

MUDFLAT PREDATION ON BIVALVES AND GASTROPODS BY *CHICOREUS CAPUCINUS* (NEOGASTROPODA: MURICIDAE) AT KUNGKRABAEN BAY, GULF OF THAILAND

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ABSTRACT. – At Kungkrabaen Bay, a small, shallow estuarine indentation located in the northern Gulf of Thailand, the intertidal predator *Chicoreus capucinus* (Lamarck, 1822) is abundant on mudflats beyond the seaward edge of the *Rhizophora* mangrove, with densities reaching 62 individuals per 100 m². There, individuals feed on a variety of bivalves and gastropods. Principal bivalve prey were the venerid clams *Anomalocardia squamosa* (Linnaeus, 1758) and *Gafrarium tumidum* (Röding, 1798), which comprised more than a quarter of all predator-prey interactions observed (n = 279) in the field. Others included *Pharella* cf. *javanica* (Lamarck, 1822) (Pharidae) and *Laternula* cf. *boschasina* (Laternulidae). Amongst the gastropods attacked and preyed upon, *Cerithidea cingulata* (Gmelin, 1791) and *C. djadjariensis* (Martin, 1899) (Potamididae) were the main prey items of *C. capucinus*. More than a third of the total number of predation occurrences involved these mudcreepers, although the cerithiids *Cerithium coralium* Kiener, 1841, and *Clypeomorus pellucida* (Hombron & Jacquinot, 1852) as well as the neritid *Clithon oualaniensis* (Lesson, 1831) were also consumed. Bivalves were invariably drilled, in most cases leaving a deep, steeply countersunk hole on either valve. There was a strong tendency for drill holes to be located on the escutcheon region of *A. squamosa*. The shells of a smaller number of potamidid mudcreepers were drilled at their mid-length, but the majority of cerithioideans were principally consumed via the shell aperture, as evidenced by perforated prey opercula. *Clithon* were either drilled through the shell apex or through the gap between the aperture shelf and closed operculum. Significant predator-prey size correlations were detected for the gastropod *C. cingulata* and for the bivalve *G. tumidum*, although such relationships were less clear for other prey items. Drill hole size was clearly dependent upon prey type, regardless of predator size. Drill holes on bivalves were significantly larger than those found on gastropod mudcreepers. A strong correlation was detected between drill hole size and predator size for the bivalves *A. squamosa* and *G. tumidum*, but not for *C. cingulata*. Intertidal muricid gastropods are usually confined to living on hard surfaces, but this study clearly shows *Chicoreus* to be a versatile and successful predator on soft substrata as well, attacking and consuming nearly all molluscs within reach on the productive mudflat except conspecifics.

KEYWORDS. – Mangroves, shell drilling, feeding ecology, predation.

INTRODUCTION

Compared to rocky shores or coral reefs in the tropics, mangrove habitats support a lower diversity of predatory muricid gastropods, and they are generally confined to available hard surfaces such as rocks, stones, mangrove roots and tree trunks. *Chicoreus capucinus* (Lamarck, 1822) (sometimes as *Murex* or *Naquetia*) is perhaps one of the more ubiquitous species associated with the mangroves in Southeast Asia (Berry, 1972; Brandt, 1974; Gribsholt, 1997). Previous work has shown that *C. capucinus* is a versatile intertidal predator with a varied diet, capable of consuming mangrove bivalves, gastropods, and crustaceans (Nielsen, 1976; Tan & Oh, 2002). These studies have, however,

focused on *C. capucinus* populations in mangrove forests or on a sandflat (Wells et al., 2001). Although the predator is also seen on mudflats, their occurrence and interactions with prey in this unlikely habitat has not been examined in any detail. Indeed, the extent and scale of predation on benthic soft substrata in the tropics is poorly known. It is generally acknowledged that crabs, fish and birds are often major predators on soft shores (Little, 2000) but predatory molluscs can play a significant ecological role as well (e.g., Vermeij, 1980a; Berry, 1982; Broom, 1982). The distribution and dietary composition of tropical muricid gastropods on soft intertidal shores are little studied, as most muricids living on soft substrata are often only found subtidally (Taylor, 1982; Ponder & Vokes, 1988). The present study attempts

to determine the abundance, diet, and method of feeding of *C. capucinus* on a mudflat immediately beyond the edge of the mangrove forest in the Gulf of Thailand.

MATERIALS AND METHODS

Location and sampling. – Observations were made during 22–28 Aug.2005 and again during 15–17 May 2006 at low tide during daylight hours on the seaward edge of the mangrove in Kungkrabaen Bay, a small (640 ha, 6.4 km²), shallow, estuarine inlet near Chanthaburi in the northern Gulf of Thailand (Fig. 1). Two sites were chosen based on accessibility: Site 1 (12°35.4'N 101°54.4'E) was located in the central region of the bay, whilst Site 2 (12°35.2'N 101°54.1'E) was near a mangrove boardwalk at the southern corner of the bay. At each site, 16 (Site 1) or eight (Site 2) 50 m transect lines were laid randomly perpendicular to the edge of the mangrove forest on the mud towards the sea. All *Chicoreus capucinus* (hereafter *Chicoreus*) individuals occurring within 1 m on either side of the transect line were carefully examined for feeding activity. This was done by looking for fresh or etching or drilling on the surface of shells being preyed upon, or confirmed by the presence of an extended proboscis inserted into the prey through a drill hole or shell aperture. Sizes of predator and prey, prey identity, as well as their position along the transect line were recorded. The total number of *Chicoreus* occurring within each transect belt was also noted to provide an estimate of predator density. For an estimation of prey abundance, three 10 × 10 cm quadrats were placed haphazardly inside

a 5 m radius circle centred at 0 m, 10 m, and 20 m along a 50-m transect line at Site 1, and similarly at 0 m, 25 m, and 50 m at Site 2. Epifaunal and infaunal organisms were collected to a depth of 10 cm in each quadrat. Organisms retained in a 1-mm mesh standard sieve were identified and quantified. In addition, the substratum sediment-size profile was obtained from sediment samples (n = 6 at each site, two surface samples taken at three positions) along transect lines at the two sites to determine if organisms displayed preference for a particular type of substratum. Sediment samples were dried to constant weight, sieved through 250, 125 and 63 µm test sieves and weighed on an analytical balance to determine the proportion of the different size classes by weight.

Drill site selection. – All prey physically handled by *Chicoreus* were individually bagged and labelled on site. Prey items were measured [shell height (SH) in gastropods; shell length (SL) in bivalves] using a dial caliper. Shell and opercular surfaces were examined carefully for drill marks under the stereomicroscope in the laboratory. In the case of potamidid and cerithiid prey, the distance between the centre of the drill hole and the apex of the shell was measured with an eyepiece graticule. The positions of the drill site in relation to the prey shell orientation (dorsal/ventral; right or left), whorl number, and shell sculpture (whether the drill hole was centred over the suture or between the sutures of adjacent whorls) were also noted. If drill marks were absent on the shells, a vice was used to break the shell to observe whether the operculum inside had been drilled. For other prey items, the shells were likewise examined, and for *Anomalocardia* and *Gafrarium*, the relative positions of drill holes were mapped onto master diagrams through a drawing tube (camera lucida) mounted on a stereomicroscope.

Drill hole size. – To determine the relationship between predator size and the size of bored drill holes, the area defined by the outline of each drill hole on respective prey was estimated. This was done by assuming the outline of each drill hole to approximate an ellipse and measuring its longest and shortest diameters under the stereomicroscope with an eyepiece graticule.

RESULTS

Predator size, abundance, and distribution. – The mean shell height of *Chicoreus* on the mudflats was 39.4 ± 0.2 mm (range 18.3–55.3 mm; n = 518). A single modal size class was observed at each of the two sites (Fig. 2), and individuals in the 35–45 mm size class comprised 80.2% of the pooled population from two sites. Juveniles (SH < 15 mm) were conspicuously absent from the mudflat. On the mudflat at Site 1, there were 12.5–55.0 ex./100 m² (mean ± SE 22.5 ± 2.9 ex./100 m²; n = 16) within 50 m from the edge of the mangrove. At Site 2, there were 11.0–62.0 ex./100 m² (mean ± SE 37.4 ± 17.4 ex./100 m²; n = 8) within 50 m from the mangrove edge. *Chicoreus* densities at the two sites sampled were not significantly different (unpaired t-test, t = 1.894, P > 0.05). However, *Chicoreus* individuals were

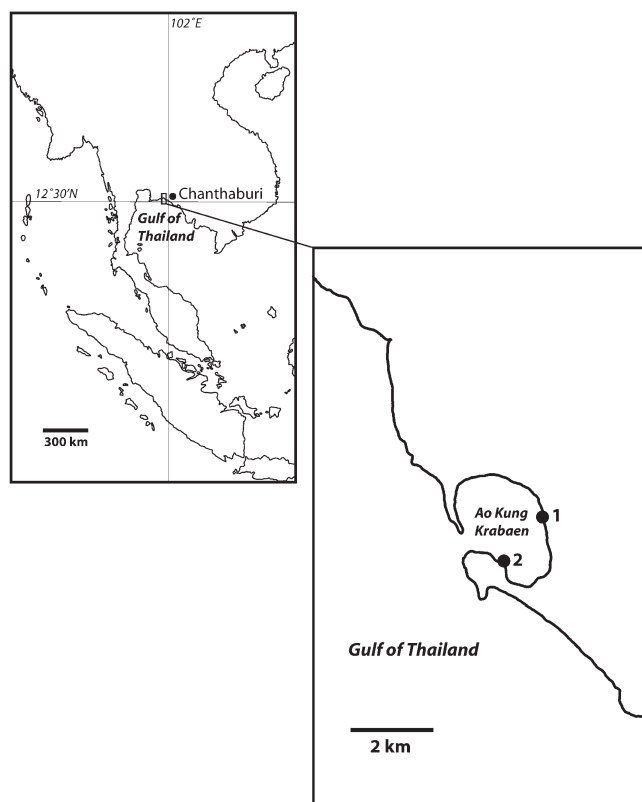


Fig. 1. Location of Kungkrabaen Bay (Ao Kung Krabaen) in the Gulf of Thailand and study Sites 1 and 2 positioned therein.

generally confined within 20 m from the mangrove edge at Site 1, whereas at Site 2, the highest densities occurred beyond 20 m along the 50 m transect line (Fig. 3). Sediment profiles of the two sites are shown in Fig. 4. A higher proportion of silt (particles < 125 µm) was present at Site 1 relative to Site 2. At each site, particle size composition along the transect line was generally comparable, except at Site 2 where there was a higher proportion of fine sand at the edge of the mangrove.

Prey abundance. – The predominant epifauna at the study sites (Table 1) comprised cerithioidean gastropods, of

which *Cerithidea cingulata* (Gmelin, 1791) occurred in densities of up to 6,000 ex./m². Two other congeners, *C. djadjariensis* (Martin, 1899) and *C. alata* (Philippi, 1849), were also observed but in considerably lower densities on the mudflat. In addition, *Clypeomorvus pellucida* (Hombron & Jacquinot, 1852) and *Cerithium coralium* Kiener, 1841, were also relatively abundant, together with the small estuarine neritid *Clithon oualaniensis* (Lesson, 1831). Shallow infaunal molluscan fauna consisted principally of venerid bivalves, of which *Anomalocardia squamosa* (Linnaeus, 1758) and *Gafrarium tumidum* (Röding, 1798) were present in densities up to 133 ex./m². *Tellina capsoides* (Lamarck, 1822) (Tellinidae) was also common (44 ex./m²) but occurred slightly deeper below the surface of the substratum. Less common were the elongate *Pharella cf. javanica* (Lamarck, 1822) (Pharidae) at the mangrove edge, as well as *Dosinia* spp. (Veneridae) and *Laternula cf. boschasina* (Reeve, 1860) (Laternulidae), which occurred in small numbers on the mudflat.

Diet. – Slightly more than half (53.9%) of *Chicoreus* individuals observed (n = 518) were associated with prey on

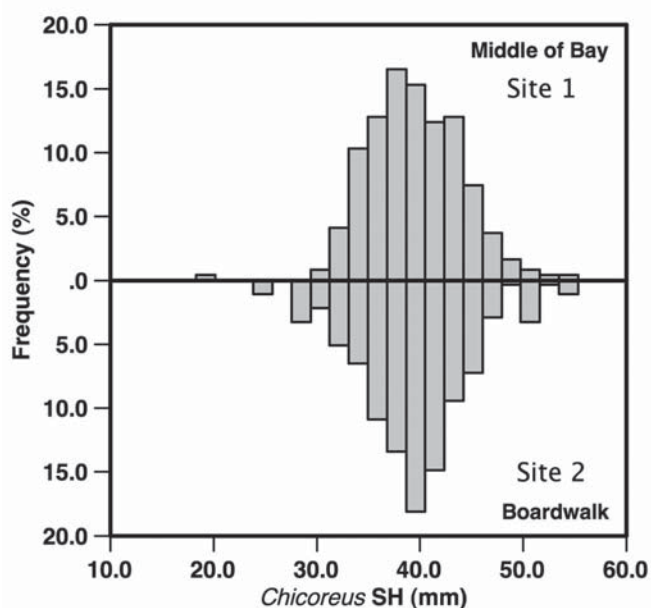


Fig. 2. Size-class distribution of *Chicoreus capucinus* at Sites 1 and 2, Kungkrabaen Bay, Gulf of Thailand. SH, shell height.

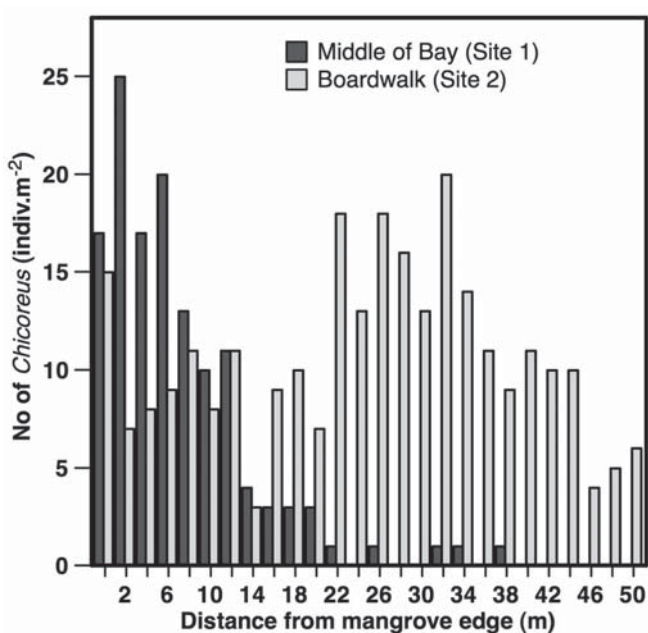
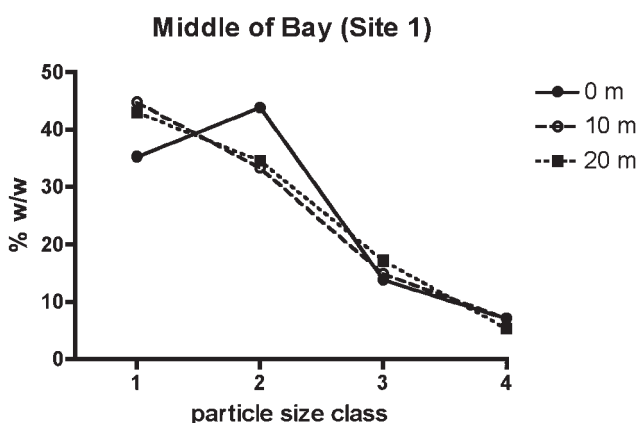


Fig. 3. Horizontal distribution of *Chicoreus capucinus* on the mudflat at Sites 1 and 2 from the edge of the mangrove (left) outwards towards the sea (right).

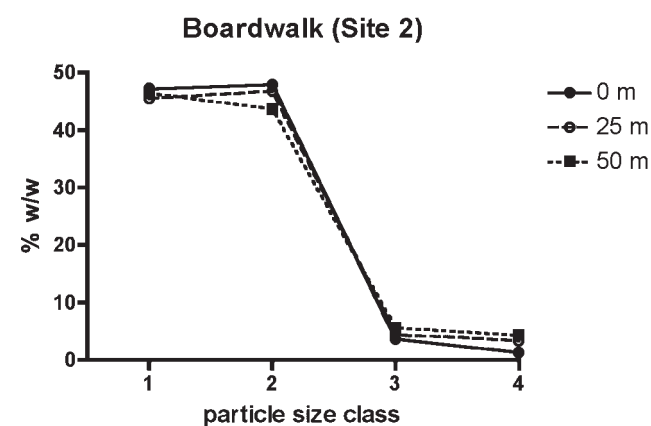


Fig. 4. Particle-size composition (percentage composition by weight) of surface sediment at Sites 1 and 2 in Kungkrabaen Bay, Gulf of Thailand. Size 1: > 250 µm; size 2 > 125 µm; size 3 > 63 µm; size 4: < 63 µm. The three lines in each graph represent the particle composition profile of the substratum at different distances along the transect line from the edge of the mangrove towards the sea.

Table 1. Abundance of epifaunal and infaunal molluscs at Kungkrabaen Bay, Gulf of Thailand, and extent of predation by *Chicoreus capucinus*, based on field observations. The proportion of individual prey items handled by *Chicoreus* might not necessarily indicate its true dietary composition, as the handling time could be different for each prey item.

| Potential/realized prey | Maximum abundance recorded on mudflat (ex./m ²) | Mean size of prey ± SE (mm) | Mean size of handled prey ± SE (mm) | Proportion of total prey handled by <i>Chicoreus</i> (%) (n = 279) |
|---|---|-----------------------------|-------------------------------------|--|
| Gastropoda | | | | |
| <i>Clithon oualaniensis</i> (Neritidae) | 142 | 6.6 ± 0.3 (n = 17) | 6.8 ± 0.2 (n = 12) | 6.8 |
| <i>Cerithidea cingulata</i> (Potamididae) | 6,000 | 8.2 ± 0.1 (n = 655) | 13.3 ± 0.3 (n = 99) | 35.8 |
| <i>Cerithidea djadjariensis</i> (Potamididae) | 200 | 12.9 ± 1.1 (n = 25) | 18.3 ± 0.9 (n = 26) | 9.3 |
| <i>Cerithidea alata</i> (Potamididae) | 9 | 18.6 (n = 1) | 16.2 (n = 1) | 0.3 |
| <i>Clypeomorus pellucida</i> (Cerithiidae) | 249 | 11.9 ± 0.6 (n = 33) | 10.5 ± 1.4 (n = 3) | 1.1 |
| <i>Cerithium coralium</i> (Cerithiidae) | 233 | 6.5 ± 0.7 (n = 13) | 15.2 ± 1.1 (n = 19) | 6.8 |
| <i>Salinator</i> sp. (Amphibolidae) | < 1 | 5.7 (n = 1) | – | 0 |
| Bivalvia | | | | |
| <i>Saccostrea</i> cf. <i>cuccullata</i> (Ostreidae) | < 1 | not measured | 13.4 ± 1.5 (n = 16) | 6.1 |
| <i>Gafrarium tumidum</i> (Veneridae) | 133 | 30.9 ± 0.4 (n = 46) | 26.6 ± 1.9 (n = 16) | 5.7 |
| <i>Anomalocardia squamosa</i> (Veneridae) | 100 | 16.8 ± 2.4 (n = 8) | 17.8 ± 0.5 (n = 77) | 27.2 |
| <i>Dosinia</i> sp. 1 | < 1 | 5.5, 7.0 (n = 2) | – | 0 |
| <i>Dosinia</i> sp. 2 | < 1 | 4.0, 4.6 (n = 2) | – | 0 |
| <i>Tellina capsoides</i> (Tellinidae) | 44 | 23.6 ± 1.9 (n = 14) | – | 0 |
| <i>Pharella</i> cf. <i>javanica</i> (Pharidae) | < 1 | not measured | 36.6, 38.2 (n = 2) | 0.7 |
| <i>Laternula</i> cf. <i>boschasina</i> (Laternulidae) | < 1 | 10.6; 14.6 (n = 2) | 14.7 (n = 1) | 0.3 |

the mudflat. Apart from two occurrences where two predators were feeding on one prey item, all other predator-prey associations were of one predator feeding on one prey item. Six species of gastropods and another six bivalve species were consumed by *Chicoreus*. Of 279 individuals observed feeding, 45.5% were feeding on *Cerithidea* spp., 27.2% on *Anomalocardia squamosa*, 6.8% on *Clithon oualaniensis*, 6.8% on *Cerithium coralium*, 6.1% on *Saccostrea* cf. *cuccullata* (Born, 1778), 5.7% on *Gafrarium tumidum*, and 1.1% on *Clypeomorus pellucida* (Table 1). Two individuals were feeding on *Pharella* cf. *javanica*. One individual was observed drilling *Laternula* cf. *boschasina* Reeve. Cannibalism was never observed.

Feeding methods. – *Cerithidea cingulata* – This mudcreeper was a major prey item for *Chicoreus*, comprising 35.8% of the total number (n = 279) of prey items seen handled by the predator. A significant positive correlation in size between predator and prey was detected (Pearson's $r = 0.377$, $P < 0.001$; Fig. 5a). Additionally, there was a strong preference in general for larger individuals (Fig. 6). A significant difference in the mean shell lengths of the pooled *C. cingulata* population on the mudflat, which comprises a sizeable juvenile cohort, and those selected by the predator, was discernible (t-test, $P < 0.001$). The majority of prey (71.7%) was attacked by drilling the operculum through the shell aperture. In all cases, the operculum was perforated by a large circular hole with a jagged outline (Fig. 7a) almost certainly caused by the

repeated rasping of the surface by the radula. Drill holes were positioned either centrally or off-centre towards the edge of the operculum. The other method of attack involved drilling the shell. Drill holes were positioned halfway along the length of the mudcreeper shell (Fig. 7b; mean ratio of distance of drill hole from apex to shell length 0.500 ± 0.01 ; $n = 28$). There was also a significant positive correlation between distance of drill hole made by *Chicoreus* from the apex of *Cerithidea* and prey shell size (Pearson's $r = 0.368$, $P < 0.001$). In relation to prey shell orientation, drill holes were more or less equally distributed over left and right lateral sides of the prey. Slightly fewer drill holes (ca. 39%) were observed on the dorsal or ventral region of the *Cerithidea* shell. Shell sculpture did not appear to influence drill site placement. Equal numbers of drill holes were found on and between sutures of adjacent whorls. The suture between the third last and fourth last whorls, as well as that between the last and penultimate whorls, were preferred over other sutural combinations. Drill holes positioned squarely on the surface of the whorls themselves were generally confined to the third (73%) and penultimate whorls (27%) only.

The choice whether to attack *Cerithidea* via the aperture by drilling the operculum, or by drilling the shell directly, does not appear to depend on prey size. There was no significant difference either in the shell size of predator (t-test, $P = 0.2268$) or prey (t-test, $P = 0.4159$) between the two groups.

Cerithidea djadjariensis: Larger in size but less common than *C. cingulata*, *C. djadjariensis* was preyed upon by *Chicoreus* in a similar pattern on the mudflat, with 73.1% of the total attacks (n = 26) being made via the aperture. In contrast to the positive relationship between prey and predator size for *C. cingulata*, no significant size correlation (Fig. 5b) was detected between *Chicoreus* and *C. djadjariensis* (Pearson's $r = 0.004$, $P = 0.493$). Whilst there were only six individuals which were drilled through the shell, the drillholes were positioned slightly nearer the apex (mean ratio of distance of drill hole from apex to shell length 0.394 ± 0.021 ; n = 6) than that observed for *C. cingulata*.

Other cerithioidean gastropods preyed upon included *Cerithium coralium* (19 ex., or 6.8% of total number observed), *Clypeomorus pellucida* (3 ex.) and *Cerithidea alata* (1 ex.). 68.4% of *C. coralium* had drill holes on the

shell, in contrast to *Cerithidea* spp., which were mostly attacked through the aperture and operculum. Although there was no significant predator-prey size correlation between *Chicoreus* and *C. coralium*, the position of the drill sites (distance from apex) was significantly correlated with the shell height of *C. coralium* (Pearson's $r = 0.802$, $P < 0.01$; n = 13). The mean ratio of distance of drill hole from apex to shell height was 0.442 ± 0.027 (n = 13). One-way ANOVA of the relative distance of the drill site in relation to prey size for *Cerithidea cingulata*, *C. djadjariensis*, and *C. coralium* did not show significant differences to suggest that drill site selection was species-specific ($F = 3.028$, $P = 0.06$).

The small (SH < 8.2 mm) neritoidean gastropod *Clithon oualaniensis* formed a small component of the diet of *Chicoreus*. All were drilled either through the dorsal shell, or attacked via the aperture by drilling at the gap between the calcareous operculum and the apertural wall.

Anomalocardia squamosa: There was no significant predator-prey size relationship (Pearson's $r = 0.052$, $P > 0.05$; n = 76) between *Anomalocardia* and *Chicoreus* (Fig. 9a). The predator exploited a wide range of prey size (SL range 7–25 mm; mode 21 mm), all of which were invariably drilled. It appeared that once drilling commenced, the drilling was almost always fatal for the bivalve, because practically all individuals observed in the process of being drilled or consumed by *Chicoreus* each possessed only one drill mark. Unsuccessful drill holes were extremely rare. All living *Anomalocardia* individuals obtained directly from the mudflat and not associated with *Chicoreus* were devoid of drill marks. *Chicoreus* showed a strong preference to locate drill sites on the escutcheon (Fig. 10), where 31.6% of drill holes were found. A small bias towards drilling the right escutcheon was observed. Only one drill hole was located at the commissure, and another over the ligament, in all prey examined. Likewise, only two individuals were drilled at the lunule. The remaining drill sites were equally distributed between the lateral surfaces of left (30.2%) and right (32.9%) valves. There appeared to be no clear preference to drill any

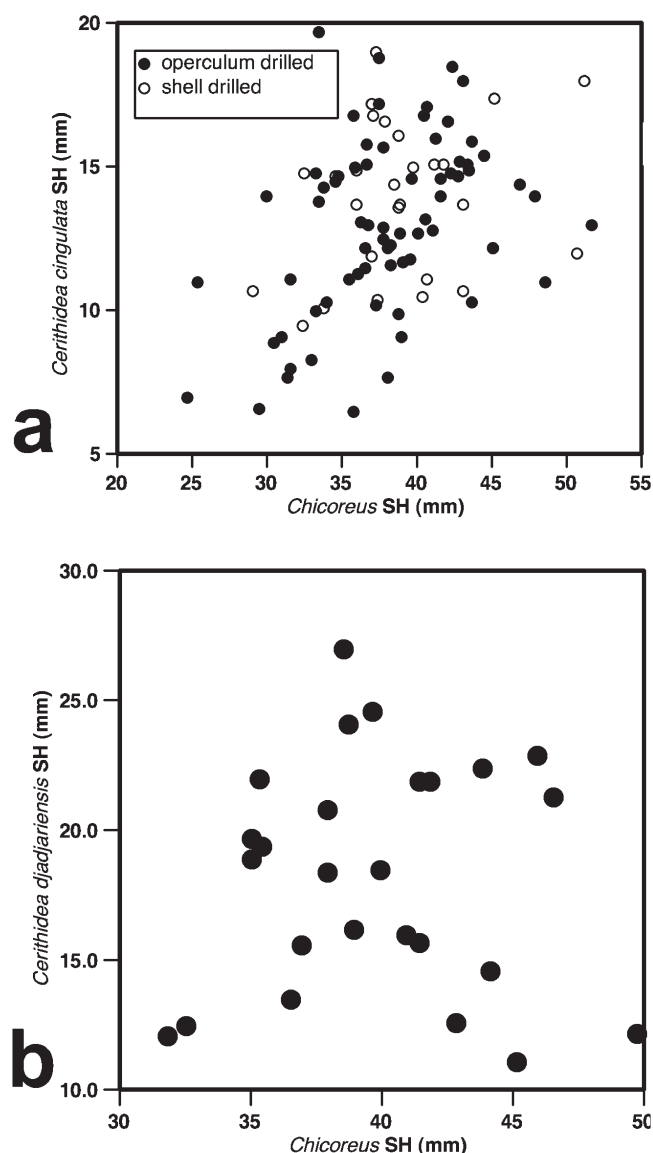


Fig. 5. Predator-prey size relationship between *Chicoreus capucinus* and two species of mudcreepers at Kungkrabaen Bay, Gulf of Thailand. Closed circles represent mudcreepers that were attacked via the aperture; open circles represent mudcreepers whose shells were drilled. a, *Cerithidea cingulata*; b, *Cerithidea djadjariensis*.

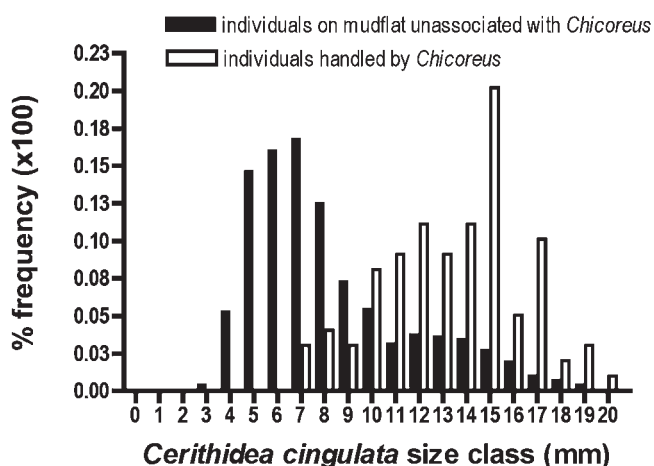


Fig. 6. Comparison of size-class distributions of *Cerithidea cingulata* occurring on the mudflat and those preyed upon by *Chicoreus capucinus* at Kungkrabaen Bay, Gulf of Thailand. A clear selection for larger mudcreepers by the predator is apparent.

particular lateral region of the valve, but edge chipping or drilling along the ventral region was never observed. Drill holes were steeply countersunk and typical of those made by drilling gastropods. These were circular or ovoid in outline, ranging 1–2 mm in diameter on the surface. The perforation on the inside wall of the valve was substantially narrower and more variable in outline, ranging 0.5–1 mm in maximum dimension.

Gafrarium tumidum: A significant positive correlation ($r = 0.699$, $P < 0.01$; $n = 16$) in predator-prey size was detected between *Gafrarium* and *Chicoreus* (Fig. 9b). Prey *Gafrarium* ranged in size between 8.5 and 34.7 mm SL (mean \pm SE 26.6 \pm 1.9 mm), whereas predator size varied between 32 and 49 mm. All *Gafrarium* individuals examined each possessed one drill mark, and no unsuccessful drill holes were observed. In contrast to that observed for *Anomalocardia*, all drill sites were located on the lateral surfaces of either valve (Fig. 11). Neither the escutcheon nor lunule region was attacked. There was no evidence for edge chipping or drilling, as also observed for other bivalve prey.

Other bivalves: Apart from *Anomalocardia* and *Gafrarium*, the oyster *Saccostrea* cf. *cucullata* was occasionally (6%; Table 1) drilled and consumed by *Chicoreus*. These oysters generally attach themselves to living or dead shells on the mudflat. *Laternula* cf. *boschasina* was likewise drilled on the posterior half of either valve, but these thin-shelled bivalves were not a major prey item of *Chicoreus* at Kungkrabaen Bay. *Pharella* cf. *javanica* was consumed through the posterior gape of the bivalve, and no drill marks were found on two individuals that were handled by the predator.

Predator-prey drill hole size relationships. – Based on the area enclosed by the approximately elliptical or circular outline of drill holes, drill hole size ranged 1.07–8.29 mm². A significant difference in drill hole size was observed between those found on bivalves (*Anomalocardia squamosa* or *Gafrarium tumidum*) and those on gastropods (*Cerithidea*

cingulata or *Cerithium corallium*) (Fig. 12a). Those made on bivalves were significantly larger (*Anomalocardia* 4.58 \pm 0.14 mm²; *Gafrarium* 5.26 \pm 0.48 mm²) than on gastropods (*Cerithidea* 1.85 \pm 0.09 mm²; *Cerithium* 2.51 \pm 0.17 mm²). Interestingly, while there was a significant correlation between drill hole size and predator size for two bivalves (*Anomalocardia* $r = 0.367$, $P < 0.01$; *Gafrarium* $r = 0.764$, $P < 0.05$), no relationship was discernible for gastropods (*Cerithidea* $r = 0.037$, $P = 0.86$; *Cerithium* $r = 0.435$, $P = 0.28$) or for the oyster *Saccostrea* cf. *cucullata* ($r = 0.648$, $P = 0.164$) (Fig. 12b).

DISCUSSION

Chicoreus capucinus forms a major epifaunal component of the mudflats of Kungkrabaen Bay in the Gulf of Thailand. Their densities (11–62 ex./100 m²) beyond the seaward edge of the mangroves are intermediate between those on the mangrove forest floor in Singapore (60 ex./100 m²; Tan & Oh, 2002) and on a sandflat in nearby Ang Sila in Thailand (1 ex./100 m²; Wells et al., 2001). The mudflat population comprises a single cohort of adult individuals, suggesting that juvenile recruitment occurs elsewhere, possibly in the mangroves where both juveniles and adults occur (pers. obs.). This observation is consistent with those made by Wells et al. (2001), in which a single cohort of adult individuals was recorded on a sandflat in the Gulf of Thailand. Unlike most other intertidal muricids in Southeast Asia, *C. capucinus* does not have a planktonic stage and embryos emerge from egg capsules as crawling juveniles (Middelfart, 1996; pers. obs.). As egg capsules are usually laid cryptically on hard substrata (Aungtonya & Vongpanich, 1997; pers. obs.) to avoid desiccation and predation, it seems likely that juveniles also spend some time in the mangroves before migrating seawards to the largely two-dimensional mudflat. Conversely, adults from the mudflat could possibly return to the mangroves to reproduce. Such ontogenetic partitioning might be necessary as the mudflat environment appears to

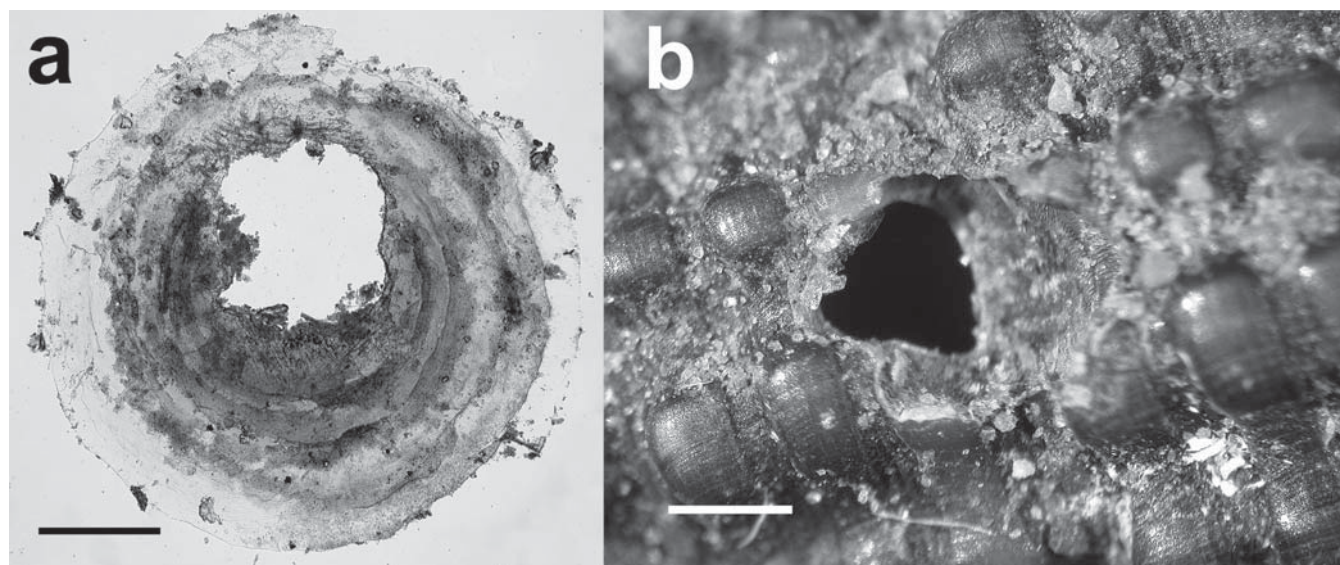


Fig. 7. Drill holes made by *Chicoreus capucinus* on the shell of the mudcreeper *Cerithidea cingulata*: a, operculum; b, sutural region. Scale bars = 500 μ m.

be less forgiving than the mangrove forest in terms of shade and protection from predators such as crabs and fish. The presence of mangroves behind the mudflat appears to be important for *Chicoreus*. A comparable habitat (based on the composition of organisms) not backed by a mangrove forest was carefully examined by Vohra (1971, 1972) and *Chicoreus* was absent.

The mudflat, however, is a veritable source of food for *Chicoreus capucinus*. Apart from the high density of

mudcreepers on the surface, large numbers of shallow infaunal bivalves occur just below the mud surface. Occurrence of predator-prey association on the mudflat (ca. 54%, this study) was comparable to those observed on the sandflat (45–72%; Wells et al., 2001), but differed considerably from the 16% recorded on the floor of the mangrove forest (Tan & Oh, 2002). This could be partly due to the decidedly higher densities of mudcreepers present on sand- and mudflats compared to the mangrove forest floor, where primary productivity is expected to be lower. Despite the abundance of *Cerithidea* on sand, predator density was lowest (Wells et al., 2001), suggesting that *Chicoreus* prefers mud to sand as a habitat. On the other hand, a soft, muddy substratum is also unsuitable, as suggested by the low densities beyond 20 m at Site 1 in Kungkrabaen Bay, where there is a higher proportion of silt (particles < 125 µm diameter). The general absence of aggregative feeding (i.e. many predators feeding on one prey item) also suggests that food is plentiful, and this is exploited well by *Chicoreus*. A total of 12 gastropod and bivalve species were consumed by *Chicoreus* on the mudflat. Apart from fast-moving epifaunal components such as nassariid gastropods and deeper infaunal elements (e.g.,

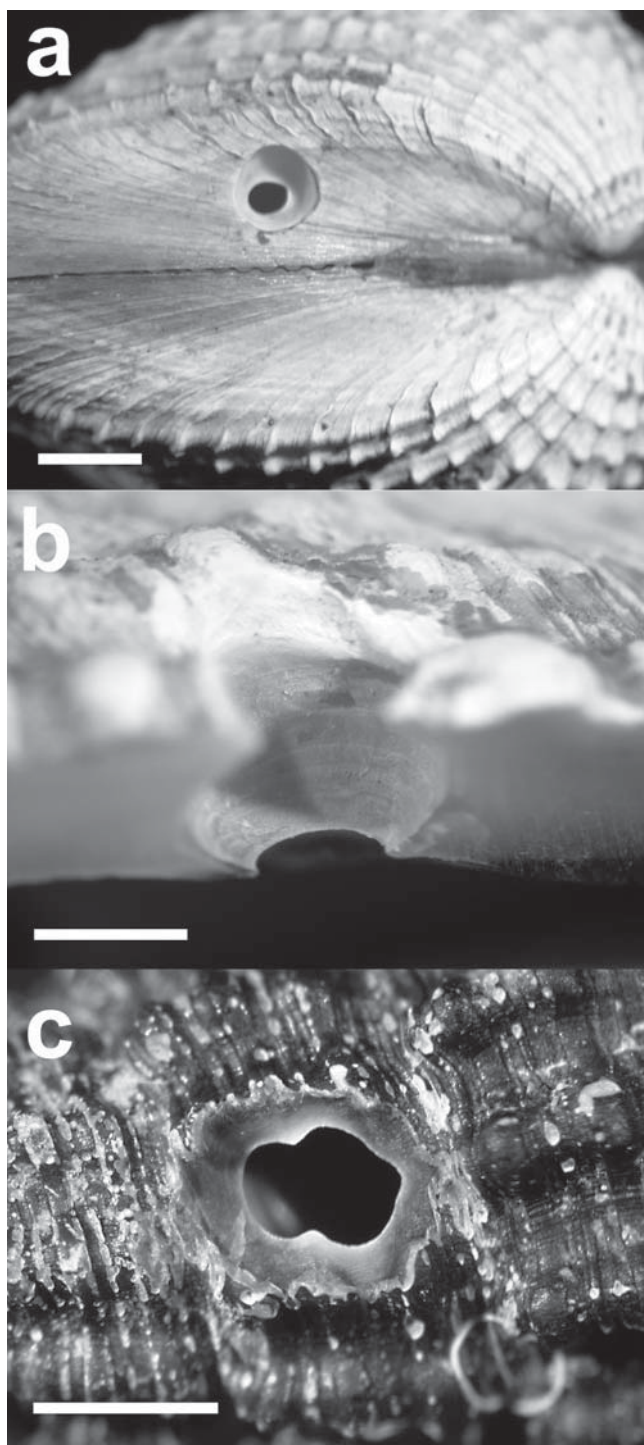


Fig. 8. Drill holes made by *Chicoreus capucinus* on the shells of: a, *Anomalocardia squamosa* (scale = 2 mm); b, *Gafrarium tumidum* (scale = 1 mm); c, *Cerithium coralium* (scale = 1 mm).

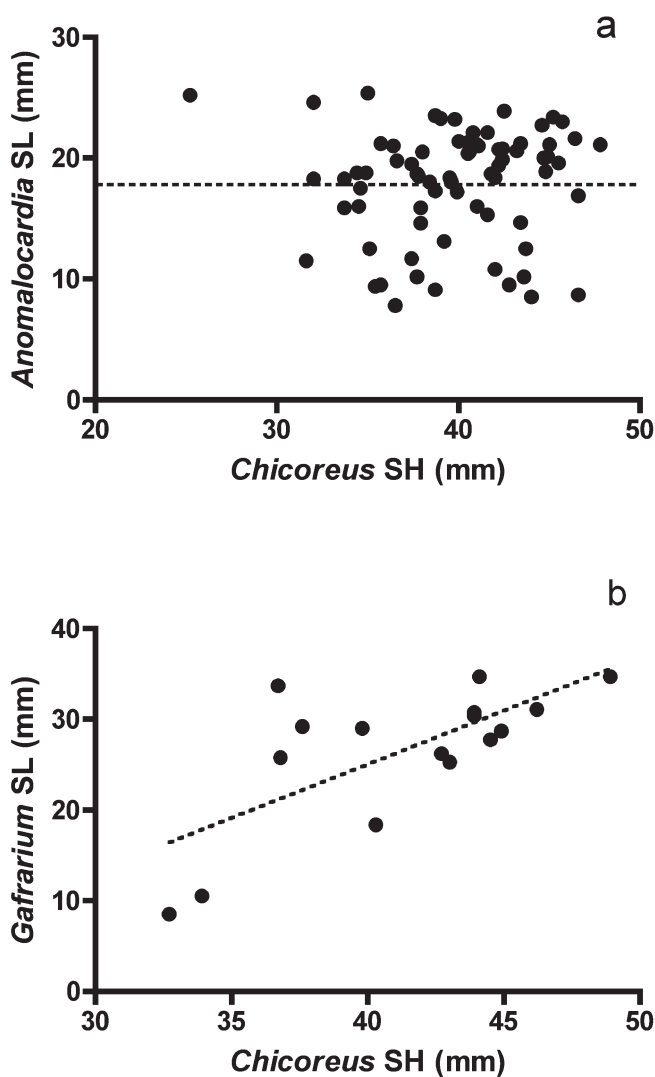


Fig. 9. Predator-prey size relationship between *Chicoreus capucinus* and: a, *Anomalocardia squamosa*; b, *Gafrarium tumidum*, at Kungkrabaen Bay, Gulf of Thailand.

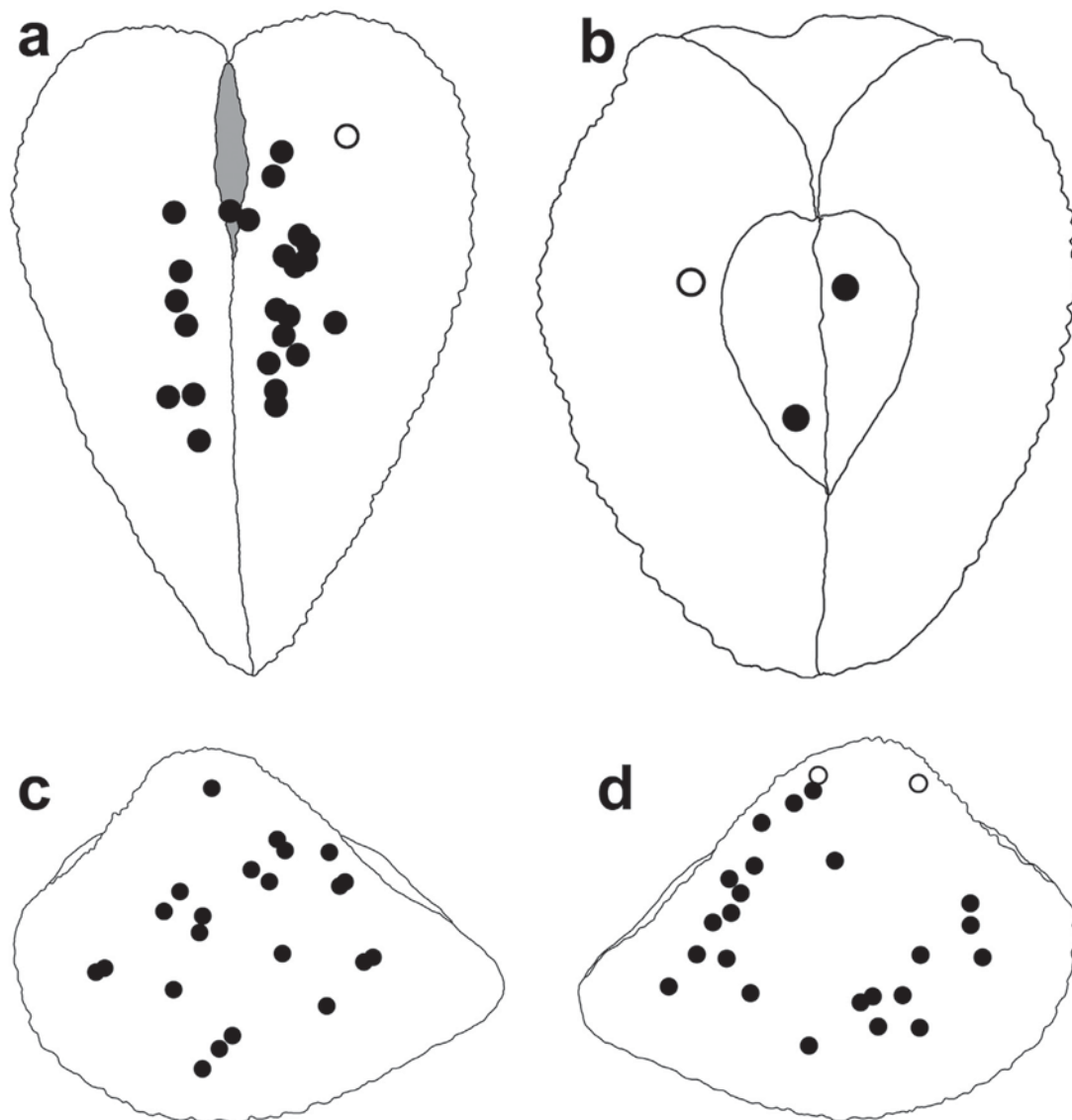


Fig. 10. Composite diagrams of drillhole positions made by *Chicoreus capucinus* on the valves of the venerid clam *Anomalocardia squamosa*: a, escutcheon region; b, lunule region; c, right valve; d, left valve.

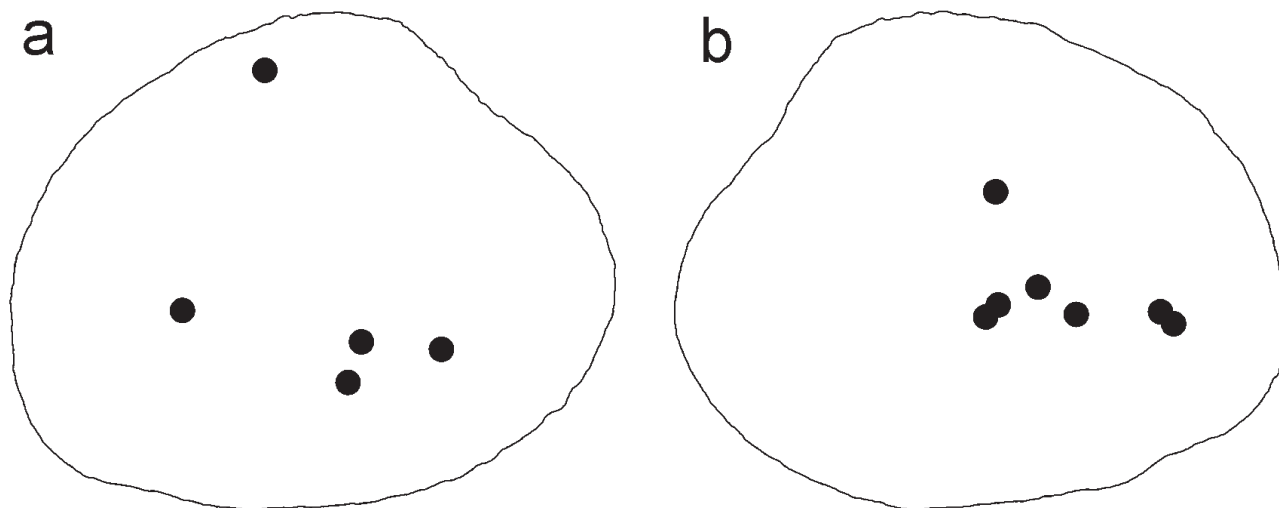


Fig. 11. Composite diagrams of drillhole positions made by *Chicoreus capucinus* on the valves of the venerid bivalve *Gafrarium tumidum*: a, right valve; b, left valve.

Dosinia spp. and *Tellina capsoides*) which are probably out of reach, nearly all molluscan fauna found on the mudflat are preyed upon by *Chicoreus*. Cannibalism was not observed. This catholic diet compares favourably with other observations made in Singapore (Tan & Oh, 2002) and Thailand (Wells et al., 2001; Printrakoon & Tëmkin, 2008) for *Chicoreus*.

Mudcreepers are an important component of the diet of *Chicoreus* on the mudflat at Kungkraabaen Bay. Potamidids were primarily attacked via the aperture, presumably by rasping through the thin corneous operculum. The cerithiids, on the other hand, were preferably drilled through their shells. It would seem advantageous not to drill the shell whenever possible, as drilling is a time- and energy consuming process, although prey-handling time has not been measured for *Chicoreus*. It is also not known if time taken to gain access to prey makes a difference to survival, given the abundance of prey. Nevertheless, the data obtained in this study suggest that apertural access is the preferred method, but at the same time, drilling was also employed selectively. The reasons for choosing to drill the shell could be related to difficulties involved in extending their proboscis through the numerous

coiled whorls of mudcreepers to reach the withdrawn animal within and operate the radula effectively. In any case, the similar positions of drill holes relative to the length of the shell of various prey mudcreeper species could suggest an optimal compromise between not breaching through a region that is devoid of the animal on one hand and drilling through earlier whorls that have been thickened on the other. It remains remarkable that directed rasping on the operculum can continue while the proboscis is coiled inside the whorls of the mudcreeper.

The relatively thick (typically 2.0–2.5 mm) bivalved shells of *Anomalocardia* and *Gafrarium* were also no obstacle to *Chicoreus*. Together they constituted more than one third of prey items drilled by the versatile predator on the mudflat. Nearly all prey gastropod and bivalve individuals examined did not possess any other drill marks other than that being made by the predator at the time of sampling. Hence each drilling attempt is more than likely to succeed, suggesting the effectiveness of *Chicoreus*. This is in contrast to the high incidence of incomplete drill holes on the valves of *Anadara granosa* (Linnaeus, 1758) made presumably by another muricid predator *Bedevea blosvillei* (Deshayes, 1830) on a seagrass bed in Indonesia (Vermeij, 1980a).

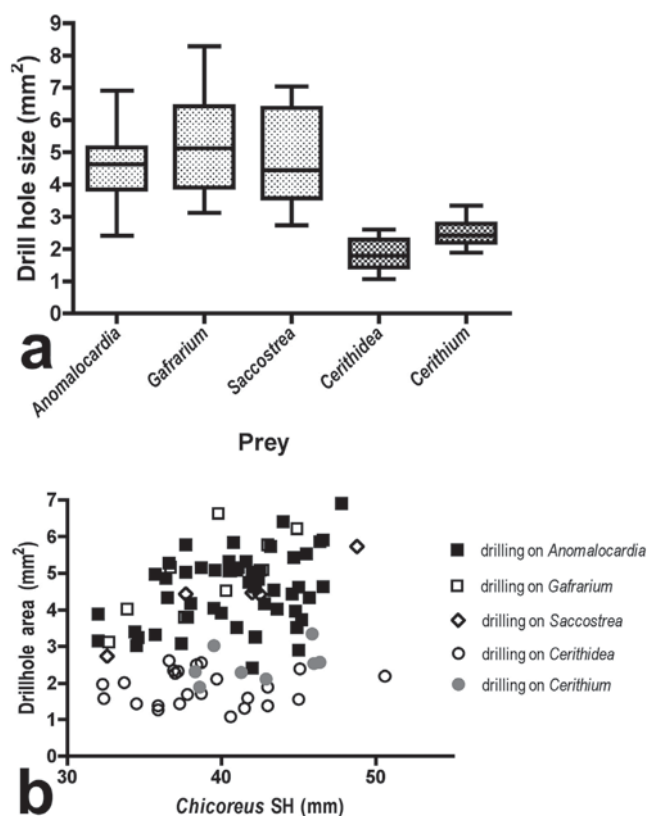


Fig. 12. Size of drill holes made by *Chicoreus capucinus* on various prey, and its relationship with predator size: a, box-and-whisker plots of drill hole size (as area defined by elliptical or circular outline of drill hole) observed on bivalves and gastropods; b, drill hole size and predator size was significantly correlated for two bivalves (*Anomalocardia*: $r = 0.367$, $P < 0.01$; *Gafrarium tumidum*: $r = 0.764$, $P < 0.05$) but no relationship was discernible for gastropods (*Cerithidea cingulata*: $r = 0.037$, $P = 0.86$; *Cerithium coralium*: $r = 0.435$, $P = 0.28$) and for the oyster *Saccostrea* cf. *cuccullata* ($r = 0.648$, $P = 0.164$).

In attacking the two venerid bivalves, *Chicoreus* clearly avoided edge drilling at the ventral margins where the valves meet. Edge drilling has been observed in a number of muricids (e.g., Taylor, 1990; Morton, 1994; Dietl & Herbert, 2005) and considered a risky activity associated with a competitive environment (Dietl et al., 2004), although this behaviour might be stereotypic. Some muricids gain access to bivalves without drilling (Broom, 1982) but in the case of *Chicoreus*, bivalves consumed were almost always drilled. Exceptions include the observations of Wells et al. (2001) for *Laternula*, which were preyed upon via the posterior gape. The general morphology of drill holes made by *Chicoreus* conforms to those described previously for other muricids (Carriker & Yochelson, 1968).

Drilling of calcareous prey opercula has been observed in other muricids (e.g., *Dicathais orbita* (Gmelin, 1791), feeding on the turbinid gastropod *Ninella*; Taylor & Glover, 1999). *Chicoreus* employed a similar method to gain access through the calcareous operculum of the neritid *Clithon oualaniensis*. However, the incidence of opercular breaching was low, and most *Clithon* individuals were drilled through the external surface of their shells.

Where organisms are comparable in size, some studies have shown significant positive relationships between predator and prey size (e.g., McQuaid, 1985; Palmer, 1988; Tan & Oh, 2002; Tan, 2003), whereas others have demonstrated equivocal relations (e.g., Taylor & Morton, 1996; Taylor & Glover, 1999; Wells et al., 2001). In this study, prey size was positively correlated with size of *Chicoreus* in *Cerithidea cingulata* and *Gafrarium tumidum*, but no correlation between predator and prey size was apparent for *Cerithidea djarjariensis* and *Anomalocardia squamosa*. Large predators are certainly capable of consuming small prey, and in some

cases, there is little to impede smaller adult predators from consuming large prey. At least in the case of *C. cingulata*, however, clearly there seems to be some directed selection by *Chicoreus* for larger mudcreepers. Small prey individuals were in general not preyed upon although they comprised the majority of the population on the mudflat. These observations parallel those at a sandflat in the Gulf of Thailand (Wells et al., 2001).

The versatility of *Chicoreus* is also amply demonstrated in their seeming ability to tune their drilling efforts according to prey type. Whereas larger predators generally drilled larger holes in bivalves, large predators were also able to drill smaller holes where needed, presumably adjusting to the thickness of the shell of prey. Drill holes were significantly smaller on mudcreepers when compared to those attempted on bivalves, regardless of predator size. Drill hole size is therefore not necessarily related to predator size, but is dependent upon the type of prey drilled.

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THAI ABSTRACT

อ่าวคู่งกระเบนเป็นอ่าวขนาดเล็ก ที่มีระดับน้ำค่อนข้างตื้นในบริเวณพื้นที่อ่าวไทยตอนบน ในพื้นที่ดังกล่าวหอยมะระดำ *Chicoreus capucinus* (Lamarck, 1822) ซึ่งเป็นผู้ล่าจะอาศัยอยู่บริเวณหาดโคลนถัดจากชายป่า *Rhizophora* ด้านติดกับทะเล หอยมะระดำบริเวณนี้มีความหนาแน่นสูงถึง 62 ตัวต่อ 100 ตารางเมตร หอยมะระดำในที่นี้กินหอยฝาเดียวและหอยสองฝาหลายชนิด โดยเฉพาะหอยเวนอริด *Anomalocardia squamosa* (Linnaeus, 1758) และ *Gafrarium tumidum* (Röding, 1798) ซึ่งเป็นเหยื่อหนึ่งในสี่ที่มีการบันทึกไว้ ($n=279$) ในสนามเหยื่ออื่นๆ ได้แก่หอย *Pharella* cf. *javanica* (Lamarck, 1822)(Pharidae) และ *Laternula* cf. *boschasina* (Laternulidae) ส่วนหอยฝาเดียวที่เป็นเหยื่อได้แก่ *Cerithidea cingulata* (Gmelin, 1791) และ *C. djadjariensis* (Martin, 1899)(Potamididae) หอยที่สืบคลานใน

โคลนเหล่านี้เป็นเหยื่อมากกว่าหนึ่งในสาม นอกจากนั้นยังมีหอย *Cerithium corallium* Kiener, 1841 และ *Clypeomorus pellucida* (Hombron & Jacquinot, 1852) และหอยเวนอริทิด *Clithon oualaniensis* (Lesson, 1831) หอยสองฝาจะถูกเจาะและเห็นร่องรอยการเจาะอย่างชัดเจนบริเวณฝาเปลือกทั้งเปลือกซ้ายและขวา โดยหอย *A. squamosa* มีแนวโน้มว่าถูกเจาะบริเวณ escutcheon หอยโพทามีคิดที่มีขนาดเล็กกว่าจะถูกเจาะบริเวณกลางลำตัว ส่วนพวก cerithoideans จะถูกกินผ่านรูเปิดของเปลือก โดยมีร่องรอยการเจาะทะเล operculum หอย *Clithon* จะถูกเจาะบริเวณยอดเปลือกหรือผ่านช่องว่างระหว่างเปลือกและ operculum นอกจากนี้ยังพบว่ามีความสัมพันธ์ระหว่างขนาดของผู้ล่าและเหยื่อด้วย โดยเฉพาะสำหรับ *C. cingulata* และ *G. tumidum* ซึ่งแต่แนวโน้มดังกล่าวไม่ชัดเจนในเหยื่อที่เป็นเหยื่อชนิดอื่น ขนาดของรูที่เจาะมีความจำเพาะกับชนิดของเหยื่อ โดยไม่สัมพันธ์กับขนาดของผู้ล่า รูเจาะในหอยสองฝามีขนาดใหญ่กว่ารูเจาะในเหยื่อที่เป็นหอยฝาเดียว โดยขนาดของรูเจาะและขนาดของเหยื่อในหอย *A. squamosa* และ *G. tumidum* มีความสัมพันธ์กัน หอยฝาเดียวกลุ่มมิวริซิดในเขตน้ำขึ้นน้ำลงมักพบอาศัยอยู่บนพื้นแข็งแต่การศึกษาในครั้งนี้แสดงให้เห็นว่าหอยมะระ *Chicoreus* มีความสามารถในการล่าเหยื่อบนพื้นที่อ่อนนุ่มด้วย และยังกินหอยเทพทูกชนิดเป็นอาหาร ยกเว้นหอยชนิดเดียวกัน

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