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Heterochely and handedness in the ridged swimming crab *Charybdis natator* from the Gulf of Suez, Red Sea

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Received 29th December 2010, Accepted 27th February 2011

Abstract

The phenomena of heterochely and handedness in the ridged swimming crab *Charybdis natator* inhabiting the Gulf of Suez were studied and related to the species feeding habit. A total of 228 crabs were collected and measured for carapace width and claw width and length. Stomach contents were examined and the different preys identified. The obtained sample consisted of 152 males and 76 females. Males were larger than females in carapace width (109.9 versus 101.6 mm). In the two sexes, right-handedness prevailed over left-handedness (66.6%, 33.4%) respectively and both phenomena were observed at a small size (70 - 80 mm CW). Slopes for claw dimensions to body size relationships for right-handed crabs were consistently steeper than for left-handed ones for males and females indicating accelerated claw growth with respect to body size. No differences were observed in the diet composition between sexes and it composed mainly of hard-bodied preys. The significance of heterochely and handedness in the feeding habit of this species is discussed.

Keywords: Heterochely, handedness, feeding habit, swimming crab, Gulf of Suez.

1. Introduction

Crabs appendages are segmentally arranged, with one pair on each segment (Crothers, 1967). The most anterior pair of thoracic limbs, the claws or chelipeds, are enlarged and chelate having evolved into appendages that are very different to the walking legs (Mearow and Govind, 1986). The cheliped is a good example of a multi-functional organ, the major uses of which include foraging, agonistic interactions, and competition for, and handling of mates (Lee and Seed, 1991). In the Brachyura, the bilateral asymmetry due to morphologically dissimilar chelae is common and is termed heterochely (Elner, 1978). The two chelae normally differ in both size and shape and are refereed as major and minor because of the size difference. The major (crusher) claw is larger, more robust and has enlarged molar-like dentition. It serves to crush prey using its greater mechanical advantage (Warner *et al*., 1982). The minor (cutter) claw is more slender, has incisor-like teeth on its biting surface and serves to manipulate the prey using finer and more coordinated movements (Pynn, 1998). On the other hand, heterochely does not always happen, some crabs have two cutters especially females and very large males (Hamilton *et al*., 1976). Several studies have reported on the relationship between heterochely and feeding habit. Major (crusher) claws are slow-acting and powerful play a role in food acquisition particularly crushing of shells of molluscs while the minor (cutter) claws which are fast-acting but weaker are specialized in capturing swimming preys (Ng and Tan, 1985; Daniels, 2001).

Handedness or laterality in crabs has been reported in species possessing dimorphic claws of unequal sizes and has been determined by the side bearing the major claw (Trott, 1987). In many heterochelous brachyuran crab species it has been found that the major chela is usually on the right hand side (Ng and Tan, 1985; Abby-Kalio and Warner, 1989; Negreiros-Fransozo and Fransozo, 2003). In some species, the distribution of right and left handedness is equal- i.e. 50% right: 50% left (Halry, 1969; Shih *et al*., 1999). Reversal of handedness occurs when a crusher is removed and the remaining pincer differentiates into a crusher after molting. A lost crusher is always replaced by a regenerated pincer-like claw (Juanes, *et al.,* 2008). Barnwell (1982) noted that most crabs with functionally dimorphic feeding claws reverse handedness following crusher loss, since a pincer can develop into a crusher in a single molt. Simonson and Steele (1981) showed that reversal was quite frequent (88%) on the first molt following crusher loss among small juvenile stone crabs.

The functional advantage of right-handedness in crabs has been reported to be linked to feeding (Elner, 1978; Ng and Tan, 1985; Abby-Kalio and Warner 1989; Seed and Hughes 1995). The size and form of the cheliped of crabs are known to be related to feeding performance and thus influence the outcomes for prey assemblages (Silva *et al.,* 2010). Many species have a particular morphology adapted to a specific use in the

feeding process (Calverie and Smith, 2007). For example, chelae may be adapted to break the shell of prey in durophagous predators (Yamada and Boulding, 1998), make generate snapping sounds or cavitation bubbles to kill prey (Versulis *et al*., 2000) or collect sediment for feeding (Crane, 1975). Detritivorous crabs have small slender claws (Seed and Hughes 1995) while the carnivorous counterparts possess enlarged chelae to facilitate predation (Mariappan *et al.,* 2000).

The swimming crab *Charybdis natator* (Herbst, 1794) (Brachyura: Portunidae) has been observed to occur in considerable amounts among the landing catches of commercial crustaceans of the Gulf of Suez (Sallam and Gaballa, 2009). This species reaches a considerably large size and both sexes display heterochely and handedness. In addition, nothing is known about the feeding habit or the diet of this species. The aim of this study is therefore to investigate heterochely and handedness in the swimming crab *Charybdis natator* and to relate these two phenomena to the feeding habit of this species.

2. Material and methods

Samples of *C. natator* were collected from El-ataka fishing center at Gulf of Suez, Red Sea, Egypt between March and June 2009. Crabs were picked from the catch, carefully handled to avoid any loss of limbs, then placed in plastic jars and fixed in 10% formalin in seawater. Each crab was examined for sex, handedness right handed, (RH) or left handed (LH) and claw type (crusher or cutter). Measurements included carapace width (CW), propodus width and length for both chelae were done. Crabs without either cheliped were excluded from the analysis. For stomach content analysis, the crab was carefully dissected and the stomach removed. It was slit open and the contents examined underneath a dissecting microscope. The contents were heavily masticated; nevertheless, different preys found were identified to the lowest taxonomic level possible. The analysis of covariance (ANCOVA) (Zar, 1984) was used to compare slopes and elevations of the regressions for right- handed versus left-handed males and females separately.

3. Results

3.1. Handedness

A total of 228 crabs were collected, 152 males with a carapace width ranges from 70 to 148.0 mm (CW) and 76 females with carapace width between 74.2-130.5 mm. Of the examined crabs, 152 (66.6%) had the right propodus and dactylus enlarged (right-handed) and 76 (33.4%) had the left propodus and dactylus enlarged (left-handed). No homochelous individuals were found. Among the 152 males, 101 (66.4%) were right-handed and 51 (33.6%) were left-handed, while amongst the 76 females, 51 (67.1%) were right-handed and 25 (33.6%) were left-handed. No significant difference in handedness between sexes was observed (X^2= 3.80; P> 0.05). All individuals (both right and left- handed) had major crusher and minor cutter chelipeds. Right-handed crabs were larger than the left-handed ones (mean= 106.8 vs. 101.7 mm) for both males and females (Table 1).

Table 1: Size ranges for males and females *Charybdis natator* with different handedness.

Sex	Handedness	Size range CW (mm)	Mean CW ± SD	N
Males	Both	70 - 148.0	106.9 ± 18.8	152
	RH	74.7 – 142.8	109.9 ± 18.4	101
	LH	70 – 148.0	100.8 ± 18.2	51
Females	Both	74.2 – 130.5	101.6 ± 11.5	67
	RH	74.2 – 130.5	100.6 ± 11.9	51
	LH	82.5 – 118.4	103.6 ± 10.2	25
Both sexes	RH	74.7 – 142.8	106.8 ± 17.1	152
	LH	70 – 148.0	101.7 ±15.9	67

Note: Legend: SD= standard deviation; N= number of individuals, RH= right-handed; LH= left-handed.

3.2. Size distribution and handedness

Figure 1 shows that both males and females exhibited handedness at a small size (70-80 mm CW). At this size range, the percentage of left-handed males was higher than right-handed ones while left-handed females were completely absent. Right–handedness prevailed over left-handedness for males throughout all size ranges (80-150 mm CW). Females showed the same trend; however, left-handed ones disappeared in sizes larger than 130mm CW.

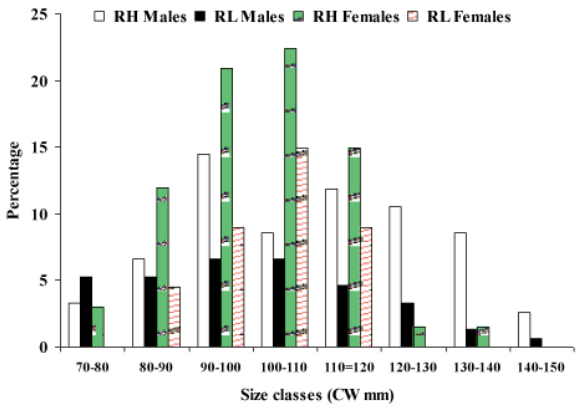

Figure 1. Size frequency distribution for males and females *Charybdis natator* with different handedness. RH= right-handed, LH=left-handed.

ISSN: 1687-4285

3.3. Relationships between claw dimensions and body size

The relationships between claw width and length for right and left-handed crabs with carapace width are shown in figure (2) and the regression equations were given in Table (2). Slopes for claw dimensions to body size relationships for right-handed individuals were consistently steeper than for left-handed individuals for both male and female crabs. ANCOVA results showed that major claw widths had higher elevations for both right-handed male and female crabs than their left-handed counterparts ($F= 3.29$, $P<0.0005$). In contrast, minor claws widths showed no differences in elevation between right and left- handed individuals ($P= 0.359$). Comparison between sexes showed that right-handed males always exhibited steeper slopes than females for all claw dimensions with respect to carapace width (all $P < 0.0001$).

Table 2. *Charybdis natator*. Regression equations for log claw width and length versus log carapace width for males and females with different handedness.

Sex	Dimension	Handedness	Equation	r^2 value
Male	Major claw width	RH	Y= 1.3735X - 1.2782	0.95
		LH	Y= 1.2802X - 1.1125	0.91
	Minor claw width	RH	Y= 1.223X - 1.0391	0.94
		LH	Y= 1.2148X - 1.0342	0.85
	Major claw length	RH	Y= 1.3293X – 0.6946	0.95
		LH	Y= 1.3752X – 0.7974	0.95
	Minor claw length	RH	Y= 1.3881X – 0.8114	0.75
		LH	Y= 1.3315X – 0.7221	0.93
Female	Major claw width	RH	Y= 1.2049X – 0.9567	0.90
		LH	Y= 1.331X - 1.2452	0.88
	Minor claw width	RH	Y= 1.1022X – 0.8302	0.88
		LH	Y= 1.1962X - 1.0331	0.91
	Major claw length	RH	Y= 1.1156X – 0.3163	0.93
		LH	Y= 1.1592X – 0.4129	0.91
	Minor claw length	RH	Y= 0.9691X – 0.042	0.85
		LH	Y= 1.9019X – 0.0811	0.91

Legend: r^2= correlation coefficient; RH= right-handed; LH= left-handed.

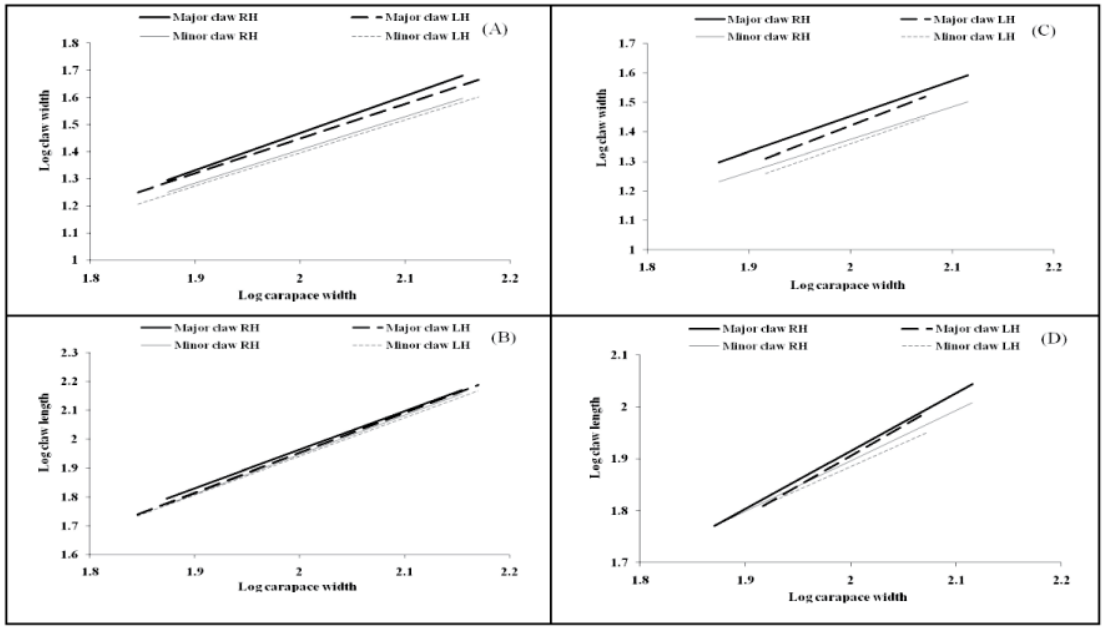

Figure 2. *Charybdis natator.* Comparison of log claw dimensions vs. log carapace width. Each panel displays either claw widths or lengths. The two pairs of bolded represents major claws, the plain pairs are for minor claws. Solid lines are for right-handed crabs, dashed/dotted lines are for left-handed crabs. (A) and (B) males, (C) and (D) females.

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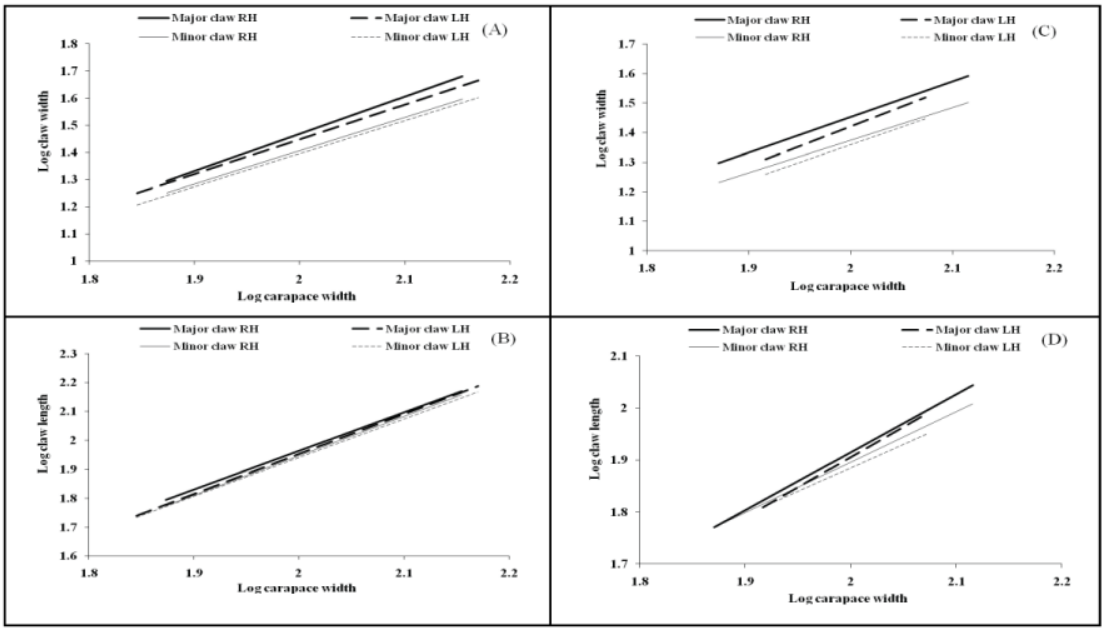

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ISSN: 1687-4285

to be cannibalistic. Marshall, *et al*. (2005) concluded that cannibalism is a widespread trait commonly observed in a wide variety of Crustacea and is frequently a response to limited food or refuge availability for vulnerable prey.

Predominance of right-handed individuals with major crusher claws in the population of *C. natator* could be explained by the need to maximize the biting force exerted on the hard-bodied preys during feeding. Heterochely has been related to the feeding technique. Seed and Hughes (1995) stated that in predatory Brachyura, the presence of the major chela on the right side facilitates handling of asymmetric hard shelled molluscan prey. Elner (1978) explained that when a crab is feeding on a mussel, the shell must be broken open and the flesh then extracted through a narrow opening. Ng and Tan (1985) reported that right handedness is due to the fact that almost all marine gastropod shells are dextral and concluded that Portunids like *Thalamita spinimana*, *Portunus sanguinolentus* and *Charybdis feriata* possess specialized teeth present at the base of the fingers of the major chela which act as peeling structures.

In conclusion, the study demonstrates that handedness appears to be one of the important factors in the determination of the allometric growth of crabs' chelipeds and therefore suggests that it could be considered a part of the morphometric studies of natural crab populations. Further studies on the relationship of this phenomenon with the feeding habit in other portunids are recommended.

References

Abby-Kalio N.J. and Warner, G.F.:1989, Heterochely and handedness in the shore crab *Carcinus maenas* (L.) (Crustacea: Brachyura). *Journal of the Linnean Society of London*, 96:19-26.

Balasubramanian, C.P. and Suseelan, C.: 1998, Natural diet of the deep water crab *Chraybdis smithii* McLeay (Brachyura: Portunidae) of the seas around India. *Indian Journal of Fisheries*, 45(4): 407-411.

Barnwell, F.H.: 1982, The prevalence of male right-handedness in the Indo-West Pacific fiddler crab *Uca vocans* (Linnaeus) and *U. tetragonon* (Herbst) (Decapoda: Ocypodidae). *Journal of Crustacean Biology*, 2: 70-83.

Calverie, T. and Smith, I.P.: 2007, Functional significance of an unusual chela dimorphism in a marine decapod: specialization as a weapon. *Proceedings of the Royal Society*, B. 271, 3033-3038.

Chu, K.H.: 1999, Morphometric analysis and reproductive biology of the crab *Charybdis affinis* (Decapoda: Brachyura: Portunidae) from the Zhujiang Estuary, China. *Crustaceana*, 72 (7) 647 - 658.

Crane, J.: 1975, *Fiddler crabs of the world (Ocypodidae: genus Uca)*, Princeton, NJ: Princeton University Press.

Crothers, J.H.: 1967, The biology of the shore crab *Carcinus maenas* (L.). *Field Studies*, 2: 407-434.

Daniels, S.R.: 2001, Allometric growth, handedness, and morphological variation in *Potamonautes warreni* (Calman, 1918) (Decapoda, Brachyura, Potamaunidae) with a redescription of the species. *Crustaceana*, 74(3): 237-253.

Elner, R.W.: 1978), *The mechanisms of predation by the shore crab, Carcinus maenas (L.), on the edible mussel, Mytilus edulis. L, Oecologia (Berl.)*, 36, Pp. 333-344.

Halry, S.R.: 1969, Relative growth and sexual maturity of the Texas ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). *Crustaceana*, 17: 285-297.

Hamilton, P.V., Nishimoto, R.T., and Halusky, J. G.: 1976, Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). *Biological Bulletin of the Marine Biology Laboratory*, Woods Hole, 150: 393- 401.

Hartnoll, R.G.: 1974, Variation in growth patterns by secondary sexual characters in crabs (Decapoda: Bracyhura). *Crustaceana*, 27(2): 131-136.

Juanes, F.; Lee. K.T.; McKnight, A. and Kellog, K.: 2008, Claw allometry in green crabs, *Carcinus maenas*: heterochely, handedness, sex. *Marine Biology*, 153: 523-528.

Jones, D.S. and George, R.W.: 1982, Handedness in fiddler crabs as an aid in grouping of the genus *Uca* (Decapoda: Ocypodidae). *Crustaceana*, 43: 100-102.

Ladle, R.J. and Todd, P.A.: 2006, A developmental model for predicting handedness frequencies in crabs. *Acta Oecologica*, 30: 283-287

Lee, S.Y. and Seed, R.: 1991, Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series*, 84: 151-160.

Mariappan, P.; Balasundaram, C. and Scmitz, B.: 2000, Decapod crustacean chelipeds: an overview. *Journal of Bioscience*, 25(3): 301-313.

Marshall, S., Warburton, K., Paterson, B. and Mann, D.: 2005, Cannibalism in juvenile blue-swimmer crabs *Portunus pelagicus* (Linnaeus, 1766): Effects of body size, moult stage and refuge availability. *Applied Animal Behavior Science*, 90: 65-82

Mearow, K.M. and Govind, C.K.: 1986, Neuromuscular properties in serially homogenous lobster limbs. *Journal of experimental Zoology*, 239: 197-205.

Negreiros-Fransozo, M. L. and Fransozo, V.: 2003, A morphometric study of the mud crab *Panopeus austrobesus* Williams 1983 (Decapoda, Brachyura) from a subtropical mangrove in South America. *Crustaceana*, 76(3): 281-294.

Ng, P.K.L. and Tan, L.W.H.: 1985, Right handedness in heterochelous calappoid and xanthoid crabs-

suggestion for a functional advantage. *Crustaceana*, 49(1): 98-100.

Pynn, H.J.: 1998, Chela dimorphism and handedness in the shore crab *Carcinus maenas. Field Studies*, 9: 343-353.

Sallam, W.S. and Gab-Alla, A.A.: 2009, Edibility assessment of the swimming crab *Charybdis natator* (Brachyura: Portunidae) from the Gulf of Suez, Red Sea, Egypt. *Egyptian Journal of Aquatic Biology and Fisheries*, 13(1): 43-54.

Seed, R. and Hughes, R.N.: 1995, Criteria for prey size selection in moluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology*, 193: 177-195.

Shih, H.T.; Mok, H.K.; Chang, H.W. and Lee, S.C.: 1999, Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies*, 38: 164-177.

Silva, A.C.; Silva, I.C.; Hawkins, S.J.; Boaventurab, D.M. and Thompson, R.C.: 2010, Cheliped morphological variation of the intertidal crab *Eriphia verrucosa* across shores of differing exposure to wave action. *Journal of Experimental Marine Biology and Ecology*, 39(1-2): 84-91.

Simonson, J.L. and Steele, P.: 1981, Cheliped asymmetry in the stone crabs, *Menippe mercenaria* with notes on claw reversal and regeneration. *Northwest Gulf Science*, 5: 21-30.

Sumpton, W.D.: 1990a, Morphometric growth and fisheries biology of the crab *Charybdis natator*, (Herbst) in Moreton Bay, Australia (Decapoda, Brachyura). *Crustaceana,* 59(2): 113-120.

Trott, T.: 1987, The prevalence of left-handedness in the painted ghost crab *Ocypode gauchaudii* H. Milne Edwards and Lucas (Decapoda, Brachyura, Ocypodidae). *Crustaceana,* 52(2): 213-215.

Versluis, M., Schmitz, B., Von der Heydt, A. and Lohse, D.: 2000, How snapping shrimp snap: through cavitating bubbles. *Science*, 289: 2114-2117.

Warner, G.F., Chapman, D., Hawkey , N. and Waring, D.G.: 1982, Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus meanas* (Crustacea: Brachyura). *Journal of Zoology*, London, 196: 431-438.

Yamada, S.B. and Boulding, E.G.: 1998, Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology*, 220: 191-211.

Yamaguchi, T.: 1994, Studies of the handedness of *Macromedaeus distinguendus* and *Leptodius exaratus* (Brachyura: Xanthidae). *Crustacean Research,* 23: 74-78.

Zar, J.H.: 1984, *Biostatistical analysis*, Prentice Hall International, 718 pages.

ISSN: 1687-4285