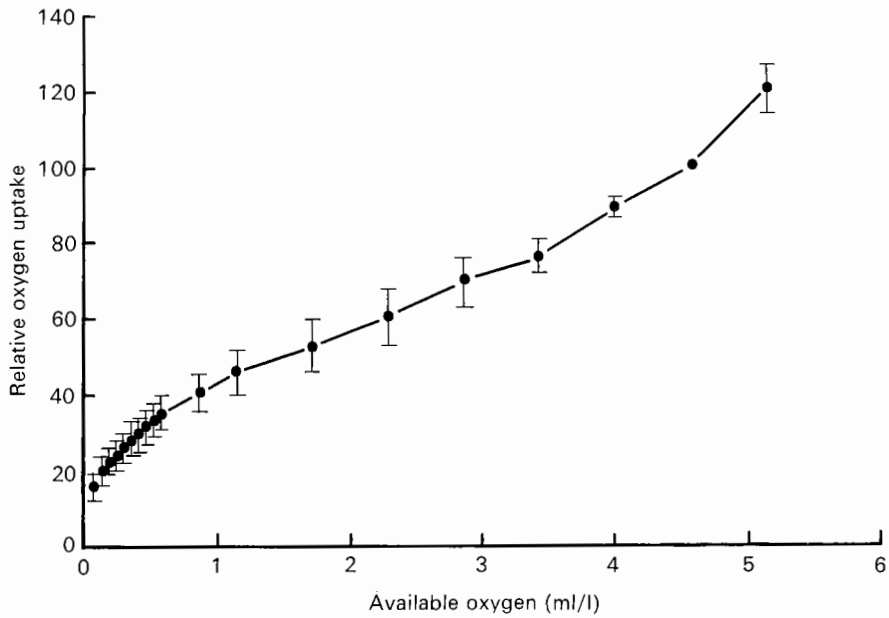

Fig. 2. Effect of oxygen tension on oxygen uptake. The bars show 95% confidence limits.

Resting oxygen uptake of starved Nassarius

Rates of oxygen uptake varied widely between individuals. Fig. 3 shows the scatter of points obtained by plotting oxygen uptake (in μl O_2/h) against dry weight of tissues (g) on logarithmic coordinates. The regression line for the points determined in March and April was:

$$\log (\text{oxygen uptake}) = 1{\cdot}78 + 0{\cdot}42 \log (\text{dry weight of tissues})$$

but r^2, the coefficient of determination, was only 0·09. The regression line therefore falls far short of significance. The regression line for the points determined in July was:

$$\log (\text{oxygen uptake}) = 2{\cdot}30 + 0{\cdot}95 \log (\text{dry weight of tissues}).$$

It is noticeable that much of the variation in log (oxygen uptake) in the measurements

made in July is accounted for by the variation in log (dry weight) ($r^2 = 0{\cdot}95$, corresponding to $0{\cdot}002 > P > 0{\cdot}001$ for 4 degrees of freedom). This is not true for the points measured in March and April when many of the females laid egg capsules in the stock tank. There was no indication of reproductive activity in July.

There was no consistent difference in oxygen uptake according to sex.

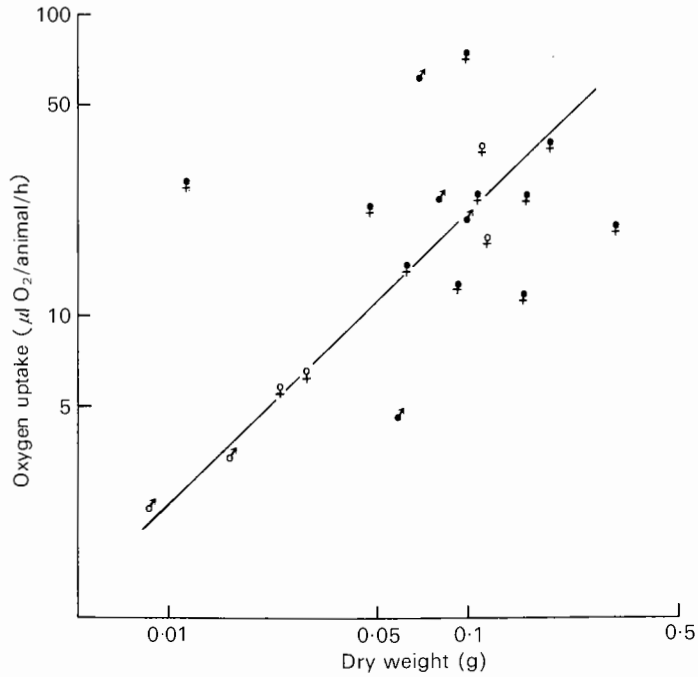

Fig. 3. Resting oxygen uptake of starved *N. reticulatus* at 80 % air saturation, according to weight and sex. Open symbols, males and females measured July 1977; closed symbols, males and females measured March/April 1977. The regression line is for the points determined in July only.

Effect of feeding on oxygen uptake and behaviour

Fig. 4 shows the oxygen uptake before, during and after feeding of the first six animals to be fed in the apparatus. They had been starved for a fortnight before the experiment and were apparently satiated by less than 0·2 g of crab gonad since they all walked away from the food after eating only part of it. Other individuals which had been starved for 5–6 weeks showed very similar increases in oxygen uptake, although after prolonged starvation most ate all the food they were offered.

It is noticeable that the increase in oxygen uptake occurred as soon after the release of food into the chamber as it was possible to take a measurement (within 2–3 min). This was almost always well before the snail had located the food. The increase was initially 3–4 times the starvation rate (Fig. 4G).

Before the release of food into the chamber, most snails had the foot expanded but were quiescent or moving very slowly. Some had retracted into the shell. As soon as the food was released the retracted snails emerged, and all snails began active movement with

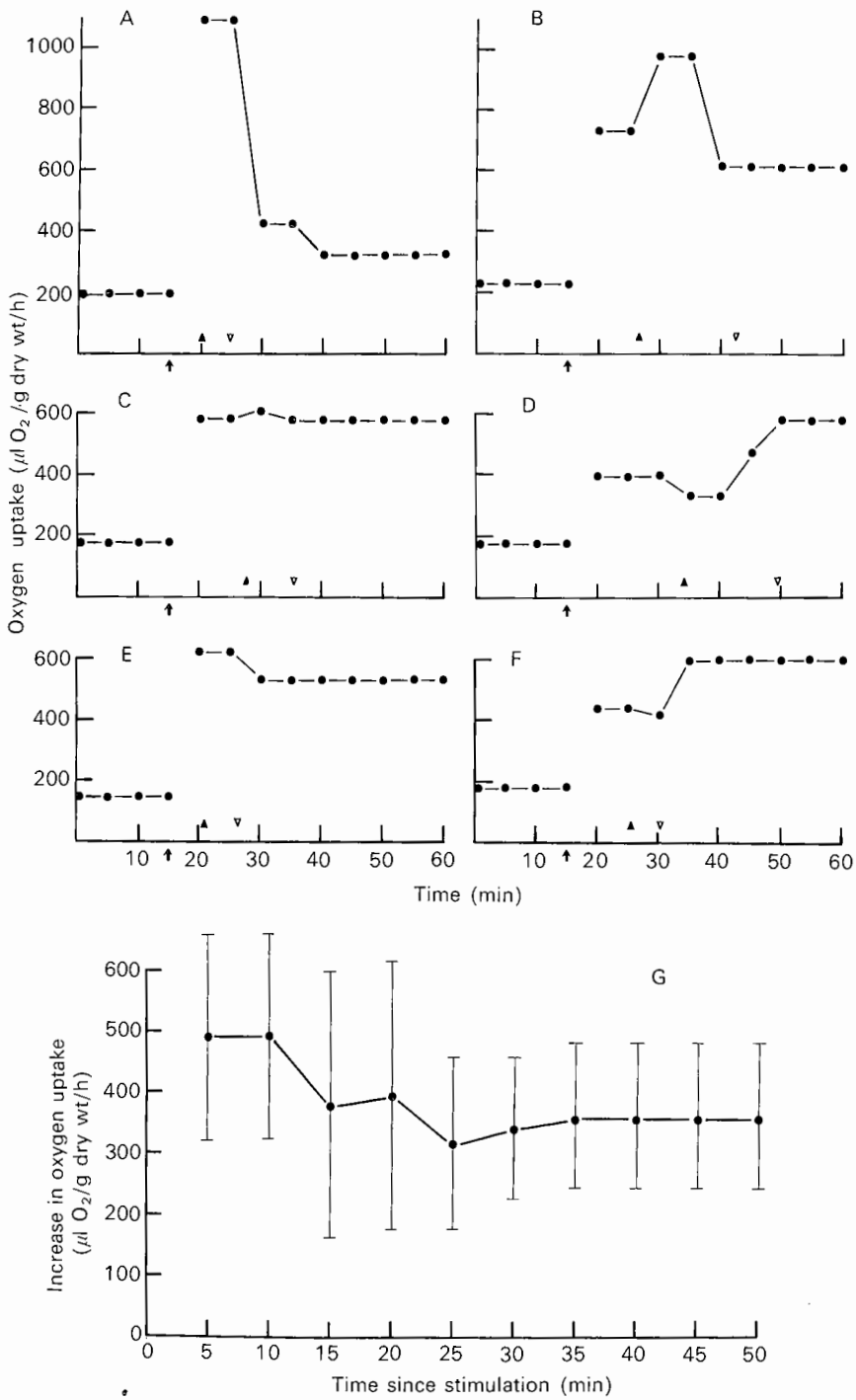

Fig. 4. Effect of feeding on oxygen uptake. (A–F) Individual responses of six snails. The arrow indicates the moment of release of food into the chamber. The upright triangle shows the moment the snail started to feed. The inverted triangle shows when it stopped feeding. (G) Averaged response of the whole group. The bars show 95 % confidence limits.

the foot fully extended and the siphon slowly waving. The proboscis was also extended. After some minutes most snails stopped moving about the chamber but continued to explore it with the extended proboscis. Owing to the confused water currents in the chamber, snails which would normally have found the food by moving upstream sometimes searched for 20–40 min before reaching it. Oxygen uptake was elevated all this

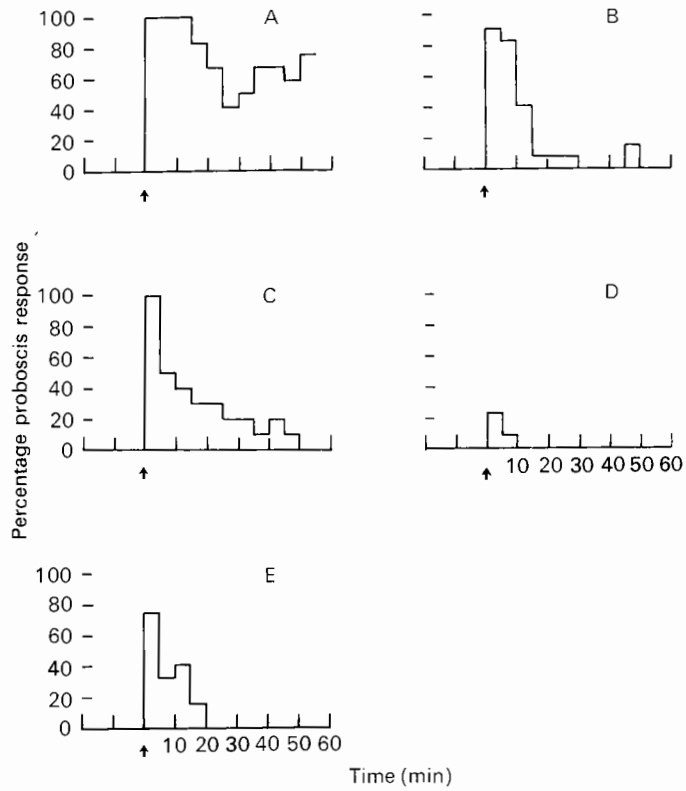

Fig. 5. Effect of feeding or chemical stimuli on the proboscis response. (A) 0·2 g crab gonad ($N = 6$). (B) Full strength *Carcinus* extract ($N = 6$). (C) 1/10th strength *Carcinus* extract ($N = 6$). (D) 1/60th strength *Carcinus* extract ($N = 11$). (E) 25 mM glycine ($N = 6$). Arrows indicate the moment of release of the stimulus into the chamber.

time, and a further increase was obvious in a few individuals when they started to feed. Fig. 5 A shows the responsiveness, as indicated by proboscis eversion, of a different group of six snails fed under the same conditions as those whose oxygen uptake was measured. Responsiveness decreased with time but was still high an hour after release of food into the chamber. Similarly, snails were very active immediately after the onset of stimulation. Activity declined a little sooner than did the proboscis response, but continued at a fairly high level for over an hour.

Fig. 6 shows that the oxygen uptake of fed snails was higher than that of starved controls for 2–3 days after feeding.

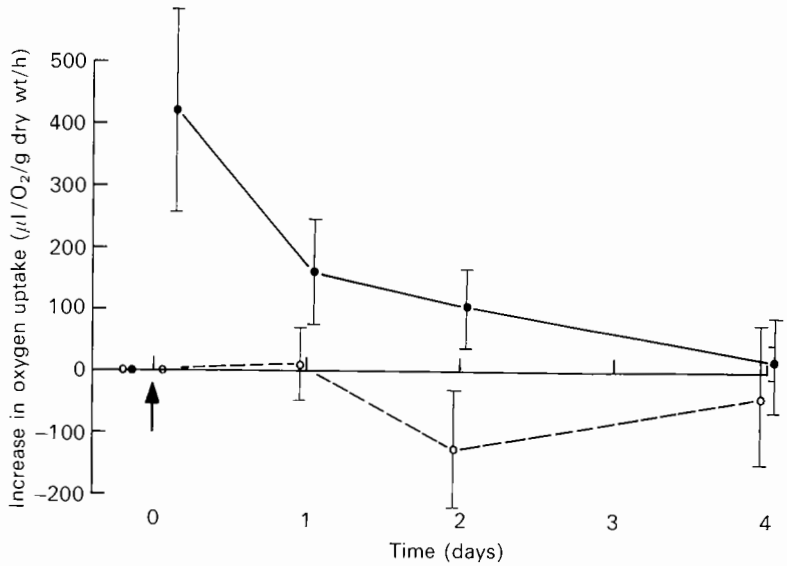

Fig. 6. Long-term effect of feeding on oxygen uptake. Solid circles represent snails fed at the arrow. Average initial starved uptake was 237 μl O_2/g dry wt/h. Hollow circles represent controls starved throughout. Average initial starved uptake was 395 μl O_2/g dry wt/h. Bars represent 95 % confidence limits ($N = 6$).

Effect of chemical stimuli on oxygen uptake and behaviour

It was clear from the foregoing experiments that ingestion of food was neither the only, nor necessarily the most important factor in elevating oxygen uptake. The chemical stimuli emanating from the food had an immediate effect on oxygen uptake. We therefore tested the responses to chemical stimuli in the absence of food. Fig. 7 shows average increases in oxygen uptake in response to three strengths of *Carcinus* extract. The full strength extract (Fig. 7A) and the 1/10th strength extract (Fig. 7B), provoked both an increase in oxygen uptake and behavioural responses including proboscis eversion in all of the starved snails tested. Extract of 1/60th strength sometimes evoked both metabolic and behavioural responses (Fig. 7C), sometimes neither (Fig. 7D). On only one occasion was there as increase in oxygen uptake without concomitant proboscis extension. A proboscis response never occurred without an increase in oxygen uptake. Although the magnitude of the initial response to the higher concentrations of crab extract was comparable with that of the response when food was available, the response did not last as long. A statistically significant effect persisted for only 20–25 min. The proboscis response of the same individuals also habituated over the same period (Fig. 5B, C, D.)

Nassarius responds behaviourally to a variety of pure chemicals, including glycine. Glycine at a final concentration in the chamber of 25 mM caused proboscis eversion and an increase in oxygen uptake in all six snails tested, as shown in Fig. 8A. The effect lasted 15–20 min, as did the proboscis response (Fig. 5E).

Nassarius shows no behavioural response to sucrose except at high concentrations. Sucrose at a final concentration of 25 mM in the chamber had no effect on the oxygen

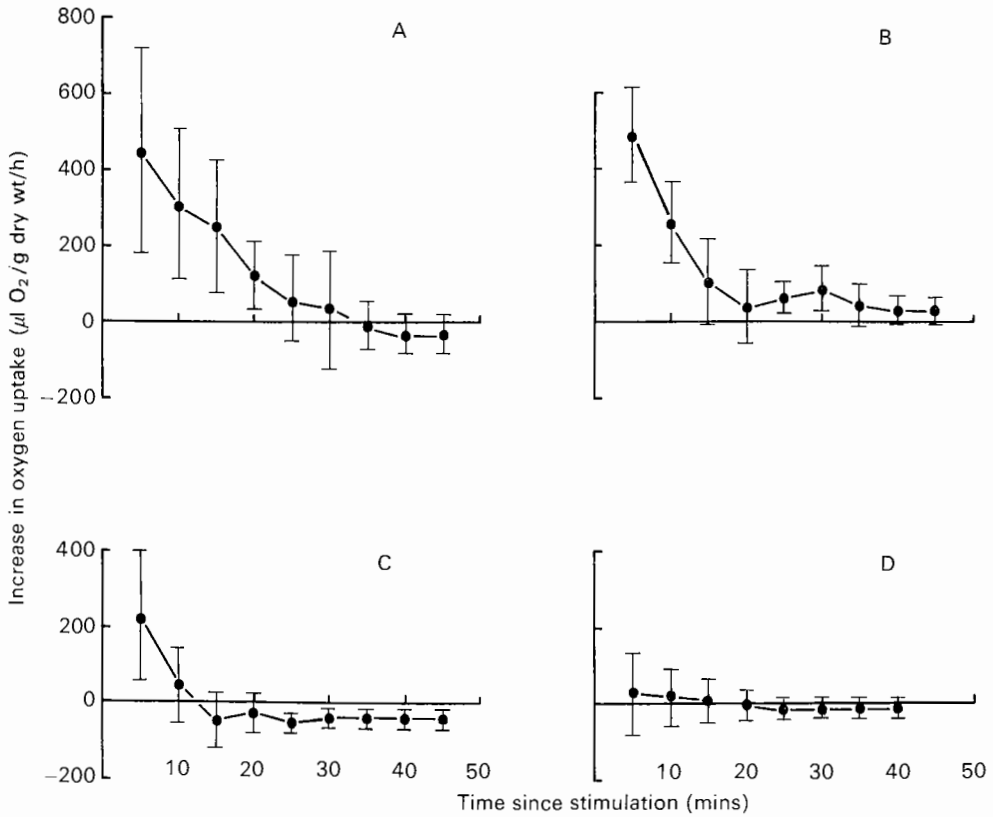

Fig. 7. Effect of food extracts on oxygen uptake. (A) Full strength extract ($N = 6$). Initial starved uptake was 200 μl O_2/g dry wt/h. (B) 1/10th strength extract ($N = 6$). Initial starved uptake was 155 μl O_2/g dry wt/h. (C) 1/60th strength extract, animals responding behaviourally ($N = 7$). Initial starved uptake was 163 μl O_2/g dry wt/h. (D) 1/60th strength extract, animals not responding behaviourally ($N = 4$). Initial starved uptake was 132 μl O_2/g dry wt/h. Bars represent 95 % confidence limits.

uptake of the six snails tested (Fig. 8B), neither did any snail evert the proboscis or show any other behavioural response.

Effect of feeding on the responses to chemical stimuli

Crab extract of 1/10th strength never failed to elicit both behavioural responses and an elevation of oxygen uptake in starved snails. After feeding, however, the same extract was sometimes ineffective. Although some individuals gave an indication of a slight response, the average oxygen uptake of four individuals was not significantly different from their unstimulated rates of uptake for 3 days after feeding. Behavioural responses were also lacking. The experiment was discontinued after 3 days.

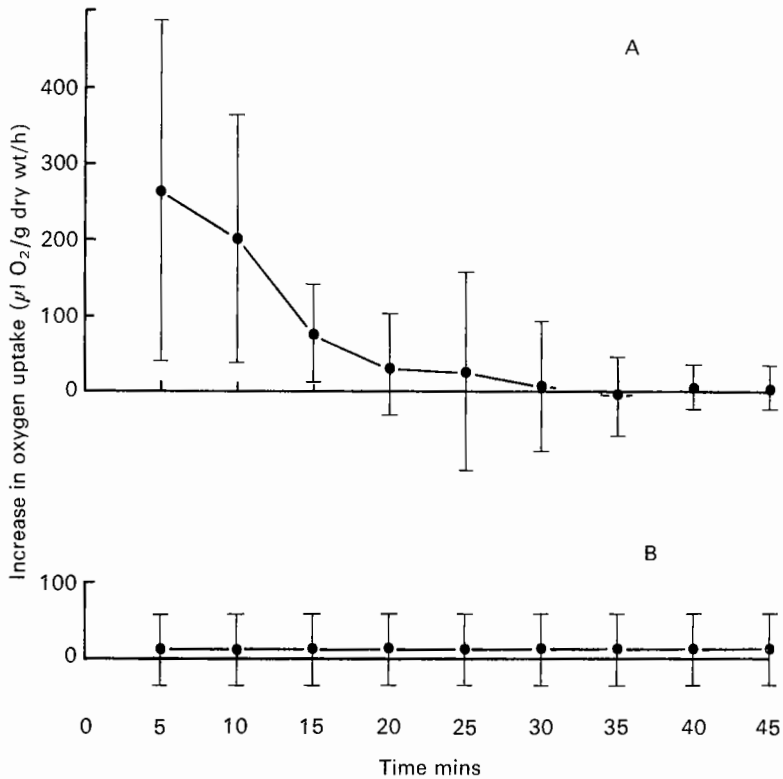

Fig. 8. Effect of pure chemicals on oxygen uptake. (A) 25 mM glycine ($N = 6$). Average initial starved unstimulated rate was 190 μl O_2/g dry wt/h. (B) 25 mM sucrose ($N = 6$). Average initial starved unstimulated rate was 97 μl O_2/g dry wt/h. Bars represent 95 % confidence limits.

DISCUSSION

According to Prosser (1973), animals fall into two classes with respect to the effect of oxygen tension on oxygen uptake. Animals in which uptake declines linearly with reduced oxygen tension are 'conformers' and those in which oxygen uptake remains constant over a wide range of oxygen tensions are 'regulators'. The terms are chosen by analogy with osmo-conformers and regulators. It is not clear, however, that the two activities are strictly comparable. Ions can be pumped actively across the animal's body surface: gas exchange, in contrast, takes place by passive diffusion. In any case, the two classes appear to be extremes of a continuum rather than strictly separate. Below some critical oxygen tension, which varies from species to species and even according to condition in a single species (Bayne, 1971), all 'regulators' become 'conformers'. 'Regulators' obviously cannot maintain their constant uptake at oxygen tensions so low that there is insufficient thermo-dynamic potential to allow diffusion through the tissues. The difference between the two classes is therefore determined by the extent to which uptake is diffusion limited. The oxygen uptake of *Nassarius reticulatus* declines more or less linearly over the range 5–1 ml O_2/l, but the line does not pass through the origin as it would if it 'conformed' to a diffusion model. At lower tensions the rate of decline is

steeper. Like other gastropods (Shumway, in preparation) it would be classified as a 'conformer' in Prosser's sense.

The individual variation of oxygen consumption of *Nassarius* measured in March and April was not attributable to the effect of size. It is likely that reproductive condition has a marked effect on oxygen uptake and accounted for some of the residual variability. It is also possible that diurnal or semilunar fluctuations in oxygen uptake occur as they do in a number of crustaceans including *Uca* species (Brown, Bennett & Webb, 1954), *Cancer pagurus* and *Maia squinado* (Aldrich, 1975). We found no evidence of such rhythms, but we did not deliberately seek them.

The value of b in the equation relating metabolism (m) to weight (w), $m = kw^b$, for *Nassarius* measured in July is high (0·95) compared with the values obtained by Shumway (in preparation) for *Nassarius* and other gastropods. There may be a seasonal variation in b. Bayne (1971) found that the summer value of b for *Mytilus edulis* was close to 1·0, whereas in the winter he obtained a value of 0·77.

Many animals display an increase in oxygen uptake after a meal (Saunders, 1963; Wallace, 1963; Thompson & Bayne, 1972). The initial phase of the increase is usually attributed to increases in activity (mechanical work of locomotion or of drawing water over the gills). It is commonly observed, however, that the observed increases in activity of effectors are inadequate to account for the magnitude of the increase in oxygen uptake (Wallace, 1963; Bayne, personal communication). This seems true also for *Nassarius*. On several occasions, although there was a clear increase in oxygen uptake, snails were no more active than they had been before stimulation. Furthermore, unstimulated snails were sometimes intermittently active with no detectable influence on oxygen uptake.

One of the most striking features of the effect is the rapidity of its onset. It occurs certainly within minutes, perhaps within seconds of chemical stimulation. This rise in respiration rate seems to be faster than that reported for cod, crabs or mussels, but the discrepancy may reflect differences in the methods of observation rather than real differences in the rate of the animals' responses.

The increase in oxygen uptake of *Nassarius* is correlated with such behavioural responses as increased activity and proboscis eversion, although the three responses do not always accompany one another. In all the experiments in which a proboscis response occurred, oxygen uptake was elevated. There was, however, no consistent difference in the rates of oxygen uptake of reactive snails during periods of proboscis eversion or withdrawal. Only on one occasion did the oxygen uptake of a starved snail increase in response to a chemical stimulus (at low concentration), without the individual also displaying a proboscis response. The behavioural responses and the elevated oxygen uptake all habituated after about the same duration of exposure to chemical stimuli. Previously fed snails, however, still had elevated oxygen uptakes but did not evert the proboscis in response to relatively high concentrations of chemical stimuli.

In general, our results seem most closely comparable with those of Thompson & Bayne (1972) for *Mytilus edulis*. They also found that sensory stimulation (with glucose, extracts of algae, or charcoal particles) caused a rise in the rate of oxygen uptake. When the stimuli were removed, oxygen uptake fell quickly back to routine levels. In contrast, *Nassarius* oxygen uptake declines after 15–30 min of continuous exposure to stimulating

chemicals. After feeding, oxygen uptake of *Mytilus* remained high for 1–2 days. The initial increase in oxygen uptake is marginally greater in *Nassarius* than in *Mytilus* (3 to 4 times the starved rate compared with 2 to 3 times); the duration of the increase is similar.

Bayne & Scullard (1977) resolved the sustained increase in oxygen uptake of *Mytilus* into two phases. The first component coincided with increases in the filtration rate and was taken to represent the mechanical cost of feeding. The second coincided with an increase in the rate of ammonia excretion and was held to represent the specific dynamic action of the food, or physiological cost of feeding.

The increase in oxygen uptake of *Nassarius* can probably also be resolved into at least two components. The first is mediated through external chemoreceptors and lasts only a short time, habituating at about the same rate as the behavioural responses. The mechanical cost of activation probably accounts for only a small fraction of the effect. The changes in the histological appearance of the salivary glands, gland of Leiblein and digestive gland which occur shortly after feeding are well known (Martoja, 1964). Release of stored secretion is followed by fresh synthesis. It is not known whether mere exposure to chemical stimuli, without feeding, affects the digestive structures, but the anticipatory elaboration of digestive enzymes might account for some of the apparent increase in the energy requirement of starved snails exposed to the smell of food. We should, however, be wary of assuming that increases in oxygen uptake necessarily indicate an increase in overall metabolism. We do not know how great a part anaerobic metabolism normally plays in *Nassarius reticulatus*.

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