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DIET OF AN INTERTIDAL PREDATOR, *MORULA FUSCA* (NEOGASTROPODA: MURICIDAE) ON ST. JOHN'S ISLAND, SINGAPORE

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ABSTRACT. — Predatory habits and diet composition of a common high intertidal predator *Morula fusca* were determined from detailed field observations during low tide. Three species of pulmonate limpets (i.e. *Siphonaria atra*, *S. guamensis* and *S. javanica*) comprised the overwhelming majority of prey items consumed by the muricid gastropod. Minor prey included other gastropods (i.e. *Turbo* sp., *Nerita undata* and *Dendropoma* sp.), bivalves (i.e. *Brachidontes* sp. and *Septifer* sp.), barnacles (*Balanus amphitrite* and *Chthmalus malayensis*) as well as the isopod *Ligia* sp.. Nearly all prey was drilled. Drill holes were typically countersunk, and were located mostly at the anterior half of the limpet shell. Predators appear to prefer smaller limpets, and compensated by feeding frequently.

KEY WORDS. — Muricid, siphonariid, drilling, drillhole, borehole, rocky shore

INTRODUCTION

Morula fusca (Küster) is a small but common high shore predator on Singapore shores, particularly on natural rocky headlands of offshore islands in the Singapore Strait. They differ from most other tropical muricid gastropods in undergoing direct development, i.e., their young hatch from egg capsules as crawl-away juveniles (Tan, 1995). This species (recently described as *Morula rumphiusi*; see Houart, 1996) also stands out in that they have a broad latitudinal distribution from tropical to temperate waters, ranging from northern Australia, through the Philippines, to Japan (Tan, 1995). Despite their wide occurrence, its ecology has only been recently elucidated in Japan (Yamamoto, 1993, 1997a, 1997b, 2004). Their ecological role on equatorial rocky shores remains unknown. This study attempts to elucidate their predatory habits from field observations in a tropical mid- to high intertidal rocky shore habitat.

MATERIAL AND METHODS

Field observations were made on the rocky shoreline of St John's Island (1°13.2'N, 103°51.03'E) during daytime low tides on ten occasions each lasting for about three hours from February to December 2007, 16 occasions between June and November 2008, and a further three occasions between November and December 2012. Some samples were also collected in July 2002. During each observation session, rock surfaces were carefully searched for *Morula fusca*. Shell heights of all *M. fusca* individuals encountered were measured with a vernier calliper and carefully examined to determine if they were feeding. If so, their prey was carefully removed and isolated individually in polythene sachets. Prey identity, size, location of drill hole (if any) and its relative position to prey shell ornamentation, as well as the condition of prey (i.e., whether the prey was consumed), were determined under a stereomicroscope in the laboratory.

RESULTS

Prey items. — A variety of prey items were consumed by *Morula fusca*, encompassing gastropods, bivalves and crustaceans (Fig. 2) that were present on the intertidal rock surfaces. However, three pulmonate limpet species (*Siphonaria guamensis*, *S. javanica* and *S. atra*) comprised 89.3% of their diet. The remaining prey items were juvenile gastropods (*Turbo* sp. and *Nerita undata*), the vermetid *Dendropoma* sp., juvenile mytilid bivalves (*Brachidontes* sp. and *Septifer* sp.), barnacles (*Balanus amphitrite* and *Chthmalus malayensis*) and an isopod (*Ligia* sp.).

Table 1. Predator size-prey size relationship of *Morula fusca* at St. John's Island, Singapore.

Predator species	Predator shell height (mm) (± S.D.)	Prey species	Prey shell length (mm) (± S.D.)	n	r	significance
Morula fusca	14.5 ± 1.6	*Siphonaria guamensis*	3.8 ± 0.8	48	0.332	P = 0.21
Morula fusca	15.6 ± 2.0	*Siphonaria javanica*	6.5 ± 2.7	49	0.363	P = 0.10

Feeding frequency. — Of a total of 662 *Morula fusca* individuals (shell height: mean = 13.6 ± 2.2 mm, range = 7.1–23.5 mm) examined during daytime low tides, only 11.3% were observed to be feeding. Not unexpectedly, the mean sizes of feeding and non-feeding individuals were not significantly different. However, *M. fusca* in the 17–19 mm size class appear to have a higher percentage (26.5%) of feeding individuals as compared to those in the smaller size classes (6.3–11.9%) (Fig. 1). The 7–9 mm, 19–21 mm, 21–23 mm and 23–25 mm size classes were not included in this data analysis as their sample sizes were too small (n < 10).

Feeding technique. — Drilling was the primary method used by *Morula fusca* to gain access to prey. Nearly all *Siphonaria* prey was drilled (100% *S. atra*, n = 2; 89.3% *S. guamensis*, n = 56; and 92.9% *S. javanica*, n = 68), as were all other gastropods, bivalves and barnacles fed upon by the muricid predator. The mean shell length of *S. guamensis* and *S. javanica* consumed but not drilled were 3.5 ± 0.6 mm (range = 2.4 – 4.0 mm, n = 6) and 5.9 ± 3.1 mm (range = 2.8 – 9.1 mm, n = 5), respectively. Drilled *S. guamensis* and *S. javanica* had respective mean shell length of 3.9 ± 0.7 mm (range = 2.0 – 5.5 mm, n = 50) and 6.4 ± 2.3 mm (range = 2.0 – 14.3 mm, n = 63). Drilled and non-drilled limpets were not tested for size difference due to the large discrepancy in their sample sizes, but limpets that were drilled appear to be larger than those that were not drilled.

Predator-prey size relationship. — There was no significant relationship between the size of *Morula fusca* and that of its prey (Table 1) – larger muricids did not feed on larger limpets as compared to the smaller muricids (Fig. 3). All *S. guamensis* consumed by *M. fusca* fell within a narrow range of 2.0–5.5 mm shell length. *Siphonaria javanica* consumed by *M. fusca* had a larger size range (shell length = 2.0 – 14.3 mm) and were also significantly larger than *S. guamensis* (t = 6.879, df = 95, P < 0.001). There is some evidence of larger muricids, especially those with shell height larger than 17 mm, avoiding smaller limpets (< 4 mm) (Fig. 3).

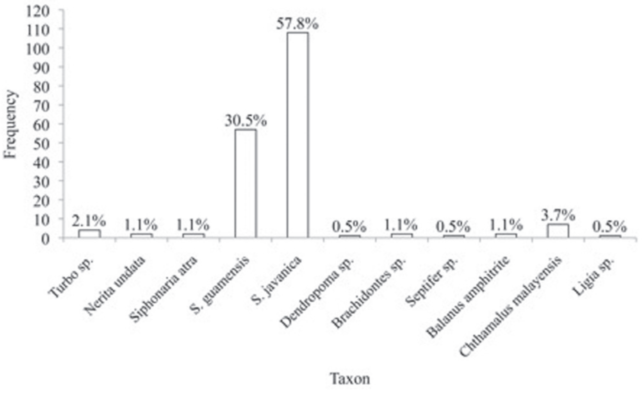

Fig. 1. Frequency of prey items consumed by *Morula fusca*. Values at the top of each column denotes the percentage of each taxon in the overall diet of *M. fusca*.

Drill hole site selection. — In *Siphonaria guamensis* (n = 53), most of the drill holes (81.1%) were located at the anterior of the shell (Fig. 4A), and the left and right side of the shell had similar frequencies of drill holes (χ^2 = 0.024, df = 1, P = 0.8759). At the shell posterior, there is also no difference in the frequency of drill holes between the left and the right sides (χ^2 = 2.000, df = 1, P = 0.1573).

In *S. javanica* (n = 68), the sites of the drill holes were also mostly at the shell anterior (Fig. 4B), but there were slightly more at the anterior right (40.9%) than at the anterior left (30.7%), although the differences were not significant (χ^2 = 1.286, df = 1, P = 0.2568). The posterior left and the posterior

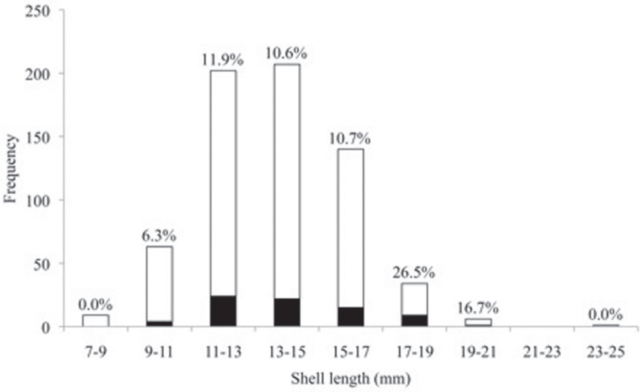

Fig. 2. Frequency of feeding ((■) and non-feeding (☐) *Morula fusca*. Values at the top of each column denotes the percentage of feeding individuals in each size class.

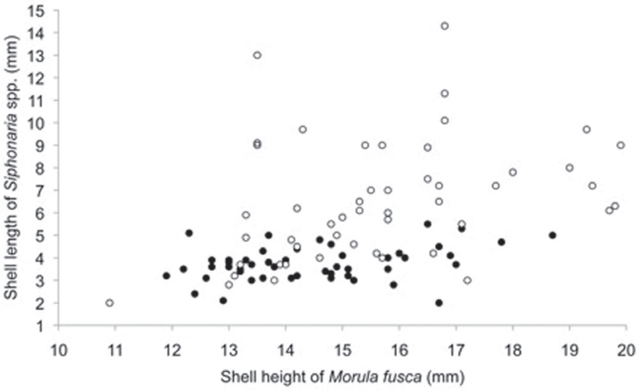

Fig. 3. Size relationship between *Morula fusca* and its prey. *Siphonaria guamensis* (•; n = 48) and *S. javanica* (◦; n = 49).

right sides of the shell have similar number of drill holes ($\chi^2 = 0.727$, df = 1, P = 0.3938). Drill holes were almost invariably located between the primary radial ribs of *S. javanica* where the shell is thinner than at the ribs.

DISCUSSION

Prey items. — The diet of *Morula fusca* at St. John's Island consisted primarily of pulmonate limpets (i.e., *Siphonaria atra*, *S. guamensis* and *S. javanica*). Other sessile and motile invertebrates were also consumed, including juvenile gastropods (*Turbo* sp. and *Nerita undata*), the vermetid *Dendropoma* sp., juvenile mytilid bivalves (*Brachidontes* sp. and *Septifer* sp.), barnacles (*Balanus amphitrite* and *Chthmalus malayensis*), but these formed only a small proportion of the prey of *M. fusca*. An individual was also observed feeding on an isopod *Ligia* sp., which is unusual because this is a fast-moving prey, so this could have been carrion. Pulmonate limpets, including *S. acmaeoides*, *S. japonica* and *S. sirius* comprised the main diet of *M. fusca* in Japan (Yamamoto, 1993, 2004). *Siphonaria* is also one of the most common prey items of *Thais* species (Taylor, 1976; West, 1988; Taylor and Morton, 1996), although siphonariids (e.g. *Kerguelenella lateralis*, *Siphonaria capensis*, *Trimusculus reticulatus*) are known to be repulsive to a variety of predators (Branch, 1981; Rice, 1985; Davenport, 1997, 2001; McQuaid et al., 1999) including the muricid *Nucella dubia* (Branch and Cherry, 1985). This has largely been attributed to the presence of polypropionate metabolites and other unpalatable chemicals in the sticky mucus produced by the lateral pedal glands (Yonge, 1960; Beukes & Davies-Coleman, 1999; Pinchuck & Hodgson, 2009). Yet, *Morula fusca* observed in this study did not avoid siphonariids but appears to select these limpets exclusively as their prey. The specific mechanism of this evolutionary advantage remains unknown but it has an important ecological implication since pulmonate limpets can be abundant organisms on intertidal shores. Thus, it appears that certain genus of muricids, such as *Morula* and *Thais*, have adapted to take advantage of this ready source of food.

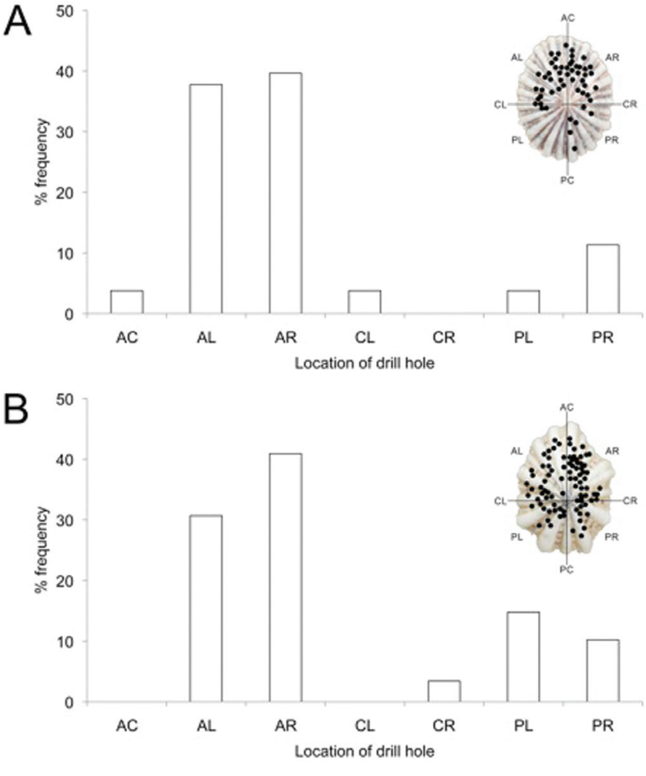

Fig. 4. Location of drill hole created by *Morula fusca* on the shells of (A) *Siphonaria guamensis* (n = 50) and (B) *S. javanica* (n = 68). AC = anterior center, AL = anterior left, AR = anterior right, CL = center left, CR = center right, PC = posterior center, PL = posterior left and PR = posterior right.

In Japan, *M. fusca* also fed on other molluscan prey but did not include crustaceans in its diet (Table 2). The consolidated data on the diet records of *M. fusca* supported the observation that primary carnivores such as *Morula* fed mainly on suspension feeders or grazers (see Little & Kitching, 1996). Despite the diversity of prey eaten, there appears to be little overlap in the diet of *M. fusca* from Singapore and those from Japan. The only taxa that are consumed by *M. fusca* in both localities are neritids, siphonariids and mytilids. This may be a reflection of the opportunistic nature of *M. fusca*, and muricid diets could be dependent on the densities of available prey. In the case of Singapore, *S. guamensis* is one of the most common intertidal organisms in Singapore (Chim & Tan, 2009).

Feeding frequency. — The frequency of *Morula fusca* individuals feeding at St. John's Island was 11.3%, which is comparable to the 8.2% documented for the same species in Japan (Abe, 1980). The slightly higher level of feeding activity could be due to its predominant use of drilling as a method to obtain access to its prey. Pulmonate limpets comprised nearly 90% of its prey and an overwhelming majority of these limpets were drilled in this study. Drilling is a time-consuming activity and the longer period required to gain access to prey means that the chances of seeing the predator feeding are increased (Fairweather & Underwood, 1983). Favourable temperature conditions in the equatorial habitat as compared to the higher latitudes could be another reason. *Morula fusca* from both localities had a feeding frequency higher than that of the other seven muricids (i.e. 0% in *Cronia margariticola*, 7.1% in *Muricodrupa granulata*, 8.3% in *Reishia luteostoma*, 1.3% in *R. bronni*, 1.8% in *R. clavigera* and 0% in *Ergalatax contractus*) except for one species (i.e. 15.3% in *Morula musiva*) studied by Abe (1980) in Japan. The high feeding frequency of *M. fusca* is surprising due to the risks involved while foraging. *Morula fusca* is known to forage during all times of the day with little preference for any tidal condition or lunar phase (Yamamoto, 1993). When submerged, foraging will increase its vulnerability to aquatic predators. It may be prone to being dislodged by waves if it drills while awash. Foraging during receding tides is also problematic due to its low tolerance to desiccation (Yamamoto, 1997a). It seems that *M. fusca* feed frequently to meet its energy requirements. In Japan, *M. fusca* is known to make seasonal migrations along the shore, possibly in search of prey (Yamamoto, 1997a). A significant amount of energy is also spent on feeding, since *M. fusca*

Table 2. Diet records of *Morula fusca* from Shirahama, Kii Peninsula, Japan (Abe, 1980; Yamamoto, 2004), Kii Peninsula, Japan (Yamamoto 1993) and St. John's Island, Singapore (this study).

Prey species	Abe, 1980	Yamamoto, 1993	Yamamoto, 2004	This study
POLYPLACOPHORA				
Undetermined species			✓	
GASTROPODA				
PATELLOGASTROPODA				
Lottia spp.			✓	
Collisella heroldi		✓		
Patelloida pygmaea	✓			
Patelloida saccharina	✓	✓	✓	
Cellana toreuma			✓	
TURBINIDAE				
Turbo sp.				✓
TROCHIDAE				
Lunella coronata	✓			
NERITIDAE				
Nerita (*Theliostyla*) *albicilla*	✓			
Nerita (*Heminerita*) *japonica*	✓			
Nerita undata				✓
LITTORINIDAE				
Nodilittorina granularis	✓			
Peasiella roepstorffiana	✓			
Unidentified species		✓	✓	
PLANAXIDAE				
Planaxis sulcatus	✓			
CERITHIIDAE				
Clypeomorus humilis	✓			
VERMETIDAE				
Dendropoma sp.				✓
SIPHONARIIDAE				
Siphonaria acmaeoides	✓		✓	
Siphonaria atra				✓
Siphonaria guamensis				✓
Siphonaria japonica		✓	✓	
Siphonaria javanica				✓
Siphonaria sirius			✓	
BIVALVIA				
MYTILIDAE				
Brachidontes sp.				✓
Septifer sp.				✓
Unidentified species		✓	✓	
CRUSTACEA				
Balanus amphitrite				✓
Chthmalus malayensis				✓
Ligia sp.				✓

gained access to its prey mostly by drilling (Yamamoto, 1993; pers. obs.).

Feeding technique. — In this study, *Morula fusca* drilled almost all of its prey, whether they were limpets (100% of *Siphonaria atra*, 89.3% of *S. guamensis* and 92.9% of *S. javanica*), other gastropods, bivalves or barnacles. However, two studies in Japan (Yamamoto, 1993, 2004) showed that limpets consumed by *M. fusca* were rarely drilled. In the first study, none of the limpets (i.e. *Siphonaria japonica*, *Patelloida saccharina* and *Collisella heroldi*) consumed by *M. fusca* were drilled, even though 78% of littorinids and all mytilids consumed were drilled (Yamamoto, 1993). In the second study, only a small percentage of limpet prey (i.e. 10% of *Siphonaria japonica*, 16% of *Lottia* spp. and 27% of *Patelloida saccharina lanx*) was drilled, probably due to the 2–3.4 times longer handling time as compared to a non-drilling method (Yamamoto, 2004). Drilling did not significantly increase the handling time for littorinids and mytilids, thus resulting in a much higher frequency of drilling in these prey (i.e. 61% of littorinids and 95% of mytilids) (Yamamoto, 2004). For *M. fusca* in Singapore, it is then possible that drilling is the preferred feeding technique because of its relatively short handling time when consuming limpets. When not drilling, *M. fusca* gained access to the flesh of limpets by inserting its proboscis through a gap between the substratum and the shell of the prey (pers. obs.). The most likely reason for the non-drilling method to be more time-consuming (and also more energy consuming) than drilling is the tight fit achieved between the contours of the rock surface and the limpet's shell margin (pers. obs.). This is often the case for limpets in a home scar. Many *Siphonaria* species, including *S. atra*, attach firmly to their home scars in response to predation (Garrity and Levings, 1983; Iwasaki, 1993; Liu, 1994; Lam, 2002). We also observed the presence of home scars for all three species of *Siphonaria* in Singapore, and this probably explains the intensive use of drilling by their muricid predators.

Predator-prey size relationship. — *Morula fusca* from a wide range of body size (approx. 12–19 mm shell height) fed on a narrow range (2.0–5.5 mm shell length) of *S. guamensis* (Fig. 3). For a similar range of body size (approx. 11–20 mm shell height), *M. fusca* consumed *S. javanica* of up to 14.3 mm shell length but also fed on *S. javanica* as small as 2.0 mm shell length. Studies on other muricids also show a similar pattern. For example, *Dicathais orbita* (10.3–30.8 mm shell height) also fed on *Siphonaria* from a narrow range of body size (3.2–5.8 mm shell length, n = 9) (Morton, 1999). There is also some evidence that indicated the preference of *Morula musiva* for smaller prey items (Abe, 1989). In intertidal habitats where the foraging window is relatively narrow, feeding on small prey items is probably more efficient and less risky because of the shorter handling time. Harper and Morton (1997) showed that *M. musiva* preferred to feed on *Isognomon legumen* because of its thinner shell even though the arcoids have higher flesh yields. *Morula marginalba* consumed juveniles of the limpet *Cellana tramoserica* 1.4 times faster than adults (Moran, 1985). *Morula fusca* compensated the small amount of energy from each prey by increasing its feeding frequency. This is possible since it is usually surrounded by an abundance of prey that is either sessile or motile. However, on a mudflat in Thailand, another muricid predator *Chicoreus capucinus* preferred to feed on larger mudcreepers despite the availability of small mudcreepers around them (Tan, 2008). Clearly choice of prey size by a predator is determined by a variety of factors that requires further study.

Drill hole site selection. — *Siphonaria guamensis* and *S. javanica* were mostly drilled at the anterior with no preference for the left and right sides. In previous studies, selective drilling has been documented for *Morula granulata* and *M. musiva*, but not for *M. fusca*. *Morula granulata* and *M. musiva* have a strong tendency of drilling at the left valve of the pearl oyster *Isognomon legumen*, at the shell margins of the oyster *Saccostrea cuccullata* and at the mid-region of the rostral shell plate of the barnacle *Tetraclita squamosa* (Taylor, 1990; Harper and Morton, 1997; Tan, 2003). There is little information regarding selective drilling by muricids on *Siphonaria*, but *S. zealandica* were usually drilled near the apex of the shell (Luckens, 1975). Holes drilled by the muricid *Dicathais aegrota* on the shell of the *Patelloida alticostata* were located somewhat randomly but were away from the apex and margin and over the gonad and digestive gland, probably to gain access to energy-rich tissues (Black, 1978). The muricid *Ocenebra lurida* drilled mostly at the posterior half of the shells of *Lottia pelta* and *Tectura scutum* (Palmer, 1988). The anterior half of *Siphonaria* contains the buccal mass, two adductor muscles, kidney and distal genitalia, whereas the gut, glandular complex, hermaphrodite gland and an adductor muscle are located at the posterior. Thus, both anterior and posterior halves of the limpet appear to be similarly nutritious. Furthermore, *M. fusca* consumed all fleshy parts when eating *Siphonaria* so it is unlikely that selective drilling was used to feed on a specific part of the animal. It is possible that the anterior was targeted to immobilise the prey since it is where the nervous ganglia and adductor muscles are located. Future experimental studies will provide important insights into drill hole site selection by boring gastropods, which remains poorly understood (see Carriker, 1981).

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