

SPECIFIC DYNAMIC ACTION DEMONSTRATED IN THE HERBIVOROUS MARINE PERIWINKLES, *LITTORINA* *LITTOREA* L. AND *LITTORINA* *OBTUSATA* L. (MOLLUSCA, GASTROPODA)

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Abstract—1. Respiration rates of starved periwinkles, *Littorina littorea* and *Littorina obtusata*, increased by 40–60% when fed their preferred algal food for 1 hr, or after having been exposed for the same period to an aqueous extract of the alga.

2. The stimulus causing the rise in metabolic rate by algal extracts is therefore thought to be chemosensory in nature, and possibly composed primarily of dissolved free amino acids.

3. The respiration rates of *L. littorea* responded only to the green alga *Enteromorpha intestinalis* while *L. obtusata* demonstrated an increase in respiration rates when fed the ubiquitous brown alga, *Ascophyllum nodosum*, and to a lesser degree to *Enteromorpha*.

4. These results compare very well to postprandial increases in oxygen consumption demonstrated in vertebrates and marine bivalves where the components of specific dynamic action (SDA) are thought to be chiefly biosynthetic costs of digestion and assimilation.

INTRODUCTION

It is well known that the intake of food, particularly protein, by animals is associated with an increase in metabolic rate, the so-called “specific dynamic action” (SDA). Specific dynamic action has been simply divided into two components, the mechanical and physiological costs of digestion (Gaffney and Diehl, 1986), while other investigators have divided the total increase in postprandial metabolic rates into several components including the costs of food acquisition, digestion and absorption, protein synthesis and costs of growth (Widdows and Hawkins, 1989). In the study by Widdows and Hawkins (1989) on the blue mussel *Mytilus edulis*, they found that the cost of growth was significantly greater than either the energetic costs associated with food acquisition or digestion and absorption, and the cost of growth scaled positively with an increase in ingested ration. In a study of SDA and protein synthesis in the crab *Carcinus maenus*, Houlihan *et al.* (1990) found that protein synthesis accounted for 20–37% of total oxygen consumption and concluded that protein synthesis incurred the highest energetic cost in this invertebrate.

In *Mytilus edulis*, a suspension feeder, sensory stimulation whether by glucose, algal extracts, or inert particles causes a transient rise in oxygen uptake (Thompson and Bayne, 1972). When unfed *Mytilus*

consume microalgae, the rise in oxygen uptake was some 2–3-fold, and remained high for 1–2 days after feeding. Shumway (1983) showed a similar response in another bivalve, *Mulinia lateralis*, while Newell and Kofoed (1977) showed a significant increase in oxygen uptake correlated with an increase in filtration rate in the filter feeding gastropod, *Crepidula fornicata*. Crisp *et al.* (1978) found a similar pattern in the behavior and metabolism of the scavenging gastropod, *Nassarius reticulatus*. Unlike *M. edulis*, which feed almost continuously and do not search, such carnivorous gastropods spend a significant amount of time not searching for food. They are aroused from quiescent times by the detection of food (Crisp, 1969, 1978) using their well developed olfactory and rheotactic responses (Dimon, 1905; Copeland, 1918; Carr, 1967; and Crisp, 1969). Crisp *et al.* (1978) also demonstrated that the recognition of food odors by *N. reticulatus* was generally accompanied by overt changes in behavior such as increased activity, proboscis eversion, and an almost instantaneous increase in oxygen uptake (Crisp, 1979). Unless reinforced by continued food stimulus, all three activities began to decline after 15–30 min. As in *Mytilus* and *Mulinia*, however, actual feeding resulted in elevated respiration rates lasting much longer; some 3–4 days duration was reported in *N. reticulatus* from a single meal.

Sensing food at a distance can be interpreted as an adaptive response in a mollusc that has limited feeding opportunities because its prey is infrequently encountered temporally and spatially. The advantage

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to a filter-feeder is less clear, but in the complete absence of food particles *M. edulis* can greatly reduce pumping activity (Thompson and Bayne, 1972, 1974), presumably saving energy.

Littorina littorea shows a preference for green and *L. obtusata* for brown algae on both European (Dongen, 1956; Watson and Norton, 1985) and on New England shores (Lubchenco, 1978; Barker and Chapman, 1990; Shumway and Crisp, unpublished data); however, food preferences in gastropods can vary with the animals' past feeding experience, as demonstrated for carnivorous neogastropods. Wood (1968) found that *Urosalpinx* was attracted to barnacles or oysters depending on which had been the dominant food in the recent past. Such "ingestive conditioning" as it has been termed has been subsequently noted in the thaidis, *Nucella lapillus* (Ekaratnc and Crisp, unpublished data), *N. emarginata* (Palmer, 1984) and in *Aeolidia papillosa* (Hall *et al.*, 1982). Surprisingly, this phenomenon was first recognized by Carefoot (1967) in the herbivore, *Aplysia punctata*. *Aplysia* that had been fed a diet of *Enteromorpha* increased the preference for this species over several others when offered, including its natural food *Plocamium* sp.

In a study of SDA in response to water borne chemical cues and direct feeding in a marine herbivore, Carefoot (1987) described SDA in the sea hare, *Aplysia*. An SDA response of herbivores might well be expected since warm-blooded ruminants display a high SDA amounting to 30–60% of food energy (Webster, 1981). To demonstrate an increased metabolic activity in herbivores, we chose two gastropods, *Littorina littorea* L. and *Littorina obtusata* L., known to feed on different intertidal algae and believed to have distinct food preferences.

MATERIALS AND METHODS

Collection of samples

Littorina littorea were obtained from the foreshore of McKown Point, Boothbay Harbor, ME, and from the Ira C. Darling Center, Walpole, ME. *Littorina obtusata* were also obtained from the Walpole location. All sites are within a few miles of Boothbay Harbor and the algal species used in this study are common at both sites.

Respiration experiments

Routine rates of oxygen uptake were measured on 24 freshly collected and numbered animals of each species. The specimens of *Littorina littorea* ranged from 0.104 to 0.69 g dry weight, and averaged 0.85 g. *Littorina obtusata* ranged from 0.0031 to 0.0082 g dry weight, and averaged 0.0051 g. These size ranges were sufficiently narrow for size differences to have no significant influence on weight-specific respiration rate, and results were therefore expressed on a per individual basis.

Oxygen consumption was measured using either a Radiometer oxygen electrode (Shumway, 1981) or micro-Winkler titrations (Burke, 1969) on individual animals held in sealed containers at 15°C and 33‰ salinity filtered sea water (0.45 µm). Both methods gave comparable results, and the activity levels of all snails was similar within experiments. The same snails were then starved for 14 days and their oxygen consumption rates measured again. Six individuals of each species were then exposed for 1 hr to one of the following stimuli: (1) feeding on *Enteromorpha* plants; (2) contact with *Enteromorpha* extract; (3) feeding on *Ascophyllum* plants; (4) contact with *Ascophyllum* extract.

The individual rates of oxygen consumption were then measured again. Extracts of each of the two algae used were prepared by blending 5 g wet weight of algae with 500 ml of filtered sea water. The resulting liquid was filtered at 0.45 µm and stored for not more than 2 days in a refrigerator.

RESULTS

Respiration experiments

Table 1 summarizes the results of the oxygen flux data. Column one gives the mean dry weight in grams of the group of six animals used in each stimulus treatment. The initial selection for equal sizes was clearly successful since the variation between the means used in each treatment differed only by $\pm 14\%$ in *L. obtusata* and by only $\pm 6\%$ in *L. littorea*.

In every case where previously starved snails were exposed to their preferred food after starvation, whether to the alga itself or to an extract prepared from it, there was a significant rise in respiration rate of from 30–70% (Table 1). Apparently the taste or odor of the crude extract was as significant as making contact with, and presumably ingesting, the preferred alga in eliciting an enhanced rate of respiration. Extracts of the non-preferred alga raised respiration rates slightly, but in the case of *L. obtusata* significantly ($P < 0.05$). Contact with the non-preferred alga itself did not change the rate of respiration significantly (Table 1).

In all samples, routine respiration rates were 40–70% above standard rates of starved animals (Table 1). The oxygen consumption of periwinkles treated with the extract of the preferred alga or feeding on the preferred alga itself for only 1 hr rose to within 15% of, or even exceeded, the routine rates of freshly collected periwinkles (Table 1). The non-preferred food or its extract was far less effective, respiration rates continuing at more than 20% below measured routine rates.

DISCUSSION

Our results for these herbivorous gastropods compare favorably with those of Crisp *et al.* (1978) and

Bayne and Scullard (1978) for *Nassarius reticulatus* and *Nucella lapillus*, respectively. It appears that these carnivorous gastropods are able to sense the odor or taste of acceptable food to which they respond by an increase in metabolic rate. In both herbivores studied here, the SDA is dependent on the strength of the chemical stimulus, being greatest when it corresponds to a preferred alga. As yet, we do not know whether the increase in metabolic rate in response to olfaction alone is temporary, as in *Nucella* (Bayne, personal communication) and *Nassarius*, or whether feeding produces a longer lasting response. A rise of the magnitude observed continuing over the long term seems probable, since enhanced respiration rates after access to preferred food correspond closely with the routine rates of animals just removed from grazing algae on the shore. Unlike carnivorous molluscs, which feed opportunistically, these herbivores have food available continuously and probably, under natural conditions, feed with few pauses, respiration proceeding at the routine rate.

The SDA response to filtered extracts of algae suggests that *Littorina* can sense a chemical or organic compound present in the alga, and pre-ingestive chemical cues have been found to influence the feeding behavior of filter-feeding bivalves (Ward and Targett, 1989). Lubchenco (1978) examined algal preferences and activities of grazing marine herbivores, and found no evidence that snails could detect algae at a distance. Watson and Norton (1985) reached a similar conclusion. Experiments and observations of behavior in the vicinity of algae support this view (Crisp and Shumway, unpublished data). There was little or no indication of orientation towards algal fronds; the success in finding them appeared to be the result of a random encounter.

Function of specific dynamic action

The rise in respiration rate following intake of food has been recognized since the time of Lavoisier, some

200 years ago (Krebs, 1964), yet it is not completely understood, and relatively few studies have been made on poikilotherms. Numerous views have been proposed to explain this almost universal phenomenon, notably the work expended in food gathering and trituration, the work of peristalsis and formation of intestinal secretions, the absorption and translocation of metabolites and the cost of synthesis in the growth of biomass or formation of propagules. For proteins, Krebs (1964) has called attention to the costs of deamination, amino acid oxidation and in ureotelic organisms, urea synthesis. Most of these activities are post-prandial, but one must also assess the magnitude of, and question the function of, the preprandial rise in metabolic activity as shown by bivalves and gastropods. In all such cases that have been investigated, the rise in respiration rate due to an olfactory, gustatory or mechanical stimulus alone is transient and small. Calculations can be made from Crisp *et al.* (1978) for *Nassarius* given a strong stimulus of crab extract on the one hand, or a meal of 200 mg wet weight crab gonad on the other. The transient preprandial olfactory stimulus lasts only *ca* 30 min and for a 0.1 g dry weight animals results in an enhanced uptake of *ca* 8 μ l O₂. The meal itself caused a rise over several days amounting to an increase of 1800 μ l O₂, over 200-fold greater. With suspension feeders, there was a similar transient rise in respiration resulting from a stimulus unaccompanied by nourishment. The effect of feeding 14 day starved *Mulinia lateralis* caused an increase in uptake of 270 μ l O₂/mg dry wt, compared with 32 μ l O₂/mg dry wt when fed particulate charcoal and 62 μ l O₂/mg dry wt when stimulated by algal extract (Shumway, 1983). Newell and Pye (1971) obtained an increase of 5–6-fold in oxygen uptake in air using a Gilson respirometer when quiescent *Littorina littorea* were compared with active individuals. Significantly, they observed alternating slow to fast rates of oxygen uptake coinciding with periods of quiescence or

Table 1. Summary of respiration experiments, carried out at 15°C and 33‰ salinity

Species and treatment	Mean dry weight (g)	Mean routine* respiration (R)	Mean standard† respiration (S)	Mean postprandial‡ respiration (T)	R/S	T/R	T/S	T-S§	t-test
<i>Littorina littorea</i>									
(a) Fed <i>Enteromorpha</i>	0.0795	0.0798	0.0553	0.0797	1.44	0.999	1.448	+0.024	+4.28
(b) Extract alone	0.0859	0.0874	0.0569	0.0747	1.53	0.855	1.315	+0.175	+11.45
(a) Fed <i>Ascophyllum</i>	0.0849	0.0829	0.0557	0.0555	1.49	0.669	0.996	-0.0002	N.S.
(b) Extract alone	0.0898	0.0825	0.0574	0.0626	1.44	0.0759	1.089	+0.0052	N.S.
<i>Littorina obtusata</i>									
(a) Fed <i>Enteromorpha</i>	0.006	0.0259	0.0165	0.0161	1.57	0.623	0.976	-0.0004	N.S.
(b) Extract alone	0.005	0.0214	0.0144	0.0165	1.48	0.771	1.133	+0.0021	+2.31
(a) Fed <i>Ascophyllum</i>	0.005	0.0246	0.0146	0.0214	1.69	0.868	1.465	+0.0068	+4.09
(b) Extract alone	0.005	0.0209	0.0134	0.0226	1.68	1.081	1.670	+0.0075	+6.71

*Routine uptake, Animals immediately after collection ${}^R V O_2 = \text{ml O}_2/\text{hr}$ per individual; †Standard uptake, Animals previously starved ${}^S V O_2 = \text{ml O}_2/\text{hr}$ per individual; ‡Postprandial uptake ${}^T V O_2 = \text{ml O}_2/\text{hr}$ per individual. (a) Fed = 1 hr feeding with named alga after starvation. (b) Extract alone = contact with particle-free extract of named alga for 1 hr after starvation; §T - S, Difference between treated and standard rates tested for mean significance by paired student *t*-test = (mean T - S)/SE of difference from six replicates); ||Exceeds critical value for *t* of 2.3 for 5 degrees of freedom corresponding to *P* < 0.05 for null hypothesis of no effect of treatment.

All oxygen flux data for individuals in ml O₂/hr.

activity, respectively. The energy lost in an abortive preprandial burst of metabolism may therefore be so small that only a minor advantage need be proposed to account for it. It can be hypothesized that the advantage, if any, lies in preparing the animal for greater searching activity especially for carnivores and scavengers, though less so in herbivores and in synthesizing initial amounts of digestive enzymes and mucus ready for food intake and immediate digestion. For the postprandial costs, some of these costs are likely to be small in the case of herbivores. The food of marine periwinkles consists largely of carbohydrate, hence the cost of deamination or urea synthesis will be small. The two species studied are found where there is abundant algae available, especially *L. obtusata* feeding on brown algae in semi-sheltered rocky shores. *Littorina littorea* is capable of feeding on the ubiquitous fucoids and kelps, but it browses preferentially on green algae. To a lesser degree, it browses on reds (Lubchenco, 1978), on sporelings on rocks (Watson and Norton, 1985) and on decaying algae at the bottom of tidepools. With these preferences, little movement over the natural environment appears necessary to search for and find food.

Specific dynamic activity coefficients in other animals

The specific dynamic activity coefficient is expressed as the increase in respired energy associated with feeding as a percentage of the assimilation rate. In some instances it is quoted as a percentage of ingestion rate. Unfortunately, the assimilation (or ingestion) rates differ according to the ration, and therefore so does the SDA coefficient. If we take the routine ration as standard, the coefficient can be expressed as

$$\text{SDA coefficient} = (R_F - R_S)/A_F, \quad (1)$$

where R_F is the routine respiration rate, R_S the standard rate (starved) rate, and A_F the assimilation rate of the fed animal.

In warm-blooded ruminants, the coefficient is high (Webster, 1981) amounting to 30–60% of utilizable energy ingested. Reptiles (Coulson and Hernandez, 1979) and fish (Jobling, 1981) have lower coefficients (19–35% and 10–25%, respectively) despite costs of deamination in a diet composed primarily of protein. Bayne and Scullard (1978) found in the carnivorous gastropod, *Nucella lapillus* that individuals fed on mussels at 8°C consumed twice the amount of oxygen which was characteristic of long-starved individuals. The SDA coefficient, therefore, was *ca* 50% of the ingested energy in *N. lapillus*, while the shore crab *Carcinus maenas* had a coefficient of only 6% of ingested energy. According to Wallace (1973) this probably represents 8–10% of assimilated energy. The largely herbivorous filter feeder *Mytilus edulis*, gave an SDA of 56% of assimilated energy (Bayne and Scullard, 1977). From the data in Shumway (1983) we calculated that the respiration ratio for

starved/fed *Mulinia lateralis* at 28‰ salinity is 0.47, giving an approximation to SDA of 53%, in good agreement with that of *Mytilus*. Planktonic copepods fed on readily assimilable microalgae yield SDA coefficients of only 16–17% of assimilated energy (Abou Debs, 1984; Kiørboe *et al.*, 1985). These estimates are widely divergent but suggest that, with certain exceptions, animals feeding on refractory plant material may spend more energy on trituration, digestion and absorption than animals feeding on easily digestible material.

Little effort has been given to a full analysis of assimilation and production on various rations to enable SDA to be partitioned accurately. For the estuarine copepod *Acartia tonsa*, Kiørboe *et al.* (1985) have analysed the components of SDA in biochemical terms. They attribute the main cost to biosynthesis for egg production, minor costs to assimilation and negligible costs to feeding, digestion and excretion. Ashworth (1969) was among the first to attribute SDA primarily to the cost of growth and Jobling (1983) has called for studies to relate increase in metabolic rates to biosynthesis and growth.

In our studies of gastropod respiration, we lack information on assimilation rates. If we approximate the SDA coefficient to the ratio $(R_F - R_S)/R_F$ where S and F denote fed and starved animals, the coefficients are $32.1\% \pm 1.0$ for *Littorina littorea* and $37.5 \pm 2.0\%$ for *Littorina obtusata*. Disregarding the cost of radular movements and locomotion, deamination and urea synthesis, the above SDA must be attributed to digestion, absorption, and translocation, or to increased biosynthetic work towards growth and reproduction as a result of feeding. These animals are spring and summer breeders so that there would be costs of production or replacement of gonads and in *L. obtusata*, material for egg capsules. The animals though still growing, were approaching maximum size so that tissue production would be small. The energy for producing enzymes, including amylases and cellulases and for digestion and movement of food in the relatively large hepatic organ and long gut of such molluscs may well be considerable. It would be valuable to compare SDA values in very small, rapidly growing littorinids, in those just maturing for the first time, and in old individuals that have ceased to grow, together with their respective assimilation and growth rates.

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