Mar Biol (2008) 153:523–528
DOI 10.1007/s00227-007-0826-6

RESEARCH ARTICLE

Claw allometry in green crabs, *Carcinus maenas*: heterochely, handedness, and sex

F. Juanes · K. T. Lee · A. McKnight · K. Kellogg

Received: 29 May 2007 / Accepted: 18 September 2007 / Published online: 13 October 2007

Abstract Claw loss and reversal of handedness during regeneration are common phenomena in heterochelous decapod crustaceans, which typically have one large 'crusher' claw on the right side and a smaller 'cutter' claw on the left. Little is known about the relative importance of claw growth vs. body growth during claw regeneration. Here the relationship between claw size and body size of green crabs, *Carcinus maenas*, was examined to test for differences in claw allometry as a function of handedness and sex, as there are differences in how males and females use their claws. A total of 730 crabs (range = 15.7–83.6 mm CW) were collected from Maine to New Jersey, USA from May to October 1997, 2000, and 2004–2005. Claw growth, particularly crushers, was accelerated in left-handed crabs and in males compared to right-handed crabs and females respectively. These differing growth strategies highlight the role of sexual dimorphism in claw usage and the importance of achieving heterochely after claw injury. These results imply that handedness should be an important factor to consider in future studies of crab morphology, behavior, and morphometrics.

Communicated by J.P. Grassle.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-007-0826-6) contains supplementary material, which is available to authorized users.

F. Juanes (✉) · A. McKnight
Department of Natural Resources Conservation,
University of Massachusetts, Amherst, MA 01003, USA
e-mail: juanes@nrc.umass.edu

K. T. Lee
Department of Biology,
University of Pittsburgh at Johnstown, Johnstown,
PA 15904, USA

K. Kellogg
Environmental Studies Program, Skidmore College,
Saratoga Springs, NY 12866, USA

Introduction

Claw loss is common among crustacean species in the wild (Juanes and Smith 1995; Mariappan et al. 2000). Because limb loss, and particularly claw loss, has important consequences for growth and survival, most crustaceans can regenerate lost limbs (see review in Juanes and Smith 1995). In most heterochelous decapod crustaceans, the larger crusher (or major) claw originally develops only on the right side of the body (Hamilton et al. 1976; Simonson and Steele 1981; Abelló 1990; Mariappan et al. 2000; Daniels 2001). Loss of this major claw leads to 'reverse handedness' whereby over several molts, the cutter (or minor claw) on the left side becomes a crusher and the regenerated claw emerges as a cutter claw. The crab thus becomes 'left-handed' (Przibam 1931; Cheung 1976; Hamilton et al. 1976; Vermeij 1977; Simonson 1985). Przibam (1931) suggested that this process represents the fastest, least energetically expensive way to return to the heterochelous condition.

Both body size and claw size have been suggested as important to survival and reproductive success (Lee and Seed 1992; Sneddon et al. 1997), and because regeneration can have a cost to growth (termed 'regenerative load' by Skinner 1985) and survival (Juanes and Smith 1995), crabs recovering from autotomy through cheliped reversal could respond in at least two ways: accelerate claw growth to achieve 'normal' heterochely as soon as possible, or minimize the cost of regeneration by maximizing body growth instead of claw growth which would lead to large body sizes with relatively small claws. Abby-Kalio and Warner (1989) examined differences in claw allometry between left-handed and right-handed male green crabs, *Carcinus maenas*. They found that left-handed crabs always exhibited slower claw growth than right-handers suggesting that body size was being maximized by left-handed individuals.

Here, we examine claw allometry of green crabs using a larger sample and a larger range of body sizes than Abby-Kalio and Warner (1989) used, and we include females to test for differences in claw growth strategies as a function of handedness and sex. Differences in claw growth between right-handed and left-handed individuals would emphasize the relative importance of achieving 'normal' heterochely vs. continued body growth after claw loss.

Materials and methods

We collected crabs by "chumming" (attracting crabs using dead menhaden as bait, then collecting them by hand) or in baited pipe traps at coastal locations in Maine (Cobscook Bay [44°54′N, 67°03′W], Wells National Estuarine Research Reserve [43°20′N, 70°33′W]), New Hampshire (Rye Beach [42°58′N, 70°45′W], Hampton Beach [42°54′N, 70°48′W]), Connecticut (Pleasure Beach [41°18′N, 72°08′W]) and New Jersey (Tuckerton, [39°36′N, 74°20′W]), USA from May to October in 1997, 2000 and 2004–2005. We sexed and measured all crabs. Measurements included: carapace width (CW, distance between the two most distal carapace spines), crusher height (maximum height of the propodus), crusher length (maximum length of the propodus), cutter height, and cutter length all in mm (±1 mm). Crabs with fully formed (i.e. not in transition or newly regenerated) left crusher claws were designated left-handed, those with fully formed right crusher claws right-handed. Crabs just beginning to undergo reversal and crabs with indeterminate handedness were removed from the analysis.

We log-transformed all measurements to satisfy regression assumptions and generated regressions of each claw dimension on carapace width for both right-handed and left-handed males and females. To test for unequal allometric relationships due to handedness, we compared the slopes and elevations of the regressions for right-handed vs. left-handed males and females separately using ANCOVA. Steeper slopes in the left-handed claw relationship would imply the importance of achieving heterochely after claw loss, whereas faster growth in the right-handed claw relationship would suggest that body growth is more important than relative claw growth. Similarity in slopes would imply that claw growth and body growth are equally important and therefore accelerated claw growth is not strongly selected for. We tested for differences in claw growth between sexes to assess the influence of sexual dimorphism by making similar comparisons of claw dimension on body size using ANCOVA, i.e. by comparing slopes and elevations of right-handed males vs. females, and left-handed males vs. females.

Smith (2004) found a latitudinal effect in crusher claw size (but not cutter-claws) in right-handed male green crabs with southern individuals (collected in Connecticut, USA) exhibiting larger claws than those collected in the northern site (Maine, USA). Here we assessed potential latitudinal effects by comparing slopes and intercepts of male and female right-handed crabs among our six sites from Maine to New Jersey. We restricted the geographical analysis to right-handed crabs as the sample size of left-handed individuals was too small for this analysis.

Results

We collected a total of 730 crabs, 337 males (range = 17.1–83.6 mm CW) and 393 females (range = 15.7–68.0 mm CW). Overall, males were larger than females (mean CW = 52.4 vs. 46.8 mm, $F = 44.015$, $P < 0.0001$), and left-handed crabs larger than right-handed crabs (53.28 vs. 50.31, $F = 11.7574$, $P = 0.0006$). Both left-handed and right-handed males were larger than females (for left-handers: 56.9 vs. 47.9 mm, $F = 26.03$, $P < 0.0001$; for right-handers: 51.1 vs. 46.5 mm, $F = 23.92$, $P < 0.0001$).

Slopes of the claw dimension to body size relationships for left-handed individuals were consistently steeper than for right-handed individuals for both male and female crabs (Appendix 1, Fig. 1), indicating accelerated claw growth with respect to body size in individuals regenerating missing limbs. All comparisons involving claw heights were significant, whereas only one claw length comparison was significant (Table 1). When slopes were the same, ANCOVA results showed that cutter lengths had higher elevations for both right-handed female and male crabs than their left-handed counterparts (Table 1). In contrast, crusher lengths in males showed no differences in elevation between right- and left-handed individuals ($P = 0.3598$).

Comparisons between sexes showed that for right-handers, males always exhibited steeper slopes than females for all claw dimensions with respect to carapace width (all $P < 0.0001$), whereas for left-handers only crusher height and length were larger in males than in females (Table 2). Slopes of cutter height and length in left-handed crabs were not significantly different between males and females, although males did have the higher elevations (all $P < 0.005$, Table 2).

There were no consistent differences among sampling locations (results not shown). Although we found significant differences in crusher height for males and females,

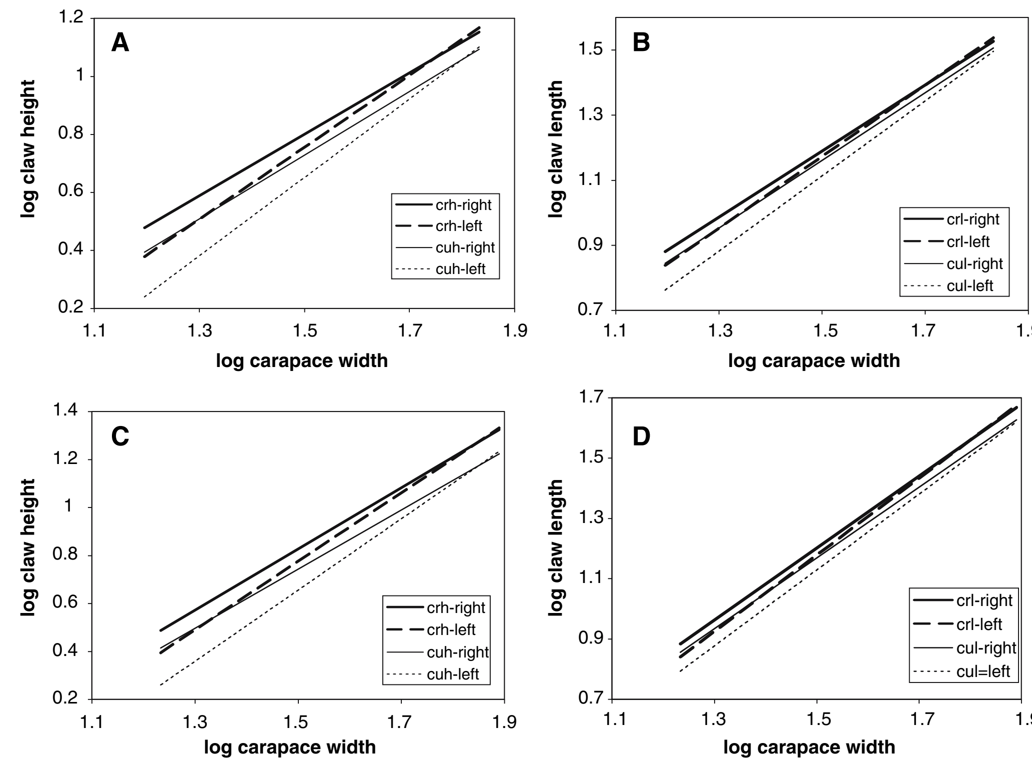

Fig. 1 *Carcinus maenas*. Comparison of log claw dimensions vs. log carapace width. Each panel displays either claw heights or lengths. The top pair of lines (*bolded*) represents crusher (major) claws, bottom pair are cutter (minor) claws. *Solid lines* are for right-handed crabs, *dashed/dotted lines* are for left-handed crabs. Only regression lines are displayed, see Appendix 1 for regression statistics. **a** and **b** females, **c** and **d** males. *crh* crusher height, *cuh* cutter height, *crl* crusher length, and *cul* cutter length

Table 1 *Carcinus maenas*. ANCOVA results for the comparison of the four claw dimensions on carapace width between right-handed and left-handed crabs analyzed separately for males and females

	Slopes		Elevations	
	F-ratio	*P*	*F*-ratio	*P*
Males				
Crusher height	6.2825	0.0127*		
Crusher length	2.8349	0.0932	0.8409	0.3598
Cutter height	14.8758	<0.0001*		
Cutter length	1.9553	0.1629	8.3876^{r}	0.004*
Females				
Crusher height	14.7635	<0.0001*		
Crusher length	4.2340	0.0403*		
Cutter height	18.3741	<0.0001*		
Cutter length	3.8236	0.0512	26.1952^{r}	<0.0001*

* indicates a significant difference. When elevations were significantly different, directionality is indicated by the superscript: *r* if right-handed individuals had higher elevations, or *l* if left-handed individuals had higher elevations

Table 2 *Carcinus maenas*. ANCOVA results for comparisons of regressions of four claw dimensions on carapace width between males and females

	Slopes		Elevations	
	F-ratio	*P*	*F*-ratio	*P*
Right-handed crabs				
Crusher height	49.6564	<0.0001*		
Crusher length	51.4879	<0.0001*		
Cutter height	16.8606	<0.0001*		
Cutter length	21.9266	<0.0001*		
Left-handed crabs				
Crusher height	6.5439	0.0115*		
Crusher length	12.9734	0.0004*		
Cutter height	1.5530	0.2147	7.8987^{m}	0.0056*
Cutter length	0.9035	0.3454	10.4470^{m}	0.0015*

* indicates a significant difference. When elevations were significantly different, directionality is indicated by the subscript: *m* if males had higher elevations, or *f* if females had higher elevations

and cutter height for females among locations, the differences were not in the predicted latitudinal pattern with larger claws in the south (Smith 2004). Instead we found that in males the largest claws were found both in the southern (New Jersey) and northern sites (Maine) with smaller values in the intermediate locations (New Hampshire, Connecticut). For female crusher heights, the highest slopes were in Connecticut and the smallest in New Hampshire.

For female cutter heights, the largest slope was also in Connecticut and the smallest in New Jersey.

Discussion

Using a large sample of green crabs collected over several years, we found consistent differences in the claw allometries of male and female crabs as well as between right-handed and left-handed individuals suggesting different claw growth strategies. The relative importance of claw growth vs. body growth after cheliped autotomy depended on handedness, claw type (crusher vs. cutter) and sex. In contrast, latitude did not have consistent effects on claw allometries likely because we used collections along a broader latitudinal extent than in previous studies (Smith 2004).

Both male and female left-handed individuals showed accelerated allometric growth in both crusher and cutter heights and lengths compared to right-handed individuals with exceptions only in claw length regressions, particularly in males. These results are in contrast to those of Abby-Kalio and Warner (1989) who found that for both claws and all dimensions (they included 2 additional ones: dactylus length and height), slopes were significantly higher for right-handed crabs. This may have been an effect of sample size, as they had smaller sample sizes than we did (157 right-handed males, 50 left-handed males), or more likely body size range, as they focused on substantially larger individuals than we did (range: 63–88 mm for LH and 55–95 for RH) which correspond to the areas where the lines converged (Fig. 1). They also did not examine females. In contrast, in a study examining claw allometry in the genus *Uca*, Rosenberg (2002) found steeper allometric slopes in regenerated claws compared to unregenerated claws.

These results suggest that handedness has an influence on claw growth relative to body growth. Because we selected individuals that had fully formed functionally heterochelous claws our results likely pertain to growth over many molt cycles (Crothers 1967). The accelerated claw growth relative to carapace width in left-handed crabs compared to right-handed crabs suggests an attempt to recover the heterochelous condition as quickly as possible. Our results show that left-handed crabs become fully heterochelous by the time they reach their maximum carapace width (i.e., left-handed and right-handed claw sizes intersect at the largest carapace widths, Fig. 1), likely also their terminal molt (Crothers 1967). Figure 1 also portrays how left handed crusher claws begin allometrically as cutter claws in right-handed individuals before the process of reversal is complete (i.e. both left crusher and right cutter claws intersect at the smallest carapace widths).

Achieving 'normal' allometric heterochely, however, may not result in complete functional recovery. In blue crabs (*Callinectes sapidus*), left crushers were always weaker and than right crushers at similar body sizes (Govind and Blundon 1985). Similarly, in red rock crabs (*Cancer productus*), a homochelous species, regenerating chelae were less powerful than first growth claws (Brock and Smith 1998). Although regenerated claws may never attain the biting strength of equally-sized intact claws, attaining the largest chela possible after autotomy is still advantageous (Lee and Seed 1992; Sneddon et al. 1997), especially if claws are used as signals. For example, Backwell et al. (2000) suggested that the faster growth of regenerated claws in *Uca annulipes* functioned as a dishonest signal, allowing crabs to bluff opponents and females into responding as if they had stronger unregenerated claws thus avoiding fights and increasing potential mating opportunities. Because *U. annulipes* populations, like most *Uca* crabs, have equal proportions of right- and left-handed individuals, handedness itself would not be an honest signal. To our knowledge, a similar experiment examining signalling in left- vs. right-handed crabs in species with a dominant handedness has not been performed.

In addition to signalling, large claw size confers a number of advantages to crabs, and particularly to male crabs. Previous work on green crabs has shown that larger claw sizes allow crabs to exploit a wider range of prey sizes (Elner 1980), and benefit males in aggressive competition for females during the mating season (Jivoff 1997). Similarly, claw height is a better indicator of claw strength than body size (Lee 1993), and claw length is a better predictor of the outcome of aggressive encounters between green crabs than body size, and the number of visual displays is greater in crabs with longer claws (Sneddon et al. 1997).

These advantages may strongly select for crabs, particularly injured crabs, to accelerate claw growth. We also expect stronger selection for regeneration of crushers (or major claws) than cutters (or minor claws) as they generally have the greater crushing force (Schenk and Wainwright 2001; Mitchell et al. 2003), are lost more often in green crabs (Abelló et al. 1994), and are most important in signalling and sexual selection (Lee 1995; Backwell et al. 2000; Mariappan et al. 2000). The relaxed selection for accelerated growth of cutter claws likely explains the majority of non-significant results involving cutter claws (no differences in cutter length slopes in males and females, and lack of difference in cutter length and height slopes between left-handed males and females), and the consistently lower r^2 in cutter claw regressions especially in left-handers (only $r^2 < 0.90$). Abby-Kalio and Warner (1989) with green crabs, and Cheung (1976) with stone crabs, *Menippe mercenaria*, also found that minor claws were generally more variable especially in left-handed individuals.

Crabs with one or more regenerating chelae, common in most crab populations (Juanes and Smith 1995), suffer a number of disadvantages. Smaller claw size or missing claws generally leads to reduced foraging efficiency (Elner 1980; Juanes and Hartwick 1990; Smith and Hines 1991; Brock and Smith 1998; but see Mathews et al. 1999) and decreased energy intake (Hartnoll 1982). Reduced energy accumulation can decrease growth increment as well as lengthen intermolt duration in crustaceans (Hartnoll 1982; Skinner 1985). Males with chela loss are found relatively less often in mating pairs and have lower mating success in lab experiments (Abelló et al. 1994). At its worst, claw loss can affect survival, as Figiel and Miller (1995) found in the crayfish *Procambarus clarkii.* Interestingly, Brock and Smith (1998) found that reduced claw efficiency was not restricted to the regenerating claw, but was also evident in the surviving claw.

In response to the severe costs of claw injury, most crabs have developed the ability to regenerate claws, but regenerating chelae may present additional growth costs (Juanes and Smith 1995). For example, Savage and Sullivan (1978) showed that injured stone crabs (*Menippe mercenaria*) allocate more energy into claw growth than uninjured counterparts. Thus claw growth can be achieved through slowed body growth. If larger body size confers an advantage, as during mating (Reid et al. 1994), a left-handed male could be at a corresponding disadvantage compared to a right-handed male of the same age. However, because claw size may be a more significant predictor of success in aggressive encounters (Lee and Seed 1992; Sneddon et al. 1997), an increased rate of crusher growth compared to body size would be advantageous. The differences in claw growth we measured between right- and left-handed individuals in both sexes (except for cutter measurements) suggest that increased claw growth of left-handers is not at the expense of body growth. However, because we cannot age crabs and therefore do not have an individual growth history, we cannot determine how long any individual took to reach maximum size. It is possible that because of regenerative costs, left-handed crabs molted more often, with relatively smaller increases in size, and may have taken longer to reach the observed maximum size. A carefully conducted laboratory experiment could quantify differences in growth allocation strategies of claw dimensions, carapace width, and instar duration between right-handed and left-handed individuals.

When comparing the sexes we found that males generally showed higher allometric claw growth than females, with the exception of cutter claws where slopes were the same but elevations were higher in males. These results are not unexpected as male crabs of many species, including green crabs, generally allocate more energy to claw growth resulting in marked sexual dimorphism in claw size/body size ratios (e.g. Crothers 1967; Mariappan et al. 2000; Daniels et al. 2001; Schenk and Wainwright 2001; Mitchell et al. 2003; Smith 2004). Males and females face different ecological trade-offs with respect to claw growth. For example, large claws, especially crushers, are a great advantage to males during mating season (Lee and Seed 1992; Abelló et al. 1994; Mariappan et al. 2000). For females, allocating energy to egg production and care may be more important than allocating energy to increasing claw size (all the females we collected, and most of the males, were beyond the size at maturity, see Crothers 1967). Female strategy may be directed more toward accumulating energy reserves for the egg-bearing period, when mechanical constraints may limit foraging success (K. T. Lee et al., unpublished data).

In conclusion, we have found that handedness is an important factor in determining claw allometric growth and that heterochely may be strongly selected for. These results suggest that in addition to interspecific (Rosenberg 2002) and regional (Smith 2004) factors, consideration of the effect of handedness should be a part of any morphological, behavioral, or morphometric study of natural crab populations, especially those with large frequencies of injury and autotomy. For example, a recent study used observed autotomy frequencies to predict the proportion of left-handed individuals of two crab species (Ladle and Todd 2006). The model underestimated the proportion of left-handed adult green crabs suggesting that there may be trade-offs between the advantages of heterochely and the disadvantages of being left-handed (Ng and Tan 1985; Shigemiya 2003).

Acknowledgments This project was funded in part by the Richard Cronin Fisheries Research Fund and the Woods Hole Scholarship Fund from the University of Massachusetts, by a Cooperative State Research, Extension, and Education Service, U.S. Department of Agriculture, MA Agricultural Experiment Station Hatch grant, and by a University of Pittsburgh at Johnstown Research Council Small Grant. We thank Connecticut College for use of space and equipment, Normandeau Associates for help with crab collections, and Rutgers University Marine Field Station, Suffolk University Friedman Field Station, and Wells National Estuarine Research Reserve for access to lab space and field sites. Writing was completed while the senior author was a Center Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California. We thank LD Smith for a thorough review of the manuscript and his insightful comments, as well as three anonymous reviewers, all of whom helped in producing a better manuscript.

References

Abby-Kalio NJ, Warner GF (1989) Heterochely and handedness in the shore crab *Carcinus maenas* (L.) (Crustacea: Brachyura). Zool J Linn Soc 96:19–26

Abelló P, Pertierra JR, Reid DG (1990) Sexual dimorphism, relative growth and handedness in *Liocarcinus depurator* and *Macropipus tuberculatus* (Brachyura: Portunidae). Sci Mar 54:195–202

Abelló P, Warman CG, Reid DG, Naylor E (1994) Chela loss in the shore crab *Carcinus maenas* (Crustacea: Brachyura) and its effect on mating success. Mar Biol 121:247–252

Backwell PRY, Christy JH, Telford SR, Jennions MD, Passmore NI (2000) Dishonest signalling in a fiddler crab. Proc R Soc Lond B 267:719–724

Brock RA, Smith DL (1998) Recovery of claw size and function following autotomy in *Cancer productus* (Decapoda: Brachyura). Biol Bull 194:53–62

Cheung TS (1976) A biostatistical study of the functional consistency in the reversed claws of the adult male stone crab, *Menippe mercenaria* (Say). Crustaceana 31:137–144

Crothers JH (1967) The biology of the shore crab *Carcinus maenas* (L.). I. The background—anatomy, growth and life history. Field Stud 2:407–434

Daniels SR (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

Elner RW (1980) The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). Mar Behav Physiol 7:15–24

Figiel CR, Miller GL (1995) The frequency of chelae autotomy and its influence on the growth and survival of crayfish *Procambarus clarkii* (Girard, 1852) (Decapoda, Cambaridae). Crustaceana 68:472–483

Govind CK, Blundon JA (1985) Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. Biol Bull 168:321–331

Hamilton PV, Nishimoto RT, Halusky JG (1976) Cheliped laterality in *Callinectes sapidus* (Crustacea: Portunidae). Biol Bull 150:393–401

Hartnoll RG (1982) Growth. In: Abele LG (ed) The biology of Crustacea. Embryology, morphology, and genetics, vol 2. Academic, NY, pp 111–119

Jivoff P (1997) Sexual competition among male blue crab, *Callinectes sapidus*. Biol Bull 193:368–380

Juanes F, Hartwick EB (1990) Prey size selection in Dungeness crabs: the effect of claw damage. Ecology 71:744–758

Juanes F, Smith LD (1995) The ecological consequences of limb loss and damage in decapod crustaceans: a review and prospectus. J Exp Mar Biol Ecol 193:197–223

Ladle RJ, Todd PA (2006) A developmental model for predicting handedness frequencies in crabs. Acta Oecologica 30:283–287

Lee SY (1993) Chela height is an acceptable indicator of chela strength in *Carcinus maenas* (Linnaeus, 1758) (Decapoda: Brachyura). Crustaceana 65:115–116

Lee SY (1995) Cheliped size and structure: the evolution of a multi-functional decapod organ. J Exp Mar Biol Ecol 193:161–176

Lee SY, Seed R (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. Mar Ecol Prog Ser 84:151–160

Mariappan P, Balasundaram C, Schmitz B (2000) Decapod crustacean chelipeds: an overview. J Biosci 25:301–313

Mathews LM, McKnight AE, Avery R, Lee KT (1999) Incidence of autotomy in New England populations of green crabs, *Carcinus maenas*, and an examination of the effect of claw autotomy on diet. J Crust Biol 19:713–719

Mitchell SC, Kennedy SM, Williams PJ, DeMont ME (2003) Morphometrics and estimates of force generation by the chelae of a North American population of the invasive green crab, *Carcinus maenas* (L.). Can J Zool 81:203–215

Ng PKL, Tan LWH (1985) 'Right handedness' in heterochelous calappoid and xanthoid crabs—suggestion for a functional advantage. Crustaceana 49:98–100

Przibram H (1931) Connecting laws in animal morphology. University of London Press, London

Reid DG, Abelló P, Warman CG, Naylor E (1994) Size-related mating success in the shore crab *Carcinus maenas* (Crustacea: Brachyura). J Zool 232:397–407

Rosenberg MS (2002) Fiddler crab claw shape variation: a geometric morphometric analysis across the genus *Uca* (Crustacea: Brachyura: Ocypodidae). Biol J Linn Soc 75:147–162

Savage T, Sullivan JR (1978) Growth and regeneration of the stone crab, *Menippe mercenaria*. Fla Mar Res Publ 32:1–23

Schenk SC, Wainwright PC (2001) Dimorphism and the functional basis of claw strength in six brachyuran crabs. J Zool 255:105–119

Shigemiya Y (2003) Does the handedness of the pebble crab *Eriphia smithii* influence its attack success on two dextral snail species? J Zool 260:259–265

Simonson JL (1985) Reversal of handedness, growth, and claw stridulatory patterns in the stone crab *Menippe mercenaria* (Say) (Crustacea: Xanthidae). J Crust Biol 5:281–293

Simonson JL, Steele P (1981) Cheliped asymmetry in the stone crab, *Menippe mercenaria*, with notes on claw reversal and regeneration. North Gulf Sci 5:21–30

Skinner DM (1985) Molting and regeneration. In: Bliss DE, Mantel LH (eds) Biology of Crustacea, vol 9. Academic, New York, pp 43–146

Smith LD (2004) Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. Mar Ecol Prog Ser 276:209–222

Smith LD, Hines AH (1991) The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shelled clams *Mya arenaria* L. J Exp Mar Biol Ecol 151:245–256

Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). Behav Ecol Sociobiol 41:237–242

Vermeij GJ (1977) Patterns in crab claw size: the geography of crushing. Syst Zool 26:138–151