



Effects of starvation on the physiology and foraging behaviour of two subtidal nassariid scavengers

Q. Zhao^a, S.G. Cheung^{a,c}, P.K.S. Shin^{a,c}, J.M.Y. Chiu^{b,*}

^a Department of Biology and Chemistry, City University of Hong Kong, Kowloon, Hong Kong

^b School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong

^c State Key Laboratory of Marine Pollution, City University of Hong Kong, Kowloon, Hong Kong

ARTICLE INFO

Article history:

Received 5 May 2011

Received in revised form 13 July 2011

Accepted 7 August 2011

Available online 31 August 2011

Keywords:

Energy budget

Gastropods

Hunger

Nassarius species

Scope For Growth

ABSTRACT

The present study investigated the effects of starvation on the foraging behaviour and physiology of two subtidal nassariids *Nassarius conoidalis* and *Nassarius siquijorensis*, which play an important ecological role in removing a large number of dead animals on the local sea bed. In both nassariid species, 8, 16 and 32 days of starvation significantly reduced the respiration and ammonia excretion rates and Scope For Growth (SFG) compared with their well-fed counterparts; the respiration and ammonia excretion rates of the starved groups decreased with increasing starvation periods. Under well-fed conditions, SFG of *N. siquijorensis* was higher than that of *N. conoidalis*. In contrast, the SFG was more negative for *N. siquijorensis* than *N. conoidalis* when starved. This study also showed that the percentage of numbers of both nassariid species that arrived at bait was affected by both distance from the bait and starvation, but not their interaction. A shorter distance and starvation increased the percentage of numbers of arrivals. A speed ranging from ~1 to 3 cm min⁻¹ was recorded for *N. conoidalis* and *N. siquijorensis* locomotion toward food. Furthermore, the majority of the starved nassariids moved toward food at a speed of ~0.18 to 1.30 cm min⁻¹ higher than their well-fed counterparts. The differential responses of the two gastropods to food availability may provide insight into the dominance of *N. siquijorensis* in Hong Kong waters.

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1. Introduction

Nassariidae in the neogastropods is one of the largest families of the Gastropoda. Representatives of the Nassariidae are considered to be “the closest attempt of an obligate scavenging life style,” although most of them are also known to be grazers, detritivores and predators (Britton and Morton, 1993, 1994; Cernohorsky, 1984; Chiu et al., 2010; Morton, 2011). For example, the intertidal *Nassarius bicallosus* emerges from sand and feeds on a film of surface inorganic and organic particles as tides recede and, when available, may also feed on carrion to supplement its natural diets (Morton, 2011). Moreover, while adults of the intertidal *Nassarius festivus* feed on surface deposits as well as carrion where it is available (Britton and Morton, 1992; Morton, 1990; Morton and Chan, 1999), the juveniles are also capable to prey on weaker, possibly near-moribund conspecifics (Chiu et al., 2010; Morton and Chan, 1997).

Sublittoral nassariids occur in great abundance in Hong Kong waters and play an important ecological role in removing a large number of dead animals on the local sea bed (Britton and Morton, 1992; Cheung, 1997; Morton, 1995; Morton and Chan, 1999). Among

the eight species of subtidal nassariid gastropods found in Hong Kong waters in a recent survey, *Nassarius siquijorensis* predominated in most of the subtidal waters and was followed by *Nassarius conoidalis*; the remaining six species were relatively uncommon (unpublished data). *N. conoidalis* was first and has only been previously reported from Hong Kong waters by Cernohorsky (1984). From 1978 to 1995, the abundance of *N. siquijorensis* in Tolo Harbour increased from 11.2% to 96% (see review by Chan and Morton, 1997). Taylor (1980) identified 93% of the gut contents of *N. siquijorensis* in Hong Kong as comprising fish bones and scales and unidentifiable tissue. Later, Taylor and Shin (1990) showed gut contents to comprise 27% sediment, 10% fish bones and scales, 9% unidentifiable tissue, 5% crustacean fragments, 18% ophiuroid ossicles, and also fragments from a variety of polychaetes, identified by their setae. *N. siquijorensis* is therefore largely a consumer of carrion. Indeed, the sporadic supply of carrion in the sea may cause periods of starvation in nassariids. Starvation was considered to be one of the most important sources of mortality, resulting in compromised population fitness (Thorson, 1950).

Scope For Growth (SFG) has been used to estimate the maximum amount of energy available for growth after fulfilling essential biological processes (Genoni and Pahi-Wohstl, 1991). Previous studies have demonstrated that SFG is a good predictor for actual growth (Baillieul et al., 1996; Beiras et al., 1994) and a sensitive

* Corresponding author. Tel.: +852 22990680; fax: +852 2559 9114.
E-mail address: jillchiu@hku.hk (J.M.Y. Chiu).

indicator of physiological stress in invertebrates (Baillieul et al., 2005; Maltby, 1992; Maltby et al., 1990; Roast et al., 1999). For example, Hu et al. (2011) has recently shown a rapid reduction in SFG in the first week of starvation in the Asian horseshoe crabs *Tachypleus tridentatus* and *Carcinoscorpius rotundicauda*.

Starvation has major consequences on the foraging behaviours in various groups of marine animals. For example, hungry dogwhelk *Nucella lapillus* foraging for mussel preys in an aquarium moved faster along straighter paths, while recently fed individuals followed tortuous search paths (Hughes and Dunkin, 1984). These behaviours would take dogwhelks away from areas of low prey density, and keep them in areas of high prey density. Frequency of prey attack by juveniles of the Japanese flounder *Paralichthys olivaceus* increased from 2 times min^{-1} to 3 times min^{-1} following 4 days of starvation (Miyazaki et al., 2000). The starved soft-bottom benthic starfish *Luidia clathrata* ingested greater numbers of prey and spent more time foraging than did recently fed individuals (McClintock and Lawrence, 1985). Furthermore, it has been suggested that hunger could override the effect of simulated predation upon a feeding assemblage in *N. siquijorensis* (Morton and Chan, 1999). Individuals that had fed within 7 days ceased feeding and departed palatable food when crushed conspecifics were added. In contrast, *N. siquijorensis* that had not fed in 7 days continued to feed when food was made available, despite the possibility of predation.

Nassariids respond immediately to the presence of food, by emerging from repose in the sediment, moving purposefully toward it and eating voraciously to satiation (Britton and Morton, 1994). Liu and Morton (1994) demonstrated that the distance for the majority of *N. siquijorensis* to detect food was 35 cm. A mean speed of 4.5 cm min^{-1} has been recorded for *N. siquijorensis* locomotion toward food (Morton and Chan, 1999). Furthermore, nassariids consume large quantities quickly, i.e. 61% of the body weight for *N. siquijorensis* in feeding bouts lasting for an average of 12 min (Liu and Morton, 1994). After feeding, they depart from the food and re-burrow quickly.

In the current study, we investigated the effects of starvation on the mortality, foraging behaviour and physiology of two nassariid gastropods *N. conoidalis* and *N. siquijorensis*. Endpoints including percent of individuals that moved toward baits placed at different distances and the speed at which they moved, SFG and the related energy budget items (i.e. absorption, respiration and ammonia excretion rates) were examined. The differential physiological responses of the two gastropods to food availability were also discussed in relation to their abundance and distribution, providing insight into the impact of food availability on the population dynamics of subtidal nassariids. Since scavengers consume carrion rapidly and those arriving from greater-than-optimal distances are not able to feed, distance may influence whether a scavenger obtains the food before it is consumed by others. A scavenger that has travelled long distances may also have a higher chance to encounter predators and risk being killed. Therefore, we hypothesised, for the first time, that distance from the potential food might influence a scavenger's decision whether or not to seek and move toward the food. Nevertheless, when prolonged starvation can result in death, hungry individuals may move more readily toward the bait in spite of long distances. We further hypothesised that hunger might override the influence of distance.

2. Materials and methods

2.1. Collection and maintenance of animals

N. conoidalis and *N. siquijorensis* adults were collected by trawling at depths between 10 and 30 m in southern Hong Kong waters (22°10'N, 114°10'E) in February 2010. Upon return to the laboratory, the gastropods were maintained in flowing seawater of a salinity of

30 psu at 24 °C and were fed ad libitum with *Metapenaeus ensis* shrimp meat once every four days for at least two weeks before experimentation (Liu and Morton, 1994). The animals did not consume the food if it was offered within three days since the last meal (personal observation).

2.2. Expt I—effects on mortality

Starvation effects were examined at three rations in 96-day experiments. The experiments were carried out with *N. conoidalis* and *N. siquijorensis*. The animals were fed ad libitum with *M. ensis* shrimp meat once either every 4, 8 or 32 days after an initial satiation. There were three rations and nine experimental chambers for each species. Each ration had three replicate chambers, and each chamber consisted of ten gastropods and 5 L seawater. There were a total of 30 *N. conoidalis* and 30 *N. siquijorensis* receiving each ration. Seawater with a salinity of 30 psu was used and maintained at 20 °C. Also, the seawater in the chambers was changed once every two days. All gastropods were examined daily and those that did not respond to the stimulation of a pipette tip were considered dead and removed from the experimental chambers.

2.3. Expt II—effects on physiology

Starvation effects were examined in 32-day experiments. The experiments were carried out with *N. conoidalis* and *N. siquijorensis*. Well-fed group was fed ad libitum with *M. ensis* shrimp meat once every 4 days (i.e. on Days 0, 4, 8, 12, 16, 20, 24, 28 and 32). Starved group was not fed after the initial satiation. The body wet weights of each gastropod right before and after the experiments were measured to the nearest 1 mg.

There were two rations (i.e. well-fed vs. starved) and six experimental chambers for each species. Each ration had three replicate chambers, and each chamber consisted of eight gastropods and 4 L seawater. Seawater with a salinity of 30 psu was used and maintained at 20 °C. Also, the seawater in the chambers was changed once every two days. Absorption rate, respiration rate, ammonia excretion rate and Scope For Growth were determined after 0, 8, 16 and 32 days post initial satiation.

2.4. Absorption rate

The absorption rate from food was calculated as follows:

$$\begin{aligned} \text{Absorption rate (Jday}^{-1} \text{ ind}^{-1}) &= \text{Food consumption rate (gday}^{-1} \text{ ind}^{-1}) \\ &\quad \times \text{Absorption efficiency (\%)} \\ &\quad \times \text{Calorific value (Jg}^{-1}) \end{aligned}$$

The gastropods were offered the shrimp meat (*M. ensis*). They became satiated and stopped consuming the remaining meat after ~1 h. The wet weights of shrimp meat before and after consumption were measured to the nearest 0.1 mg. The wet weight of shrimp meat consumed in each experimental chambers was then determined and the dry weight was calculated using a linear regression equation established in a preliminary experiment: $W_{\text{dry}} = 0.1929W_{\text{wet}} - 0.0277$ ($n = 35$, $r^2 = 0.952$, $SE = 0.046$, $P < 0.001$)

W_{dry} and W_{wet} are the dry weight and wet weight of shrimp, respectively.

Absorption efficiency was measured as follows (Conover, 1966):

$$\text{Absorption efficiency} = (F - E) / (1 - E)F \times 100$$

where F = ash-free dry weight:dry weight ratio of shrimp meat, E = ash-free dry weight:dry weight ratio of faeces.

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