Heterochely and handedness in the river crab, Potamon potamios (Olivier, 1804) (Decapoda, Brachyura).

HETEROCHELY AND HANDEDNESS IN THE RIVER CRAB, *POTAMON POTAMIOS* (OLIVIER, 1804) (DECAPODA, BRACHYURA)

BY

MASSIMILIANO SCALICI[1,3]) and FRANCESCA GHERARDI[2])

[1]) Università degli studi "Roma Tre", Dipartimento di Biologia, Viale G. Marconi 446, I-00146 Rome, Italy

[2]) Università degli Studi di Firenze, Dipartimento di Biologia Animale e Genetica "Leo Pardi", Via Romana 17, I-50125 Florence, Italy

Many decapods show asymmetry in the size and shape of their chelae, a phenomenon commonly known as heterochely. This may be related to the diverse functions that the two chelae exert for food acquisition, courtship display, or territorial defence (e.g., Mariappan et al., 2000). The majority of brachyurans are right-handed (e.g., Williams & Heng, 1981; Bartwell, 1982; Ng & Tan, 1985; Abby-Kalio & Warner, 1989), contrary to Hartnoll's (1982) claim that "there is no preference for handedness" in most heterochelous decapods. Heterochely is well documented in freshwater decapods, but, differently from the marine species, they have been poorly analysed until now (Daniels, 2001).

In this study, we investigated heterochely in a population of the freshwater crab, *Potamon potamios* (Olivier, 1804), family Potamidae, a species distributed in the Sinai, the Jordan River system, the Litani River, mainland Greece, the south-eastern Aegean islands, and southern Anatolia (Brandis et al., 2000). We analysed the data collected during the summer of 1988 by Gherardi & Micheli (1989) on 139 females and 148 males from a population on the western shore of the Dead Sea. Crabs were sexed, and the length (CL) and width (CW) of the carapace, together with the length (ChL), width (ChW), and height (ChH) of the two chelae, were measured using Vernier callipers. Of the 287 crabs examined, 75.3% were right-handed (R) and the remaining 24.7% were left-handed (L), without a significant difference between sexes ($\chi^2 = 3.16$, df $= 127$, $P > 0.05$). Relative frequencies of R and L individuals per size class are shown in fig. 1. The percentage of L individuals significantly increased with CL in females (Spearman test: $r_s = 0.74$, $t = 2.14$, df $= 29$, $P = 0.039$), in males ($r_s = 0.66$, $t = 2.32$, df $= 39$, $P = 0.047$), and in the whole population ($r_s = 0.71$, $t = 2.28$, $P = 0.037$).

[3]) Author for correspondence; Fax: +39.655176321; e-mail: scalici@uniroma3.it

Crustaceana 81 (4): 507-511
Also available online: www.brill.nl/cr

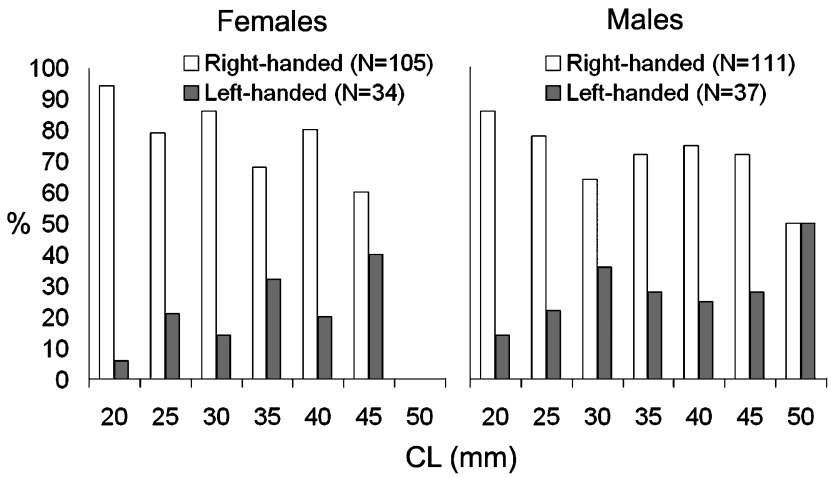

Fig. 1. Percentage of left- and right-handed *Potamon potamios* (Olivier, 1804) per size class (each of 5 mm carapace length (CL) interval) in the two sexes.

We compared ChW of the larger chela for each size class between R and L individuals of both sexes and found significant or nearly significant differences (table I). In contrast, such a comparison for ChL and ChH of the larger chela and for all measures of the smaller chela did not lead to significant values. Neither did we find any significant difference between similar-sized individuals of the two sexes (t-test, P always >0.05, for both chelae).

Our results are clear in showing that *P. potamios* is heterochelous, independent of its sex, and that it is most often right-handed (cf. Pretzmann, 1971). The usual explanation for the possession of an enlarged cheliped in freshwater crabs is its specialized role during feeding (Daniels, 2001). The faster growth of one chela has

TABLE I

Larger chela width: comparison between right- and left-handedness of *Potamon potamios* (Olivier, 1804) for both sexes after Student's t-test (significant values in **bold**); "–" means 0 individuals; CL, carapace length

CL (mm)	Right-handed vs. left-handed					
	Females			Males		
	t	df	*P*	t	df	*P*
<29	**3.61**	**20**	**0.0006**	**2.39**	**20**	**0.026**
30-35	1.02	13	0.053	1.06	13	0.054
36-40	0.061	11	0.064	**2.48**	**20**	**0.022**
41-45	**3.93**	**19**	**0.009**	**3.49**	**11**	**0.024**
46-50	–	–	–	**0.84**	**8**	**0.048**
51-55	–	–	–	0.24	8	0.061

also been related to its wider use during fighting (Vannini et al., 1983), the larger chela acting as an effective weapon for the acquisition of resources (e.g., burrows; Raubenheimer, 1986), the defence of hatchlings (Liu & Li, 2000), or the access to females (Cornew, 1990; Daniels, 2001). The role of heterochely in intersexual selection is poorly known in freshwater decapods and, when investigated, it has been questioned (Aquiloni & Gherardi, 2007; cf. Oliviera & Custodio, 1998 for fiddler crabs). Neither is there evidence of whether heterochely and handedness in *P. potamios* are the result of genetic predisposition as suggested for *Carcinus maenas* (Linnaeus, 1758) (cf. Ladle & Todd, 2006), or of preferential use of either of the two chelae during the larval or juvenile phase, as found in *Cancer productus* Randall, 1839 (cf. Smith & Palmer, 1994).

When *P. potamios*' size classes were analysed separately, the frequency of left-handed individuals was found to increase with body size, ranging from 10% to 40 and 50% in females and males, respectively. These are relatively high values, considering that usually the frequency of left-handed individuals in freshwater crabs does not exceed 10%, e.g., in *Potamon gedrosianum* Alcock, 1909 (cf. Schneider, 1971); in *Geotelphusa dehaani* (White, 1852) (cf. Yagamuchi & Takamatsu, 1980); in *P. fluviatile* (Herbst, 1785) (cf. Gherardi et al., 1987). Higher frequencies were only found in the Potamonautidae (see Daniels, 2001) but data are not sufficient to allow for a comparison between that family and the Potamidae.

The frequency of handedness reversal (in the form of the crusher being replaced by a cutter) seems to increase with growth in *P. potamios*, as a possible consequence of bigger, and presumably older crabs losing the larger chela more likely than the smaller ones (see Lewis, 1969). In other decapods, handedness reversal takes place 3-4 moults after the loss of the larger chela (Sardà, 1983; Simonson, 1985) and the populations are characterized by the presence of individuals with unusually small chelae (Takeda & Yamaguchi, 1973; Cheung, 1979; Govind & Blundon, 1985). In the population of *P. potamios* analysed no homochelous crab or crab with irregular or small chelae was found, but handedness was recognized even in individuals with regenerated chelipeds. It has often been said that crabs regenerate the lost chela after a single moult; however, no clear evidence for this assumption exists in the literature for either marine, or freshwater species. Therefore, it seems unlikely the observed heterochely could be referred to a reversal event. In some cases, handedness reversal was assumed to occur when size ratio between the two chelae was particularly high [e.g., 94 : 6 in *Potamonautes depressus depressus* (Krauss, 1843), 71 : 29 in *Potamonautes sidney* (Rathbun, 1904), 58 : 42 in *Potamonautes brincki* Stewart, 1997 females: see Daniels, 2001]. However, analyses of both size and shape of the chelae in hatchlings, together with records of reversed handedness during ontogeny (in *Necora puber* (Linnaeus, 1767), cf. Norman & Jones, 1991), seem more informative to solve this issue.

The increased frequency of left-handed *P. potamios* individuals with growth requires additional explanations. We may hypothesize that right-handed crabs are more often preyed upon than left-handed ones, simply because they are more frequent in the population. In fact, left-handed juveniles accounted for no more than 10% of the population, and this might reduce their likelihood of being preyed upon. Alternatively, for unknown reasons, left-handed crabs might increase their ability to survive during growth.

Additional studies are obviously needed to answer the questions here addressed about the proximate and ultimate causes of heterochely in freshwater crabs, and of their putative reversal of handedness.

REFERENCES

ABBY-KALIO, N. J. & G. F. WARNER, 1989. Heterochely and handedness in the shore crab *Carcinus maenas* (L.) (Crustacea: Brachyura). Zool. Journ. Linn. Soc., London, **96**: 19-26.

AQUILONI, L. & F. GHERARDI, 2007. Mutual mate choice in crayfish: large body size is selected by both sexes, virginity by males only. Journ. Zool., London, (in press).

BARTWELL, F. H., 1982. The prevalence of male right-handedness in the Indo-west Pacific fiddler crabs *Uca vocans* (Linnaeus) and *U. tetragonon* (Herbst) (Decapoda: Ocypodidae). Journ. Crustacean Biol., **21**: 70-83.

BOTT, R., 1967. Potamidae (Crustacea, Decapoda) aus Afghanistan, Westasien und dem Mittelmeerraum (eine Revision der Untergattung *Potamon* s. str.). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, **130**: 7-13.

BRANDIS, D., V. STORCH & M. TÜRKAY, 2000. Taxonomy and zoogeography of the freshwater crabs of Europe, North Africa, and the Middle East. Senckenbergiana Biologica, **80**: 5-56.

CORNEW, S., 1990. Aspects of the biology of the Cape River crab *Potamonautes perlatus* (M. Edw.) with particular reference to feeding biology: 1-27. (B.Sc. (Hons.) Thesis, University of Cape Town, Cape Town).

CHEUNG, T. S., 1979. A biostatistical study of the functional consistency in the reversed claws of the adult male stone crab, *Menippe mercenaria* (Say). Crustaceana, **31**: 137-144.

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

GHERARDI, F., S. GUIDI & M. VANNINI, 1987. Behavioural ecology of the freshwater crab, *Potamon fluviatile*: preliminary observations. Invest. Pesq., Barcelona, **51**: 389-402.

GHERARDI, F. & F. MICHELI, 1989. Relative growth and population structure of the freshwater crab, *Potamon potamios palestinensis*, in the Dead Sea area (Israel). Israel Journ. Zool., **36**: 133-145.

GOVIND, C. K. & J. A. BLUNDON, 1985. Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. Biol. Bull., Woods Hole, **168**: 321-331.

HARTNOLL, R. G., 1982. Growth. In: L. G. ABELE, The biology of Crustaecea, **2**, Embryology, morphology and genetics: 111-196. (Academic Press, New York).

LADLE, R. J. & P. A. TODD, 2006. A developmental model for predicting handedness frequencies in crabs. Acta Oecol., **30**: 283-287.

LEWIS, J. E., 1969. Reversal of asymmetry of chelae in *Calappa* Weber, 1795 (Decapoda: Oxystomata). Proc. Biol. Soc., Washington, **82**: 63-80.

LIU, H. & C. LI, 2000. Reproduction in the freshwater crab *Candidiopotamon rathbunae* (Brachyura: Potamidae) in Taiwan. Journ. Crustacean Biol., **20**: 88-99.

MARIAPPAN, P., C. BALASUNDARAM & B. SCHMITS, 2000. Decapod crustacean chelipeds: an overview. Journ. Biosci., **25**: 301-313.

NG, P. K. L. & L. W. H. TAN, 1985. "Right handedness" in the heterochelous calappoid and xanthid crabs, suggestion for functional advantages. Crustaceana, **49**: 98-100.

NORMAN, C. P. & M. B. JONES, 1991. Limb loss and its effect on handedness and growth in the velvet swimming crab *Necora puber* (Brachyura: Portunidae). Journ. nat. Hist., London, **25**: 639-645.

OLIVIERA, R. F. & M. R. CUSTODIO, 1998. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. Ethol. Ecol. Evol., **10**: 241-251.

PRETZMANN, G., 1971. Ergebnisse einiger Sammelreisen nach Vorderasien, I. Teil: Zwei neue Unterarten von Süßwasserkrabben. Ann. Naturhistor. Mus., Wien, **75**: 473-475.

RAUBENHEIMER, C. D., 1986. Aspects of the biology of the freshwater crab, *Potamonautes sidneyi*, with particular reference to general seasonality and female aggression: 1-97. (M.Sc. Thesis, University of Natal, Durban).

SARDÀ, F., 1983. El proceso de la regeneraciòn de quelas en la cigala *Nephrops norvegicus* (L.). Inv. Pesq., Barcelona, **47**: 113-123.

SCHNEIDER, P., 1971. Zur Biologie der Afghanischen Flusskrabbe *Potamon gedrosianum*. I. Lebensweise, Verbreitung, Morphologie und systematische Stellung. Bonner Zoologische Beiträge, **22**: 305-321.

SIMONSON, J. L., 1985. Reversal of handedness, growth, and claw stridulatory patterns in the stone crab *Menippe mercenaria* (Say) (Crustacea: Xanthidae). Journ. Crustacean Biol., **5**: 281-293.

TAKEDA, M. & T. YAMAGUCHI, 1973. Occurrence of abnormal males in a fiddler crab, *Uca marionis* (Desmarest), with notes on asymmetry of chelipeds. Proc. Japanese Soc. syst. Zool., **9**: 13-20.

VANNINI, M., F. GHERARDI & M. PIRILLO, 1983. Aggressive communication in *Potamon fluviatile*: role of size, color and other visual cues. Crustaceana, **45**: 203-209.

WILLIAMS, M. J. & P. K. HENG, 1981. Handedness in males of *Uca vocans* (Linnaeus, 1758) (Decapoda, Ocypodidae). Crustaceana, **40**: 215-216.

YAMAGUCHI, T. & M. TAKAMATSU, 1980. Ecological and morphological studies on the Japanese freshwater crab, *Geotelphusa dehaani*. Journ. Sci. Biol., Kumanoto, **15**: 1-27.

First received 22 May 2007.
Final version accepted 10 September 2007.