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The feeding strategy of the predatory *Gyrineum natator* (Gastropoda: Neotaenioglossa: Ranellidae) in the Cape d'Aguilar Marine Reserve, Hong Kong, with a review of sulphuric acid use in prey access by the Tonnoidea and experimentally derived estimates of consumption

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Under conditions of otherwise enforced starvation in filtered seawater and with only oysters (*Saccostrea mordax*) to feed on, an individual of *Gyrineum natator* consumed > 98%, on average, of its body weight of oyster tissues each week (> 14% per day). When other potential food, such as sediment, organic debris and other newly settled sessile organisms, was available to a similar-sized conspecific living in conditions of unfiltered seawater (in addition to oysters), the oysters only accounted for 1.52% of its average weekly diet (0.21% per day). This was because of the 12 proffered oysters, only four were consumed in contrast to the 12 eaten by the individual in filtered seawater. All the oysters were accessed through large holes made in their shells. It is generally understood that the salivary glands of confamilial ranellids produce secretions of sulphuric acid from greatly enlarged salivary glands and this is demonstrated herein for *G. natator* also. It is believed that it was these secretions that made the holes in the oyster shells. It, therefore, seems that *G. natator* uses sulphuric acid to attack prey only when more easily obtained food is not available. It may also be used in defence. A comparison of consumption rates for a range of scavenging and predatory gastropod taxa shows that representatives of the Nassariidae consume (much) more than predators because of their opportunistic lifestyles. *Gyrineum natator* generally eats similar amounts to other predators, although the increased difference in estimated consumption (~10%) between this species and another similar-sized ranellid, *Linatella caudata*, might be because the latter did not use sulphuric acid to access its prey. Its enforced use in this study of *G. natator*, therefore, might represent the increased costs of using the acid to access the proffered oyster prey.

Keywords: consumption; oyster prey; attack method; sulphuric acid; salivary glands

Introduction

The Tonnoidea comprises approximately seven families of predatory gastropods (Bouchet and Rocroi 2005) although the systematics of this diverse group of caenogastropods is still debated. Moreover, the feeding biology of most representatives of these familial taxa are undescribed, adding to the systematic confusion. The best understood tonnoideans in terms of their feeding biology are representatives of the Tonnidae and Cymatiidae (or Cymatiinae), as will be discussed. Conversely, the diets and feeding strategies of the Ranellidae are poorly known.

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The Ranellidae (or Ranellinae) with the fossil *Ranella olearium* Lamarck being recorded widely from Central Europe, and with the family's origins in the Paratethys of the Miocene (97–26 million years ago) (Landau et al. 2009) comprises a rich assemblage of relatively small predators. Hitherto, however, the only study of any other representative of the family (or subfamily) was by Morton (1990a), who described the feeding biology of *Linatella caudata* (Gmelin), bearing in mind that this genus too has been placed by some in the Cymatiinae. Notwithstanding, *L. caudata* was shown to feed, in Hong Kong, upon a variety of sheltered rocky shore species, most notably the arcoid *Barbatia virescens* (Reeve) followed by the rock oyster *Saccostrea cucullata* (Born), and then the ascidian *Styela plicata* Lesuer plus, less favoured, the barnacle *Balanus amphitrite* Darwin and the turban shell *Lunella coronata* (Gmelin). Morton (1990a) also showed that *L. caudata* possesses sulphuric-acid-secreting salivary glands but the predator did not, however, seem to use this acid to access its prey, but rather the radula was used to scrape a hole in either the shell or test and the proboscis was inserted into the penetrated animal. It was concluded that perhaps the acid was used for defence, to externally digest its accessed prey or, possibly, to attack less accessible prey.

Gyrineum natator (Röding) is distributed widely throughout the Indo-West Pacific (Henning and Hemmen 1993). It has been recorded from the Seto Inland Sea in the north (Inaba 1982) south to Omishimi Island, Yamaguchi Prefecture, southern Japan, (Beu 1999), south to the Yellow Sea, the East China Sea, Taiwan Strait, South China Sea, Vietnam, Malaysia, Singapore, Brunei, Sunda Strait (Indonesia) and the Andaman Sea. In the Indian Ocean it occurs as far west as the Arabian Gulf and all down the East African coast as far as Beira, Mozambique. It is also distributed well into the Pacific Ocean as far east as New Guinea and the Maldives, although it has not been reported from the Philippines and neither New Caledonia nor Australia (Beu 1998), but other species do occur here (Wilson 1993).

The exposed rocky shore *G. natator* appears to be the ecological equivalent of sheltered rocky shore. *L. caudata* in Hong Kong waters (Morton 1990a). In Hong Kong, *G. natator* was reported by Taylor (1980), from an analysis of gut contents, to principally eat green algae, although the remains of polychaetes, amphipods, sponges and holothurians (spicules), were also identified – suggesting that these were consumed either with the algae or represented carrion or, possibly, predation behaviour. Similarly, in the Cape d'Aguilar Marine Reserve in Hong Kong, where the species is common, *G. natator* was found to be feeding upon, again from an analysis of gut contents, algae, bryozoans and sponges (Taylor and Morton 1996). It was concluded, therefore, that the species is a generalist browser. Such a conclusion was also reached for *G. natator* by Neo et al. (2001), who showed that in Thailand (Phuket), the species fed mainly on algae (47%), sponges (43.5%) and hydroids (31.2%) and occasionally, and possibly, polychaetes and barnacles – as in Hong Kong.

The aims of this study were to investigate the method(s) of feeding and consumption exhibited by *G. natator* under conditions of starvation in the laboratory and, thereby, elaborate on the above, field-derived, generalization that the species is an indiscriminate browser of intertidal and shallow subtidal epibionts. And, thereby, also, if possible, set its feeding behaviour, diet and consumption into the overall picture of tonnoidean predation that has been little elaborated.

Materials and methods

Feeding behaviour

Permission was given for 14 individuals of *G. natator* to be collected from the Cape d'Aguilar Marine Reserve and experimented upon. As an initial experiment, the 14 individuals of *G. natator* were held in aquaria of the Swire Institute of Marine Science of the University of Hong Kong on the shores of the Cape d'Aguilar Marine Reserve, along with individuals of the species that typically occur with it under the smaller and moveable boulders that occupy the shallow sub-tidal waters of Lobster Bay within the reserve (Morton and Harper 1995, Figure 6). Such species commonly included the gastropods *Monodonta labio* (Linnaeus) and *Nerita albicilla* Linnaeus, the bivalves *Hormomya mutabilis* (Gould) and *Chama reflexa* Reeve, the sea star *Coscinasterias acutispina* (Stimpson) and the sponge *Tethya aurantia* (Pallas). The institute's sea-water supply is untreated so that aquarium-entrained species are held under near-ambient conditions. After 1 month of observations, this experiment was abandoned because none of the species had been consumed by *G. natator*, and this will not be reported upon further. Field observations, however, recorded that individuals of *G. natator* were often associated with small, scattered, individuals of the rock oyster *Saccostrea mordax* Gould that occur in more sheltered mid- to low-tide pools and cryptic habitats also in Lobster Bay.

Accordingly, another longer-term, but still trial, experiment was established in which two of the 14 individuals of *G. natator* of approximately the same shell height, that is 34.6 and 33.6 mm, were held in separate trays of, again, ambient seawater [20°C (± 2°C) and 32‰ salinity] each with 12 rock oysters that had all been carefully removed from the shores outside the marine reserve using a solid scalpel and small hammer so that none of them was damaged. The oysters were also cleaned of any adhering material and organisms with a toothbrush and checked carefully for any sign of shell damage. Twenty-four more cleaned oysters were held under identical conditions as the two experimental aquaria, but without *G. natator*, as mortality controls. Similarly, two other *G. natator* individuals were held in separate trays and remained unfed except for what the seawater supply provided. One of these trays was cleaned, as with the experimental conspecific with oysters, whereas the other control was not.

One of the two experimental aquaria and one of the two *G. natator* controls were supplied with unfiltered ambient seawater whereas the second experimental aquarium was supplied with seawater (at the same rate) that had been filtered through a fibreglass column. The floor and walls of the latter aquarium only (plus one of the controls; see above) were, moreover, cleaned scrupulously every day for 16 weeks when, as will be described, the experiment ended. Hence, the *G. natator* individual occupying this aquarium (and its control) had nothing to feed on except the oysters, whereas the other individual had oysters plus any sediment or "fouling" organisms that settled out from the ambient seawater and which it could potentially consume. The *G. natator*-alone controls and the oysters-alone controls were therefore held in similarly filtered and cleaned and un-filtered seawater trays as the two experimental predators plus their potential oyster prey. Neither the oysters alone nor the *G. natator* alone controls suffered any mortality and will not be reported upon further.

Each experimental oyster was damp-weighed (to the nearest 0.1 g) before the start of the experiment, which lasted for 16 weeks, that is, as will be described, when all 12 individuals in the filtered seawater aquarium had been attacked and consumed by the resident *G. natator* individual. Subsequently, the shells of the oysters that had been consumed were damp-dried and re-weighed (to the nearest 0.1 g) to obtain an approximate estimate of how much flesh (wet weight) had been consumed. Similarly, when the experiment was concluded after 16 weeks, the two *G. natator* individuals were re-weighed, boiled in water and their tissues were removed from the shells, damp-dried, and weighed (to the nearest 0.1 g), to obtain measures of shell and wet tissue weights.

Separately, 34 individuals of *S. mordax* were obtained from shores outside the Cape d'Aguilar marine reserve's Lobster Bay. After weighing, the tissues of these individuals were removed from their shells, damp dried and weighed, again to the nearest 0.1 g. Such data were used to construct total weight versus wet tissue weight regressions that would be used to obtain estimates of consumption for the two experimental *G. natator* individuals. Similarly, the shell heights of five of the 12 remaining (including the two controls) individuals of *G. natator* were measured (to the nearest 1 mm) and total and shell weights, and wet tissue weights (all to the nearest 0.01 g) were recorded. These five individuals plus the same data obtained for the two experimental animals (see above) were used to construct shell height versus wet tissue weight regressions. Using the two regressions for *S. mordax* and *G. natator* wet tissue weights it has been possible to obtain derived estimates of consumption for the two experimental predators over the 16-week period of study.

Statistical analyses

As noted above, the measurements of the total weight, shell weight, mantle water and wet tissue weights of the 34 individuals of *S. mordax* and seven individuals of *G. natator* plus the shell heights of the latter, were used to estimate the consumption rates of the predator upon the oysters in filtered and unfiltered seawater, both with oysters, respectively. Values obtained for total weight (TotW), wet tissue weight (WW) of both species, plus shell height (SH) of *G. natator*, were Log(x + 1) transformed to optimize linear correlations. The linear regression, Log(WW + 1) = –0.462 + 0.470[Log(TotW + 1)] (n = 34, r^2 = 0.637, $p \leq 0.001$), obtained between the 34 *S. mordax* total weights (Figure 3) and wet tissue weights, was used to estimate the wet weights of the predated individuals identified in Table 1. Similarly, the linear regression, Log(WW + 1) = –4.788 + 1.492[Log(SH + 1)] (n = 7, r^2 = 0.817, $p \leq 0.01$), obtained between shell heights and wet weights of the seven *G. natator* individuals (Figure 4) was used to estimate the wet weights of the two individual predators used in the feeding experiment (Table 1). Statistical calculations were carried out using SigmaPlot v.11.0.

Foregut anatomy and histology

Three of the remaining seven individuals of *G. natator* collected from the shores of the Cape d'Aguilar Marine Reserve were anaesthetized in equal parts of 7.5% magnesium chloride and ambient seawater, preserved in 5% formaldehyde and dissected to demonstrate details of foregut anatomy. Subsequently, the salivary and pharyngeal

Table 1. Numbers (and individual weights) of oysters (*Saccostrea mordax*) consumed by two equal-sized *Gyrineum natator* individuals over a period of 16 weeks in two conditions of filtered and unfiltered seawater (columns A and B). Also identified are the derived wet tissues of the oysters consumed (columns C and D) and the wet weights of oyster tissues consumed^{-1} derived wet weight of predators^{-1} expressed as percentages (columns E and F).

Column	A	B	C	D	E	F
Week	Total weight of oysters attacked in filtered seawater (with *Gyrineum*, 34.6 mm SH)	Total weight of oysters attacked in unfiltered seawater (with *Gyrineum*, 33.6 mm SH)	Wet tissue weight of oyster tissues consumed in filtered seawater (with *Gyrineum*, 34.6 mm SH))	Wet tissue weight of oyster tissues consumed in unfiltered water (with *Gyrineum*, 33.6 mm SH)	% wet weight of oyster tissues consumed in filtered seawater water (with *Gyrineum*, 34.6 mm SH)	% wet weight of oyster tissues consumed in un filtered seawater water (with *Gyrineum*, 33.6 mm SH)
1	5.4 g	9.1 g	0.51 g	0.87 g	69.22	131.55
	1.9 g	2.2 g	0.04 g	0.09 g	5.16	13.11
	13.4 g		1.20 g		164.85	
2	10.6 g		0.99 g	–	135.58	
3			–	–		
4	43.8 g		2.76 g	–	377.35	
	2.6 g		0.15 g		20.43	
	34.9 g		2.39 g		327.48	
5		5.3 g	–	0.50 g		74.97
6			–	–		
7			–	–		
8			–	–		
9			–	–		
10			–	–		
11	1.9 g		0.04 g	–	5.16	
12	17.9 g		1.50 g	–	206.07	
13			–	–		
14			–	–		
15	3.4 g	2.1 g	0.26 g	0.07 g	36.12	10.82
	4.3 g		0.38 g		51.85	
	3.4 g		0.26 g		36.12	
16			–	–		
Oyster eaten Total:	12 (143.5 g)	4 (18.7 g)	10.48 g	1.52 g	98.78	1.52
Average per week:	0.77 (11.96 g)	0.25 (4.68 g)	0.65 g	0.01 g		

gland tissues of these individuals were removed and preserved in Bouin's fluid overnight and, following routine histological procedures, sectioned at 6 μm. Alternate slides were stained in either Ehrlich's haematoxylin & eosin or Masson's trichrome. These sections were used to determine the histological features of the two glands.

Salivary and pharyngeal gland pH

Small pieces of the salivary and oesophageal glands were excised from each of the final four individuals of *G. natator* and homogenized separately in 2 ml of de-ionized and double-distilled water using a Kinematica CH-6010 polytron homogenizer and the pH of the resultant eight liquids was measured with an HI 8114 digital pH meter.

Sulphuric acid production

The remaining portions of the salivary glands of the three individuals of *G. natator* used in the above anatomical and histological studies were divided into two pieces. The first three such pieces were given three consecutive baths in 3.2% sodium chloride. The glands were then immersed in 1% barium chloride for 50 minutes and subsequently fixed in 10% formaldehyde. The three other pieces of the glands from the same individuals were not bathed in barium chloride and became the controls. Following routine histological procedures, 6-μm thick transverse sections of the six pieces of glands were lightly counterstained in eosin and examined under phase-contrast microscopy for the presence and distribution of barium sulphate crystals.

The pharyngeal gland of one of the individuals used in the anatomical and histological studies described above of *G. natator* was removed and divided into two portions. These were treated in the same way as above, the second piece serving as a control. The above tests for barium sulphate crystals are positive for the presence of sulphuric acid-secreting cells in marine molluscs (Thompson 1983) and has been used successfully by this author (Liang and Morton 1988) to detect the presence of the same acid-secreting cells in the pallial organ of *Atrina pectinata* (Linnaeus) (Bivalvia: Pinnidae).

Results

Gyrineum natator possesses a pleurembolic proboscis and this is seen in its extended state in Figure 1 where the living animal is illustrated from the ventral aspect crawling on an upturned sheet of glass immersed in seawater. The cephalic tentacles of *G. natator* are short and stubby with eyespots located towards their outer bases. The extended, radula-tipped, proboscis is longer and is mottled brown, as are the tentacles and siphon.

Feeding behaviour

In the experimental controls, no oysters nor either of the two *G. natator* died over the course of the 16-week experimental period. Every one of the 16 individuals of *S. mordax* consumed by *G. natator* in each of the pair of experiments, (all 12 in the

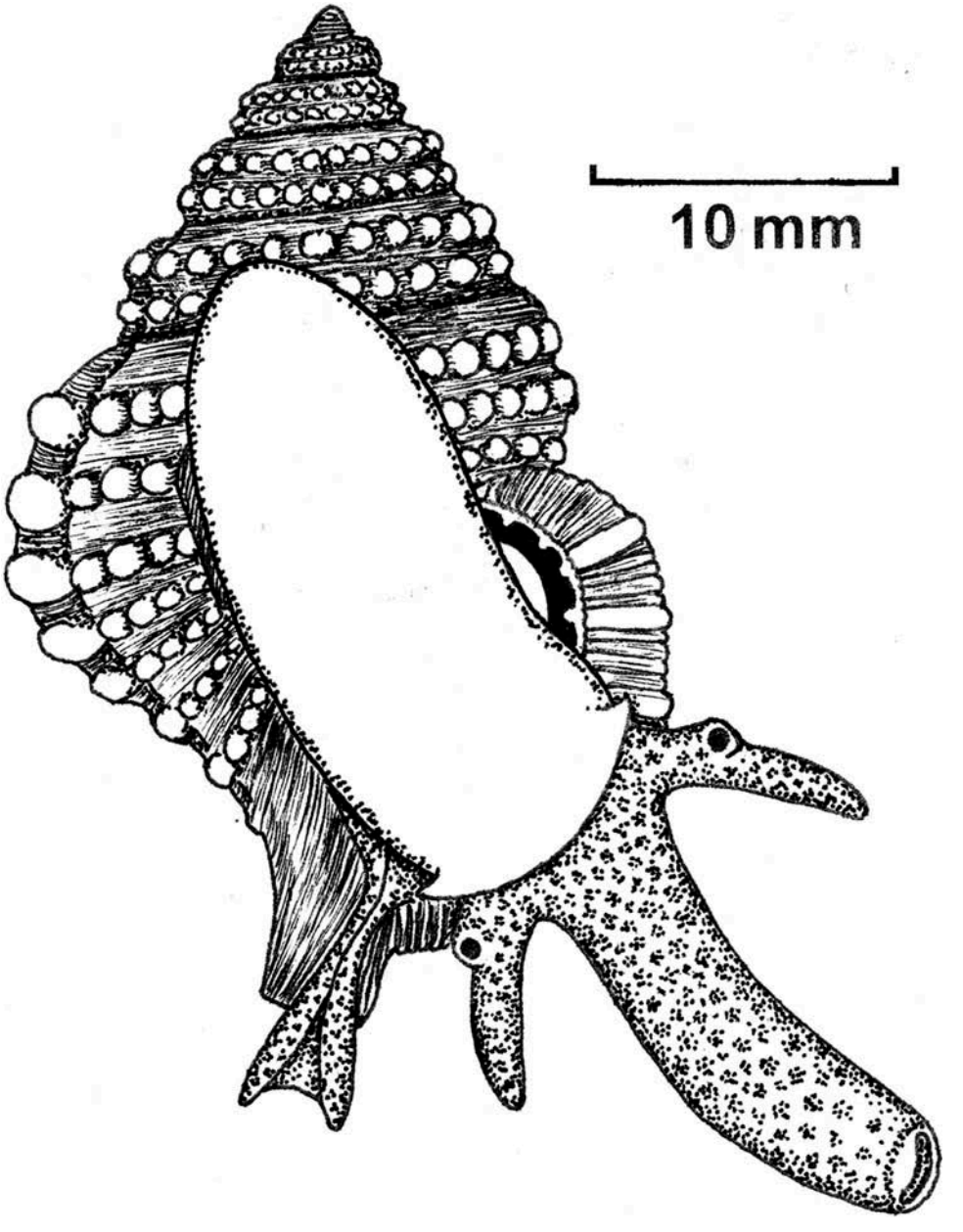

Figure 1. *Gyrineum natator*. The living animal as seen from the ventral aspect crawling on an upturned sheet of glass immersed in seawater, and showing the extended proboscis.

filtered seawater aquarium, four of 12 in the unfiltered seawater aquarium) were attacked by the creation of holes in their shells, typically marginally. Four of these are illustrated in Figure 2. In Figure 2A, a small circular, irregular, hole had been made in the upper right valve of one oyster's shell. In all the other shells, three of

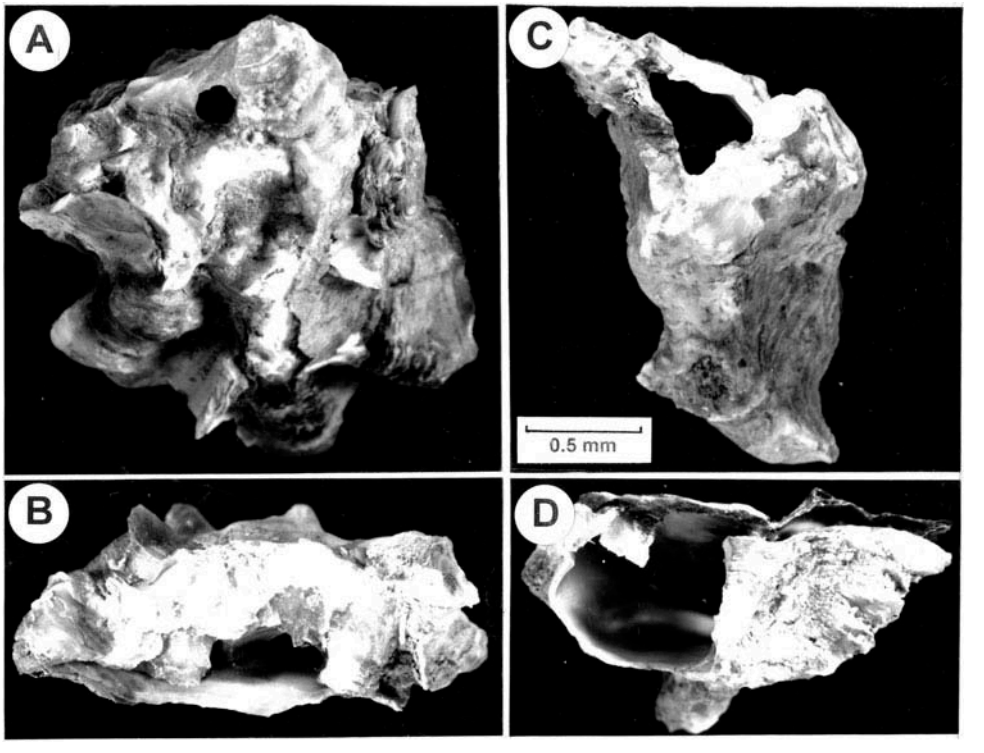

Figure 2. *Gyrineum natator*. The holes made in four shells (A–D) of *Saccostrea mordax* by individuals held in experimental aquaria. Only A shows a near-circular access hole, but other irregular ones (B–D) appear to have been created by acid attack as there would be no need for the radula alone to make such large holes.

which are illustrated in Figure 2B–D, the holes were much larger and highly irregular and quite unlike the stereotypical holes created by muricid and naticid predatory gastropods (Carriker 1981).

Table 1 shows the results of the feeding experiments. In the scrupulously cleaned aquarium fed with filtered seawater all 12 oysters were consumed by the resident *G. natator* (shell height of 34.6 mm) within a period of 16 weeks (Table 1, Column A). In contrast, only four oysters were eaten by a conspecific *G. natator* of the same approximate shell height (33.6 mm) (Table 1, Column B) in the unfiltered water aquarium, In terms of total and weekly average oyster weights, this amounted to 143.5 g and 18.7 g, respectively, and 11.96 g and 4.68 g, again respectively.

The linear relationship between the Log(x + 1) total weight and the Log(x + 1) wet tissue weight of the 34 *S. mordax* individuals are shown in Figure 3. The obtained r^2 value was 0.637 (p = <0.001). The relationships between Log(x + 1) shell height and Log(x + 1) wet tissue weight of the seven individuals of *G. natator*, including the two experimental animals, are shown in Figure 4. The obtained r^2 value was 0.817 (p = 0.01). Based on these results, it was possible, given the values of wet tissue weight estimated for the two experimental individuals of *G. natator* (shell heights of 34.6 and

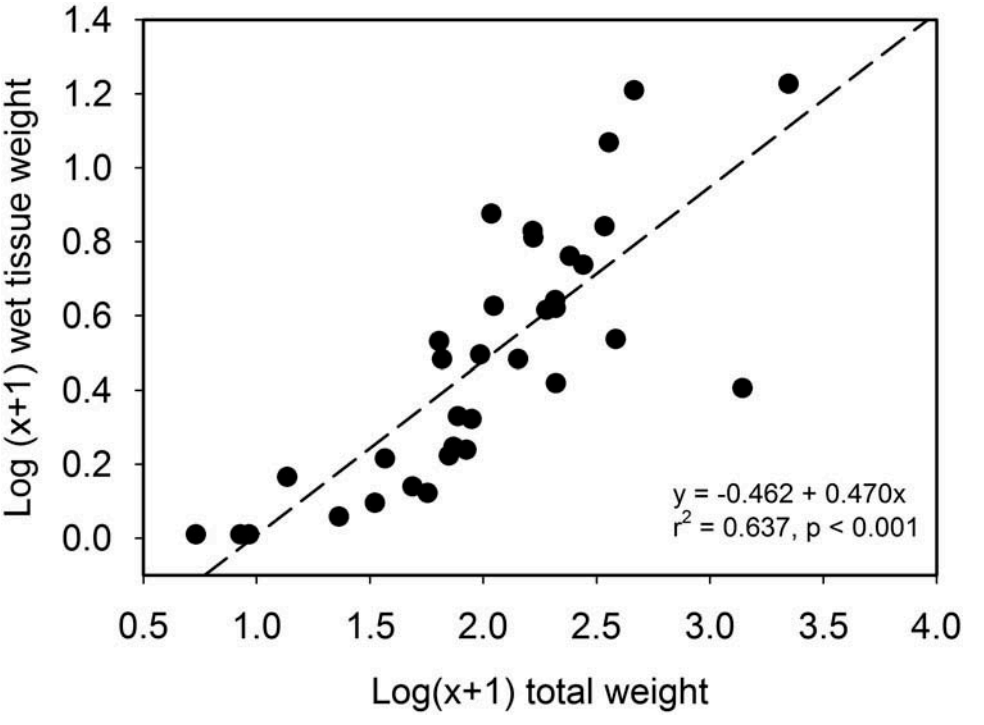

Figure 3. *Saccostrea mordax*. The relationship between total weight [Log(TotW + 1) (in grams)] and wet tissue weights [Log(*W* + 1) (in grams)] of the 34 oyster individuals.

33.6 mm), to calculate values for the wet tissue weights of each individual oyster consumed during the 16-week-long experiments. These calculated values are identified in Table 1, Columns C and D for the *G. natator* individuals in filtered and unfiltered seawater, respectively. In summary, the *G. natator* in filtered seawater consumed a total of 10.48 g of wet oyster tissue equalling 0.65 g each week. The *G. natator* individual in unfiltered seawater consumed a total of 1.52 g of oyster wet tissue, equalling only 0.095 g each week. Similarly, using estimated wet tissue weight figures obtained for the two individuals of *G. natator* (Figure 4), it was possible to then calculate how much oyster tissues had been consumed over the course of the 16-week experiment and each week in terms of their wet tissue weights and expressed as percentages (Table 1, Columns E & F, for the predators in filtered and un-filtered seawater, respectively). Over the 16-week period, the *G. natator* in filtered seawater consumed 98.78% of its own wet tissue weight, whereas the conspecific in unfiltered seawater consumed only 1.52%. This amounted to 14.11% per day and 0.21% per day, respectively.

Percentage accumulated values of wet oyster tissue weight/predator wet tissue weight consumed by the two *G. natator* individuals each week of the 16-week period are presented in Figure 5. *Gyrineum natator* in filtered seawater consumed seven oysters in the first 4 weeks, followed by a long period of repose when it consumed five more oysters over the final 5 weeks of the experiment. The resulting graph appears as a highly profiled asymptotic curve. Conversely, the *G. natator* individual

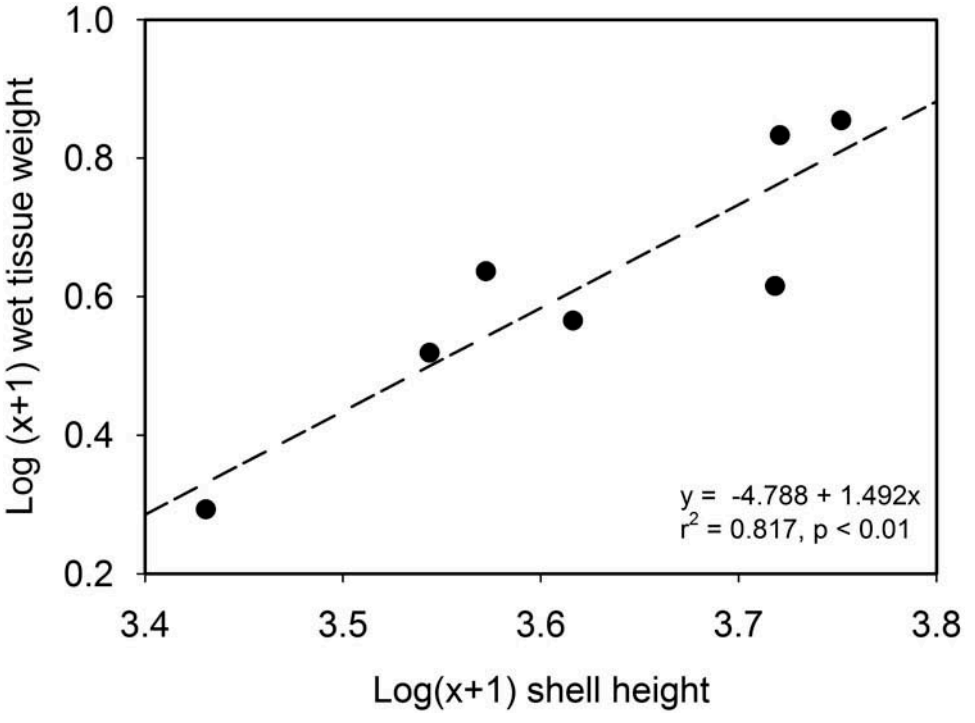

Figure 4. *Gyrineum natator*. The relationship between shell height (in mm) and wet tissue weights [Log(W + 1) (in grams)] of seven individuals including the two experimental animals with shell heights of 34.6 and 33.6 mm.

in unfiltered seawater consumed two oysters in the first week, another one in week 5 and then another one in week 15 creating a low profiled asymptotic curve.

Foregut anatomy and histology

The foregut anatomy of *G. natator* is seen from the dorsal aspect in Figure 6. It shows the pleurembolic proboscis containing the mouth with an anterior radula contained within its radula sac. Paired salivary ducts empty into the mouth and, along with the oesophagus, pass through the nerve ring. The ducts arise from a pair of hypertrophied salivary glands, which are also associated dorsally with a single pharyngeal gland.

The histology of the salivary and associated pharyngeal glands of *G. natator*, as termed by Andrews and Thorogood (2005) but identified as salivary and oesophageal glands by other, earlier, authors are illustrated in Figure 7. Figure 7A is a transverse section through one of the paired salivary glands and the associated pharyngeal gland. The whole structure is contained within a muscular sheath and each salivary gland tubule contains a central cluster of barium sulphate crystals. New, developing, tubules are located peripherally in the gland while the structure opens into a lumen that is surrounded by the tubules of the pharyngeal gland. A peripherally developing, pyramidal, salivary gland tubule (Figure 7B) with a basal length of ~40 μm comprises squamous cells some 5 μm tall. These tubules also contain distinctive barium sulphate

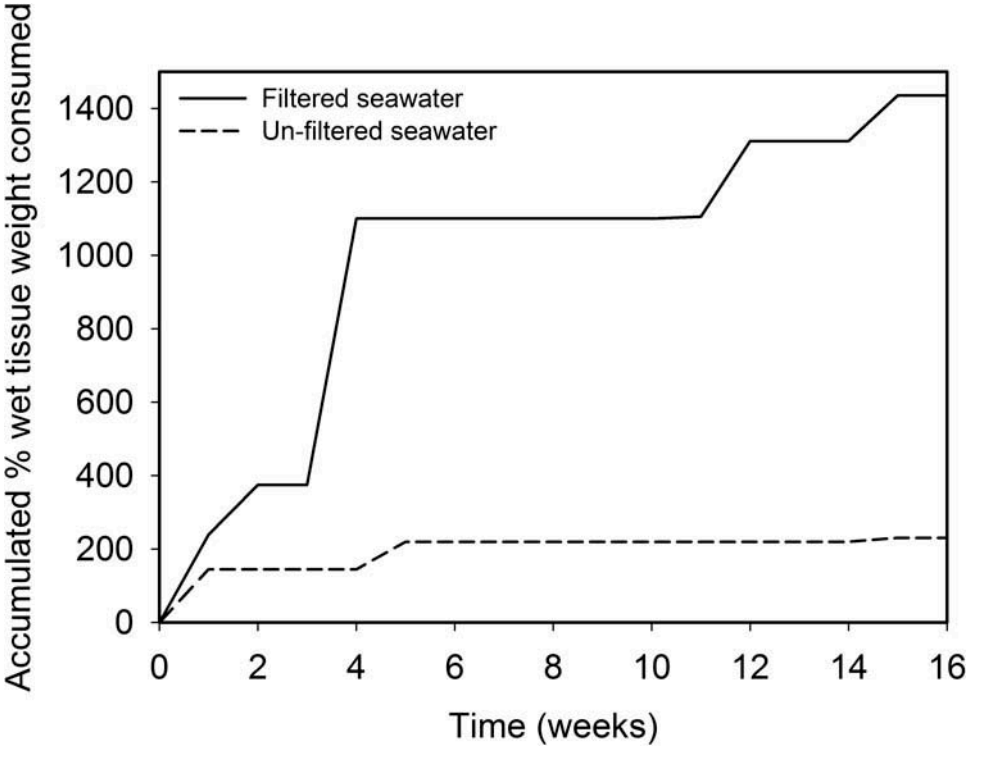

Figure 5. *Gyrineum natator*. The accumulated % wet tissue weights of oyster tissues consumed by the two approximately equal-sized individuals of *G. natator* held in filtered and unfiltered seawater aquaria.

crystals. Fully developed salivary gland cells are columnar, ~40 μm tall containing barium sulphate crystals ~4 μm in diameter (Figure 7C). Figure 7D is a transverse section through a pharyngeal gland tubule, which are ~ 60 μm in diameter. Each tubule comprises basophilic mucous cells interspersed with what have described as storage cells by Andrews and Thorogood (2005) for other muricid and nassariid caenogastropods. In transverse section (Figure 7E), the salivary gland/pharyngeal gland duct is about 170 μm in diameter. It comprises basophilic mucous cells interspersed regularly by distinctively ciliated cells with long, ~50 μm, cilia.

Salivary glands and pharyngeal gland pH

The obtained pH values of the salivary glands of the four individuals of *G. natator* were 2.8, 3.1, 3.3 and 3.6 (x = 3.2). The obtained pH values of the pharyngeal glands of the same four individuals were 8.1, 8.5, 8.7 and 9.2 (x = 8.6).

Sulphuric acid secretion

The irrigation with barium chloride of tissues thought to harbour soluble sulphates gives rise to the *in situ* precipitation of barium sulphate (Thompson 1983), which can

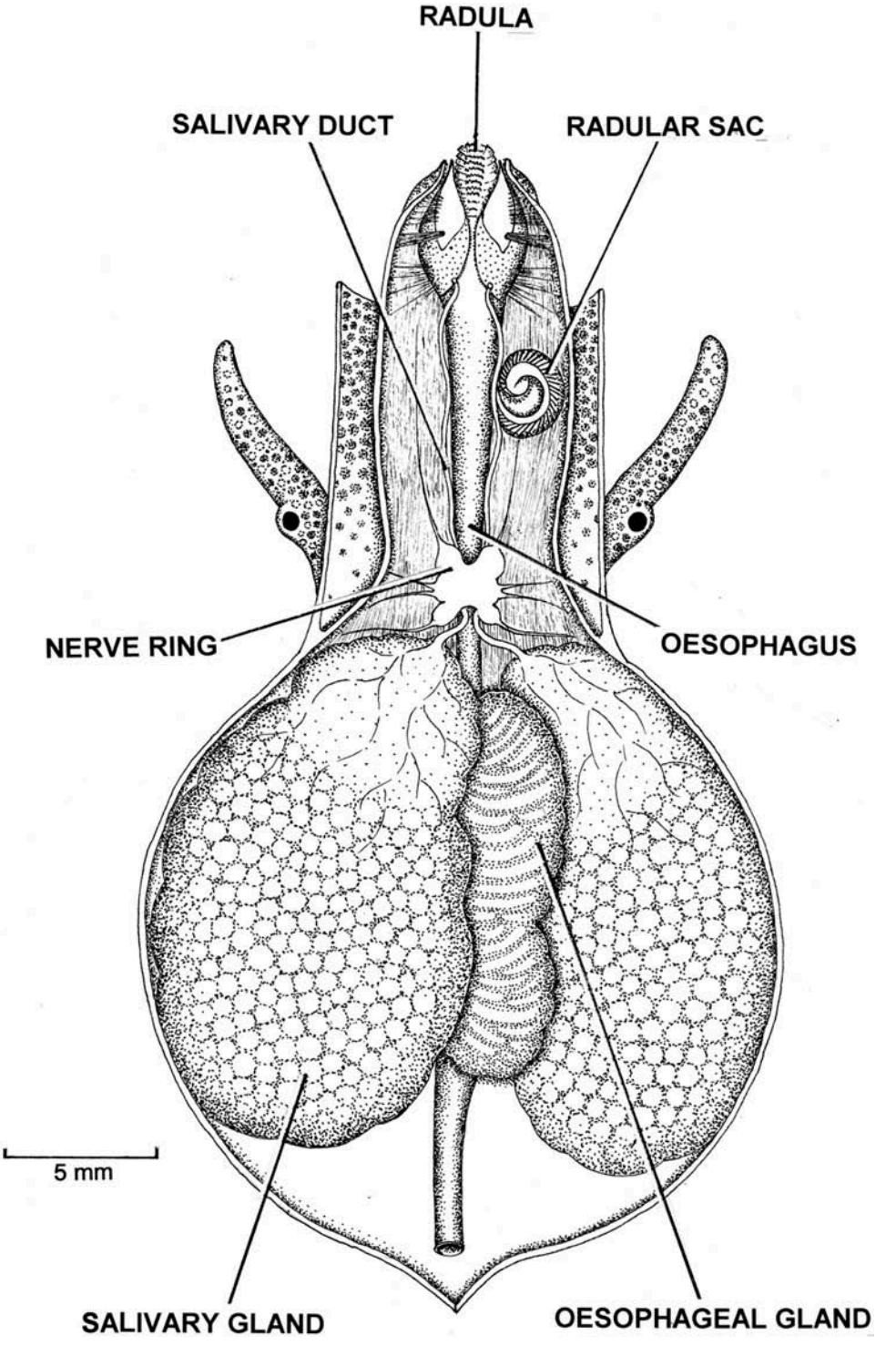

Figure 6. *Gyrineum natator*. The foregut anatomy, as seen from the dorsal aspect, and showing the hypertrophied and paired salivary glands and the single pharyngeal (oesophageal) gland. Redrawn after Taylor (1998).

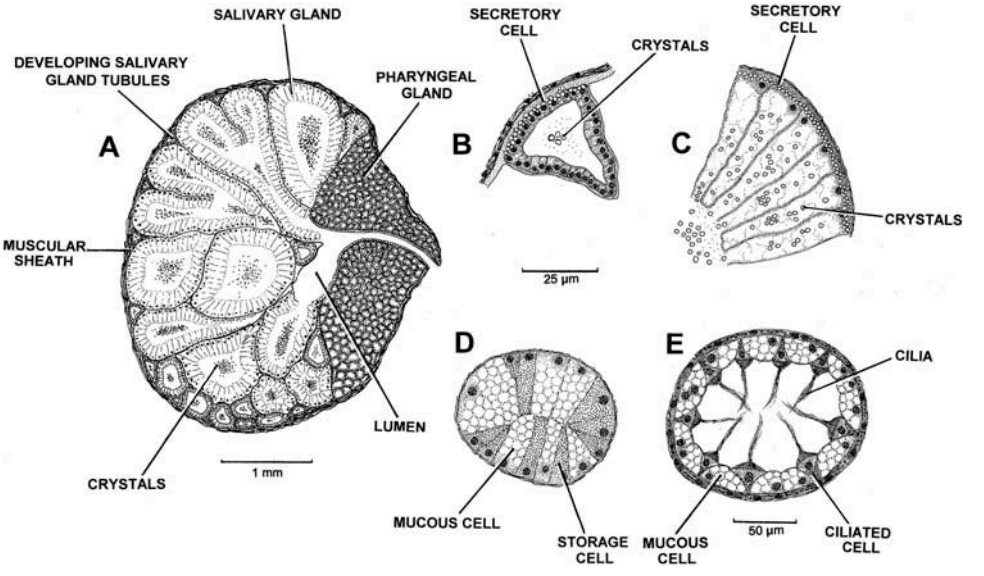

Figure 7. *Gyrineum natator*. (A) A transverse section through one of the paired salivary glands and the associated pharyngeal (oesophageal) gland; (B) developing salivary gland tubules at the outer edge of the salivary gland; (C) fully developed sulphuric acid producing salivary gland cells; (D) a transverse section through a pharyngeal (oesophageal) gland tubule; (E) a transverse section through the salivary gland/pharyngeal gland duct.

be recognized in sections under phase-contrast microscopy as hyaline crystals. The results of irrigating the salivary glands of three individuals of *G. natator* for 50 minutes, as suggested by Liang and Morton (1988), are illustrated in Figure 8. These phase-contrast micrographs of the salivary glands of the three untreated control individuals of *G. natator* are shown in Figure 8A–C. The barium chloride-treated individuals (Figure 8D–F) exposed the tall (40 µm) columnar, acid-secreting cells most of which contained bright, hyaline, barium sulphate crystals that were not identifiable in the untreated controls.

Figure 9 illustrates barium chloride-treated phase-contrast micrographs of the salivary (Figure 9A) and the pharyngeal (oesophageal) (Figure 9B) glands of *G. natator* both after treatment with barium chloride for 50 minutes. The treated salivary gland contained bright, hyaline, barium sulphate crystals that were not identifiable in the pharyngeal gland.

Discussion

As noted in the introduction to this paper, the Tonnoidea Suter, 1913 comprises approximately seven families of predatory gastropods, although the systematics of this diverse group is still debated (Beu 1998). Bandel and Riedel (1994) and Riedel (1995) suggested the name Cassoidea for this suite of Neotaenioglossa, although the name Tonnoidea was conserved by Beu (1988, 1998) and accepted by Bouchet and Rocroi (2005). It is therefore used herein. According to Bouchet and Rocroi (2005), the Tonnoidea comprises the Tonnidae, Bursidae, Laubierinidae, Personidae,

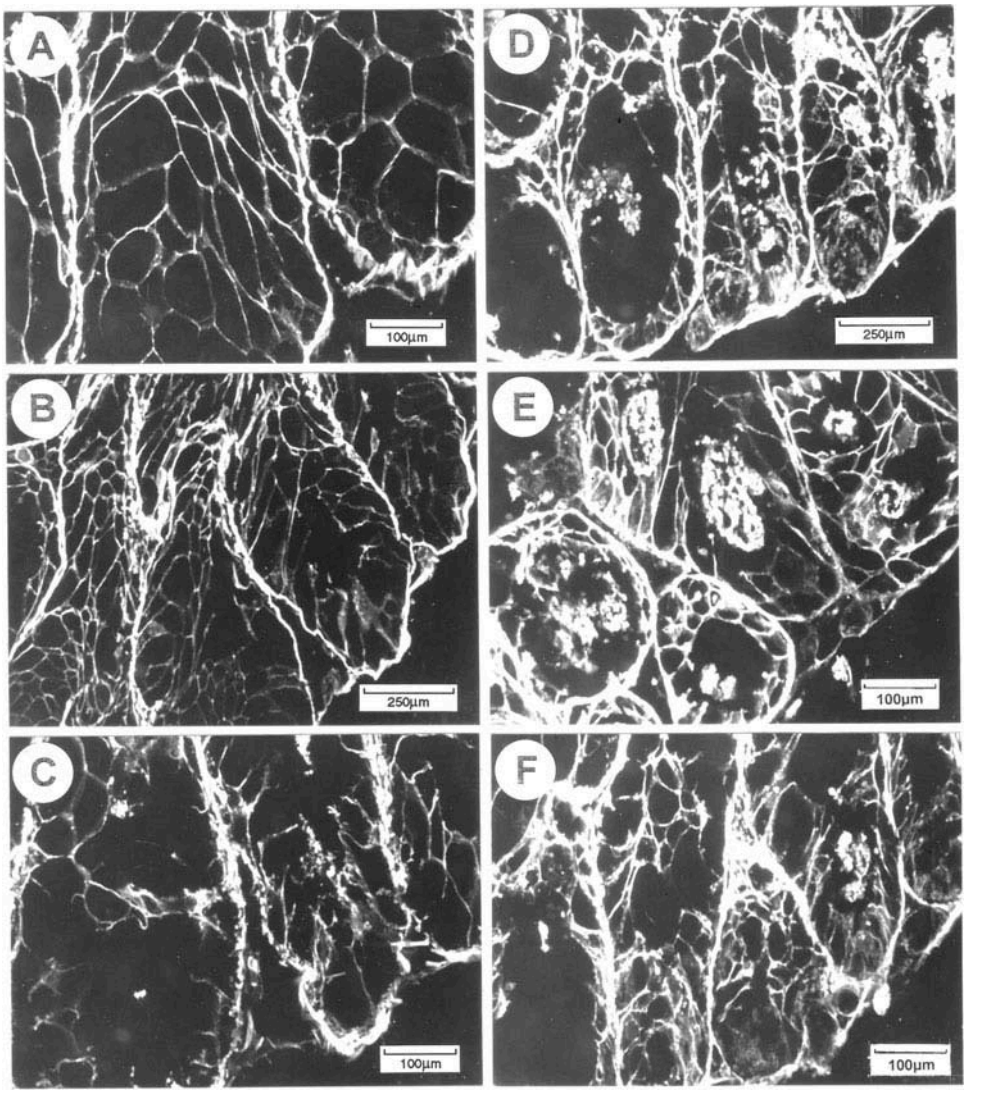

Figure 8. *Gyrineum natator*. Phase-contrast micrographs of the salivary glands of three individuals following treatment with barium chloride for 50 minutes. (A–C) Three untreated controls; (D–F) three treated individuals.

Pisanianuridae, Ranellidae and Cassidae, the last named considered a sub-family of the Ranellidae, although Beu (2008) elevated it to family status. In addition, some authorities consider the Cymatiidae to be but a subfamily of the Ranellidae whereas others consider the two to constitute distinct families.

Resolution of this confused taxonomy is not, however, the principal subject of this paper – although it is believed that studies of diet and feeding strategy could help in this matter. At this time, however, it is only necessary to state that *G. natator* is currently regarded as a member of the Ranellidae (or Ranellinae), but is sometimes

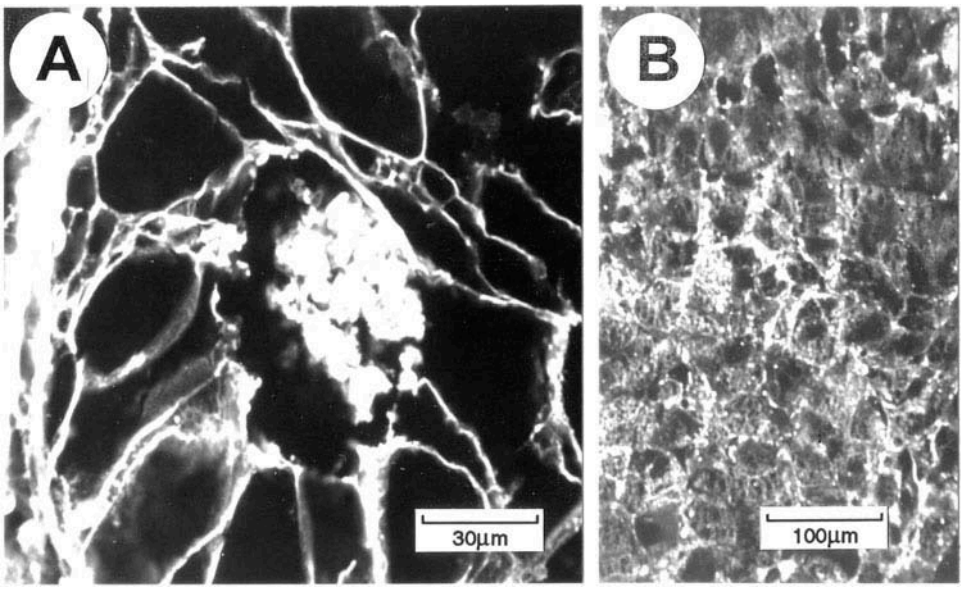

Figure 9. *Gyrineum natator*. Phase-contrast micrographs of (A) the salivary gland and (B) the pharyngeal (oesophageal) gland after treatment with barium chloride for 50 minutes.

placed in the Cymatiidae (or Cymatiinae) according to which authority one acknowledges. This study therefore investigated the diet, method of feeding and consumption of *G. natator*. With, as demonstrated herein, huge salivary glands secreting (as also demonstrated herein) sulphuric acid, the question to be answered is: why are such structures and secretions needed by *G. natator* when, in field-derived observations and subsequent analyses of stomach contents, the evidence suggests that it is an indiscriminate browser of algae and epibionts of the rocky intertidal and shallow subtidal (Taylor 1980; Taylor and Morton 1996; Neo et al. 2001)?

With no known answer to this vexing question, this study attempted to answer it by forcing, through selective starvation, individuals of *G. natator* to feed on bivalve (oyster) prey. The study also sought to set the feeding activities of *G. natator* into the overall picture of tonnoidean predation that has been little elaborated.

Species of *Tonna* (Tonnidae), such as *Tonna zonatum* (Green), feed almost exclusively, as far as is known, on holothurians swallowed whole (Morton 1991, Figure 1). Earlier, however, Weber (1927) had suggested that the salivary glands of *Tonna galea* (Linnaeus) secrete sulphuric acid to either pacify or access their prey, although the study by Morton did not conclude this. Interestingly, however, Bigatti et al. (2010) showed that *Odontocymbiola magellanica* (Gmelin), (Volutidae), a muricoidean distantly related to tonnoideans, produced not an acid, but a strongly alkaline (pH 10) secretion from its salivary and accessory salivary glands. This was used to immobilize and relax its gastropod and bivalve prey, allowing them to be consumed alive. Interestingly, the pharyngeal glands of *G. natator* individuals examined in this study had an average pH value of 8.6.

Species of *Charonia* (Tritonidae) have similarly been suspected of producing either a venom or sulphuric acid from a proboscis gland to either pacify or access

their prey. The suggestion of venom seems to have been proposed for species of *Charonia* by Panceri (1868) and an acid by Pelseneer (1935), which, it was suggested, was used to drill a hole through the calcareous skeletons of its echinoderm prey (Hirsch 1915). As recorded by Bandel (1984, p. 104), however, an individual of *Charonia variegata* (Lamarck), similar to *Tonna zonatum* (see above), swallowed a holothurian whole. Small asteroids and the detached arms of bigger sea stars were also swallowed whole, the latter one by one. Similarly, Bandel (1984) never observed *C. variegata* drilling a hole through the calcareous skeletons of echinoderms, although he did observe the predator gaining access to the interior of an echinoid by drilling a hole (but using the radula) through the buccal membrane that surrounds the Aristotle's lantern, "*where no calcareous plates are present*" (my italics), and only organic matter has to be penetrated. Okutani (2000, p. x) also illustrated, *Charonia lampas* (Linnaeus) feeding on *Ceratonardoa semiregularis* (Müller and Troschel) (Ophidiasteridae) in a like manner in Japanese waters. Scheibling (1980) observed *C. variegata* feeding on the sea star *Oreaster reticulatus* Müller and Troschel at St Croix in the US Virgin Islands in the Caribbean and described it as follows (p. 115): "The triton initially ingested the soft internal tissues of *O. reticulatus* penetrating the mouth or aboral body wall with its proboscis. Subsequently, the collapsed body wall was gradually engulfed. The duration of feeding was 2 to 4d." In a laboratory aquarium in the Açores, Morton (2012) reported upon *C. lampas* feeding on the sea star *Ophidiaster ophidianus* (Lamarck) but not piercing the skeleton of its non-envenomated sea star prey to suck out the tissues but, rather, simply consuming the whole arm autotomized by the prey. Finally, and most recently, Morton and Pires (2013) observed *C. lampas* in the field in the Açores feeding on *Marthasterias glacialis* (Linnaeus) by orally removing a dorsal skeletal spine and feeding on the tissues beneath through this hole. Hence, in none of the cases where predation by species of *Charonia* has actually been observed, neither acidic nor venomous secretions have been ascribed to the feeding process.

Although this paper is not concerned with phylogeny, the widely-accepted linkage between the tritons and other representatives of the Ranellidae and, especially, the Cassidae within the Cassoidea (Riedel 1995) seems to have led to the assumption that, like these other, well-known, acid-producing predators, prey capture in species of *Charonia* also involves such chemicals. As described above, there is, however, little actual evidence that this is so. Moreover, the most recent construction of a phylogenetic tree for the Caenogastropoda based on morphological characters (Simone 2011, Figure 20), identified *Charonia laevigata* located in its own clade, separate from the Cassidae and other representatives of the Ranellidae, suggesting that the Tritonidae discussed above should be separated from the other tonnoidean families. In this conclusion, the suggestion of Simone is supported by evidence that species of the Cassidae, in contrast to the Tonnidae, Tritonidae (see above) and Bursidae [Beu 1998; for example, *Bursa cruentata* (Sowerby) and *B. granularis* (Röding) (Houbrick and Fretter 1969)], are said to inject an acidic/venomous saliva into their prey to paralyse them (Hughes and Hughes 1981) and then, as described for *Phalium bisulcatum* Schubert and Wagner (Cassidae) feeding on an echinoid (*Brissus* sp.) by Hughes (1985, p. 626), cut "out a disc of the test using a secretion of the proboscis gland, rich in sulphuric acid".

Representatives of the Ranellidae, often linked closely systematically with the Tonnidae and Tritonidae, "appear to have rather generalist diets" (Taylor 1998,

p. 190). In the North Pacific, Kohn (1983), reported that *Fusitron oregonensis* Redfield feeds upon echinoids, asteroids, ophiuroids, tunicates, bivalves, gastropods, chitons, polychaetes and carrion although tunicates and echinoids were the preferred prey (Young 1985). The southern Australian *Argobuccinum pustulosum* (Solander in Lightfoot, 1786) attacks the ascidian *Sycozoa cerebriformis* (Quoy and Gaimard) (Coleman 1981). In southern Australia too, *Mayena* (= *Ranella*) *australasiae* (Perry, 1811) eats ascidians, but also consumes carrion (Laxton 1971). Day (1969) showed that the South African *Argobuccinum argus* Gmelin feeds, in the laboratory, on the intertidal, tube-dwelling, sedentary polychaete *Gunnarea capensis* (Schmarda) (Bustamante and Branch 1996). Day (1969) also showed that the acid secretion produced by *A. argus* was 33% more effective in dissolving calcium carbonate than 0.47N sulphuric acid alone and, further, that salivary gland secretions of *A. argus* were more effective in dissolving the shells of *Macoma* sp. (Bivalvia) prey than 1 N acid alone due to the added ingredient of a chelating agent in the saliva.

There is also evidence that representatives of two other tonnoidean families produce sulphuric acid to access their prey. *Species of Cymatiinae* [or Cymatidae, according to different authors] *mainly feed on other molluscs* (Taylor 1998, p. 192). *Cymatium gemmatum* (Reeve), *Cymatium nicobaricum* (Röding) and *Cymatium parthenopeum* (von Salis) eat gastropods (Houbrick and Fretter 1969; Adam 1979) whereas *Cymatium pileare* Linnaeus, *Cymatium aquatile* (Reeve), *Cymatium intermedia* Pease, 1869 and *Cymatium muricinum* (Röding) feed on bivalves (Houbrick and Fretter 1969; Taylor 1984) including, in Australia, the cultivated oyster *Crassostrea rhizophorae* (Guilding) (Littlewood 1989) and cultivated tridacnid clams (Govan 1994). This latter author elaborated upon these observations subsequently (Govan 1995). Here, the author showed that *Cymatium muricinum* repeatedly "stabs" its tridacnid prey with its proboscis and that (p. 19) "Within minutes the clam begins to relax and die" and is then eaten. Such observations suggest strongly that some kind of venom was injected into the prey to narcotize it. Govan (1995) also showed that other species of *Cymatium*, notably *Cymatium aquatile* (Reeve), *Cymatium pileare* (Linnaeus) and *Cymatium nicobaricum*, also attacked juvenile giant clams [*Tridacna gigas* (Linnaeus)] in a similar manner, although the latter species also consumed the gastropod *Cerithium tesselatus* (Wood, 1828).

Also in Australia, and New Zealand, *Cymatium parthenopeum* (von Salis) [as *Monoplex australasiae* (Perry, 1811)] eats bivalves and ascidians (Laxton 1971). In the Mediterranean, *Cabestana cutacea* (Linnaeus) and *Cymatium corrugatum* (Lamarck) eat ascidians whereas *Cymatium parthenopeum* [as *Monoplex parthenopeus* (Salis-Marschlins)], also here, prefers bivalves and ascidians (Troncoso and Russo 1990). Hughes (1986) *showed that* in an aquarium *Galeodea echinophora* (Linnaeus) fed on *Echinocardium cordatum* Pennant, 1777. Every few days, each *predator* emerged from the sand and foraged. On detecting an *urchin*, the proboscis was extended on to the prey and a small area of test was cleared of spines. A disc was cut from the softened test, leaving a hole ~2 mm in diameter. All flesh, except the gut, was then removed from the prey, the entire procedure taking between 1 and 3 hours. Newly hatched juveniles also attached themselves to adult *urchins* and commenced feeding on either the epithelium between the spines or the tube feet. Fänge and Lidman (1976) suggested that the salivary glands of *Cassidaria* (= *Galeodea*) *echinophora* secrete sulphuric acid, which is hyperosmotic and has a pH of < 1. These authors suggested

that this acid secretion, and those of other marine predatory gastropods, might function either in defence or feeding.

The large paired and mono-lobed salivary glands of *Cymatium intermedius* (Morris) (Andrews et al. 1999, Figure 1A) produce secretions that are known to be toxic (West et al. 1998). Andrews et al. (1999) noted that, in *Cymatium intermedius*, only the posterior regions of the salivary glands produced sulphuric acid crystals whereas the anterior regions produced mucus. Accordingly, the posterior regions of the salivary glands and the pharyngeal gland of *G. natator* were sectioned for this study and, as illustrated in Figures 8 and 9, only the former and not the latter were shown to produce crystals of barium sulphate. The question remains, however, and in light of the study by Morton (1990a) upon the ranellid *L. caudata*, which suggested that the sulphuric acid-producing salivary glands of this species were not used in prey penetration, in this case an ascidian but also the arcoid *Barbatia virescens* (Reeve), what is the function of the same acid produced by *G. natator*?

In addition to hard-shelled prey penetration, as demonstrated herein for *G. natator*, it seems possible that the acidic secretion could also be used in defence or, perhaps, in digestion. The functions of the various secretions produced by the foregut glands of *Cymatium intermedius* have been discussed by Andrews et al. (1999) but since the pH of none of them was measured, it is only possible to speculate about the alkaline pharyngeal gland secretions. Perhaps they too play a role in digestion or function to neutralize the acidic salivary gland secretions once they have fulfilled their function(s).

As noted earlier, *G. natator* has been considered to be a generalist browser (Taylor 1980; Taylor and Morton 1996; Neo et al. 2001) of the rocky intertidal in Hong Kong and Thailand. That is, analyses of gut contents identified green algae and the remains of sponges, bryozoans, polychaetes, amphipods and holothurian spicules in its diet plus polychaete and barnacle setae. Conversely, as demonstrated herein, however, under conditions of no-alternative starvation in filtered seawater, *G. natator* readily attacked proffered oysters by creating holes in the shells of such prey items with, analysis of the salivary glands suggest, sulphuric acid. In only one case was a near-spherical hole created in the shell of an oyster (Figure 2A). All the others (Figure 2B–D) were large and irregular. The proffered prey, *S. mordax,* is a species adapted to high-energy, but low-productivity, waters (Lam and Morton 2004) and it therefore seems possible that species such as this on the shores of the Cape d'Aguilar Marine Reserve are attacked by *G. natator* using an acidic secretion, with a pH of ~ 3.2, produced by the large, paired, salivary glands, when other browsable food items are not available to it.

It seems possible too that sulphuric acid is an expensive secretion to not only produce but also to store (although there are no data regarding this) and its use in feeding is, therefore, restricted to times when other food items are not obtainable – as possibly demonstrated herein (Figure 5). That is, under conditions of enforced starvation, *G. natator* consumed > 98% of its body weight each week or > 14% of its wet tissue weight per day. When other potential food, such as sediment, organic debris and other newly settled sessile organisms were available to a similar-sized conspecific (in addition to oysters), the oysters only accounted for 1.52% of its average weekly diet or 0.21% of its wet tissue weight per day.

The conclusion reached by this admittedly trial experiment [with no opportunity for a fully replicated study but supported by field-based estimates of diet (Taylor 1980; Taylor and Morton 1996; Neo et al. 2001)] is that *G. natator* normally simply

browses on organic sediments lodged in rocky intertidal and shallow subtidal crevices and small living sessile animals and only resorts to the sulphuric acid accessing of prey when it is forced, of necessity, to do so – as demonstrated herein. Possibly, too, the acidic secretion is used for either defensive or gut neutralizing purposes, the former also suggested for another ranellid, *L. caudata*, in Hong Kong by Morton (1990a). Interestingly, Houbrick and Fretter (1969) showed that *Cymatium pileare* and *Cymatium muricinum* both feed on bivalves, notably *Crassostrea gigas* (Thünberg) and *Ostrea sandwichensis* Sowerby, but did not explain how.

As noted above, sulphuric acid is possibly energetically expensive to produce and store. Nevertheless, both individuals of *G. natator* experimented upon in this study used it in the first week of study to attack oysters and the individual held in filtered seawater used it again in the fourth week. There then followed, for this individual, a 6-week period of abstinence. The nassariid *Bullia digitalis* (Dillwyn) feeds every 7–10 days (Stenton-Dozey and Brown 1988) as do other nassarids, Morton (1990b) and Cheung (1994) estimating that *Nassarius festivus* (Powys) eats between 50 and 60% of its body weight in a single meal, as does the subtidal *Nassarius siquijorensis* (A. Adams) (Liu and Morton 1994). Once fed to satiation, however, subsequent meals are smaller (Cheung 1994; Liu and Morton 1994). Cheung and Wong (2001) showed experimentally that *N. festivus* grew fastest when fed every 2 days (high ration), followed by those that fed every 7 days (medium ration). Individuals lost weight when fed every 21 days (low ration). As illustrated in Table 2, however, the above nassariids are opportunistic scavengers and feed voraciously when the opportunity arises and such feeding bouts are followed by long periods of quiescence until another such opportunity presents itself (Morton and Britton 1991; Britton and Morton 1993). Such voracity leads to consumption estimates of > 20% per feeding bout per day.

True gastropod predators are, however, somewhat different from scavenging nassariids although consumption figures can still be impressive. These are identified in Table 2, wherein most values are expressed in terms of wet weights and although a few, for example, Paine (1965) and Edwards and Hubner (1977), are expressed in terms of dry weight, such values typically show a difference of but 1–2% from those of wet weight (Morton 1990a). Two-week-old hatchlings of the melongenid whelk *Hemifusus tuba* (Gmelin) ate approximately 92% of their body weight (of carrion) each day, which equates to > 40% of their wet tissues weight per day. In subsequent weeks, however, this figure declined progressively and fell to between 3–4% per day for adults (Morton 1985, 1986; Mortem 1987). A similar situation has been demonstrated for the naticid *Polinices duplicatus* (Say) which consumes between 14 and 18% of its wet tissue weight per day as juveniles (Turner 1949). This falls to a maximum of 5–6% per day in adults (Edwards and Huebner 1977) but rises again to 15% per day in reproductively active individuals (Ansell 1981). Adults of other predatory gastropods reveal similar order levels of consumption. In Californian waters, *Navanax inermis* (Cooper) (Philinoidea: Aglajidae) feeds on cephalaspideans and nudibranchs (such as *Hermissenda crassicornis* Eschscholtz, *Polycera atra* MacFarland and *Dirona picta* MacFarland in Cockerell and Eliot), consuming between 6.2 and 9.5% of its body weight per day (Paine 1965).

Similarly, Morton and Chiu (1990) showed that on Hong Kong sandy beaches *Philine orientalis* Adams, 1854 (Opisthobranchia: Philinidae) attacks a

Table 2. Calculated consumption rates of different taxa of Gastropoda; (wet tissue weight of prey per wet tissue weight of predator consumed per day.).

Species	Family	Prey	Consumption	References
Navanax inermis	Aglajidae	Cephaspidea and Nudibranchia	6.2–9.5% per day	Paine (1965)
Philine orientalis (adults)	Philinidae	Bivalves	2.2–6.7% per day	Morton and Chiu (1990)
Polinices duplicatus (juveniles)	Naticidae	Bivalves (*Mya arenaria*)	14–18% per day	Turner (1949)
Polinices duplicatus (adults)	Naticidae	Bivalves (*Mya arenaria*)	Maximum of 5–6% per day	Edwards and Huebner (1977)
Polinices duplicatus (reproductively active adults)	Naticidae	Bivalves	15% per day	Ansell (1981)
Hemifusus tuba (adults)	Melongenidae	Bivalves	4% per day	Morton (1985)
Hemifusus tuba (2-week-old juveniles)	Melongenidae	Carrion	92% per day	Morton (1986)
Hemifusus tuba	Melongenidae	Hatchling sibling cannibalism	<2% per day	Mortem (1987)
Bullia digitalis (juveniles)	Nassariidae	Carrion	138% per day	Stenton-Dozey and Brown (1988)
Bullia digitalis (adults)	Nassariidae	Carrion	18% perday	Stenton-Dozey and Brown (1988)
Nassarius festivus (adults)	Nassariidae	Carrion	Between 50-60% per meal (per day)	Morton (1990b) Cheung (1994)
Nassarius pyrrhus (adults)	Nassariidae	Carrion	20% per meal (per day)	Morton and Britton (1991)
Nassarius mendicus (adults)	Nassariidae	Carrion	20% per meal (per day)	Britton and Morton (1993)
Nassarius siquijorensis (adults)	Nassariidae	Carrion	A maximum of 60.6% per day	Liu and Morton (1994)
Cymatium muricinum	Cymatiiidae	Bivalves (*Tridacna gigas*)	2–7% per day	Govan (1995)
Linatella caudata (adults)	Ranellidae	Bivalves (*Barbatia virescens*)	2.9–4.0% per day	Morton (1990a)
Gyrineum natator (adults)	Ranellidae	Bivalves (*Saccostrea mordax*)	14% per day	This study

variety of mostly shelled prey but in the laboratory consumed between 2.2 and 6.7% of their wet tissue weights per day when fed on the bivalve *Tapes philippinarum* (Adams and Reeve). Only one estimate of consumption exists for representatives of the Cymatiidae, a taxa generally considered to be related to the Ranellidae. This is of *Cymatium muricinum* feeding on *Tridacna gigas* by Govan (1995). This author recorded an average daily consumption rate of between 3 and 7% of the species' total and dry tissue weights per day although values fluctuated widely.

Perhaps the most important comparison with *G. natator* is, however, with a second ranellid, also in Hong Kong. When feeding on bivalves, that is, *Barbatia virescens* (Reeve), *L. caudata* consumed between 2.9 and 4.0% of its wet tissue weight per day (Morton 1990a), which is within the same range determined for *Cymatium muricinum* by Govan (1995). This is low in comparison with *G. natator* (~14% per day) but information on the reproductive state of neither of these species was available at the study times. Bearing in mind that neither *L. caudata* nor *Cymatium muricinum* used their sulphuric acid potential to access their prey (Morton 1990a; Govan 1995), whereas the *G. natator* in the filtered seawater aquarium was forced to, in order to access its sole choice of oyster prey, the ~ 10% difference in estimated consumption between these similar-sized ranellids and cymatiids might, therefore, represent the increased costs of using the acid to access bivalve prey.

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