

RESEARCH ARTICLE

Chela asymmetry in a durophagous crab: predominance of right-handedness and handedness reversal is linked to chela size and closing force

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ABSTRACT

The swimming crab *Portunus trituberculatus* is a durophagous brachyuran. Right-handed crabs are predominant, but left-handed crabs are also found in nature. Left-handedness may arise from loss of the right crusher. We examined whether heterochely (morphology) was correlated with differences in closing force (physical property) and handedness (behaviour). The closing force was stronger in larger chela with greater apodeme height and handedness resided in the chela with stronger closing force. With loss of the right chela (autotomy), handedness transitioned from the right to left chela, and all crabs were left-handed thereafter. Reversed handedness was accompanied with a reduction of size and closing force in the regenerated right chela, and growth of the original left chela. After handedness reversal, dentition on the left dactylus of the newly-converted crusher was close to that of the original right crusher, but did not attain the same shape, even after 10 moults. Left-handed crabs were significantly worse than right-handed crabs at crushing hard-shelled prey. Chela formation was symmetrical in the zoea, and heterochely and right-handedness started in the megalopa, regardless of maternal handedness. Since the left chela is capable of being the crusher, heterochely may be caused by differences in morphogenetic velocity between the right and left chelae, under a signal discriminating right from left. Right-handedness is an attribute of *P. trituberculatus*, that would be inheritable across generations. It is probable that right-handedness was used in the earliest durophagous crabs, and this trend has been succeeded to extant species.

KEY WORDS: *Portunus trituberculatus*, Durophagy, Handedness reversal, Autotomy, Linked morphogenic and functional regulation, Ontogeny, Evolution

INTRODUCTION

A prominent feature of the chelae of decapod crustaceans is lateral asymmetry (heterochely) in shape and size. One dimorphic chela is identified as the ‘crusher’, and is generally equipped with occlusive morphology and leverage capable of strong crushing forces, whereas the ‘cutter’ on the other side generates weaker forces and

is used for manipulating and cutting food or for grooming (Lee, 1995; Seed and Hughes, 1995). Heterochely is fully functional in the male fiddler crab *Uca*, where the major chela is used for display and combat (Levinton et al., 1995; Rosenberg, 2002).

Heterochely is also well-developed in durophagous crabs (i.e. those preying on hard-shelled prey) (Seed and Hughes, 1997; Schenk and Wainwright, 2001). Durophagous brachyurans include Calappidae (Lewis, 1969), Cancridae (Warner and Jones, 1976; Vermeij, 1977; Yamada and Boulding, 1998), Portunidae (Brown et al., 1979; Abby-Kalio and Warner, 1989; Seed and Hughes, 1995, 1997), Xanthidae (Brown et al., 1979; Blundon, 1988) and some other taxa (Vermeij, 1977; Seed and Hughes, 1995). With the exception of superficially homochelous cancrids, most durophagous brachyuran crabs also have asymmetrical chelae, usually with the right chela being the crusher and the left being the cutter (e.g. Lewis, 1969; Vermeij, 1977; Brown et al., 1979; Abby-Kalio and Warner, 1989; Seed and Hughes, 1997; Schenk and Wainwright, 2001). Right-handedness thus may be predominant in most durophagous crabs.

The proportion of right-handedness often differs among decapod crustaceans. Herrick (1909) found that 1266 specimens of the American lobster *Homarus americanus* possessed left crushers and right pincers, whereas 1164 possessed the opposite configuration. Yamaguchi (1977) also found that the proportion of right-handed and left-handed males of the fiddler crab (*Uca lactea*) was approximately even; out of 8088 males, 4071 were right-handed, and 4017 were left-handed. These crustaceans begin post-larval development with symmetrical chelae. In the lobster, the trigger that determines handedness is chela use at the critical juvenile stage (Govind, 1989). Once cheliped laterality is determined, the presence of a crusher on one side inhibits the other side from becoming a crusher (Govind, 1992). By contrast, in the fiddler crab, one of the male chelipeds is spontaneously lost at the post-larval stage to regenerate as a minor one, while the remaining one develops into a major chela (Yamaguchi, 1977). Thus, heterochely and handedness in these animals arises through different developmental mechanisms, although the resulting predicted and observed proportions of right and left-handedness are equal.

The crusher is often lost by autotomy, and a new cheliped is regenerated one or two moults later. If the right crusher is lost, the left cutter is converted to the new crusher. This phenomenon is known as ‘handedness reversal’ (Emmel, 1907; Przibram, 1931; Lewis, 1969; Govind and Pearce, 1988; Pynn, 1998). In the blue crab *Callinectes sapidus*, the proportion of right-handed crabs decreased from 100% in the smallest crabs to 74% among the largest crabs (Hamilton et al., 1976). Handedness reversal may provide a mechanism for explaining this trend. Simonson (1985) assumed that in the stone crab *Menippe mercenaria*, handedness reversal following chela loss was the most likely cause of an observed

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List of symbols and abbreviations

C1	first crab stage
Z4	fourth stage of zoea
L-cr	left crusher
L-cu	left crusher
M	megalopa
R-cr	right crusher
R-cu	right cutter
α	tooth on the dactyle
α -L	α on the left dactyle
α -R	α on the right dactyle
β	teeth on the propodus
β -L	β on the left propodus
β -R	β on the right propodus

decrease from initial 100% right-handedness to 80% among crabs in natural populations (see also Abby-Kalio and Warner, 1989; Norman and Jones, 1991).

In *Callinectes sapidus*, the mechanical advantage of newly converted crushers has been found to be greater than that of original cutters, but less than that of original crushers (Govind and Blundon, 1985). The same pattern has been reported in the red rock crab *Cancer productus* (Brock and Smith, 1998). In *Menippe mercenaria*, a normal stridulatory pattern on the major chela was not regained on a regenerated chela (Simonson, 1985). However, in the shore crab *Carcinus maenas*, regenerated chelae may grow to the same size as original chela (Pynn, 1998). Of note is that chela growth is accelerated in the left crusher after reversal of handedness (Juanes et al., 2008). So it may be possible for the newly converted left crusher to attain the same size as the original major chela. The relationship between the morphological and functional properties of newly converted major chelae and those of the right chelae regenerated after autotomy is as yet unclear.

In the shore crab *Carcinus maenas*, all individuals are, by birth, destined to bear the crushing chela on the right side of the body (Przibram, 1931). In *Cancer productus*, juvenile crabs also go on to

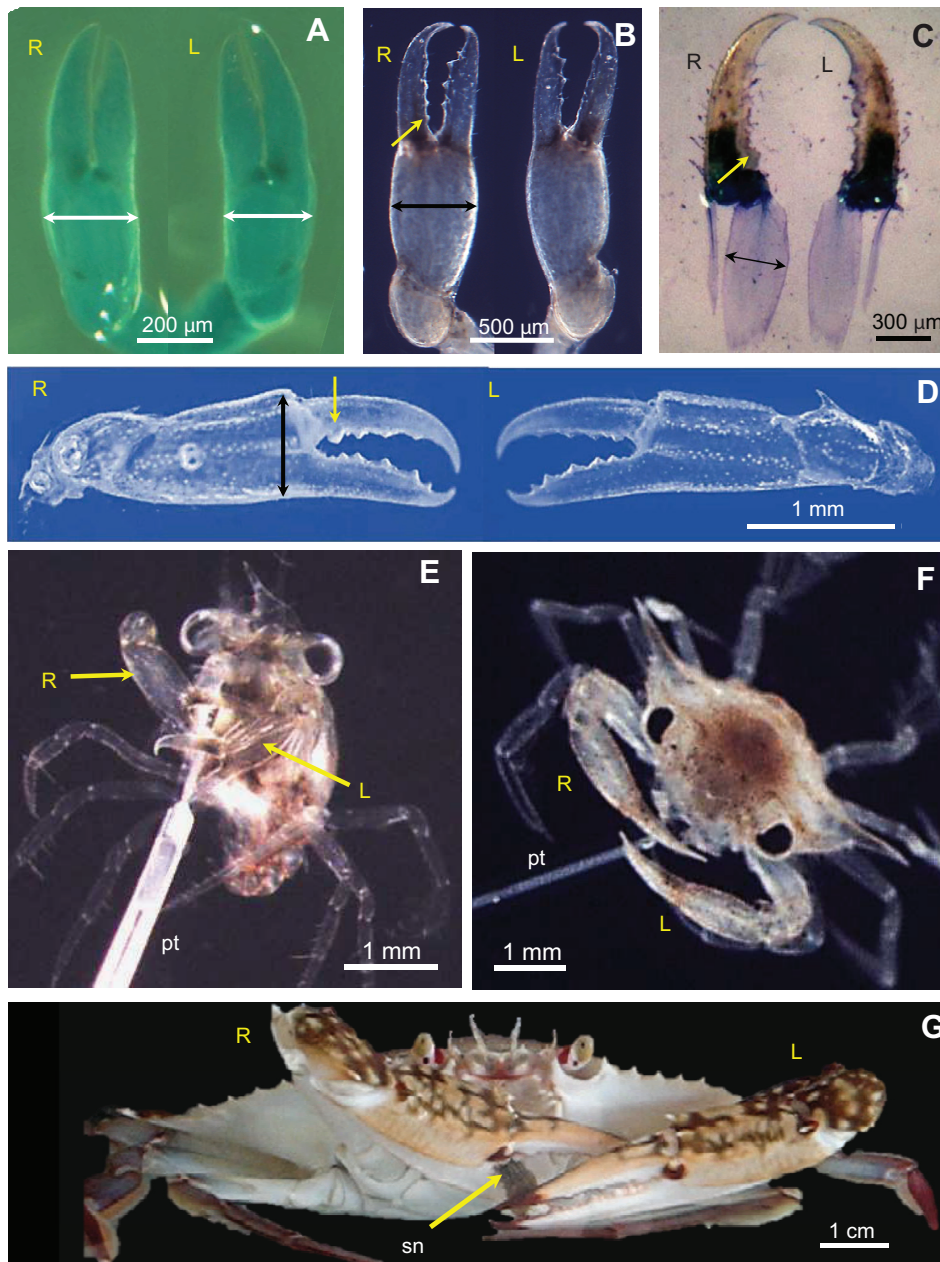


Fig. 1. Morphology of the cheliped and feeding behaviour of the swimming crab *Portunus trituberculatus*. (A) Right and left chelae from zoea (Z4). R, right cheliped; L, left cheliped. Note that chelipeds are shown in frontal view, so the right cheliped is presented on the left side and the left cheliped is shown on the right side in all figures. Double-headed arrows indicate propodus height. (B) Megalopa chelipeds. The yellow arrow indicates a canine of the right dactylus (movable finger). (C) Closer apodeme of a juvenile crab (C1). The apodeme height (double-headed arrows) was measured. Yellow arrow indicates a canine on the right dactylus. (D) Morphology of the right and left chelae in the first crab stage (C1). The propodus height (double-headed arrows) was measured. Yellow arrow indicates a canine on the right dactylus. (E) Feeding experiment on a megalopa, which repeatedly tried to crack the fine PFA tube (pt) with the right chela (R). The left chela (L) was used for grasping the PFA tube. (F) Feeding experiment on a juvenile crab (C1). Only the right cheliped was employed for cracking the glass tube. (G) Shell-cracking behaviour. Hard-shelled snails (sn) or bivalves (arrow) are carried to the mouth by either chela, and then they are broken by the right chela.

develop right-handedness (Smith and Palmer, 1994). In other brachyurans, cheliped asymmetry begins at post-larval development (Hamilton et al., 1976; Govind and Blundon, 1985; Simonson, 1985; Pynn, 1998; Ladle and Todd, 2006) similar to that of *Homarus* (Emmel, 1908; Govind and Pearce, 1989) and *Uca* (Yamaguchi, 1977). Analysis of a critical period in which handedness is determined would be essential for understanding formation of chela asymmetry.

The swimming crab *Portunus trituberculatus* is a durophagous brachyuran with heterochely. Right-handed crabs are predominant in this species, but a small number of left-handed crabs are found in nature. The frequency of left-handedness seems to increase with growth of crabs. To determine whether this increasing frequency is due to handedness reversal, we examined whether handedness (behaviour) is closely connected with heterochely (morphology) and differences in closing force of the chela (physical property). Next, to investigate the main factor to cause handedness reversal, we focused on morphological and physiological changes between the right and left chelae before and after autotomy.

For investigation of development of chela asymmetry, it is necessary to determine a critical period where handedness is determined. For this purpose, crabs with and without autotomy were tracked for more than 1 year from the larval stages to mature specimens. In addition, to determine whether right-handedness is a property by birth, zoeas collected from right- and left-handed females were reared in aquaria.

A further question arose as to the predominance of right-handedness. If left-handedness is caused by the loss of the right crusher chela, the majority of left-handed crabs would originally be right-handed. Right-handedness may be an attribute of durophagous crabs. The predominance of right-handedness in durophagous species is explained in terms of inheritability of handedness.

MATERIALS AND METHODS

Morphological parameters of chelae: chelae size, dentition and apodeme height

At the Okayama Fishery Institute, zoeas of *Portunus trituberculatus* (Miers 1876) hatched from 20 ovigerous females are reared in several large aquaria every year. When they attain the third (C3) or fourth (C4) crab developmental stage, most of these crabs are released into the Seto Inland Sea. A portion of these crabs were retained in aquaria for experiments. More than 300 crabs, including males and females, were kept individually in plastic cages (40 cm long×30 cm wide×30 cm high), each of which was placed in a shallow aquarium. Juvenile crabs were also kept individually in a small aquarium made of a plastic cylinder with mesh at the bottom (7–15 cm in diameter and 10–20 cm high). Other experiments were done using mature crabs purchased from the Fishery Cooperation at Yorishima, Okayama prefecture, and kept in the aquaria.

P. trituberculatus has four zoea stages (Z1–Z4) and one megalopa stage (M) before the first crab stage (C1). Zoeas were fixed with 3% formalin (v/v) for 1 day, and were then transferred to a solution of 70% ethanol and 2.5% glycerol for preservation. The propodus height was measured under a biological microscope (Optiphoto, Nikon Co. Ltd., Tokyo, Japan). Chela size was represented by the propodus height (Fig. 1A). The cuticle of megalopa are easily broken, so megalopae were placed in PBS (phosphate-buffered saline), and frozen at -80°C . Juvenile crabs were fixed with a solution of 70% ethanol and 2.5% glycerol until cheliped measurement. Propodus height of megalopa and juvenile crabs (black arrows in Fig. 1B,D) was measured under a biological microscope, a stereomicroscope (SZX 12, Olympus Co. Ltd., Tokyo, Japan) or using digital vernier callipers.

The magnitude of the force exerted by chela is closely related to the area of the closer apodeme, onto which the closer muscle is inserted (Warner and Jones, 1976; Seed and Hughes, 1995). The closer apodeme was absent in

zoea, but was found in megalopa (Fig. 1C). The closer apodeme height was measured under the biological microscope up to C3–C4 crab stages, and was measured by use of digital vernier callipers thereafter.

Asymmetry was found in the shape and size of the teeth arranged on the dactylus and propodus as well as the chela size. The height of these teeth was measured under a profile projector (V-12, Nikon Co. Ltd., Tokyo, Japan) or under the stereomicroscope if the former was not possible. We determined morphogenetic stage where these teeth (α -R and α -L) appeared, and further examined how their shape was altered by autotomy.

Feeding experiment

When soft-shelled prey such as annelids, squid, small fish and mysid shrimps were given to crabs, they were immediately captured with both chelipeds and directly carried to the mouth. Thus, soft-shelled prey were not useful for testing handedness. Handedness was clearly apparent when preying on hard-shelled items. Bivalves such as *Ruditapes philippinarum*, *Phacosoma japonicum* or *Cyclina sinensis* were adequate for testing handedness of mature crabs (carapace width more than about 12 cm). The left cheliped was often used for secondary crushing following the first attack with the right chela. When these bivalves were partially crushed and fed to crabs, the frequency of left chela use increased. Hence, handedness of mature crabs was determined using bivalves with undamaged shells (Movie 1).

However, these clams (*R. philippinarum*, *P. japonicum* and *C. sinensis*) were too big for small crabs (5–10 cm in carapace width). Smaller snails such as *Granata lyrata* and *Reticunassa festiba* (5–10 mm in shell diameter) were given to these immature crabs. The size and hardness of these snails were adequate for judging the handedness of immature crabs. (When these snails were fed to mature crabs, they were easily crushed by the mandibles with use of both chelipeds).

Even small snails such as *G. lyrata* were too big to determine the handedness of megalopae and juvenile crabs (C1 and C2), but soft-shelled prey such *Artemia* larvae and small mysid shrimps were broken by the

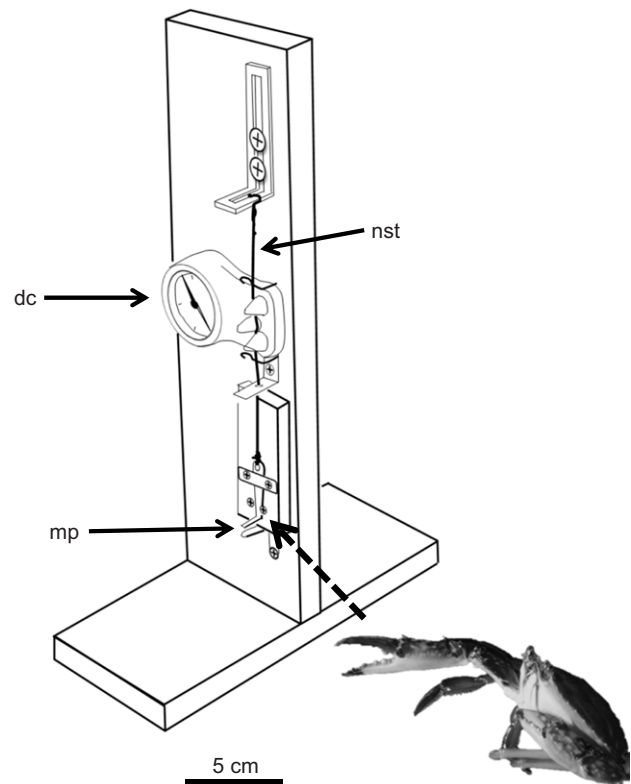


Fig. 2. Apparatus to estimate closing force of the chela. dc, drag checker; mp, right-angled metal plate; nst, nylon string. Closing force was measured at the middle of the chela.

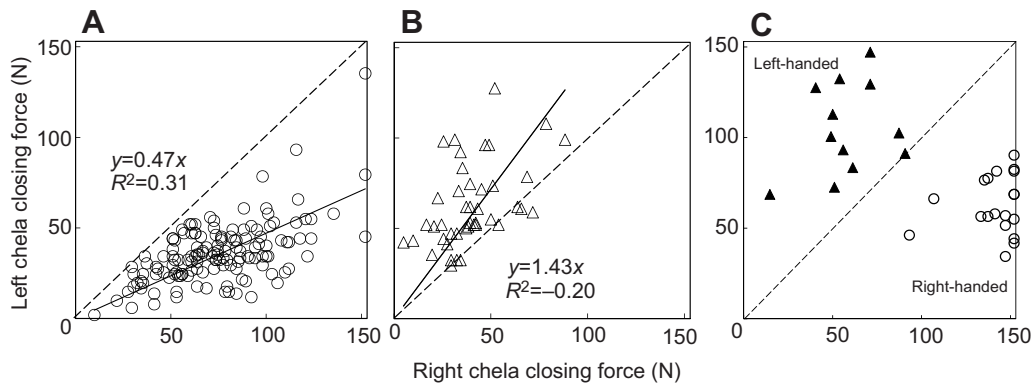


Fig. 3. Difference in closing force between right and left chelae in crabs. (A) Closing force (N) of right and left chela in individuals with larger right chela (open circles). (B) Closing force (N) of right and left chela in individuals with larger left chela (open triangles). The dashed lines indicate equal closing force for right and left chelae. Solid lines indicate the regression. R^2 , coefficient of correlation. (C) Comparison of the closing force between right and left chela in right- and left-handed crabs. Open circles, right-handed crabs; filled triangles, left-handed crabs. The dashed line indicates equal closing force (N) for right and left chelae. The closing force of eight individuals (right-handed crabs) exceeded the maximum level (150 N) of measurement (shown on the right edge of the figure). All crabs were collected from the field, but note that the proportion of handedness is not reflective of that in the field.

mandibles without use of chelipeds. We therefore prepared PFA tubes (300 μm external diameter, and 100 μm internal diameter) for feeding experiments. Mysid shrimps were homogenized in glass and ultrasonic homogenizers, and then injected into the PFA tubes using a syringe. The hardness of PFA tubes was adequate for determining handedness of megalopae and juvenile crabs (Fig. 1E,F). Hard-shelled prey was given to crabs according to their carapace size (Fig. 1G).

Measurement of closing force and measurement of the apodeme height

The crushing power of crab chelae primarily depends on the magnitude of the force that can be generated by the closer muscle. We estimated crushing power as closing force. Closing force was estimated using a Drag Checker (Bouz Production Co. Ltd., Tokyo, Japan). Slender, right-angled metal plates were fixed to the board at the top and the bottom (Fig. 2). The upper, movable, metal plate could pull a strong nylon string through the Drag Checker. The space between the opposing metal plates was less than 1 cm, and was adjusted according to chela size. Each crab was picked from its cage in the aquaria, and the slender opposing metal plates were pinched by the chela at the same time. Closing force was measured at around the centre of the dactylus. One of two types of Drag Checker, i.e. DC-1005 (0–5 kgf) or DC-1015 (0–15 kgf) was used depending on crab size. After estimation of the closing force (N) of the right and left chelae, the apodeme height was measured for the same specimens after freezing. Coefficients of regressions between these measurements were estimated using Excel (Microsoft).

Influence of maternal handedness

Zoeas were obtained from both right- and left-handed mature females. They were separately reared in aquaria and the handedness of megalopae and the first crab stage (C1) were determined.

Long-term experiment to estimate handedness reversibility

Megalopae were randomly collected from a big aquarium, and were divided into two groups. Each group was further divided into 4–5 small aquaria. One group (control) was kept without autotomy of the right chela. In another group, the right chela was autotomized at the first crab stage (C1). The handedness of each crab was determined four times, until the juvenile crabs attained stage C12 to C14. For the first test, handedness was determined by the feeding experiment (Fig. 1E–G). The second test used the snail *G. lyrata*. The third and fourth tests were done using PFA tubes. Crabs were fed on mysids and other animals between these experiments.

Immobilization of the right chela

Megalopae were collected from the communal aquarium, and kept in small aquaria. Two experiments were performed. In the first (adhesion 1), use of the right chela was immobilized using a quick-drying adhesive (cyanoacrylate) applied after each moult (five times from C1 to C5). Handedness was tested by the feeding experiment (Fig. 1E–G). Dentition was also examined at these same stages. In the second experiment (adhesion 2), use of the right chela was immobilized using adhesive at the first (C1) and second (C2) crab stages. Dentition and behaviour were inspected at stage C10.

RESULTS

Close relationships among chela size, closing force and handedness

Relationships between chela size and closing force were determined for more than 300 mature crabs that were individually kept in the aquaria. Chela size was represented by propodus height. As shown

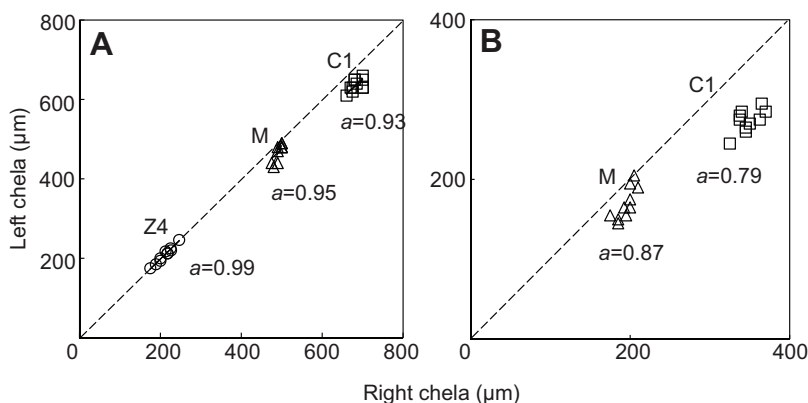


Fig. 4. Ontogeny of chela asymmetry. (A) Relationship between right and left chela size. Chela size is represented by propodus height. Z4, zoea; M, megalopae; C1, first crab stage. The dashed line indicates equal height in the right and left chelae. Number of individuals used for each experiment: Z4=10, M=10 and C1=11. (B) Generation of chela asymmetry (apodeme). The apodeme is not found in zoea. Number of individuals used for each experiment: M=10 and C1=10.

Table 1. Handedness of the larval and juvenile crabs born from females with different handedness

Aquarium	Maternal female		Megalopa			First crab stage (C1)		
	Number	Handedness	Right handedness	Left handedness	Both	Right handedness	Left handedness	Both
No. 1	1	R	24	0	2	7	0	1
No. 2	2	R	23	0	0	12	0	0
No. 3	2	R	28	0	0	–	–	–
No. 4	2	R	–	–	–	10	0	0
No. 5	1	L	28	0	2	9	0	0
No. 6	2	L	36	0	0	18	0	0
No. 7	2	L	22	0	0	15	0	0
Total	12		161	0	4	71	0	1

in Fig. 3A, when the right chela was larger than the left, the closing force of the right chela was always greater than that of the left. Conversely, for the crabs with larger left chela, the closing force of the left chela was stronger than the right (Fig. 3B).

Mature crabs were collected from the Seto Inland Sea, and were starved for more than 2 months. The closing force was measured in each individual (Fig. 3C). Handedness was determined using the feeding experiment (Fig. 1G). Nineteen of 31 crabs possessed larger right chela, the other 12 crabs possessed larger left chela. For right-handed crabs, the right chela was always stronger than the left. Conversely, for left-handed crabs, the left chela was stronger than the right. Thus, handedness is determined as the chela with the stronger closing force. The mean closing force of the major chela in the right-handed crabs was more than 141.3 ± 15.6 N. (The closing force of 8 out of 31 individuals exceeded 150 N, maximum force that could be measured by the apparatus illustrated in Fig. 2). The mean closing force of the major chela was 105.0 ± 24.0 N for left-handed crabs.

Ontogeny of chela asymmetry

Chelipeds in *P. trituberculatus* (Fig. 1A) first appeared as an immovable structure at the second zoeal stage (Z2). Chela size was symmetrical up to the last stage (Z4) of zoea (Fig. 4A). The cheliped of zoeas was not employed for feeding; prey (rotifers and *Artemia* larvae) were caught by the maxillipeds and other appendages. Chela asymmetry was first detected in megalopae (Fig. 1B and Fig. 4A) and the closer apodeme (Fig. 1C) was also observed first in megalopae (Fig. 4B). Asymmetry in apodeme height became much more obvious in juvenile crabs (Fig. 1D and Fig. 4B).

Influence of maternal handedness

Ovigerous females with different handedness (7 females with right-handedness, and 5 females with left-handedness) were kept in separate aquaria, and zoeas were randomly collected. Handedness of megalopae and crabs in the first stage was determined in a feeding experiment. As shown in Table 1, 75 of

77 megalopae (97%) and 29 of 30 first crabs (97%) from right-handed females were right-handed. The remaining two megalopae and one crab used both chelae. Eighty-six of 88 megalopae (98%) and all 42 crabs (100%) were right-handed, with the remaining two megalopae using both chelipeds. This indicates that megalopae start out right-handed irrespective of the handedness of maternal females. Right-handedness therefore seems to be an attribute of this species.

Irreversible reverse-handedness

Crabs at the first stage (C1) were randomly collected from aquaria 17 days after hatching, and were divided into two groups (each of 36 individuals): a control group (without autotomy) and an experimental group in which the right chela was autotomized by pinching the basement of the cheliped with fine forceps. Both groups were separately reared through subsequent crab stages (up to C14 stage). Handedness was determined by feeding experiments (Fig. 1E–G). In the control group, the right-handedness was maintained throughout the experiment (Table 2). For the autotomized group, the right chela regenerated after one or two moults. Handedness transitioned from the right to left chela, and all crabs were left-handed thereafter. Right-handedness never reappeared in crabs with loss of the right chela.

Decrease of the closing force in the regenerated right chela, and increase in the left chela

Fig. 5A compares the closing force between right and left chela in right- and left-handed crabs reared in the aquarium (Table 2). In the right-handed crabs (control), the closing force of the right chela was always stronger than that of the left chela. The mean closing force was 32.5 ± 11.4 N on the right chela and 16.5 ± 6.7 N on the left chela. In the left-handed crabs (a group in which the right chela was autotomized at stage C1), the mean closing force was 29.6 ± 12.7 N in the left chela (crusher) and 12.6 ± 7.7 N in the right chela (Fig. 5B). Thus, the closing force of the right chela decreased to 39% in the autotomy group. By contrast, the

Table 2. Feeding experiment to examine whether the right-handedness reappears

Experiment (date)	Day 0	Day 23–25			Day 140–142			Day 344–346			Day 382–383		
	(22 Jun 2012)	(15–17 Jul 2012)			(9–12 Nov 2012)			(1–3 Jun 2013)			(10–11 Jul 2013)		
Handedness	—	R	L	no	R	L	no	R	L	no	R	L	no
Control	36	36	0	0	21	0	1	15	0	0	10	0	0
Autotomy on day 0	36	0	36	0	1 ^a	13	0	0	9	0	0	6	0
Crab stage	C1	C5–C6			C11–C12			C11–C13 ^b			C12–C14		
Total carapace width (cm)	0.5	1.8–3.2			8.3–13.3			10.6–14.1			11.0–15.6		
Carapace width (cm)	0.3	1.3–2.3			6.4–10.2			8.1–10.8			8.5–12.2		

no: no response to the snail. ^aThe left cheliped was lost at ecdysis on day 47. ^bNumber of molts drastically decreases in the second year.

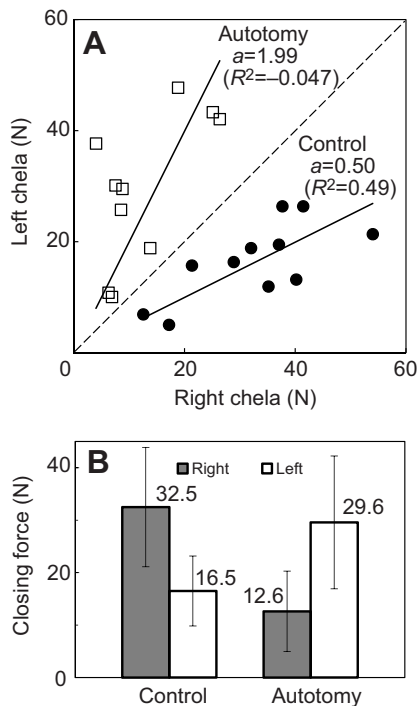


Fig. 5. Difference of closing force between the right and left chela in crabs with and without autotomy. (A) Closing force (N) in right-handed (control) and left-handed crabs (autotomy). Filled circles, control group; open squares, autotomy group. The dashed line indicates equal chela height in the right and left chelae. (B) Comparison of the closing force between right and left chela in right-handed (control) and left-handed crabs (autotomy). Values are means \pm s.d.

closing force of the left chela increased to 1.8 times that of the control group.

Statistically significant differences were detected between right and left chela both for crabs without autotomy (paired *t*-test,

d.f.=10, $t=6.237$, $P<0.001$) and crabs with autotomy of the right cheliped (paired *t*-test, d.f.=9, $t=5.199$, $P<0.001$).

Alteration of chela size and handedness reversal after autotomy

Fig. 6A indicates growth of chela size in one crab without autotomy. The difference between right and left chela size increased with moult number. However, the ratio was always within 1.10- to 1.19-fold (Table 3). When the right cheliped was autotomized at C1 (two crabs), the right chela regenerated after two moults (C3) and chela size reversed from right to left (Fig. 6B). A feature of note was that the left chela (L-cr) was 141% (mean) as large as the regenerated right chela (R-cu) (Table 3). The ratio rapidly decreased to 116–113% over C4–C6 and was 107–111% thereafter. Thus, chela size rapidly increased in the newly converted left crusher.

Fig. 6C summarizes the chela size relationship of the specimens with or without autotomy of the right chela. Crab stages used for measurement were C12–C14 (see Table 2). The regenerated right chela became the minor chela (R-cu), but its size was a little larger than the left chela (L-cu) of the control group with no autotomy. A statistically significant difference was detected in the intercept of each two regressions (d.f.=11, $t=2.260$, $P=0.0451$ between R-cr and L-cr; and d.f.=11, $t=3.097$, $P=0.0102$ between R-cu and L-cu). Thus, alteration never returned to the original relationship before autotomy.

Growth of chela dentition and morphological changes after autotomy

Fig. 7A (top panel) shows the right and left chelae of a mature female (frontal view), and dentition on the dactylus (movable finger) and propodus (immovable finger). In the right-handed crab, a sharp canine, α -R (top and middle panels in Fig. 7A) that was observed at the base of the right dactylus significantly enhances chelae mechanical advantage. In contrast, the tooth (α -L) had a groove on the left dactylus. A paired tooth (β) was also observed on the propodus (bottom panel in Fig. 7A). While the right molar (β -R)

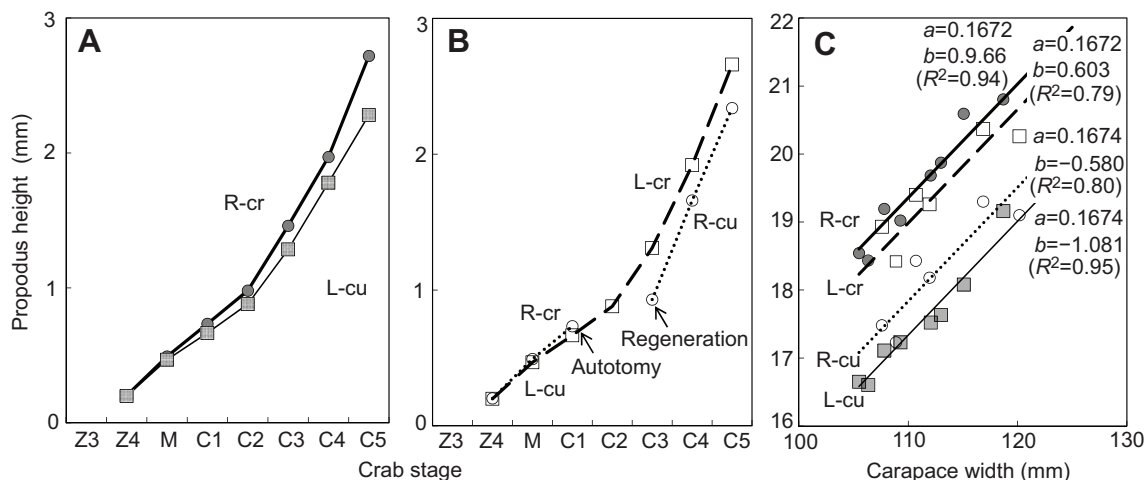


Fig. 6. Chela size asymmetry with growth is altered by autotomy. (A) Growth of chela size (propodus height) in crabs without autotomy (control). R-cr: chela on the right. L-cu: chela on the left (left cutter). Z, M, and C indicate zoea, megalopa and crab, respectively. Data were obtained from one individual. (B) Alteration of chela size relation after autotomy at C1. Open squares with dashed line indicate growth of the left chela. Note that function of the left chela changes from cutter (L-cu) to crusher (L-cr) after autotomy of the right chela. Open circles with dotted line indicate growth of the right chela before (R-cr) and after (R-cu) autotomy. Data show the mean values of two individuals. (C) Relationship of chela size with or without autotomy. Black circles (R-cr) and grey squares (L-cu) indicate growth of the right crusher and left cutter without autotomy (control group). Open circles (R-cu) and open squares (L-cr) indicate growth of the right cutter and left crusher after loss of the right chela (autotomy group). Measurements were made on crabs (Tables 2 and 3) on day 390 (C12–C14). *a*, the intercept of each regression line; R^2 , coefficient of determination. Data were obtained from measurement of 8 (control) and 6 (autotomy) individuals.

Table 3. Growth (propodus height) of the left chela and conversion to the crusher after autotomy of the right chela

		Crab growth stage											
		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
Control	R-cr (mm)	0.73	0.98	1.46	1.97	2.72	3.80	5.0	6.7	8.0	9.9	12.7	16.2
	L-cu (mm)	0.67	0.88	1.29	1.78	2.28	3.44	4.4	5.7	6.9	8.5	11.2	14.5
	R/L	1.10	1.11	1.14	1.11	1.19	1.10	1.13	1.17	1.16	1.16	1.13	1.12
Autotomy	R-cu (mm)	Au	Abs	0.93 ^a	1.66	2.34	3.32	4.6	5.8	7.3	8.8	10.9	14.6
	L-cr (mm)	0.67	0.88	1.31	1.92	2.66	3.76	5.0	6.3	8.1	9.6	11.9	15.6
	L/R			1.41	1.16	1.14	1.13	1.09	1.09	1.11	1.09	1.09	1.07

R-cr, right crusher; R-cu, right cutter; L-cr, left crusher; L-cu, left cutter; Au, right chela was autotomized at stage C1 (the first crab); Abs, Absence of the right chela. Note that in the same stage, the crusher chela is larger in the control group (R-cr) than in the autotomy group (L-cr).

^aA small chela regenerated on the right.

had a vertical groove (type I), that on the left propodus (β -L) had vertical and cross grooves (type II).

After the loss of the right major chela (R-cr) at C1, the tooth of the newly converted left crusher (α -L) developed, and the shape was close to that of a canine (Fig. 7B, top panel). Nevertheless, the shape of the left chela did not attain the same shape as that of the original right chela, even 10 moults after autotomy. In the regenerated right dactylus (R-cu), the tooth (α -R) was smaller than that of the original left cutter (L-cu). Comparison of Fig. 7B (middle panel) with Fig. 7A (middle panel) shows that the tooth shape (α -R) was similar

to the molar of the original left cutter (L-cu) in that it was partitioned by a vertical groove (type I), even after several moults.

The molar of the right propodus (β -R) had a vertical groove in the original right crusher (Fig. 7A, bottom panel). This tooth had both vertical and cross grooves after regeneration (Fig. 7B, bottom panel). The molar on the left propodus (β -L) was much the same as that of the original left cutter (type II). Thus, the molar of the right propodus (β -R) was altered from type I to type II after autotomy, but that of the left propodus (β -L) was of much the same type as before (type II).

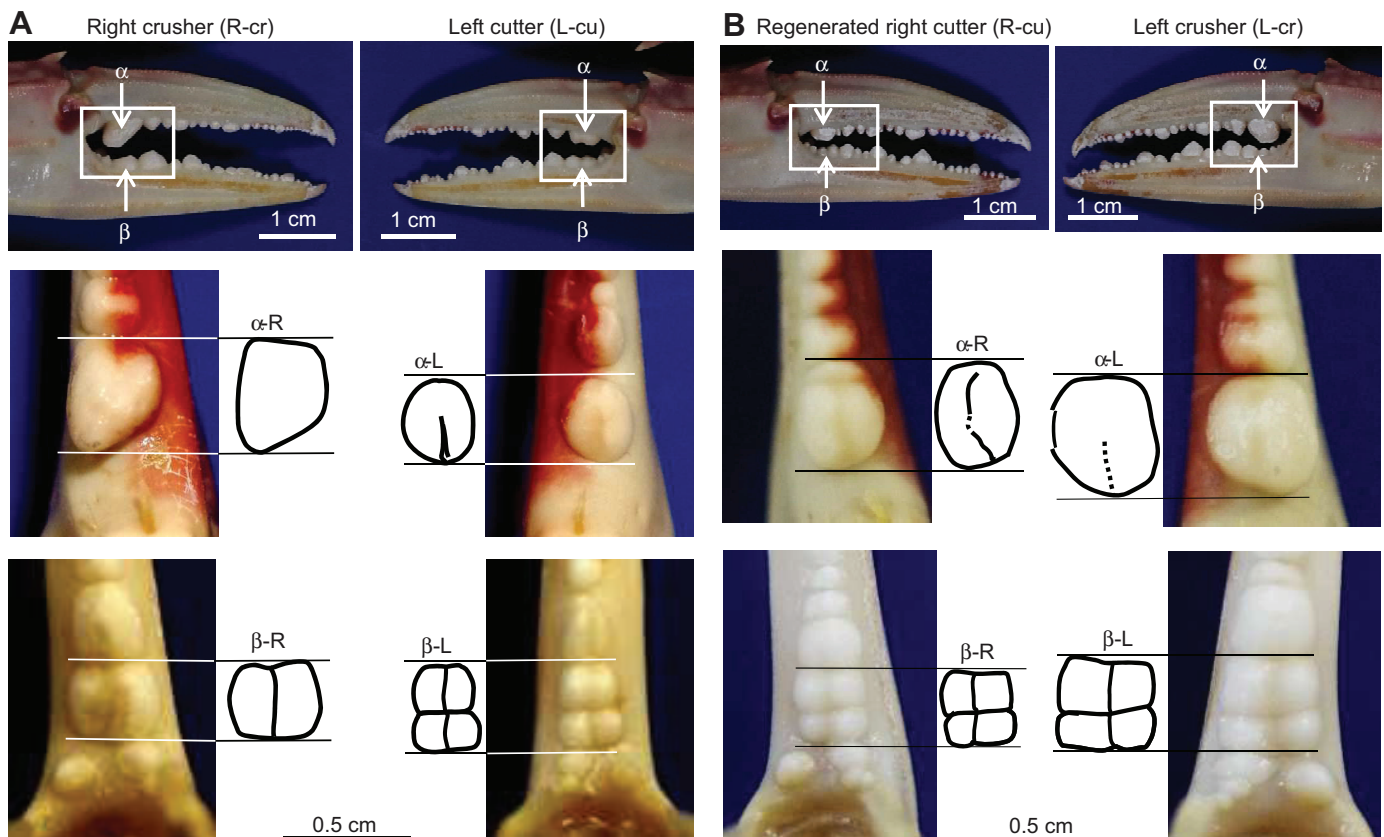


Fig. 7. Comparison of dentition on the dactylus and propodus between control group and autotomy group. (A) A female at the crab stage C13 (i.e. 13th moult). Top panels: dentition of the right and left chelae of mature crabs. The chela consists of dactylus (upper, movable finger) and propodus (lower, immovable finger). We have focused on the teeth at the bases of the dactylus and propodus (boxed area). α indicates the tooth on the dactylus, and β shows the tooth on the propodus. Middle panel: tooth shape on the right dactylus (α -R), and that of the left dactylus (α -L). A sketch of each tooth is shown to the right or left of the image. The vertical line on α -L indicates a shallow groove. Bottom panels: tooth shape on the right propodus (β -R) and left propodus (β -L). A sketch of each tooth is shown at the right or left of the image. There is a vertical groove on β -R (type I) and vertical and cross grooves on β -L (type II). (B) Top panels: dentition of a regenerated right chela (R) and the original left chela (L) after loss of the original right chela. The right chela was autotomized at C1 and dentition was inspected at crab stage C13 (a female). Middle panels: the shape of the dactyle tooth in the regenerated right cutter (α -R) and the newly converted left crusher (α -L). Bottom panels: the shape of the tooth on the propodus. β -R, regenerated right cutter; β -L, converted left crusher.

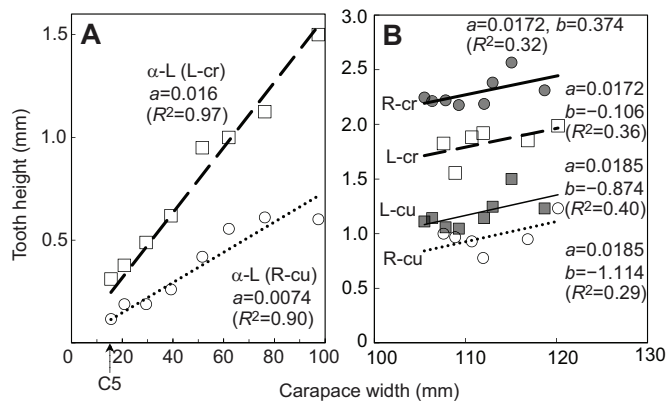


Fig. 8. Regeneration and growth of the tooth on the dactylus. (A) Growth of the tooth on the dactylus after regeneration at C3. α -L (open squares), tooth on the left; α -R (open circles), tooth on the right. (B) Relationship between tooth height and carapace width, with and without autotomy (C12–C14). Black circles (R-cr) and grey squares (L-cu) indicate growth of the right crusher and left cutter, respectively (control group). Open circles (R-cu) and open squares (L-cr) indicate growth of the right cutter and left crusher after the loss of the right chela, respectively (autotomy group). Lines are regression lines. a , the slope of each group; R^2 , coefficient of determination. Measurements were made on the crabs shown in Tables 2 and 3. Data were obtained from measurement of 8 control and 6 autotomy individuals.

Fig. 8A shows the change in tooth size (height) between the right and left dactylus after autotomy of the right chela in C1 (Table 2). The right chela was regenerated in C3, and measurement was done from stage C5. The tooth height (α -L) in the newly-converted left crusher (L-cr) was taller than that (α -R) of the regenerated right cutter (R-cu), and this difference became larger with age (number of moults). As well as the chela size (Fig. 6C), tooth height of the left crusher (L-cr) was less than that of the original right crusher (R-cr) (Fig. 8B). Tooth height of the regenerated right cutter (R-cu) was smaller than that of the original left cutter (L-cu). A statistically significant difference was detected in the intercept of each two regressions (d.f.=11, $t=7.349$, $P<0.001$ between R-cr and L-cr; and d.f.=11, $t=3.547$, $P=0.0046$ between L-cu and R-cu).

Allometric relationships between apodeme height and closing force

Fig. 9A shows allometric relationships between the closing force [$\log(y)$] against the closer apodeme height [$\log(x)$] in the major (R-cr) and minor (L-cu) chelae of the right-handed crabs (control group) and Fig. 9B indicates those in the major (L-cr) and minor (R-cu) chelae of the left-handed crabs (autotomy group). In the control group, the mean apodeme height of the right chela was 17.1 ± 1.5 mm (R-cr), but was 11.1 ± 1.6 mm (R-cu) in the autotomy group (a decrease of 65%). The mean closing force was 139 ± 19 N (R-cr) in the control group, but was 58 ± 20 N (R-cu) in the autotomy group (decrease of 42%). However, in the autotomy group, the apodeme height of the left chela was 12.5 ± 1.6 mm (L-cu) and 14.7 ± 1.0 mm (L-cr) (1.17-fold increase). The closing force was 63 ± 16 N in the control group, and was 105 ± 24 N in the autotomy group (1.68-fold increase).

A statistically significant difference was detected among the mean apodeme heights of the four chela groups (one-way ANOVA, $F_{3,63}=44.17$, $P<0.001$; Tukey's HSD test, $P<0.05$). When the major right chela (R-cr) was lost, apodeme height and closing force of the regenerated new chela (R-cu) were smaller than those of the original left chela (L-cu) (Fig. 9C). Since handedness always resides in the chela with stronger closing force (Fig. 3C), the original left chela (L-cu) should be converted to the major chela (L-cr) with regeneration of the right cheliped.

Crabs with two crusher chelae

Right chelipeds were made immovable using adhesive several times at each moult (Table 4). Handedness was examined by feeding experiments at C11–C13 stages, along with chela morphology. For the control group, all crabs showed right-handedness; and for the autotomy group, all crabs showed left-handedness. In the first chela-immobilizing experiment (adhesion 1), six out of 13 individuals showed right-handedness (Rcr-Lcu). In the other seven individuals, the left chela became a crusher as well as right crusher (Rcr-Lcr) (see also Fig. 10, top panel). The second experiment (adhesion 2) was carried out on seven individuals. Four crabs possessed a right crusher and a left cutter (Rcr-Lcu), but the other three crabs had

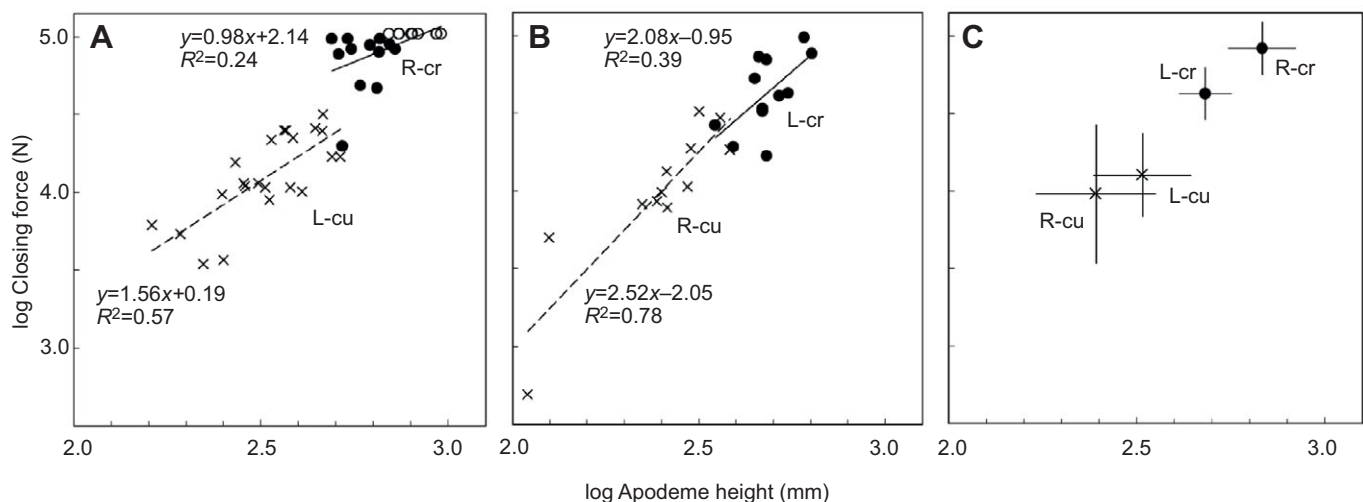


Fig. 9. Allometric relations between the apodeme height and the closing force. (A) Right-handed crab. Filled circles (R-cr) show the right chela (open circles indicate crabs in which the closing force exceeded maximum value of the apparatus), and crosses (L-cu) show left chela. (B) Left-handed crab. Filled circles (L-cr) indicate the left chela and crosses (R-cu) indicate the right chela. (C) The mean value with standard deviations in each chela. R-cr, right crusher; R-cu, right cutter; L-cr, left crusher; L-cu, left cutter. The closing force (N) of the right and left chelae was estimated in 22 right-handed and 12 left-handed crabs that were newly collected from the field.

Table 4. Effect of immobilization of the right chela

	Morphology			No. of crabs
	R-cr–L-cu	R-cu–L-cr	R-cr–L-cr	
Control	9	0	0	9
Autotomy	0	6	0	6
Adhesion 1	6	0	7	13
Adhesion 2	4	0	3	7

R-cr, right crusher; R-cu, right cutter; L-cr, left crusher; L-cu, left cutter.

crushers on both chelae (Rcr-Lcr). When the right cheliped was released from adhesion, both chelae were used for feeding. Frequency of right and left chelae use differed somewhat in each individual (data not shown). Nevertheless, the right crusher was never converted to a cutter.

For the crabs with both crushers (Rcr-Lcr), the tooth of the left chela (α -L) was a sharp canine, as well as that on the right dactylus (α -R) (Fig. 10, middle panel). The molar on the left propodus (β -L) was of much the same type (type I) as the right molar (β -R) (Fig. 10, bottom panel). (While the canine was very sharp in the right dactylus, it was somewhat rounded in the left dactylus.) Type I molars were seen on the left propodus in only two out of 10 specimens (Table 5). Six had type II molars, and the molar of the other two crabs were different between type I and type II.

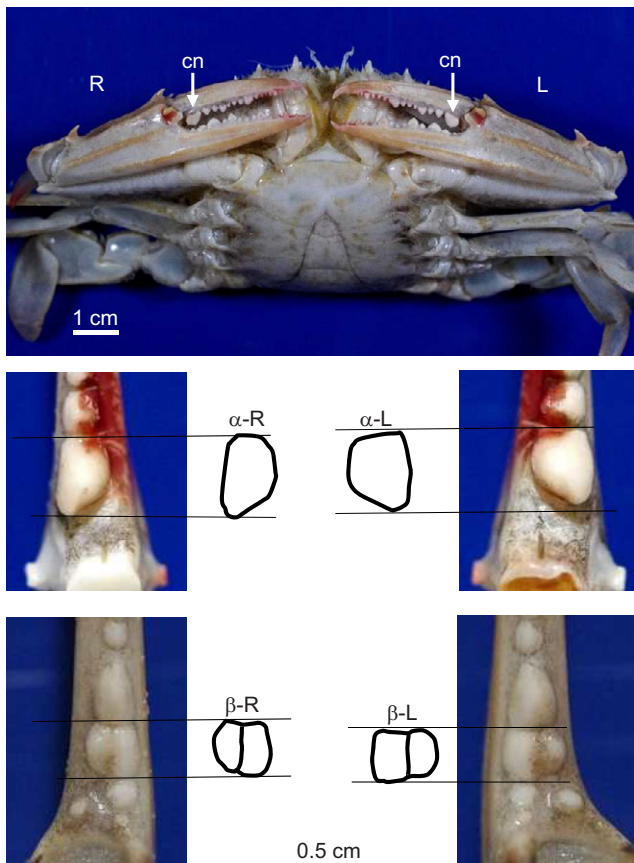


Fig. 10. Expression of the left crusher by immobilization of the right chela. Top panel: a male crab with major chelae on both sides (frontal view). Arrows (cn) indicate the tooth (canine) on each dactylus. Middle panels: tooth (canine) on each dactylus. α -R, a canine on the right dactylus; α -L, a canine on the newly formed left crusher. A sketch of each tooth is shown. Bottom panels: contrast of tooth (molar) shape between the original right crusher (β -R) and newly formed left crusher (β -L). Inspection at C12 stage.

Difference in shell-crushing success between the right- and left-handed crabs

The ratio of success in shell crushing was compared between right- and left-handed crabs that had been kept from the megalopa stage (Table 2). A feeding experiment was carried out using a small, hard-shelled snail, *Reticunassa festiba*. The proportion of crabs successfully crushing shells increased with the growth of crabs (Fig. 11A) but it varied widely among individuals, therefore, the success ratio at each size was normalized (Fig. 11B). The level of success in shell crushing was significantly affected by the factor handedness (logistic regression, z -test, $P=0.009$) and size (z -test, $P<0.001$). Thus, it is obvious that right-handed crabs were better at crushing hard-shelled prey than left-handed crabs.

DISCUSSION

Left-handedness caused by loss of the right chela

Bilateral cheliped asymmetry is a prominent feature of decapod crustaceans (Emmel, 1907; Herrick, 1909; Przibram, 1931; Govind, 1989, 1992; Palmer, 2004, 2012). In many durophagous crabs, crusher chelae occur on the right side of the body and cutters occur on the left (e.g. Lewis, 1969; Hamilton et al., 1976; Vermeij, 1977; Juanes and Hartwick, 1990; Seed and Hughes, 1995; Pynn, 1998; Schenk and Wainwright, 2001; Ladle and Todd, 2006; Juanes et al., 2008). The ratio of left-handedness may be different in species and habitat (Hamilton et al., 1976). The shore crab *Carcinus maenas* was found to be 79% right-handed and 21% left-handed in nature, and it was suggested that left-handedness may have been caused by loss of the right chela (Abby-Kalio and Warner, 1989). Handedness reversal in the velvet crab *Necora puber* is also thought to be due to autotomy of the major cheliped (Norman and Jones, 1991). The proportion of *Callinectes sapidus* possessing the crusher chela on the right decreased with age (size) from 100% in very small crabs to 74% in larger sized crabs (Hamilton et al., 1976).

In *Portunus trituberculatus*, among more than 300 mature individuals, 75% had a right crusher and left cutter, 25% had the opposite configuration (Fig. 3A,B). The chelipeds that first appeared were symmetrical (Fig. 1A and Fig. 4A) but megalopae were right-handed (Fig. 1B,E, Fig. 4A,B). As shown in Table 1, right-handedness occurs in the megalopae irrespective of maternal handedness. This may indicate that right-handedness is a property of *P. trituberculatus* at birth. When the right cheliped was autotomized, handedness was reversed with change of the chela size (Tables 2, 3 and Fig. 6B). Handedness reversal did not occur when the minor chela is autotomized. Thus, handedness reversal always occurs from right to left chela and left-handedness is fixed with the change of chela size and closing force (Tables 2 and 3). Hence, the proportion of left-handed crabs should increase with growth in nature. It is highly plausible that the majority of these left-handed crabs must have experienced autotomy of the original right crusher.

Handedness linked to greater closing force

In crustaceans with heterochely, the crusher chela has a greater mechanical advantage and a larger closer muscle volume than the cutter chela (Elner and Campbell, 1981; Warner et al., 1982; Blundon, 1988; Schenk and Wainwright, 2001). A difference in closer muscle composition has been suggested in the lobster *Homarus americanus* (e.g. Lang et al., 1977; Govind et al., 1981). In the blue crab *Callinectes sapidus*, however, fibre composition was not different between the crusher and cutter of individual crabs (Govind and Blundon, 1985). Furthermore, there may be no bilateral asymmetry between closer muscles in terms of motor neurons or size and number of sensory axons (Govind and Blundon,

Table 5. Dentition of crabs with a crusher chela on both sides

	β-R			β-L			No. of crabs inspected
	Type I (V)	Type II (V+C)	Others	Type I (V)	Type II (V+C)	Others	
Control	9	0	0	0	9	0	9
Autotomy	0	4	2	0	6	0	6
Adhesion 1	7	0	0	1	4	2	7
Adhesion 2	3	0	0	1	2	0	3

β-R, molar on the right propodus; β-L, molar on the left propodus; V, vertical groove; C, cross groove. Others, teeth with three to six small projections; adhesion 1, use of the right chela was immobilized using a quick-drying adhesive (cyanoacrylate) applied after each moult (C1–C5); adhesion 2, use of the right chela was immobilized using adhesive at the first (C1) and second (C2) crab stages.

1985). This could suggest that different closing forces between the asymmetric chelae result from differences in the volume of the closer muscle and the mechanical advantage.

Closing force is a function of the stress produced per cross-sectional area of muscle, the cross-sectional area of the closer muscle and the mechanical advantage of the lever arm to the length of the lever arm (Warner and Jones, 1976; Vermeij, 1977; Elner and Campbell, 1981; Schenk and Wainwright, 2001; Swanson et al., 2013). In *P. trituberculatus*, closing force was proportional to the apodeme size (Fig. 9A,B) and handedness always resided in the chela with stronger closing force (Fig. 3C). Greater apodeme height and chela size may be closely related to the volume of the closer muscle, and handedness would then depend on the chela with stronger closing muscle.

Irreversible handedness and remodelling of the chela operating system

As indicated in Fig. 5A,B, the mean closing force of the right chela was 32.5 N in the control group and decreased to 12.6 N in the autotomy group. In contrast, the mean closing force of the left chela was 16.5 N in the control group, and increased to 29.6 N in the autotomy group. In Fig. 9A (control group), the apodeme height of the right chela (R-cr) was much larger than that of the left chela (L-cu). This relationship was reversed in the autotomy group (Fig. 9B): the apodeme height of the left chela (L-cr) was larger than the right chela (R-cu). The chela with stronger closing force transitioned from the right to left chela (Fig. 9C). Since handedness is linked with the chela with stronger closing force (Fig. 3C), handedness should also transition from the right to the left chela in the autotomy group. With transition of handedness, the left chela further grew bigger (Table 3). Chela function could therefore change from right to left, possibly via the central nervous system.

Decapod crustaceans with asymmetrical chelae

In the fiddler crab *U. lactea*, the proportions of right-handed and left-handed males are nearly equal (Yamaguchi, 1977), but in the

other species such as *U. vacans* and *U. tetragonon*, almost all males are right-handed (Barnwell, 1982). In *U. lactea*, chelae of individual crabs are symmetrical up to the juvenile crab stage and heterochely occurs after spontaneous loss of either chela, resulting in the equal proportions of right- and left-handed individuals. When both chelae remained intact or were lost at the same time, symmetry was fixed as paired major or minor chelae (Yamaguchi, 1977). These results indicate that loss of either chela is an important factor that triggers asymmetry.

In the lobster *Homarus americanus*, the critical period for chela differentiation was delimited to occur in the fifth stage; the development of chela asymmetry required at least 5 days in the presence of a substrate such as oyster chips (Govind and Pearce, 1989). A four-step mechanism in chela asymmetry has been proposed for *H. americanus* (Govind, 1992).

In *P. trituberculatus*, the left chela was not lost at metamorphosis (Fig. 1A,B and D), so it is clear that asymmetry is not triggered by loss of either chela in the larval stage. The crusher chela was also formed on the left side by immobilization of the right chela (Fig. 10 and Table 4). In the lobster, once cheliped laterality is determined, the presence of a crusher on one side inhibits the other side from becoming a crusher (Govind, 1992). Handedness and reversed handedness in *P. trituberculatus* may be explained physiologically as follows. With generation of chela asymmetry (Fig. 1B, Fig. 4A and Fig. 6A), the presence of a larger right chela may inhibit the opposite chela from becoming a crusher. When the crusher chela is lost by autotomy (Table 2), or is immobilized by the adhesive (Fig. 10), suppression on the opposite chela would be lost. Then the opposite chela grows bigger to become a crusher (Table 3). Presence of newly converted crusher may inhibit the regenerated chela from becoming a crusher.

Megalopae in the brachyurans are transitional forms between zoea and crab, and morphological changes in internal anatomy and external shape are most pronounced in the postembryonic stage (Felder et al., 1985). Chela asymmetry in *P. trituberculatus* may develop through two morphogenetic steps (Fig. 12A). In the first

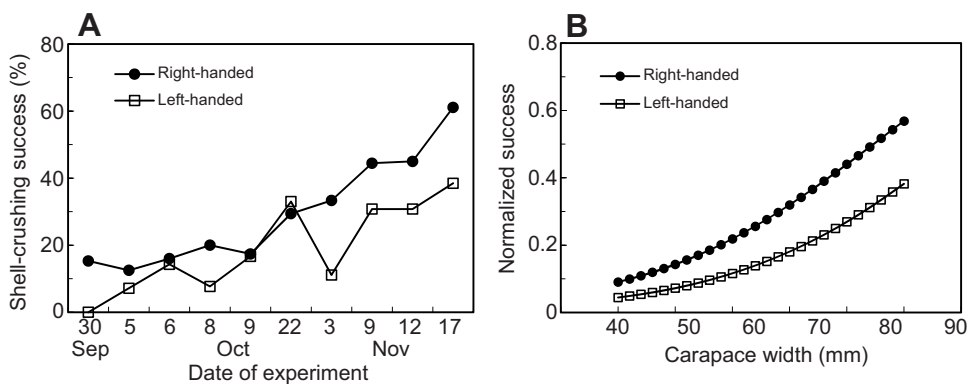


Fig. 11. Analysis of shell-cracking success between the right and left chelae with growth of crabs. (A) Original data. Number of crabs used for measurement each day: 21–27 for the right-handed crabs, and 13–15 for the left-handed crabs. Each data point is the mean of these crabs. Measurements were made of crabs shown in Table 2. (B) Normalization of the original data for statistical treatment. Right-handed: $\text{logit}(y)=0.052x-4.37$; left-handed: $\text{logit}(y)=0.052x-5.13$.

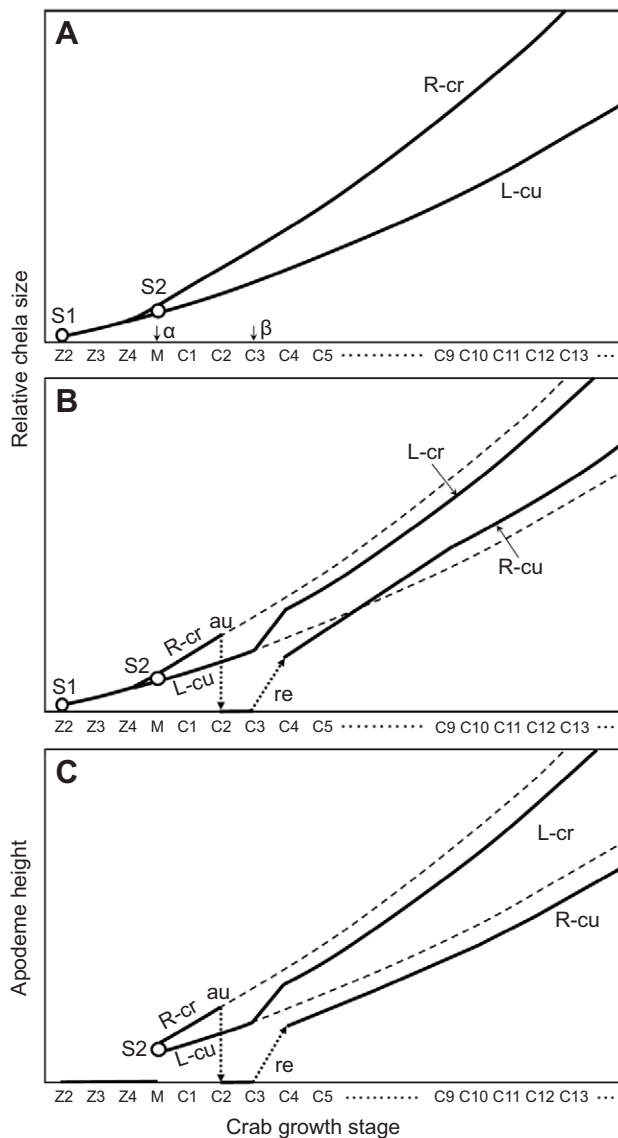


Fig. 12. Development of chela asymmetry and alteration of handedness before and after loss of the major chela. (A) Ontogeny and enlargement of chela asymmetry. A crab with no history of autotomy. R-cr and L-cu indicate the right crusher and the left cutter, respectively. Chela first appears as a symmetrical structure (s1) at the second stage of zoea. Asymmetry appears at the megalopa (s2). Difference in tooth morphology (α and β in Fig. 7A) appears in the megalopa for the dactylus, and in C3 for the propodus, respectively. The growth curve is generally step-like due to moulting, but is drawn as a straight curve here for clarity. (B) Alteration of chela size after the loss of the major chela (R-cr): the case where the right chela is lost at stage C2 and the right chela (R-cu) is regenerated at stage C4. The point of autotomy (au) is indicated. Chela regeneration (re) is shown by dotted line. The dashed curves indicate growth in the case where the right chela is not autotomized. (C) Alteration of apodeme height after the loss of the right chela (R-cr). Note that the closer apodeme height of the regenerated right chela (R-cu) is smaller than that of the original left cutter (L-cu, lower dashed curve).

step (s1), chela shape is symmetrical (see also Fig. 1A and Fig. 4A). Asymmetry starts at the second step (s2). Differences in chela formation in the morphogenetic steps may be the primary cause of asymmetry. Asymmetry depends not only on chela size (Fig. 4A) but also on the apodeme height (Fig. 4B). The developmental stage where asymmetry in tooth morphology (α and β) appears may be different between dactylus and propodus (Fig. 12).

The first sign of chela asymmetry was seen in the megalopa stage, with a prominent tooth on the right dactylus (Fig. 1B), a difference in chela size (Fig. 4A) and closer apodeme height (Fig. 4B). Since right-handedness was not influenced by maternal handedness (Table 1), morphogenetic facilitation of the right chela would occur spontaneously at metamorphic stage, under a signal distinguishing right from left.

Comparison of Fig. 7A,B (middle panels) indicates that in the autotomy group, the shape and size of the tooth on the left dactylus (α -L) was close to that on the original right crusher (α -R), although the molar on the propodus remained similar to type II (bottom panels in Fig. 7A,B). These morphological differences were observed more than 1 year after autotomy, in C12–14 individuals (Table 2). Most crabs have two moults in the second year, and only one moult in the third year (Hamasaki, 1997). The teeth (especially β -R) in the newly converted left crusher could not attain the same shape as that of the major chelae of the right-handed crab (Fig. 7B), even if autotomy occurred at a young age.

Shell-cracking behaviour

Handedness may be advantageous for feeding on hard-shelled preys and for fighting, especially in durophagous brachyurans (Seed and Hughes, 1995, 1997). The advantage of right-handedness has been typically accounted for as an adaptation for opening dextrally coiled shells (e.g. Ng and Tan, 1985; Dietl and Hendricks, 2006). In the xanthid crab *Eriphia smithii*, left-handed crabs had more difficulty in breaking the shell aperture of large individuals of the dextrally coiled snail *Planaxis sulcatus* (Shigemiyu, 2003). However, left-handedness may not have any disadvantage for left-handed crabs in either feeding or agonistic behaviour (Ladle and Todd, 2006).

In *P. trituberculatus*, the proportion of success in shell crushing increased with growth in both right- and left-handed crabs (Fig. 11A). Left-handedness arose from loss of the right crusher and the regenerated right chela was always smaller than the left chela (Fig. 6B,C). The closing force of the newly converted left chela (L-cr) was always less strong than that of the original right crusher (R-cr) (Fig. 5B and Fig. 9C). When compared in the same carapace size, the closing force of the major chela (R-cr or L-cr) was significantly stronger in the right-handed crab. Hard-shelled preys given to crabs were snails such as *Granata lyrata* and *Reticunassa festiva* with 5–10 mm diameters. Crabs cracked the snails in the same manner regardless of handedness. Differences in the closing force between right and left chela would result in higher proportion of success in shell crushing in the right-handed crabs (Fig. 11B). This suggests that right-handed crabs clearly have advantage in feeding and agonistic behaviour.

Predominance of right-handedness in the durophagous crab

Handedness may be advantageous for feeding on hard-shelled prey and for fighting in durophagous brachyurans (Vermeij, 1977; Brown et al., 1979; Govind and Blundon, 1985; Seed and Hughes, 1995, 1997; Sneddon et al., 1997; Yamada and Boulding, 1998; Schenk and Wainwright, 2001). In most durophagous brachyuran crabs right-handedness may be predominant (e.g. Lewis, 1969; Vermeij, 1977; Brown et al., 1979; Abby-Kalio and Warner, 1989; Seed and Hughes, 1997; Schenk and Wainwright, 2001).

In *P. trituberculatus*, left-handedness is caused by autotomy (or injury and malfunction) of the original right crusher (Table 2). In addition, right-handedness appeared in the megalopae regardless of maternal handedness (Table 1), suggesting that right-handedness is an attribute of this species. Heterochely may

occur as a result of differences in morphogenetic velocity between the right and left chela (Fig. 4A,B, Fig. 6A and Fig. 8B), under a signal discriminating right from left. Right-handedness could be inheritable across generations.

The heterochely of the durophagous fossil crab *Megaxantho zoque*, from the Cretaceous period (Vega et al., 2001; Dietl and Vega, 2008) clearly suggests right-handedness. The brachyuran fossil record indicates that most taxa had appeared by the early Eocene (see fig. 3 in Brösing, 2008). Although *M. zoque* became extinct at the end of the Cretaceous (Vega et al., 2001), the diversity of durophagous brachyurans greatly increased from the late Cretaceous to the early Eocene (see fig. 3 in Oji et al., 2003; and table 1 in Schweitzer and Feldmann, 2010). Most existing brachyuran groups that forage for hard-shelled prey consist of right-handed species. A possible explanation for the predominance of right-handedness is that they are the descendants of the durophagous brachyurans that appeared in the Cretaceous.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

N.M.: experiments and production of all figures and tables. M.H.-O., S.D., M.K. and M.G.: crab maintenance and preparation of the experimental animals. Y.T. and T.N.: statistical treatment of the data. M.S.: experiments and writing of the paper.

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Supplementary information

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