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CHELAE FORCE GENERATION AT VARIABLE GAPE SIZES IN THE MUD CRAB, *SCYLLA OLIVACEA* (BRACHYURA: PORTUNIDAE)

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ABSTRACT. — Chelae crushing forces produced by crabs at a single specific gape size have been explored in numerous studies, but very rarely are multiple gape sizes tested. Here, we investigated the chela strength generated at differing gape sizes of the mangrove mud crab, *Scylla olivacea*. Crabs were induced to grip metal levers fixed to a modified digital pull-push force gauge to generate a force reading. Crushing forces produced by the proximal and distal regions of chelae were significantly different ($P<0.05$). The major chela of *Scylla olivacea* had a mechanical advantage compared to its minor chela. Overall, as gape size widened, the force generated increased until an optimal (i.e., greatest force achieved) gape size was attained. Thereafter, a decline in force generation was recorded. The optimal gape size has important implications for foraging behaviour, including prey selection and handling time.

KEY WORDS. — crushing force, tropical, Southeast Asia, *Myomenippe hardwicki*, mechanical advantage, optimal foraging theory

INTRODUCTION

The mud crab (*Scylla olivacea*) is a species of Portunid found in coastal waters throughout the Indo-Pacific (Keenan et al., 1998; Le Vay, 2001; Walton et al., 2006). It is commercially important for local fisheries and aquaculture in tropical and subtropical Asian countries (Keenan, 1999; Le Vay, 2001; Walton et al., 2006). Recent overexploitation of these crabs has resulted in the decline of natural stocks in the wild (Le Vay, 2001). Despite its economic importance, little is known about the ecology, behaviour, and physiology of *Scylla olivacea*. This species is large (adult carapace width ranges from 95.0–133.9 mm; Keenan et al., 1998) and heterochelous; comprising of a major 'crusher' and minor 'cutter' claw, as with most other crabs in the infraorder Brachyuran (Keenan et al., 1998). Even though their major chela is capable of crushing substantial shelled prey (Vermeji, 1977), no study to date has quantified the forces that can be generated by *Scylla olivacea* claws.

The chelae of crabs are multifunctional, employed in many aspects of their behaviour, including sexual displays, territorial defence, and the capturing and manipulation of prey (Seed & Hughes, 1995). In several Brachyuran crabs, both the major and minor chelae aid in feeding (Vermeiji, 1977). The major chela has large, blunt molariforms present on its opposing planes near the hinge of the chela's pollex and movable dactyl (Vermeiji, 1977; Seed & Hughes, 1995). This enables a strong force to be delivered to a focused area—ideal for crushing shelled molluscs (Vermeiji, 1977; Seed & Hughes, 1995). Conversely, the smaller minor chela lacks large molariforms, and is used mainly for holding and manipulating prey (Vermeiji, 1977; Zipser & Vermeiji, 1978; Govind & Blundon, 1985; Seed & Hughes, 1995).

Tropical brachyuran crabs are known to prey extensively on hard-shelled molluscs (e.g., Vermeiji, 1977; Seed & Hughes, 1995; Ling et al., 2008). They also have larger chelae, probably a consequence of reduced energetic constraints of the crab at higher temperatures (Vermeiji, 1977; Seed & Hughes, 1995). *Scylla olivacea* has a large and heavy major chela (Vermeji, 1977) however, its natural diet have not been documented. Gut content analysis and behavioural observations of its close relative, *Scylla serrata*, suggests that it feeds mainly on bivalves and small crabs as well as scavenging (Hill, 1976, 1979; Williams, 1978). The greater muscle volume found in large tropical crab chela enables more force to be generated (Mitchell et al., 2003), thus allowing the species that possess them to consume larger prey than temperate crabs (Vermeiji, 1977; Zipser & Vermeiji, 1978).

The force generated by chelae can be partly attributed to their mechanics. The chela is analogous to a frictionless lever system, with the force applied by the closer muscle depending on the mechanical advantage of the dactyl (Warner & Jones, 1976), i.e., the ratio of the length between the pivot and the dactyl's proximal tip (L_1, Fig. 1A, B), and the length between the pivot and the point on the dactyl (L_2, Fig. 1A, B) where the item to be crushed is positioned

(Warner & Jones, 1976; Vermeij, 1977). The resultant force generated by the chelae is attributed to the size of its closer muscle and the lever system of the chelae (Lee & Seed, 1992). Consequently, the mechanical advantage of the dactyl of each claw determines the effective force generated—up to 800 N in some species (Vermeiji, 1977).

The strength generated by crab chelae has been documented in several species (Warner & Jones, 1976; Vermeji, 1977; Preston et al., 1996; Seed & Hughes, 1997; Claussen et al., 2008). Studies have generally focused on determining the mechanical advantage of the claw in relation to chelae sizes (Vermeij, 1977; Blundon & Kennedy, 1982; Seed & Hughes, 1995). Other research has investigated the sarcomere lengths of the chelas' closer muscle and how this relates to forces generated (Warner & Jones, 1976; Taylor et al., 2000). One similarity among all these studies is that the measurements of the crushing forces were conducted at a fixed chela gape size. Only Ling et al. (2008) examined the effects of increasing chelae gape size on force generation (and it was not even the focus of their work); they found that the chelae closing force of *Myomenippe hardwicki* decreased with increasing gape size. However, Ling et al. (2008) did elaborate on what might be causing this decrease. Here, we investigated the effects of increasing gape sizes on the chelae closing force of *Scylla olivacea*. We hypothesized that chela strength would begin to decrease at larger gape sizes. To test this, the magnitude of force generated by the chela was measured at multiple gape sizes using a modified push pull force gauge.

MATERIAL AND METHODS

Experimental organisms. — Six live mud crabs, *Scylla olivacea*, were obtained from a local market in Singapore. Individuals with any signs of injuries or ill-health were avoided. Only crabs of similar sizes (carapace width: 110.78 ± 1.41 mm) and chelae heights (major chelae: 42.08 ± 0.44 mm; minor chelae: 37.30 ± 0.27 mm) were chosen. The animals were maintained at the marine aquarium in the Department of Biological Sciences, National University of Singapore, in rectangular plastic tanks (28 × 15 × 17 cm; length × width × height). A continuous supply of air was provided and crabs were kept for a maximum duration of two weeks to reduce behavioural or health changes that might confound the experimental results. The crabs were fed daily on a diet of frozen fish and, occasionally, cockles. Before feeding, the crabs were observed to crush the cockles with either the distal or proximal region of their major claw, suggesting that bivalves could be part of their natural diet.

Chelae closing force measurements. — The peak chelae-closing forces generated by *Scylla olivacea* chela at different gapes (the distance between dactyl and propus) were measured using a digital push-pull force gauge (IMADA DPS-50) connected to a double lever by a steel cord (following Ling et al., 2008). The lever arms contained a pair of notches for the crabs to grip. During each trial, a crab was randomly selected, placed in a plastic container (45 × 30 × 12 cm; length × width × height) and induced to attack by nudging it gently with the lever arms. When both the dactyl and propus of the chela were in place within the two notches of the apparatus (Fig. 1C), the peak force generated during 10 s from the onset of the pinch was recorded. The force pulse generated by chelae tended not to extend beyond this time period (Boulding, 1984; Seed & Hughes, 1995). Measurements of the crushing force generated were taken at the proximal and distal regions of both the major and minor chela (Ling et al., 2008). Three replicate measurements were taken for each gape size of each crab and individuals were provoked to pinch for no more than five minutes. In addition, chelae region and gape size to be measured were randomly selected for each trial. Gape sizes were varied at 2-mm intervals. For all crabs, the maximum gape sizes measured for both major and minor chela at the proximal region was 14 mm. The largest gape size for the distal region of the major chela was 28 mm, whereas the maximum gape size measured for the distal region of the minor chela was 26 mm.

Data analysis. — All statistical analyses were conducted using SPSS 16 (SPSS). Wilcoxon signed ranks test was used to determine the differences in mean force generated between the distal and proximal regions of the major and minor chelae.

RESULTS

Comparison of mean crushing forces generated by the proximal and distal regions showed that the major chelae was capable of delivering a greater crushing force than the same regions on the minor chelae. The force generated by the two claws could differ up to 94.0 N and 253.9 N at the distal and proximal regions respectively. In addition, the strength generated at the proximal region of the claw was significantly greater than the distal region of the claw. This trend was observed for both major and minor chelae. Wilcoxon signed ranks test showed significant differences in the mean force generated by the proximal (128.8 N ± 93.8 S.E) compared to the distal (34.1 N ± 33.7 S.E.) region of the major chela ($Z = -2.201$; $p<0.05$). Likewise, Wilcoxon signed ranked tests also showed significant differences in the mean force generated by the proximal (42.6 N ± 18.0 S.E.) compared to the distal (19.1 N ± 9.2 S.E.) region of the minor chela ($Z = -2.023$; $p<0.05$). The maximum force generated by each individual was at a different gape size (Figs. 2, 3).

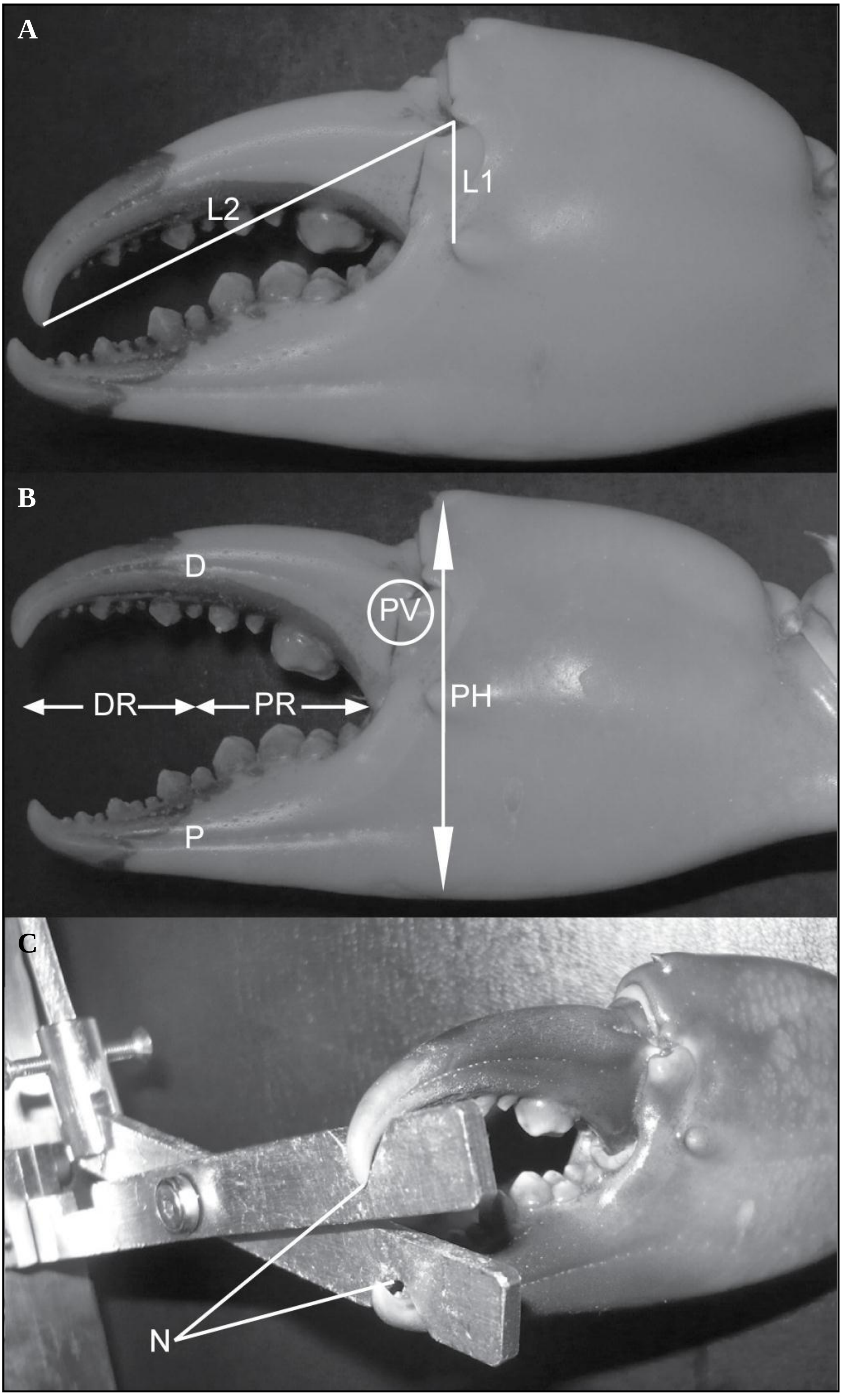

Fig. 1. Major chela of mud crab (*Scylla olivacea*). A, illustrating the lengths of L_1 and L_2 that contribute to the chela's mechanical advantage; B, illustrating the morphometric features measured: D=dactyl; P=propus; D_R=distal region; P_R=proximal region; P_V=pivot; P_H=propal height; C, gripping onto the apparatus' lever arms. N=notches that allow the crab to grip onto.

For most crabs, an inverse relationship was observed between the chela strength generated at the proximal region and gape sizes for both major and minor chelae (Fig. 2A, B). While variable, the peak force was usually generated when the major claw had a gape size of 12 mm and the minor claw at 10 mm (Fig. 2A, B). Thereafter, crushing force generated would decrease with increasing gape sizes. The maximum peak force generated by the proximal region recorded was 330.1 N ± 21.9 S.E. at gape size of 12 mm whereas the lowest recorded was 10.8 N ± 0.3 S.E. at gape size 4 mm (Fig. 2A). For the minor chela proximal region, the highest peak force recorded was 76.2 N ± 8.4 S.E. at 10 mm while for the lowest peak force recorded for this region was 8.7 N ± 2.3 S.E. at gape size 4 mm (Fig. 2A). Two of the crabs however, continued to exhibit increasing chelae strength in their major claws up to the maximum gape size (Fig. 2A). This was also observed for the minor chela of one crab (Fig. 2B).

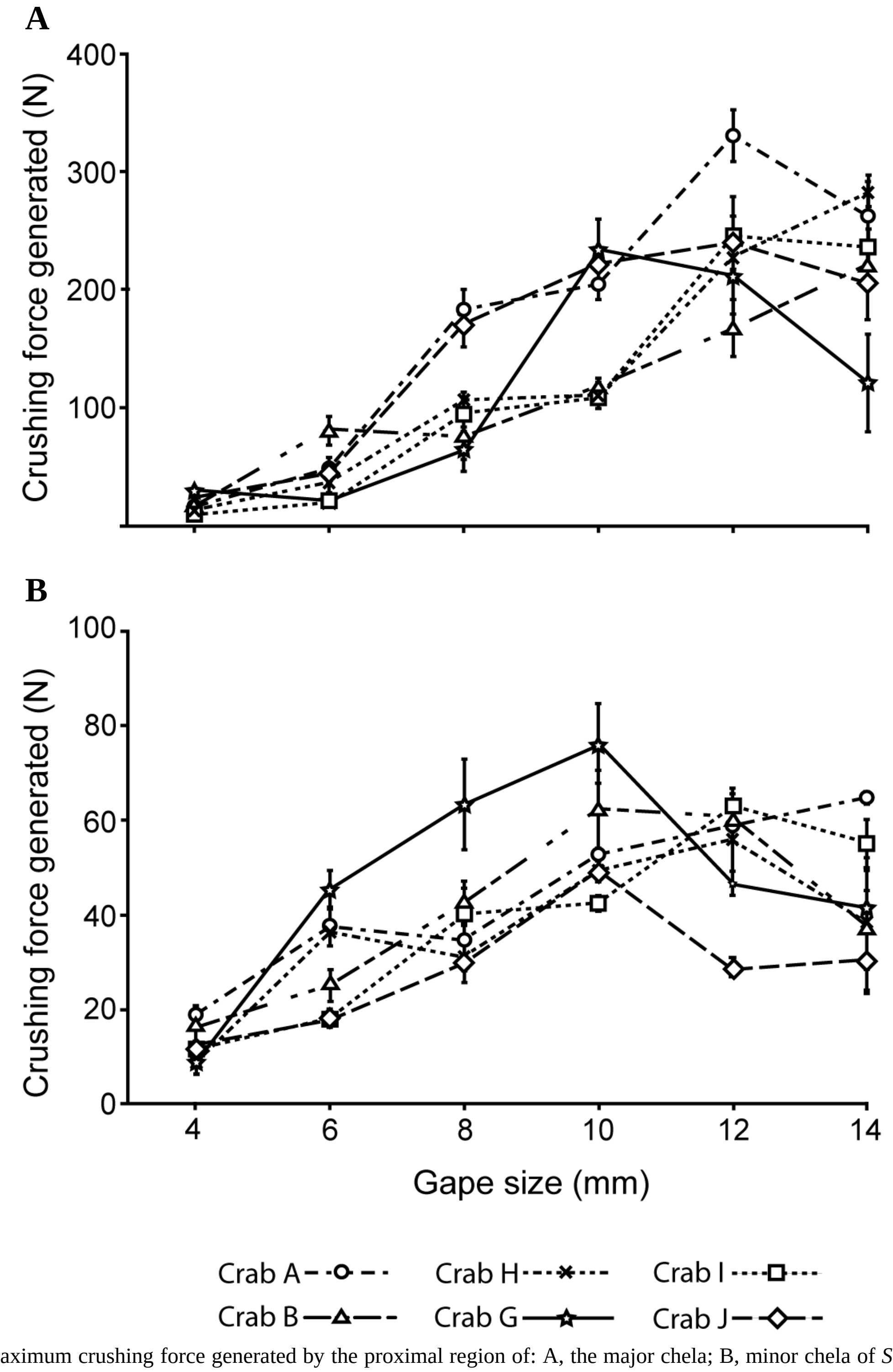

Fig. 2. Mean maximum crushing force generated by the proximal region of: A, the major chela; B, minor chela of *Scylla olivacea* at increasing gape sizes at 2 mm intervals (n=3). Error bars indicate standard error.

Chela strength generated by the distal region fluctuated with gape sizes for both chelae (Fig. 3A, B). The maximum forces generated were often at gape sizes ranging between 10–14 mm and 18–26 mm (Fig. 3A, B). The highest peak force generated by the distal region of the major chela was 140.1 N ± 16.0 S.E. at a gape size of 22 mm whereas the lowest peak force generated in this region was 5.3 N ± 0.7 S.E. at gape size 4 mm. For the minor chela distal region, the highest peak force recorded was 46.1 N ± 2.2 S.E. at gape size 16 mm whereas the lowest force was 5.3 N ± 0.7 S.E. at gape size 4 mm.

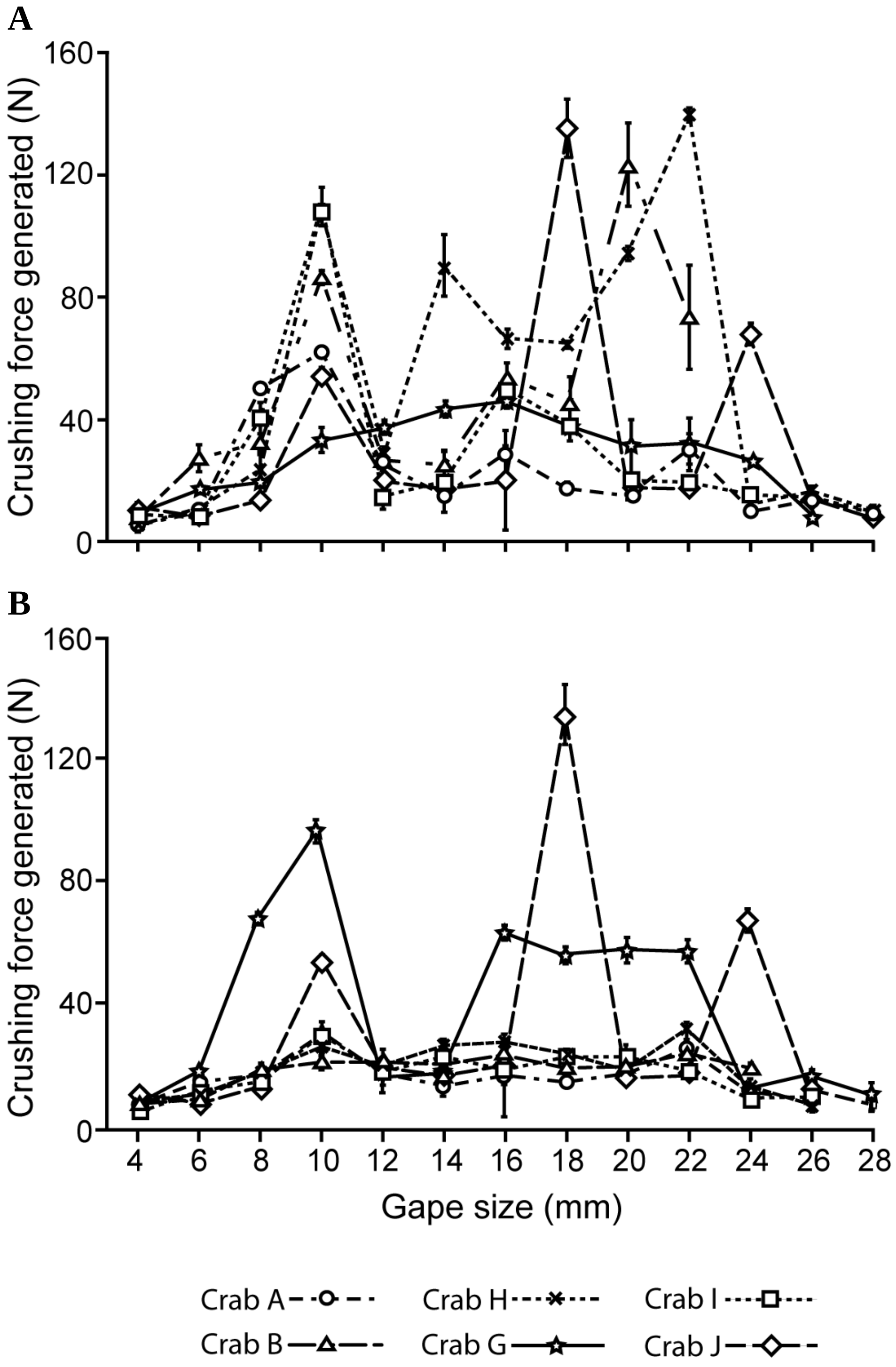

Fig. 3. Mean maximum crushing force generated by the distal region of: A, the major chela; and B, the minor chela of *Scylla olivacea* at increasing gape sizes at 2 mm intervals (n=3). Error bars indicate standard error.

DISCUSSION

The closing force generated by crab chelae at multiple gape sizes has only been examined once before (Ling et al., 2008). While Ling et al. (2008) demonstrated an eventual decrease in force generated when the chelae of *Myomenippe hardwicki* opened beyond its optimal (i.e., greatest force achieved) gape size for both its proximal and distal regions, in the present study this was only observed for the proximal region of *Scylla olivacea* claws. For the distal region of the chelae, the maximum force varied among gape sizes. Disparity in the pattern of crushing forces generated between the two crab species could be attributed to differences in their chelae morphology and associated mechanical advantage. As with other studies (e.g., Ling et al., 2008), our results showed a significant difference in the mean force generated between the distal and proximal region of both the major and minor chela.

The angle of pinnation of the sarcomeres has been used previously to predict the strength of crab chelae (Schenk & Wainwright, 2001; Mitchell et al., 2003). This angle is formed between the muscle fibres and the closer apodeme in the chela (See Schenk & Wainwright, 2001). As muscle fibres shorten when the chela closes, its angle of pinnation increases. Crabs with larger mean angle of pinnation of its sarcomeres also have greater mechanical advantage and therefore stronger claws (Schenk & Wainwright, 2001). Here we propose that, beyond an optimal gape size, the muscle fibres of the chela gradually lengthens and the angle of pinnation decreases. This results in a reduced force generated as gape size increases. Both the proximal and distal regions of *Myomenippe hardwicki* claws exhibited this trend (see Ling et al., 2008) whereas, for *Scylla olivacea*, this was only observed for the proximal region of both claws. Here, and in Ling et al. (2008), the optimal gape size for the maximum crushing force generated varied among the specimens. These inconsistencies among individuals could be explained by the differences in muscle development as a result of handedness reversal during early intermoults and/or environmental cues (Abby-Kalio & Warner, 1984; Govind & Blundon, 1985; Smith & Palmer, 1994). In addition, individual behaviour of the crabs and their feeding strategies (Taylor et al., 2000) may also affect the crushing force generated.

The greater crushing force generated in the proximal region compared to the distal region of the claw can be attributed to the chela lever system. Warner & Jones (1976) were the first to analyse force generation by treating the chela as a lever system and this approach has been incorporated in numerous subsequent studies (see Blundon & Kennedy, 1982; Seed & Hughes, 1997; Schenk & Wainwright, 2001). Vermeij (1977) and Seed (1993) noted that prey placed nearer the chela pivot (proximal region) will be subjected to greater crushing forces generated than prey nearer the claw tips due to the corresponding higher mechanical advantage. Only smaller prey, however, can be accommodated in the proximal region owing to the limited maximum gape size achievable.

Decreasing chela strength generated beyond optimal gape sizes influences prey selection. Optimal foraging theory predicts that prey specialisation occurs within the capabilities of the predator, to maximise its energy intake with minimal time spent on foraging (Hughes & Elner, 1979). It has been suggested that the physical characteristics of a molluscan prey, such as their shape, structure, and toughness of their shells, are factors limiting crab predation (Zipser & Vermeiji, 1978; Boulding, 1984). Boulding (1984) noted that crab predators tend to have difficulty handling and subduing large shelled prey. Here we have shown how large gape sizes can result in a reduction in forces generated. This may result in the crab repeatedly loading prey items larger than their optimal gape size in order to crush them, leading to increased handling times. This makes the crab more vulnerable to predators (Boulding & Labarbera, 1986; Seed & Hughes, 1995; Ling et al., 2008) and reduces time available for foraging (Boulding, 1984). In addition, repeated loading of a large prey can induce damage via micro-cracks and abrasion of the chela (Boulding & Labarbera, 1986; Taylor et al., 2000).

There exists a substantial body of literature concerning chela strength, but it only reports forces generated at a single gape size. In the present study, we demonstrated that the crushing forces generated by *Scylla olivacea* chela will decrease once an optimal gape size is exceeded. Ling et al. (2008) found a similar trend for this in *Myomenippe hardwicki*. While the exact cause of this pattern was not investigated here, we propose that future studies examine chela closer muscle efficiency in relation to the strength generated at varying gape sizes. Such research would provide a better understanding into the mechanics of the chela, beyond the present lever system interpretation. Overall, the relationship between gape size and force generated has substantial implications for foraging behaviour, especially prey selection and handling time and should be further investigated for its potential influence on the crab and mollusc co-evolutionary arms race.

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