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

BY

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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 ( $r_s = 0.71$ ,  $t = 2.28$ ,  $P = 0.037$ ).

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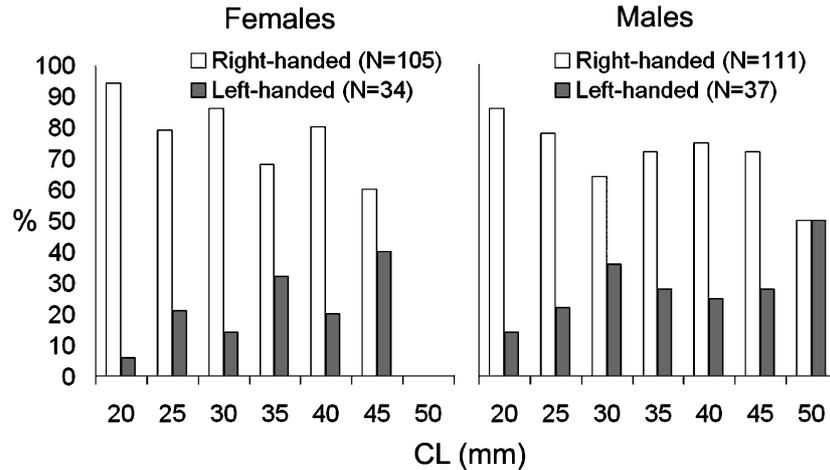


Fig. 1. Percentage of left- and right-handed *Potamon potamios* (Olivier, 1804) per size class (each of 5 mm carapace length (CL) interval) in the two sexes.

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	<b>3.61</b>	<b>20</b>	<b>0.0006</b>	<b>2.39</b>	<b>20</b>	<b>0.026</b>
30-35	1.02	13	0.053	1.06	13	0.054
36-40	0.061	11	0.064	<b>2.48</b>	<b>20</b>	<b>0.022</b>
41-45	<b>3.93</b>	<b>19</b>	<b>0.009</b>	<b>3.49</b>	<b>11</b>	<b>0.024</b>
46-50	—	—	—	<b>0.84</b>	<b>8</b>	<b>0.048</b>
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.

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