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S G Cheung, W H Wong. EFFECT OF FOOD AVAILABILITY ON THE ENERGETICS OF THE INTERTIDAL SCAVENGING GASTROPOD NASSARIUS FESTIVUS. Vie et Milieu / Life & Environment, 2001, pp.181-188. hal-03192143

**HAL Id: hal-03192143**

**<https://hal.sorbonne-universite.fr/hal-03192143>**

Submitted on 7 Apr 2021

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## EFFECT OF FOOD AVAILABILITY ON THE ENERGETICS OF THE INTERTIDAL SCAVENGING GASTROPOD *NASSARIUS FESTIVUS*

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NASSARIUS  
GASTROPOD  
GROWTH  
MAINTENANCE RATION  
FOOD AVAILABILITY

**ABSTRACT.** – Individuals of the intertidal scavenging gastropod *Nassarius festivus* (Powys) were kept at one of the four ration levels in the laboratory for ten weeks. The fastest growth (shell and somatic tissue) was observed when individuals were fed once every two days (high-ration) and followed by those fed once every seven days (medium-ration). Individuals lost weight when fed once every 21 days (low-ration), or unfed throughout the experiment. Maintenance ration was  $16.5 \text{ J day}^{-1} \text{ ind}^{-1}$  and could be met by a food ration of one meal every 8.2 days. Positive values of gross growth efficiency (P/C) were obtained for the high- and medium-ration group and were estimated at 4.2 and 2.1%, respectively. As food availability decreased, the proportion of consumed energy expended on respiration (R/C) increased from 6.7% for the high-ration group to 25.1% for the unfed group. Results are discussed with respect to the unpredictable food supply to this obligate scavenger.

NASSARIUS  
GASTÉROPODE  
CROISSANCE  
RATION DE MAINTIEN  
RESSOURCES NUTRITIVES

**RÉSUMÉ.** – Des individus du Gastéropode nécrophage *Nassarius festivus* ont été élevés au laboratoire en recevant une des quatre rations de nourriture pendant 10 semaines. La croissance la plus rapide (coquille et tissu somatique) est observée lorsque les individus sont nourris une fois tous les deux jours (ration élevée), immédiatement suivie par ceux qui sont nourris une fois tous les sept jours (ration moyenne). Les individus nourris une fois tous les 21 jours (basse ration) ou restés à jeun pendant toute la durée de l'expérience perdent du poids. La ration de maintien s'établit à  $16,5 \text{ J jour}^{-1} \text{ ind}^{-1}$  et correspond à une ration de un repas tous les 8,2 jours. Les valeurs positives de croissance brute (P/C) sont obtenues pour les groupes ayant reçu les rations forte et moyenne, et sont estimées à 4,2 % et 2,1 % respectivement. Lorsque la nourriture disponible décroît, la part de l'énergie consommée due à la respiration (R/C) augmente de 6,7 % pour le groupe nourri avec la ration la plus élevée et de 25,1 % pour le groupe resté à jeun. La discussion des résultats porte notamment sur le fait que les ressources nutritives de ce nécrophage exclusif sont aléatoires.

### INTRODUCTION

The neogastropods Nassariidae are one of the largest families of the Gastropoda with more than 300 species and most of them are presumed exclusively scavengers of carrion (Cernohorsky 1984). Intertidal species of this family commonly inhabit eulittoral soft shores having moderate to broad tidal ranges and low exposure to wave energy. As food supply to these animals is sporadic, these gastropods may undergo starvation for long periods of time. Four intertidal species of *Nassarius* are found in Hong Kong with *Nassarius festivus* being the

dominant species (Britton & Morton 1992). When food is available, *N. festivus* moves towards food rapidly and consumes large quantities of it quickly, about 50-60% of the body weight (Morton 1990, Cheung 1994). In the face of hunger, however, *N. festivus* can survive >100 days without food (Morton 1990) and reduce energy expenditure by reducing activity (Cheung 1994). This animal, however, abandons a meal in the face of the risk of predation when food availability is equal to or more than one meal every 14 days. A further decrease in the food availability increases the risk of starvation to such an extent that the animal will feed, despite the risk of being consumed (Morton *et al.* 1995).



Hong Kong is facing an overfishing problem and nutrient enrichment in the surrounding waters. Such environmental perturbations are suggested to be responsible for the decrease in benthic species diversity which is reflected in a reduction of neogastropods and an increase in the number of scavenging gastropod species of Buccinidae and Nassariidae, e.g. *N. festivus* (Morton 1993). These scavengers now assume an important ecological role as cleaners which help in preventing further degradation of the marine environment (Morton 1993). For *N. festivus*, energy expenditure on individual activities has been reported by Cheung (1994) and the effect of food availability on fecundity by Cheung & Lam (1999). The objectives of this study included the investigation of the effect of food availability on the energetics of *N. festivus* and the determination of the maintenance ration for this species.

## MATERIALS AND METHODS

**Maintenance of the animals:** Individuals of *Nassarius festivus* (shell length: 9.02–1.60 mm) were collected from the sandy beach at Lok Wu Sha, Tolo Harbour, Hong Kong and acclimated in laboratory conditions for one week (salinity: 30‰, temperature: 20°C) prior to experimentation. During acclimation, individuals were allowed to feed to satiation everyday on excised short-necked clams, *Tapes philippinarum* collected from the same site. The individuals of *N. festivus* were then exposed to one of the three ration levels with food provided once either every 2, 7 or 21 days which were considered as the high-, medium- and low-ration group, respectively. The fourth treatment group was unfed throughout the experiment, except at the start of the experiment and was labelled as the unfed group. Ten individuals of *N. festivus* from each treatment group were placed in two plastic vials with five individuals each. Plastic vials of all the four treatment groups were then placed in a fish tank. Three fish tanks were prepared to act as replicates. Therefore, there were thirty individuals of *N. festivus* for each treatment group and the experiment lasted for ten weeks.

**Food consumption:** Five individuals of *N. festivus* from each treatment group were allowed to feed to satiation on excised *Tapes philippinarum*. The time spent feeding was calculated as the time between when the proboscis was everted and retracted (Cheung 1994). The number of individuals fed and the time spent feeding by each individual was recorded. The initial and final body wet weight (after consumption by *N. festivus*) of *T. philippinarum* was measured to the nearest 0.1 mg. As *T. philippinarum* loses weight after immersion in water, 3 individuals were placed in water for 15 minutes, which was about the time an individual of *N. festivus* spent feeding, and the weight change was used to adjust the computed consumption rate. The mean consumption rate per meal per individual was then calculated by dividing the

obtained values by a factor of five. The experiment was repeated twice.

The wet weight of *T. philippinarum* consumed by *N. festivus* was converted into the dry weight using a linear regression relating wet weight (WW) and dry weight (DW):  $DW = 0.22 \times WW + 0.01$  ( $r^2=0.96$ ,  $P<0.005$ ) (Cheung 1994). Energy gained from consumption of *T. philippinarum* was calculated using the mean calorific value of the tissue of *T. philippinarum*, i.e. of 20.46 KJ g<sup>-1</sup> dry wt (Cheung 1994).

**Shell growth:** The shell length of each of the 30 individuals of *N. festivus* from each treatment group was measured to the nearest 0.01 mm every seven days for ten weeks using vernier calipers. To calculate the amount of energy allocated to shell production, the measured increase in shell length was converted into shell weight by a regression equation relating shell weight to shell length. The equation was computed from 20 individuals with shell lengths of between 6.90 and 14.10 mm and was calculated as  $\text{Log shell weight (g)} = 2.64 \times \text{Log shell length (mm)} - 3.64$  ( $n = 30$ ,  $r^2 = 0.97$ ). The organic content of the shell was determined by drying 4 empty shells in an oven at 80°C for 48 h and then ashing in a muffle furnace at 500°C for 8 h. The percentage weight lost was considered as the organic content of the shell which was determined as  $3.23\% \pm 0.23$  (1SD). Using the calorific value of the organic matter of shell, which was 20.82 KJ g<sup>-1</sup> (Edwards & Welsh 1982), the energy allocated to shell growth was calculated.

**Somatic growth:** The body wet weight of each of the 30 individuals of *N. festivus* from each treatment group was measured every 7 days for 10 weeks. The body wet weight was determined by an electronic balance to the nearest 0.1 mg after being blotted dry. The weight of the body tissue was obtained by subtracting the shell weight, which was predicted by the regression, from the body wet weight. The water content of the body tissue of *N. festivus* was found to be 75% (unpublished data), this value was used for converting tissue wet weight into tissue dry weight. The calorific value of body tissue was determined by drying the body tissue of five individuals of *N. festivus* at 105 °C for 48 h. The dried tissue of each individual was then ground into powder, mixed with benzoic acid and pressed into pellets. The pellets were then burnt using the Parr semi-micro bomb calorimeter and the mean calorific value of body tissue was estimated at 16.61 KJ g<sup>-1</sup> dry wt. The energy allocated to tissue growth was computed from the change in the tissue weight and the calorific value of the tissue.

**Oxygen consumption:** The oxygen consumption rate was measured on nine occasions, at 7-day intervals. Twelve individuals of *N. festivus* from each treatment group were used. Because of the small size of the individuals, two individuals were placed in each container filled with 50 ml seawater, so there were six measurements for each treatment group. Three containers without animals were used as controls. To minimize disturbance, individuals were allowed to stay in the containers for 30 min before the experiment started. The seawater inside containers was then renewed and the containers were sealed for 90 min. Initial and final oxygen levels in each container were measured using a Clarke-type pola-



rographic oxygen meter. The decrease in oxygen tension was less than 25% of full saturation. Oxygen consumption rate ( $\text{mg O}_2 \text{ hr}^{-1} \text{ ind}^{-1}$ ) was then calculated after correction for the control. Energy expended on respiration was calculated from the amount of oxygen consumed and the conversion factor of  $13.98 \text{ J mg}^{-1} \text{ O}_2$  (Ivlev, 1934).

**Statistical analysis:** As no significant difference in the above measurements was found among the three replicates of each treatment group, data of the three replicates were pooled and differences among treatment groups were compared using two-way repeated measure ANOVA. Considering the number of meals taken by each treatment group was different, the effect of time on each parameter was tested separately for each treatment group by Kruskal-Wallis one-way ANOVA. Percentage data were arcsine transformed prior to analysis.

## RESULTS

### Food consumption

In this 10-week experiment, all individuals from the low-ration group fed on all the occasions whereas the percentage number of individuals fed for the medium-ration group ranged from 96.7 to 100% and that for the high-ration group ranged from 73.3 to 100%. The mean percentage number of individuals that fed in this 10-week experiment was  $92.0 \pm 7.7\%$  (1SD),  $99.3 \pm 1.4\%$  and  $100 \pm 0\%$

for the high-, medium- and low-ration group, respectively. The percentage number of individuals that fed did not change significantly with time for all the three ration groups as tested by Kruskal-Wallis one-way ANOVA ( $P > 0.05$ ). Since the total number of meals taken by different treatment groups was different, the percentage number of individuals that fed for the three ration groups were compared by two-way repeated measures ANOVA, using data from weeks when all the three ration groups fed. The percentage number of individuals that fed was significantly lower for the high-ration group as compared with the medium- and low-ration group, the effect of time and the interaction between time and ration, however, were not significant ( $P < 0.05$ ).

The mean time spent feeding for the high-, medium- and low- ration group was 12.2, 20.9 and 22.4 min, respectively. The effect of time, ration and the interaction between ration and time were statistically significant ( $P < 0.05$ ) with longer time spent feeding as food availability decreased (Fig. 1).

Food consumption per meal did not vary significantly ( $P > 0.05$ ) with time for all treatment groups (Fig. 2). The mean food consumption per meal throughout the experimental period was 22, 30 and 24 mg wet wt meal $^{-1}$  ind $^{-1}$  for the high-, medium- and low-ration group, respectively, and was neither significantly affected by ration nor the interaction between ration and time (two-way repeated measure ANOVA,  $P > 0.05$ ). The accumulated dry

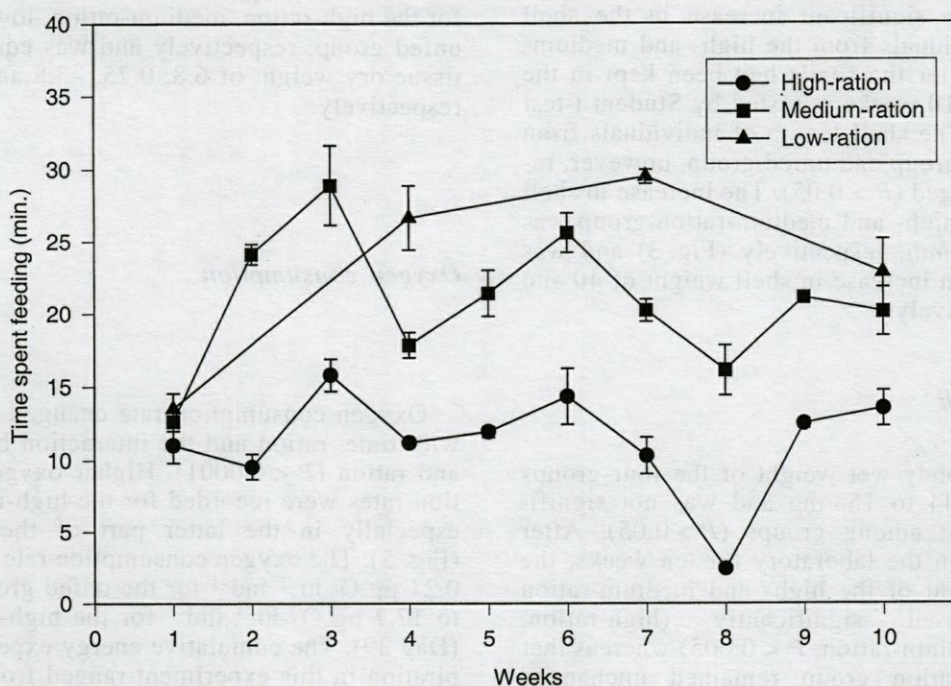


Fig. 1. – *N. festivus*. Mean time spent feeding ( $\pm$  S.E.) for individuals fed at one of the four ration levels.



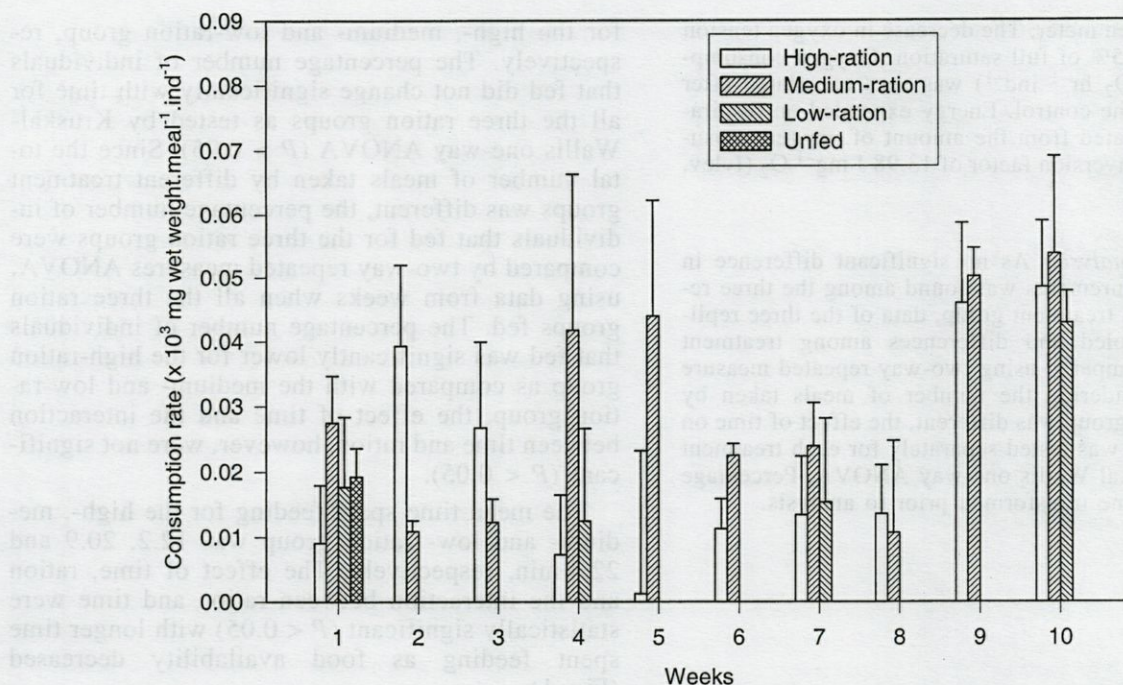


Fig. 2. – *N. festivus*. Food consumption rate ( $\pm$  S.E.) for individuals fed at one of the four ration levels. The \* indicates data of the high-ratio group obtained on day 9 instead of day 8.

weight of clam tissue consumed by an individual of *N. festivus* in 10 weeks was 164, 75, 29 mg for the high-, medium- and low-ratio group, respectively.

### Shell growth

There was a significant increase in the shell length of individuals from the high- and medium-ratio group after the snails had been kept in the laboratory for 10 weeks as tested by Student t-test ( $P < 0.0001$ ). The shell length of individuals from the low ratio group and unfed group, however, remained unchanged ( $P > 0.05$ ). The increase in shell length for the high- and medium-ratio group was 1.38 and 0.80 mm, respectively (Fig. 3) and was equivalent to an increase in shell weight of 40 and 22 mg, respectively.

### Somatic growth

The initial body wet weight of the four groups varied from 144 to 154 mg and was not significantly different among groups ( $P > 0.05$ ). After keeping them in the laboratory for ten weeks, the body wet weight of the high- and medium-ratio group increased significantly (high-ratio,  $P < 0.001$ ; medium-ratio,  $P < 0.005$ ) whereas that for the low-ratio group remained unchanged ( $P > 0.05$ ) and that for the unfed group decreased ( $P < 0.0005$ ). The final body wet weight increased

significantly with ration (Fig. 4) as tested by one-way ANOVA followed by Student-Newman-Keuls (SNK) multiple range test ( $F=23.1$ ,  $df=3,116$ ,  $P < 0.0001$ ).

After subtracting the shell weight from the body wet weight, the change in the tissue wet weight at the end of the experiment was 9, 1, –5 and –23 mg for the high-ratio, medium-ratio, low-ratio, and unfed group, respectively and was equivalent to a tissue dry weight of 6.8, 0.75, –3.8 and –17.3 mg, respectively.

### Oxygen consumption

Oxygen consumption rate changed significantly with time, ration and the interaction between time and ration ( $P < 0.0001$ ). Higher oxygen consumption rates were recorded for the high-ratio group, especially in the latter part of the experiment (Fig. 5). The oxygen consumption rate ranged from  $0.21 \mu\text{g O}_2 \text{ hr}^{-1} \text{ ind}^{-1}$  for the unfed group (Day 18) to  $17.7 \mu\text{g O}_2 \text{ hr}^{-1} \text{ ind}^{-1}$  for the high-ratio group (Day 39). The cumulative energy expended on respiration in this experiment ranged from 73 J  $\text{ind}^{-1}$  for the unfed group to 224 J  $\text{ind}^{-1}$  for the high-ratio group (Table I).



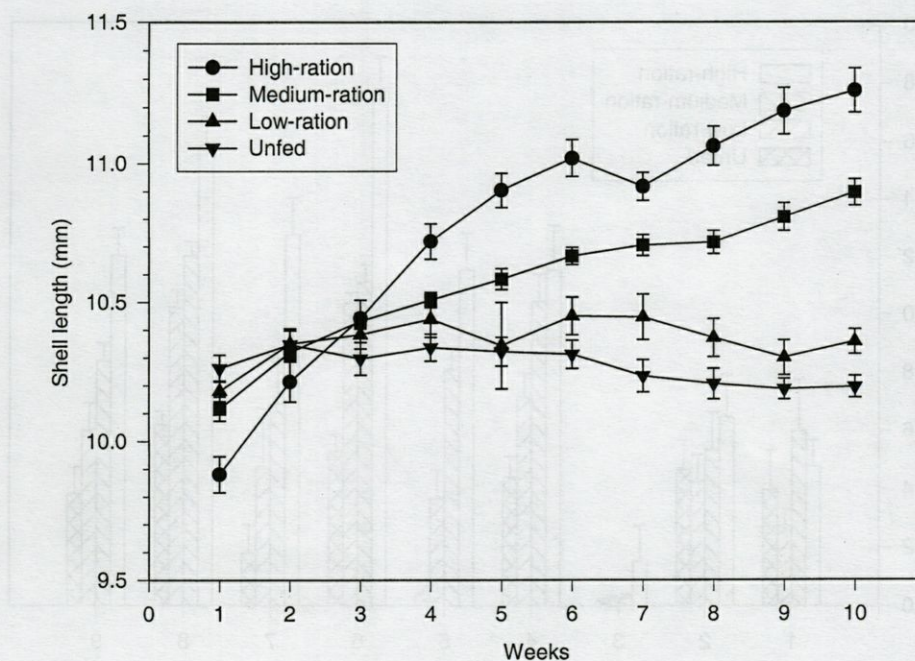


Fig. 3. – *N. festivus*. Growth in shell length ( $\pm$  S.E.) for individuals fed at one of the four ration levels.

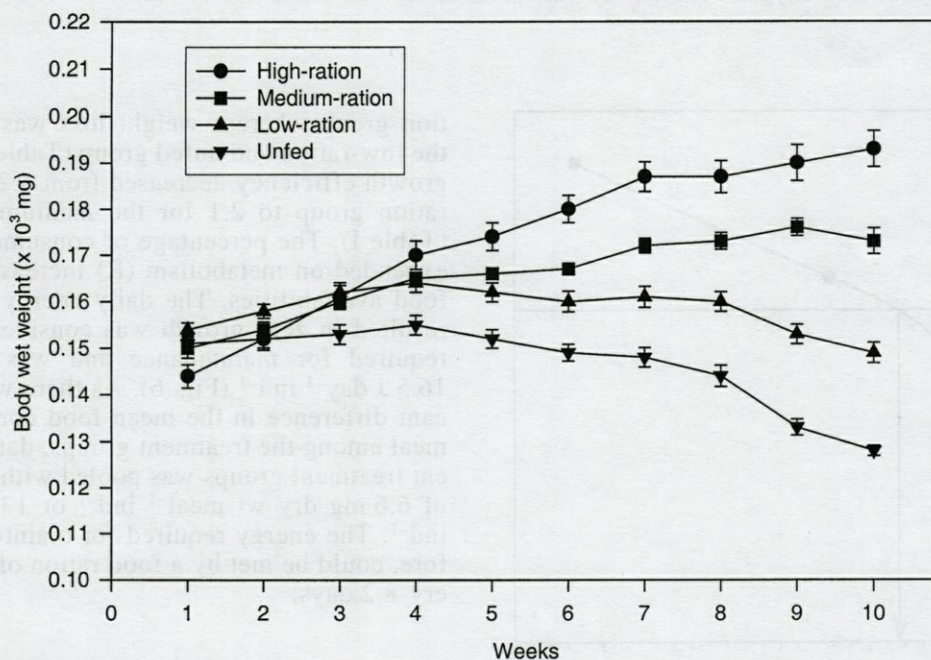


Fig. 4. – *N. festivus*. The change in the body wet weight ( $\pm$  S.E.) for individuals fed at one of the four ration levels.

Table 1. – Energy budget of *N. festivus* (J individual<sup>-1</sup>) in terms of consumption (C), production of soma (Pg) and shell (Psh), and respiration (R).

Food ration	C (J)	Psh (J)	Pg (J)	R (J)	Psh + Pg (J)	(Psh + Pg)/C x 100 (%)	R/C x 100 (%)
High	3353	27	113	224	140	4.2	6.7
Medium	1543	15	17	163	32	2.1	10.6
Low	602	0	-63	117	-63	---	19.4
Unfed	291	0	-287	73	-287	---	25.1



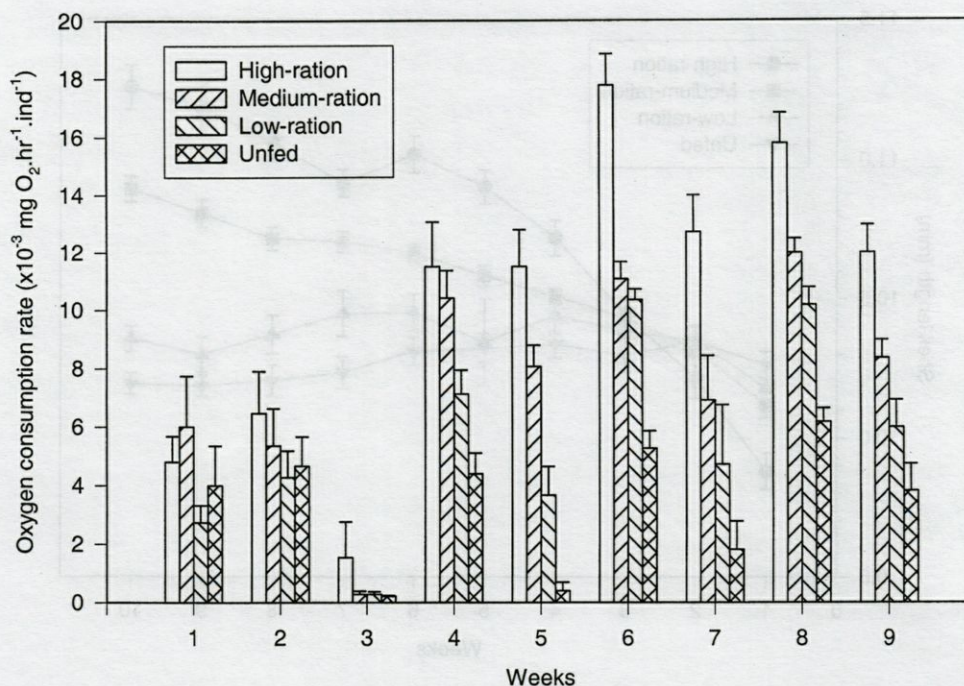


Fig. 5. – *N. festivus*. Mean oxygen consumption rate ( $\pm$  S.E.) for individuals fed at one of the four ration levels.

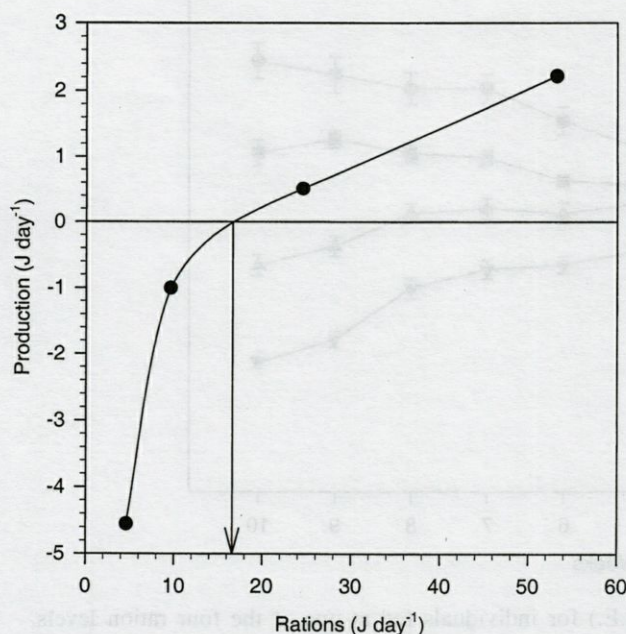


Fig. 6. – *N. festivus*. Production as a function of ration. Maintenance ration is considered as the ration level that results in zero growth, i.e. production = 0 J day<sup>-1</sup>.

#### Maintenance ration

In this 10-week experiment, positive energy balance was obtained for the high- and medium-ra-

tion group whereas weight loss was observed for the low-ratio and unfed group (Table I). The gross growth efficiency decreased from 4.2 for the high-ratio group to 2.1 for the medium-ratio group (Table I). The percentage of consumed energy (C) expended on metabolism (R) increased at reduced food availabilities. The daily energy intake which resulted in zero growth was considered as energy required for maintenance and was estimated at 16.5 J day<sup>-1</sup> ind<sup>-1</sup> (Fig. 6). As there was no significant difference in the mean food consumption per meal among the treatment groups, data from different treatment groups was pooled with a mean value of 6.6 mg dry wt meal<sup>-1</sup> ind<sup>-1</sup> or 135.04 J meal<sup>-1</sup> ind<sup>-1</sup>. The energy required for maintenance, therefore, could be met by a food ration of one meal every 8.2 days.

#### DISCUSSION

A common response during periods of reduced food availability is a reduction in the rate of oxygen consumption (Bayne & Newell 1983) so as to conserve energy. This may be due to a depression in the level of activity, a depletion of energy reserves, or a loss of material from the gut. However, for predators or scavengers that must seek out their food, a decline in standard (or resting) rate of metabolism may be offset against higher activity as the search for food is increased (Bayne & Newell



1983). The present study showed that oxygen consumption rate of the unfed group did not decrease with time of starvation. Higher oxygen consumption rates obtained for individuals maintained at higher rations were largely attributed to the growth of the animals. A similar independence of oxygen consumption from starvation was reported for *Thais lamellosa* (Stickle & Duerr 1970) and *N. festivus* (Morton 1990). The oxygen consumption rate of the latter remained constant when it was starved for 45 days and was reduced to about one third as periods of starvation increased to 60 days or more. For scavengers to conserve energy, spending a longer time in the sand when starved and coming out immediately once food is available should be a better strategy than reducing standard (resting) metabolism. This also explains why the proportion of consumed energy allocated to respiration in this study increased from 6.7% for the high ration group to 25.1% for the unfed group. Such an increase in R/C following stress was also observed in predatory gastropods *Polinices alderi* (Ansell 1982) for which the values increased from 11.1% under optimal conditions of growth and reproduction to 32.7% where growth was poor and no reproduction occurred.

The amount of food consumed per meal by *N. festivus* did not vary significantly with rations and is probably attributed to the limit set by the size of the gut. Individuals maintained at lower rations, however, spent a longer time feeding. Similar results were reported for the burrowing scavenging prosobranch *Bullia digitalis* (Stenton-Dozey *et al.* 1995) and the predator *Thais lapillus* (Bayne & Scullard 1978) and may be due to physiological deterioration that leads to a reduction in the functioning efficiency of the proboscis (Hughes 1986, Stenton-Dozey *et al.* 1995). The feeding time of field populations of *N. festivus* was reduced significantly when the number of conspecifics increased from 10 to 20 (Morton & Yuen 2000). Some *N. festivus*, unable to penetrate the cluster of feeding individuals gathering on dying clams in the field, were observed to turn away (Cheung 1994). With competition from conspecifics in the field, a slower feeding rate of *N. festivus* following starvation would ultimately affect meal size. Another constraint on feeding time in the field is the risk of predation. Morton *et al.* (1995) reported that *N. festivus* would abandon a meal in the face of the risk of predation when food availability was equal to or more than one meal every 14 days, although a further decrease in the food availability would increase the risk of starvation to such an extent that the animal would feed, despite the risk of being consumed. The maintenance ration of *N. festivus* was estimated at  $16.5 \text{ J day}^{-1} \text{ ind}^{-1}$  which could be met by having one meal every 8.2 days. This, however, was determined under laboratory conditions where individuals of *N. festivus* were free from

competition and predation and they were allowed to feed to satiation. As predation and competition are two constraints on feeding time, the maintenance ration in the field could only be met by having a meal at 8.2 day intervals. Nevertheless, the calculated maintenance ration helped to explain why *N. festivus* individuals are willing to risk their life for food for periods of starvation more than 14 days as reported by Morton *et al.* (1995) because individuals are now in negative energy balance.

ACKNOWLEDGEMENTS. – We thank Desmond O'Toole and two anonymous reviewers for constructive comments on the manuscript, C Y Wong for technical assistance, and K T Wu for providing data on wet weight: dry weight ratio for *N. festivus*. The work described in this paper was substantially supported by a grant from CityU (Project No. 7000588).

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Reçu le 25 juin 2001; received June 25, 2001

Accepté le 7 août 2001; accepted August 7, 2001