J. Mar. Biol. Ass. U.K. (2002), **82**, 967–969
Printed in the United Kingdom

Behavioural responses of the netted dogwhelk *Nassarius reticulatus* to olfactory signals derived from conspecific and nonconspecific carrion

J. Davenport* and P.G. Moore

University Marine Biological Station Millport, Isle of Cumbrae, Scotland, KA28 0EG.
*Corresponding author, present address: Department of Zoology & Animal Ecology and Environmental Research Institute, University College Cork, Lee Maltings, Prospect Row, Cork, Ireland. E-mail: jdavenport@zoology.ucc.ie

Netted dogwhelks *Nassarius reticulatus* were offered standardized olfactory signals derived from flesh of: cod (*Gadus morhua*), starfish (*Asterias rubens*), shore crabs (*Carcinus maenas*), mussels (*Mytilus edulis*), periwinkles (*Littorina littorea*), dog whelks (*Nucella lapillus*) and netted dogwhelks. *Nassarius reticulatus* responded positively to all signals except the conspecific one. Positive responses to extracts were in the order (strongest to weakest): *Gadus*, *Carcinus*, *Nucella*, *Mytilus*, *Asterias*, *Littorina*. Starved *Nassarius reticulatus* buried in sand emerged rapidly to feed on crushed *C. maenas*, but remained buried when offered crushed conspecifics. These data confirmed the hypothesis that *N. reticulatus* would not respond positively to the smell of conspecific carrion, to avoid emerging from the substratum while neighbours were being predated. However, a second hypothesis, that strength of response to olfactory signal was proportional to taxonomic distance between *N. reticulatus* and the source of carrion was not supported by the data.

INTRODUCTION

The netted dogwhelk, *Nassarius reticulatus* (L.) (=*Hinia reticulata, Nassa reticulata*), like many whelks, is usually regarded as an obligate scavenger. There is a large literature devoted to scavenging by nassariid gastropods (see Britton & Morton, 1994 for review), and to the problems of life as a scavenging whelk (e.g. McKillup & McKillup, 1997). Whelks have well developed olfactory detection mechanisms that allow them to find prey or carrion. Studies on scavenging nassariids have already revealed marked food preferences. For example: the related Asian species *Nassarius festivus* prefers fish and molluscan baits above other carrion items (Morton & Yeun, 2000).

Nassarius reticulatus relies on the rapid detection and location of carrion that is intermittently and unpredictably available. It spends most of its life buried just beneath the surface of muddy sand in shallow subtidal areas, though it does penetrate the intertidal zone to a limited extent. Nassariid whelks have long been known to have a spectacular behavioural reaction to the scent of food if they have been starved for some time. This response is particularly well-developed in *N. reticulatus* which responds within seconds to the smell of food by emerging from the substratum and travelling towards its source (sometimes over distances of several metres), eats enormous meals in relation to body size within a few minutes of encountering carrion, and demonstrates great post-prandial increases in oxygen consumption (Crisp et al., 1978). After meals, whelks move away from carrion items and rebury themselves quickly.

The small size of *N. reticulatus*, and its short-duration foraging trips, suggest that foraging and feeding are periods of vulnerability to predation. A priori, olfactory information derived from carrion can fall into three categories: (a) the normal scent of the animal concerned; (b) chemicals leaking from freshly-damaged tissues; and (c) chemicals resulting from processes of breakdown and decay. For an animal like *N. reticulatus*, living within a substratum, olfactory information could report the presence of a potential meal—or the presence of a predator, or of a damaged conspecific that had been attacked (cf. McKillup & McKillup, 1994, 1995). The study reported here was designed to test two hypotheses:

1. That *N. reticulatus* would not respond positively to the smell of conspecific carrion.
2. That *N. reticulatus* would respond more positively to carrion, the greater the taxonomic distance between itself and the carrion source (on the principle that olfactory cues would be less similar to those provided by conspecific carrion).

The second hypothesis stemmed from earlier published (Moore & Howarth, 1996) and unpublished observations made by the author. Thus JD collected *N. reticulatus* for an earlier study (Crisp et al., 1978) and found that fish and crab baits were effective, while limpet baits were not.

MATERIALS AND METHODS

Collection and maintenance

Specimens of *Nassarius reticulatus* were collected by SCUBA diving. Fish baits were placed on the bed of the Fairlie Channel, close to the Isle of Great Cumbrae, Scotland, UK and left to soak. Whelks were caught by hand as they moved over the substratum surface towards the baits. On return to the laboratory they were placed in tanks supplied with running seawater at ambient temperature.

All whelks to be used in behavioural experiments were individually identified with bee tags (numbered and coloured plastic discs about 3 mm in diameter) attached near the apex of the shell with cyanoacrylate adhesive. Before use in behavioural experiments, whelks were deprived of food for a minimum of two weeks.

Extract preparation

Extracts of a variety of potential carrion sources (including *N. reticulatus* itself) were used to test the behavioural responses of the whelks. Extracts were each freshly-prepared in the following standardized fashion. Three grams wet weight of flesh was added to 100 ml of filtered seawater and homogenized. The solution was then coarse and fine filtered to yield the extract. The following species were used to prepare extracts: cod (*Gadus morhua*), starfish (*Asterias rubens*), shore crabs (*Carcinus maenas*), mussels (*Mytilus edulis*), winkles (*Littorina littorea*), dog whelks (*Nucella lapillus*) and netted dogwhelks (*Nassarius reticulatus*). Filtered seawater was used as a control. In the case of cod, only myotomal muscle was used in extracts, while in the case of crabs gonadal material was used. In all other species all soft tissue was used.

Experimental protocol

To conduct an individual experiment, ten bee-tagged *N. reticulatus* that had been starved for a minimum of two weeks and never previously used in experiments were first placed in an aquarium (previously cleaned with hot freshwater and detergent) containing 5-l of aerated, filtered seawater. All experiments were conducted at laboratory temperature (~15°C). The whelks were left for 1 h to acclimatize to their surroundings and become stationary. Next, aeration was stopped and the airstones removed. Five ml of the prepared extract were added to the water by spraying over the whole surface of the water with a hypodermic syringe. The timing and type of subsequent response shown by each whelk was noted. Responses identified were as follows: syphon waving, shell rocking and twisting, initiation of movement around the aquarium, and proboscis eversion. After 5 min, and again after 10 min, 5 ml aliquots of extract were added, to give a total of 15 ml added. Observation was continued until 15 min had elapsed, or until all ten *N. reticulatus* had everted their proboscides if this occurred earlier. A 15 min experimental period was chosen because Crisp et al. (1978) found that *N. reticulatus* became unresponsive to food extracts beyond such a period.

For each extract tested and for controls in which filtered seawater rather than flesh extract was sprayed onto the water surface, the above experimental procedure was repeated until a total of 50 whelks had been tested (i.e. 5 replicates in each case).

Observations with substratum present

Two separate observations were carried out, using ten starved (>2 weeks) experimentally-naïve *N. reticulatus* in each case. First, a 5-l aquarium was set up in which the bottom was covered with clean fine sand and the aquarium filled with aerated, fine-filtered seawater. The whelks were placed on the sand and left overnight to burrow. Next day a crushed-crab bait (*Carcinus*) was placed on the surface of the sand. Whelk behaviour was observed for 30 min. Second, the experiment was repeated (with a cleaned aquarium and new sand) but using three crushed *N. reticulatus* as bait.

RESULTS

Qualitative observations

Control whelks showed virtually no reaction to addition of filtered seawater to their aquaria. Occasional animals everted the tip of the proboscis briefly, but this was also seen in starved animals living in the holding tanks. In contrast, whelks responded to cod and crab extract with an impressive display. Within 1–2 min of extract being added, all animals showed syphon-waving, usually accompanied by shell-rocking. They started to move rapidly around the aquarium. Proboscis eversion usually followed, sometimes to a great length (30–50 mm). The proboscis was often everted for several minutes. Animals remained active throughout the 15 min experiment, and several climbed the walls of the aquarium to the water surface. Responses to starfish, winkle, mussel and dogwhelk extracts were much less dramatic. Virtually all *Nassarius reticulatus* showed syphon waving and most started to move around the aquarium. However, fewer animals showed proboscis eversion, and then mostly for a few seconds and to a limited extent. Whelks continued to exhibit activity for 15 min in response to mussel extract, but in the case of the other extracts most animals were inert by the time 10 min had elapsed.

The response to *N. reticulatus* extract was quite different. All animals showed syphon movement, shell-rocking and movement around the aquarium, but only one animal out of 50 showed proboscis eversion (for a few seconds). All response ceased before the second addition of extract.

Quantitative analysis

Frequency of proboscis eversion was the most clear-cut behavioural response and was analysed statistically (Tables 1 & 2). These data confirm that the intensity of response differs for different extracts. Cod flesh elicited the strongest response, closely followed by crab gonad extract. Responses

Table 1. *Proboscis eversion response in* Nassarius reticulatus *exposed to extracts of various animals for 15 minutes. Means (of 5 replicates, 10 whelks per replicates) and standard deviations (SDs) were calculated after arcsine transformation of raw data.*

Extract	Mean proportion of whelks showing everted probosces	SD
Gadus	0.984	0.244
Carcinus	0.902	0.400
Nucella	0.666	0.151
Mytilus	0.654	0.234
Asterias	0.584	0.299
Littorina	0.538	0.285
Nassarius	0.020	0.045
Control (filtered seawater)	0.020	0.045

https://doi.org/10.1017/S002531540200646X Published online by Cambridge University Press

Table 2. *Results of one-way analysis of variance (ANOVA) and Tukey's pairwise comparisons of data described in Table 1. One-way ANOVA performed on arcsine-transformed data demonstrated a highly significant variation in response to extracts (*P<0.0005*). Columns and rows below show results of Tukey's pairwise comparisons.*

	Control	*Nassarius*	*Littorina*	*Asterias*	*Mytilus*	*Nucella*	*Carcinus*	*Gadus*
Gadus morhua	●	●	●	●	●	●	n.s.	–
Carcinus maenus	●	●	●	n.s.	n.s.	n.s.	–	
Nucella lapillus	●	●	n.s.	n.s.	n.s.	–		
Mytilus edulis	●	●	n.s.	n.s.	–			
Asterias rubers	●	●	n.s.	–				
Littorina littorea	●	●	–					
Nassarius reticulatus	n.s.	–						
Control	–							

●, significant difference between pairs ($P<0.05$); n.s., no significant difference.

to starfish, mussel, winkle and dogwhelk extracts could not be distinguished from each other, but all showed significant differences from controls. The response to *N. reticulatus* extract was quite different—as far as proboscis eversion was concerned the extract elicited no stronger reaction than filtered seawater.

Observations with substratum present

Within five minutes, nine out of the ten *N. reticulatus* offered *Carcinus* as bait had emerged from the sand and reached the carrion source. By the end of the experiment they had all reburied themselves. In contrast, no whelks emerged when the carrion was *N. reticulatus* itself, even though the whelks were starved.

DISCUSSION

The experimental results clearly demonstrate that *Nassarius reticulatus* responds differently to conspecific carrion odours than to all other carrion items offered. In a bare aquarium the smell of conspecific carrion triggered activity (an escape reaction?) but none of the pre-feeding eversion of the proboscis shown in response to other carrion signals. Unreplicated observations on buried, starved *N. reticulatus* showed that they remained buried when crushed conspecifics were available as potential food on the surface of the substratum, in contrast to the rapid emergence shown in the presence of crab bait. Hypothesis 1 is therefore supported—*N. reticulatus* does not respond positively to conspecific carrion. This presumably protects the whelk against emerging from the substratum when a near neighbour has been attacked by predators, and is a reflection of the trade-off between risks of starvation and predation (cf. McKillup & McKillup, 1994; Morton et al., 1995; Morton & Chan, 1999).

The other data collected indicate that *N. reticulatus* responds more strongly to crab and fish extracts than to molluscan extracts, but the moderate response to *Asterias* carrion, and the positive response to *Nucella* (the nearest taxonomic neighbour tested) carrion indicate that Hypothesis 2 is not supported.

The authors are grateful to Mr K. Cameron for collection of specimens, and to Ms Julie Strang for technical assistance.

REFERENCES

Britton, J.C. & Morton, B., 1994. Marine carrion and scavengers. *Oceanography and Marine Biology. Annual Review*, **32**, 369–434.

Crisp, M., Davenport, J. & Shumway, S.E., 1978. Effect of feeding and of chemical stimulation on the oxygen uptake of *Nassarius reticulatus* (Gastropoda, Prosobranchia). *Journal of the Marine Biological Association of the United Kingdom*, **58**, 387–399.

McKillup, S.C. & McKillup, R.V., 1994. The decision to feed by a scavenger in relation to the risks of predation and starvation. *Oecologia*, **97**, 41–48.

McKillup, S.C. & McKillup, R.V., 1995. The responses of intertidal scavengers to damaged conspecifics in the field. *Marine and Freshwater Behaviour and Physiology*, **27**, 49–57.

McKillup, S.C. & McKillup, R.V., 1997. Effect of food supplementation on the growth of an intertidal scavenger. *Marine Ecology Progress Series*, **148**, 109–114.

Moore, P.G. & Howarth, J., 1996. The foraging reactions of marine scavengers: relatedness to bait, carcass damage and hunger. *Journal of Sea Research*, **36**, 267–273.

Morton, B. & Chan, K., 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. *Journal of Experimental Marine Biology and Ecology*, **240**, 213–228.

Morton, B., Chan, K. & Britton, J.C., 1995. Hunger overcomes fear in *Nassarius festivus*, a scavenging gastropod on Hong Kong shores. *Journal of Molluscan Studies*, **61**, 55–63.

Morton, B. & Yuen, W.Y., 2000. The feeding behaviour and competition for carrion between two sympatric scavengers on a sandy shore in Hong Kong: the gastropod, *Nassarius festivus* (Powys) and the hermit crab, *Diogenes edwardsii* (De Haan). *Journal of Experimental Marine Biology and Ecology*, **246**, 1–29.

Submitted 9 May 2002. Accepted 30 September 2002.