Autotomy patterns in the Japanese mitten crab, *Eriocheir japonica*

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**Abstract.**— Autotomy is a common phenomenon in crustaceans and has been extensively studied. The Japanese mitten crab, *Eriocheir japonica*, is an important fisheries species in Japan, but autotomy patterns of this species have seldom been reported. Therefore, in this study, we examined the autotomy patterns for *E. japonica* in both growth and reproduction habitats. Our results indicated that a high proportion (more than 26%) of *E. japonica* lost appendages, and autotomy rate was positively correlated with crab size. There was no significant difference in autotomy frequency between sexes, and single appendage loss was the most common form of autotomy. Appendages on the left and right sides had an equal probability of loss. The observed autotomy frequency was significantly different from the expected frequency, which suggests that in *E. japonica* the autotomy event is dependent on each other. Moreover, appendage loss in *E. japonica* was affected by habitat type and season.

**Key words:** appendage loss, size, habitat, morphological maturity

**Introduction**

Autotomy is the behavior of an animal shedding a part of its body in response to abiotic or biotic stress (Juanes & Smith, 1995; Fleming et al., 2007). This behavior has been confirmed in many invertebrate and vertebrate species, with caudal autotomy among lizards probably the most well-known example (Maginnis, 2006; Fleming et al., 2007; Bateman & Fleming, 2009). A variety of factors can trigger autotomy, but the main cause has been considered sublethal predation (Juanes & Smith, 1995; Fleming et al., 2007; Lindsay, 2010). In addition, other factors, such as human activities, physical disturbance, and chemical stimulation can also induce autotomy (Fleming et al., 2007).

In decapod crustaceans, autotomy is also a common phenomenon (Juanes & Smith, 1995; Fleming et al., 2007; Lindsay, 2010). On the one hand, this behavior has multiple benefits. For example, the autotomized appendages can distract a predator’s attention, therefore increasing the animals’ chance of survival (Robinson et al., 1970; Davis et al., 2005; Maginnis, 2006). On the other hand, autotomy has some disadvantages. For instance, loss of appendages could reduce an animal’s locomotion ability and foraging efficiency, which in turn could reduce predator avoidance ability and growth (Kuris & Mager, 1975; Smith, 1990; Juanes & Smith, 1995; Brouwer et al., 2006). In addition, chelipeds play an essential role in mate competition, and the absence of this appendage could decrease mating success (Smith, 1992; Abello et al., 1994). These individual-level effects could be projected as population-level effects by reducing population growth and recruitment (Bennett, 1973; Harris, 1989; Smith, 1990; Lindsay, 2010).

Autotomy has been extensively studied in decapod crustaceans (Needham, 1953; McVean, 1976; Sekkelsten, 1988; Spivak & Politis, 1989; Smith & Hines, 1991; Smith, 1990; Abello et al., 1994; Mathews et al., 1999; Davis et al., 2005; Dvoretsky &
Autotomy patterns vary among species despite the prevalence of autotomy in decapods. In some species, such as *Callinectes sapidus* and *Carcinus maenas*, chelipeds are the most frequent autotomized appendages (Needham, 1953; Smith, 1990), while in *Chionoecetes bairdi* and *Paralithodes camtschaticus*, chelipeds are least likely to be autotomized (Edwards, 1972; Dvoretsky & Dvoretsky, 2009), and in *Cyrtograpsus angulatus*, the third and fourth walking legs suffer the highest frequency of injury (Spivak & Politis, 1989). Differences in autotomy patterns may result from different body shape characteristics in different species.

The Japanese mitten crab, *Eriocheir japonica* (De Haan, 1835), is an important fisheries species widely distributed in Japan, Korea, and the Russian island of Sakhalin (Kobayashi, 1999b). This crab is a catadromous species, which grows in freshwater (the growth area) and reproduces at sea (the reproduction area) (Kobayashi, 1999b). Ecological information on this crab is well-known (Kobayashi & Matsuura, 1991; Kobayashi, 1999a, 2002, 2012), however information on autotomy patterns in *E. japonica* is limited. To date, only one quantitative study on autotomy in *E. japonica* was conducted in the reproduction area where only adult individuals were collected (Kobayashi & Matsuura, 1997). Autotomy patterns of juvenile *E. japonica* in freshwater areas still remain unknown. Therefore, in this study, we quantified the autotomy patterns in *E. japonica* both in their growth and reproduction areas.

**Materials and Methods**

A field investigation was conducted from May 2014 to April 2015 in the Banda River, Chiba Prefecture, Japan (34.9753°N to 34.974°N, 139.776°E to 139.775°E). Specimens were collected with a hand-held net (mesh size = 1.0 mm) by turning over stones in the river and intertidal area.

At the laboratory, crabs were sexed on the basis of abdomen morphology, and carapace width (CW) was measured with a digital caliper to the nearest 0.01 mm. The number and position of lost and regenerated appendages (chelipeds, first to fourth walking legs, right or left side of the body) were recorded. The regenerated appendage could be identified easily as it is generally smaller than the contralateral appendage (Smith, 1990; Dvoretsky & Dvoretsky, 2009). Appendage loss occurred occasionally as a result of injuries caused by collection operations. These fresh injuries were excluded from analyses.

In order to test whether the probabilities of autotomizing each appendage were independent, we calculated the expected autotomy frequencies based on binomial distribution. The expected and observed frequencies were compared with a chi-square test. All statistical analyses were performed using R version 3.1.0 (R Development Core Team, 2014).

**Results**

**Samples**

In total, 649 specimens of *E. japonica* were collected comprising 326 males and 323 females. The sex ratio did not differ significantly from a 1 : 1 ratio ($\chi^2 = 0.014$, $p > 0.05$). Male crabs had a CW varying from 8.22 to 50.06 mm, with a mean size of 21.70 ± 10.25 mm CW. The size of females varied from 7.75 to 59.98 mm CW, with an average size of 21.86 ± 11.92 mm CW. There was no significant difference in crab size between males and females ($t = -0.184$, $p > 0.05$).

**Incidence of autotomy**

Among the specimens collected, 170 individuals had lost their appendages. Size frequency distributions of intact and injured crabs are presented in Fig. 1. The average size of injured crabs (27.27 ± 13.48 mm) was significantly
larger than intact crabs ($19.83 \pm 9.40$ mm) ($t = -6.643, p < 0.001$).

**Effects of sex and side**

Of 170 individuals injured, 83 were male and 87 were female, amounting to 135 and 154 appendages lost, respectively (Fig. 2). No significant difference was found between sexes ($\chi^2 = 1.249, p > 0.05$). Additionally, there was no significant gender difference between autotomy frequency and appendage types ($\chi^2 = 3.7808, p > 0.05$), which implied the frequency of autotomy in *E. japonica* was independent of sex.

Among the 289 lost appendages, 143 occurred on the left side and 146 occurred on the right side. The autotomy frequencies did not differ significantly between left and right sides ($\chi^2 = 0.031, p > 0.05$).

Since there was no sex or side effect on *E. japonica* autotomy pattern, we pooled sex and side data together to analyze whether each appendage type had equal probability of loss. All appendages did not have equal probability of loss ($\chi^2 = 23.232, p < 0.001$); the ratio between overall missing chelipeds and walking legs was significantly higher than the expected ratio of 1 : 4 ($\chi^2 = 18.439, p < 0.001$). All walking legs had the same loss probability ($\chi^2 = 5.485, p > 0.05$).

**Body size effect**

Mixed-gender data were used to analyze the relationship between autotomy rate and crab size. Considering the number of large crabs was few (Fig. 1), crabs larger than 45 mm CW were classified as one group.

The autotomy rate and number of lost limbs per crab were both positively correlated with crab size (Fig. 3). When crab size was less than 25 mm CW, autotomy rate remained more or less constant at just below 20%. However, when crab size was larger than 25 mm CW, autotomy rate was greater than 35% and climbed progressively as crab size increased. Further-
more, autotomy rate was recorded higher than 50% when crab size was beyond 40 mm CW (Fig. 3a). The number of autotomized appendages per crab was less than 0.4 when CW ≤ 25 mm; when CW > 25 mm, it was larger than 0.5, especially when CW > 40 mm, crabs lost more than one appendage on average (Fig. 3b). On the basis of above results, we roughly divided the severity of autotomy in this species into three levels: slight (CW ≤ 25 mm), moderate (25 mm < CW ≤ 40 mm) and severe (CW > 40 mm) (Fig. 3). Both autotomy rate and number of missing appendages were significantly different among different levels of autotomy (ANOVA, p < 0.05).

**Observed versus expected**

As illustrated above, male and female crabs have similar autotomy patterns: chelipeds are the appendage type autotomized most often and walking legs have equal probability of loss. Therefore, the expected probability of loss was calculated by consolidating male and female data.

The probability of loss of a cheliped (\(p_c\)) was calculated as:

\[
p_c = \frac{\text{Number of lost chelipeds}}{\text{Number of possible chelipeds}} = \frac{87}{649 \times 2} = 0.067
\]

Similarly, the probability of loss of a walking leg (\(p_w\)) was calculated as:

\[
p_w = \frac{\text{Number of lost walking legs}}{\text{Number of possible walking legs}} = \frac{202}{649 \times 8} = 0.0389
\]

*E. japonica* has two chelipeds and the probability of losing \(x\) chelipeds (\(x = 0, 1, 2\)) was calculated as:

\[
p_{\text{chelipeds}}(x) = \binom{2}{x} p_c^x (1 - p_c)^{2-x}
\]

This crab has eight walking legs and the chance of losing \(x\) walking legs (\(x = 0, 1, 2 \ldots\)) was calculated as:

\[
p_{\text{walking leg}}(x) = \binom{8}{x} p_w^x (1 - p_w)^{8-x}
\]

For instance, the chance of a crab losing three appendages was calculated as follows:

\[
p_{\text{chelipeds}}(0) \times p_{\text{walking leg}}(3) + p_{\text{chelipeds}}(1) \times p_{\text{walking leg}}(2) + p_{\text{chelipeds}}(2) \times p_{\text{walking leg}}(1).
\]

The observed and expected autotomy frequencies are shown in Fig. 4. Significant differences were detected between the observed and expected autotomy frequencies (\(\chi^2 = 514.185, p < 0.001\), Fig. 4). Crabs losing one appendage were observed less frequently than expected; as for others, observed frequencies were more frequent than expected (Fig. 4).

From the population of *E. japonica* in Banda River, 15.56% lost one appendage, whereas, only 2.16% lost four or more appendages. Crabs that lost more than five appendages were seldom observed and we found only one crab that lost all of its eight walking legs. Therefore, single appendage autotomy was most common in this species.

In multiple appendage autotomy events, adjacent appendage autotomy was prevalent. Adjacent appendages are regarded as (1) appendages which are successive on the same side, or (2) appendages which have the same position.
on both sides (Juanes & Smith, 1995). Adjacent appendage autotomy occupied 48.78%, 92.86%, and 100% among crabs autotomizing 2, 3, and ≥ 4 appendages, respectively.

**Effect of habitat and season**

The average size of injured crabs in the intertidal area (45.29 ± 6.48 mm) was significantly larger than injured crabs in the river (21.90 ± 9.87 mm) \((t = 17.344, p < 0.001, \text{Fig. 5})\). Autotomy rate of crabs in the intertidal area (69.64%) was significantly higher than crabs in the river (22.09%) (Fisher’s exact test, \(p < 0.001\)). In addition, among injured *E. japonica*, crabs from the intertidal area exhibited more multiple appendage autotomy events (58.97%) than crabs from the river (35.11%) (Fisher’s exact test, \(p = 0.009\)).

In intertidal areas, crabs are not available all year round due to their unique life history (Kobayashi, 1999b). Furthermore, given the limited number of specimens collected from the intertidal area in our study, we only considered the seasonal difference of autotomy in *E. japonica* from the river. In this study, we divided the year into four seasons: spring (March to May), summer (June to August), autumn (September to November) and winter (December to February). Autotomy levels of *E. japonica* were not consistent among seasons (Fisher’s exact test, \(p < 0.001\)). There was no significant difference in autotomy rate between the spring and summer (Fisher’s exact test, \(p > 0.05\)). However, autotomy levels in the spring and summer were significantly higher than in the fall (Fisher’s exact test, \(p < 0.001\)). Due to an extremely small number of crabs collected during the winter, no statistically significant difference in autotomy levels was observed between winter and other seasons. However, as shown in Fig. 6, autotomy levels in spring and summer were obviously higher than autotomy levels in fall and winter.

**Discussion**

As a common phenomenon in crustaceans, autotomy has been frequently studied (Juanes & Smith, 1995; Fleming et al., 2007; Lindsay, 2010). The incidence of autotomy in crustaceans is generally high (~19% to 32%), with much variance among species (Lindsay, 2010). For instance, in small *C. maenas*, only 1.7% of individuals lost their appendages (Sekkelsten, 1988), while in female *C. angulatus*, the injury rate was about 80.0% (Spivak & Politis, 1989). In this study, the injury level of *E. japonica* was within this range. As a catadromous species, *E. japonica* grows in rivers and migrates to the sea after maturity (Kobayashi, 1999b). This explained why the size of injured *E. japonica* in the intertidal area was larger than in the river.

The autotomy pattern of *E. japonica* has been studied in the intertidal area by Kobayashi & Matsuura (1997). Consistent with our re-

![Fig. 5. Size frequency distribution of injured *Eriocheir japonica* in river and in intertidal areas.](image)

![Fig. 6. Seasonal autotomy levels in *Eriocheir japonica* from the river.](image)
results, injury frequency in the intertidal area was high (43.16%). However, contrary to the previous study (Kobayashi & Matsuura, 1997) which indicated that larger adult E. japonica did not show any significant site specificity of appendage loss, our results suggested that in both sexes, E. japonica were prone to losing the chelipeds (Fig. 2). These might reflect the size differences of appendage. The enlarged chelipeds have multiple functions in E. japonica, including combat, foraging, signaling displays, and courtship (Hartnoll, 1974; Kobayashi, 1999a), which certainly increase the risk of exposure to predators and entanglement during molts (Edwards, 1972; Spivak & Politis, 1989; Smith, 1990; Maginnis, 2006; Fleming et al., 2007; Dvoretsky & Dvoretsky, 2009).

Crustacean autotomy patterns are generally found to be independent of sex, which might imply causes of autotomy, such as predation, are sex independent (Juanes & Smith, 1995). Nevertheless, exceptions were found in some species, such as C. angulatus (Spivak & Politis, 1989), and C. maenas (McVean, 1976). These sex differences might result from different intrasexual interactions or physical differences (Fleming et al., 2007).

Kobayashi & Matsuura (1997) only collected large-sized adult E. japonica from the intertidal area, and thus their study of injury in E. japonica was independent of size. In our study, we sampled various sizes of E. japonica and found injured crabs were significantly larger than intact crabs. Moreover, our results verified Kobayashi & Matsuura’s (1997) hypothesis that autotomy level in E. japonica is positively correlated with crab size. Similar positive correlations have also been confirmed in C. maenas (McVean, 1976), C. angulatus (Spivak & Politis, 1989), and Hemigrapsus sanguineus (Davis et al., 2005). Nonetheless, we should note that a positive pattern is not consistent among crustacean species, with other patterns, such as negative and parabolic correlations have also been found in certain species (Davis et al., 2005).

In our study, the severity of autotomy in E. japonica was divided into three levels. In an attempt to explain this phenomenon, we discuss the following four reasons: molting cycle, physical disturbance, anti-predator ability, and intraspecific competition.

Firstly, the regeneration opportunity of a lost
Appendage is related to molt frequency. Crab molting frequency declines as body size increases (Leffler, 1972; Spivak & Politis, 1989; Smith, 1990; Smith & Hines, 1991; Juanes & Smith, 1995). In brachyuran crabs, the size of chelipeds in males and morphology of abdomens in females has been recognized as a secondary sex characteristic, which can be used to estimate morphological size of maturity (Hartnoll, 1974, 1978). We estimated morphological size of maturity in *E. japonica* by different methods (discriminant function analysis and piecewise regression analysis) (Corgos & Freire, 2006; Williner et al., 2014). According to our analysis, both male and female *E. japonica* achieved morphological sexual maturity at around 25 mm CW (Fig. 7, unpublished). As a result of frequent molting in *E. japonica* prior to morphological maturity, lost appendages have a higher chance of being regenerated and resuming normal size, which may explain the lower level of detected autotomy in *E. japonica* less than 25 mm CW. It has been verified that in juvenile *E. sinensis*, the regenerated new appendages appear the same as normal appendages after the regeneration interval (He et al., 2016). However, after achieving morphological maturity, crabs have a longer intermolt period and the potential for complete regeneration is reduced (Skinner, 1985; Kobayashi, 2012). As a result, subsequent autotomies accumulate in adult crabs and injury rates are high.

Secondly, physical disturbances are different in different habitats. Injuries to *E. japonica* in intertidal areas occur more frequently than to crabs in rivers. In addition to crab size, there are differences between the two habitats. This phenomenon might partially result from differences in physical environmental conditions. Environment conditions in intertidal areas are more turbulent than in rivers, so that crabs inhabiting intertidal areas are more vulnerable to injury. Severe injuries were found during the investigation in the intertidal area (Fig. 8). The effect of habitat on autotomy levels has been confirmed in other species. A previous study revealed that lizards living near roads were more exposed to predators or vehicle traffic than those living further from roads, and thus a higher autotomy frequency was found (Bateeman & Fleming, 2009). Habitat-related patterns of injury have also been verified among Jamaican gorgonians (Wahle, 1985).

Thirdly, the anti-predator response in animals depends on their body size (Wahle, 1992). Smaller crabs are unlikely to escape from their

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**Fig. 8.** *Eriocheir japonica* with injuries (both crabs were collected from an intertidal area).
predators by autotomizing appendages as strikes are often fatal. However, larger crabs tend to respond to predators with aggressive displays. Instead of being eaten, larger crabs may autotomize their appendages and escape (Wahle, 1992; Fleming et al., 2007).

Fourthly, male-male competition for mates during the reproductive season has been observed in many brachyuran crabs, including *E. japonica* (Hartnoll, 1969; Kobayashi & Matsura, 1997). Agonistic interactions during this process would likely lead to an increase in appendage injury.

Seasonal variation in autotomy levels was confirmed in *E. japonica* from the river. One possible explanation is the seasonal variation in the intensity of competition and predation. Compared to cold seasons, animals are more actively foraging, and *E. japonica* are more abundant during warm seasons, which would result in high levels of predation and competition. A temporal difference in autotomy has also been confirmed in *E. japonica* in the sea: from the beginning to the end of the reproductive season, autotomy increases (Kobayashi & Matsura, 1997).

Autotomy frequency in *E. japonica* did not show any right or left side preference. In the majority of crustaceans, autotomy is symmetrical because autotomy-causing agents and the direction of escape are unpredictable and random in brachyuran crabs (Smith, 1990; Dvoretsky & Dvoretsky, 2009). However, bilateral asymmetry in autotomy distribution was found in certain species, such as *C. maenas* (Needham, 1953) and *P. camtschaticus* (Dvoretsky & Dvoretsky, 2009).

Multiple appendage autotomy events occurred more frequently than expected (Fig. 4), indicating that appendage autotomy events are not independent. One possible explanation is that prior appendage loss would reduce the animal’s locomotion ability and make the animal more vulnerable to predators (Needham, 1953; McVean, 1976; Shirley & Shirley, 1988). The prevalence of adjacent appendage injury in multiple appendage autotomy events provides another possible explanation by indicating that crabs can lose more than one appendage in a single attack event (Spivak & Politis, 1989; Smith & Hines, 1991).

In crustaceans, different appendages have different functions, and loss of appendages would result in a reduction of individual fitness. For example, loss of appendages would decrease growth rate and increase mortality by reducing an animal’s foraging efficiency and predator avoidance ability (Smith & Hines, 1991; Mathews et al., 1999; Davis et al., 2005; Brouwer et al., 2006; He et al., 2016). In natural environments, crabs with lost appendages would be at a competitive disadvantage. As a result, they would be excluded from suitable habitats and likely have lowered mating success (Smith, 1992; Abello et al., 1994). A theoretical model illustrated that nonlethal injury could influence population stabilization (Harris, 1989). Bennett (1973) suggested that population growth of *C. pagurus* would decrease by 3% due to autotomy. Further studies are needed to elucidate the potential impacts of appendage loss on *E. japonica*.

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