Invasion risk assessment of Chinese mitten crab in Japan

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Doctoral Dissertation

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博士学位論文内容要旨
Abstract

専　攻 Major	Applied Marine Biosciences	氏　名 Name	ZHANG ZHIXIN
論文題目 Title	Invasion risk assessment of Chinese mitten crab in Japan チュウゴクモクズガニの日本への侵入リスクに関する研究		

The Chinese mitten crab *Eriocheir sinensis* (H. Milne Edwards, 1853), is an important aquaculture species natively distributed in eastern Asia. This species, however, has been regarded as a notorious invasive alien species outside its native range and successfully established populations in some European countries and North America. The invasion of Chinese mitten crab has caused substantial ecological and economic damage in recipient ecosystems. For instance, *E. sinensis* may compete with or predate on native species; more recently, this species was found to be a carrier of the crayfish plague pathogen and might infect native crayfish species. Chinese mitten crab is a catadromous species, which grows in rivers and migrates to estuarine environment for reproduction. This complex life cycle makes it difficult for people to understand its population dynamics and develop effective eradication strategies. *E. sinensis* has also been designated as an invasive species in Japan and two adult specimens were recently found in Tokyo Bay. Despite this fact, live Chinese mitten crabs are imported from China to Japan for human consumption every year. In 2017, about 87 tons of *E. sinensis* were imported to Japan with a value of approximately 320 million JPY. This invasive species is believed to have negative impact on Japanese ecosystems, such as competition with or predation on native species; thus far, however, no study has been performed to explore the potential ecological impact of *E. sinensis* on native Japanese species, especially on its congener Japanese mitten crab *Eriocheir japonica*. The objectives of this study were to analyze the population dynamics of Chinese mitten crab by a matrix population model approach and examine its possible interactions with native *E. japonica* under laboratory conditions.

In the first chapter, I constructed a periodic matrix population model for *E. sinensis* based on published information about its life history. The life cycle of this species was divided into two seasons: summer and winter and each season contained three stages. Transition probabilities during summer and winter were estimated based on previous studies. An elasticity analysis was performed to identify the most import parameters in regulating population growth of Chinese mitten crab. Model simulation results suggested that population growth of *E. sinensis* in suitable habitat would be larger than 1 and reproductive values of this species increased with developmental stage. The results of elasticity analysis suggested that water temperature and mortality rate during larval development contribute most to population growth. Therefore, the larval stage is the most critical in the life history of Chinese mitten crab and the estuarine environment deserves more attention when evaluating its future invasion risk because this is the habitat in which larvae occur. The modeling also suggested that considerable long-term efforts are required to eradicate this pest once it becomes established, which highlights the importance of taking control measures at the early stages of invasion.

In the second chapter, I examined shelter competition between invasive *E. sinensis* and native *E. japonica* under laboratory conditions. Only male individuals were used to eliminate the effect of sex differences. Shelter competition trials were conducted in pairs of one adult native and one adult invasive crab in different size combinations. A resident-intruder model was used in this experiment and interactions between the two opponents were registered by a drive recorder. Crab behaviour frequency and fight duration were analyzed. My results suggested competition between the two species was size-dependent: *E. japonica* always successfully defended shelter when competing with size-matched or slightly larger *E. sinensis*; *E. sinensis* only evicted *E. japonica* from shelter when its size was 1.1 times larger than that of *E. japonica*. The two species exhibited different behavioural patterns: compared with *E. sinensis*, *E. japonica* frequently displayed positive behaviour (approach, walking leg contact, chela contact) and seldomly displayed negative behaviour (retreat). Fight duration reached maximum when two opponents had a similar probability of wining. My results highlight the important role of strong native competitors in controlling invasion success, and invasive *E. sinensis* may be unlikely to exclude native *E. japonica* from its habitat by direct competition for shelter.

In the third chapter, I investigated the potential predatory impacts of invasive *E. sinensis* on native *E. japonica*. To achieve this goal, I first studied the cannibalism patterns in native *E. japonica* and then compared cannibalism with the intensity of predation by invasive *E. sinensis* on juvenile *E. japonica*. In cannibalism experiments, I examined the possibility of cannibalism in intermolt *E. japonica* in relation to predator–prey size difference, predator sex, prey density, and presence of alternative food and shelter under laboratory conditions. Predator crabs were starved for 48 h and then exposed to smaller conspecifics as prey for 24 h, after which the number of dead/injured prey was recorded. My results indicated that *E. japonica* cannibalizes conspecifics when the relative size difference between cannibal and victim becomes large. Males were more cannibalistic than females. The presence of alternative food and shelter effectively mitigated cannibalism. Based on these results, I hypothesize that the segregated distribution pattern of *E. japonica* along river courses may be an evolutionary adaptation to reduce intraspecific predation. In cannibalism and predation comparison experiment, adults of the two species were regarded as predators and they were fed before experiment. Each trial contained one predator and five juvenile *E. japonica*. The results suggested no significant difference was detected among treatments and all predators predated intensively on juvenile *E. japonica*.

Finally, the invasion risk of Chinese mitten crab in Japan was discussed on the basis of current results. In Japan, there are limited suitable estuarine environments for the larvae of *E. sinensis*. Around these estuaries, native Japanese mitten crab populations are already distributed. This competitively superior native species may act as a form of biotic resistance and prevent the establishment of invasive *E. sinensis* in Japan. But we should be cautious that invasive *E. sinensis* may adversely influence native *E. japonica* populations in other ways, such as pathogen transmission and hybridization. Further studies are required to address these issues. Several management strategies are proposed to control Chinese mitten crab in Japan. Strict management measures should be taken to prevent the escape of live *E. sinensis* from food market. In addition, appropriate ballast water management strategies should be developed to prevent the further introduction of larvae of this pest via ballast water discharge.

Publications

Zhang, Z., Yokota, M., & Strüssmann, C. A. Potential competitive impacts of the invasive Chinese mitten crab *Eriocheir sinensis* on native Japanese mitten crab *Eriocheir japonica*. Hydrobiologia (in press).

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Presentations

Zhang, Z., Yokota, M., & Strüssmann, C. A. (2015). Invasion risk analysis of Chinese mitten crab in Japan using life history model. The 53rd Annual Meeting of Carcinological Society of Japan, October 10–11, Tokyo, Japan

Zhang, Z., Yokota, M., & Strüssmann, C. A. (2017). Competitive and predatory impacts of invasive Chinese mitten crab on native Japanese mitten crab. The JSFS 85th Anniversary-Commemorative International Symposium, September 22–24, Tokyo, Japan

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Zhang, Z., Yokota, M., & Strüssmann, C. A. (2018). Potential competitive impacts of the invasive Chinese mitten crab on native Japanese mitten crab. The ninth international Crustacean Congress, May 22–25, Washington, D.C., USA

Chapter 1

General Introduction

1.1 Introduction of Chinese mitten crab

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards, 1853), is a wide–spreading aquatic species natively distributed in eastern Asia, extending from South of China to the western Korean Peninsula (Fig. 1.1) (Zhao et al., 1988; Dittel and Epifanio, 2009; Sui et al., 2011; McLay, 2015). This species is catadromous, which grows in freshwater habitats and migrates to the estuarine environments after sexual maturity for the purpose of reproduction (Zhao et al., 1988; Dittel and Epifanio, 2009; Blumenshine et al., 2012). Due to the delicacy and high commercial values, Chinese mitten crab is regarded as an important aquaculture species in its native ranges, especially in China (Zhao et al., 1988; Wang et al., 2006; Cheng et al., 2008; Sui et al., 2011; Wang et al., 2016). Its aquaculture production has increased rapidly in recent years and reached nearly 800 thousand tonnes in 2014 (Fig. 1.2) (FAO, 2016).

Despite the commercial importance within native ranges, *E. sinensis* has been regarded as an annoying invasive alien species outside native range (Veldhuizen and Stanish, 1999; Herborg et al., 2003; Rudnick et al., 2005; Dittel and Epifanio, 2009; Brockerhoff and McLay, 2011). Invasive species have been considered as a serious global environmental problem and posed substantial threat to global species biodiversity and ecosystem services in the recipient areas (Lodge, 1993; Vitousek et al., 1996; Higgins et al., 1999; Riul et al., 2013; Vorsino et al., 2014). Invasive *E. sinensis*, not an exception of this phenomenon, has successfully invaded some European and North American countries (Fig. 1.1), and caused considerable ecological, economic, and human health impact (Schrimpf et al., 2004; Rudnick and Resh, 2005; Gollasch, 2006; Dittel and Epifanio, 2009; Webster et al., 2015; Wójcik et al., 2015). There is widespread agreement that the invasion of Chinese mitten crab is mainly caused by ballast water discharges, live import, and religious practices of animal release (Cohen and Carlton, 1997; Rudnick et al., 2000; Shiu and Stokes, 2008; Dittel and Epifanio, 2009; Low et al., 2013; Yeomans and Clark, 2016).

1.2 Chinese mitten crab in Japan

The Chinese mitten crab has also been designated as an invasive alien species in Japan according to the Japanese Invasive Alien Species Act (Ministry of the Environment, Government of Japan, 2004). Despite the invasive status in Japan, live adult *E. sinensis* are imported from China to Japan as edible delicacies every year. In 2017, about 87 tons of live Chinese mitten crab were imported to Japan with a value of approximately 320 million JPY (Ministry of Agriculture, Forestry and Fisheries, Japan) (Fig. 1.3). In addition, this invasive species was once cultured in Chiba and Yamagata prefectures around the year 2000 by releasing juveniles into paddy fields (Takeda and Koizumi, 2005; Kobayashi, 2012). In 2004, two adult female specimens were found in Tokyo Bay, Japan (Takeda and Koizumi, 2005), and there is a possibility that Chinese mitten crab may establish populations in Japan. Up to now, however, the invasion risk of Chinese mitten crab in Japan still remain unstudied. As pointed out by Therriault and Herborg (2008), two aspects should be considered in invasion risk assessment: probability and impact. Thus far, the population dynamics of *E. sinensis* still remains unclear due to its complex catadromous life style. Besides, this species has been designated as an invasive alien species in Japan, but its potential impact in Japan remains unknown. In particular, there is native Japanese mitten crab *Eriocheir japonica* in Japan, which belongs to the same genus with *E. sinensis*. Two species share a number of similar biological characteristics, including morphology, life history, and feeding habit (Table 1.1). The possible interactions between the two species remain unclear.

1.3 Study objectives

In order to solve above remaining problems, I conducted the present study. The objectives of my research were to analyze the population dynamics of Chinese mitten crab by using a periodic matrix population model and examine its potential interactions with native Japanese mitten crab under laboratory conditions.

The Chinese mitten crab is an important commercial species in China and has received extensive studies; therefore, information on its life history is well known. On the basis of life history information from published literature, I developed a periodic matrix population model for *E. sinensis* to better understand its population growth in Chapter 2. The key factors in regulating the population growth were identified by an elasticity analysis. In addition, the efficacy of possible control strategies to reduce the abundance of *E. sinensis* was estimated.

Invasive species could negatively influence native ecosystems through various mechanisms; among them, competition and predation might be the most extensively studied interactions. Previous studies elucidated that asymmetry of competition between invasive and native species plays an essential role in species displacement (Usio et al., 2001). If the native *E. japonica* was more aggressive than invasive *E. sinensis*, the native crabs might act as a form of biotic resistance and prevent the invasion of invasive *E. sinensis*. On the contrary, if invasive *E. sinensis* was competitively superior, the native *E. japonica* might be competitively excluded from their suitable habitats, which would increase the susceptibility of native species to natural enemies. Therefore, to investigate the asymmetry in competitive ability between native *E. japonica* and invasive *E. sinensis*, I performed shelter competition experiments between the two species under laboratory conditions in Chapter 3.

For the purpose of identifying predatory impact of invasive *E. sinensis* on native *E. japonica*, I examined the asymmetry in intra– and interspecific predation on juvenile *E. japonica* under laboratory conditions in Chapter 4. Previous stomach content analysis studies indicate that *E. japonica* and *E. sinensis* have the same food habits: both are omnivorous and opportunistic (Jin et al., 2003; Kobayashi, 2009). Therefore, I hypothesize that both native *E. japonica* and invasive *E. sinensis* may be capable of predating on juvenile *E. japonica*. Cannibalism (intraspecific predation) is a common phenomenon in decapod crustaceans; up to now, however, no research has been conducted to investigate the cannibalism patterns in *E. japonica* and little information is available on the degree of cannibalism in this species. Therefore, in Chapter 4, I first examined the possibility of cannibalism in intermolt Japanese mitten crab in relation to predator–prey size difference, predator sex, prey density, and presence of alternative food and shelter under laboratory conditions. Then I compared cannibalism with the intensity of predation by adult *E. sinensis* on juvenile *E. japonica*.

I summarized the results of present study in Chapter 5 and discussed the invasion risk of *E. sinensis* in Japan. Several management strategies were proposed to control this invasive species in Japan.

Figures

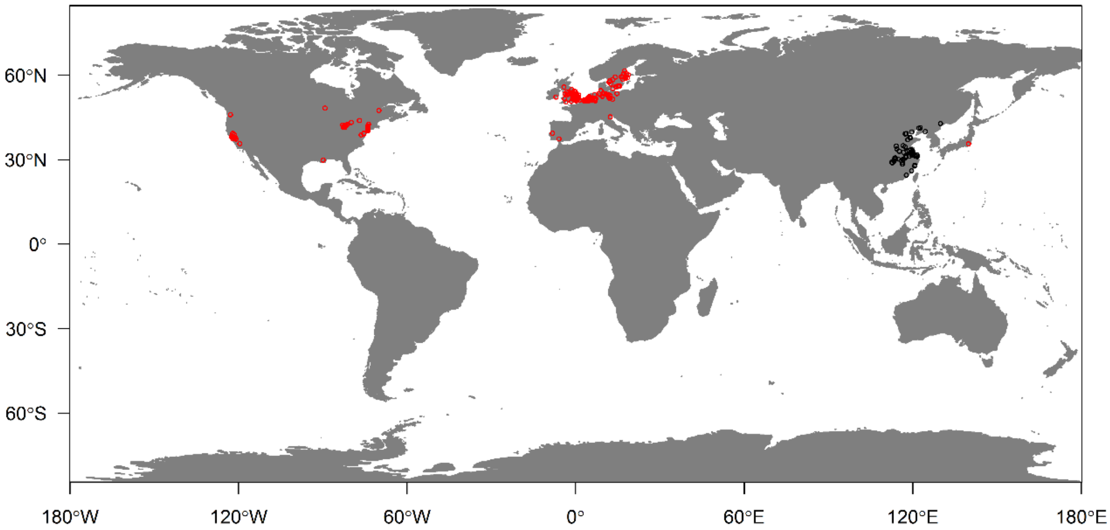


Fig. 1.1 Worldwide occurrence records of the Chinese mitten crab *Eriocheir sinensis*. Black points represent the occurrence records of Chinese mitten crab in its native range. Native distribution data was collected from previous studies (Zhao et al., 1988; Tang et al., 2003; Sui et al., 2009; Xu et al., 2009; Kang et al., 2016). Red points indicate the occurrence records of *E. sinensis* in its invasive range, which were obtained from the Global Biodiversity Information Facility (http://www.gbif.org) and the Nonindigenous Aquatic Species (https://nas.er.usgs.gov).

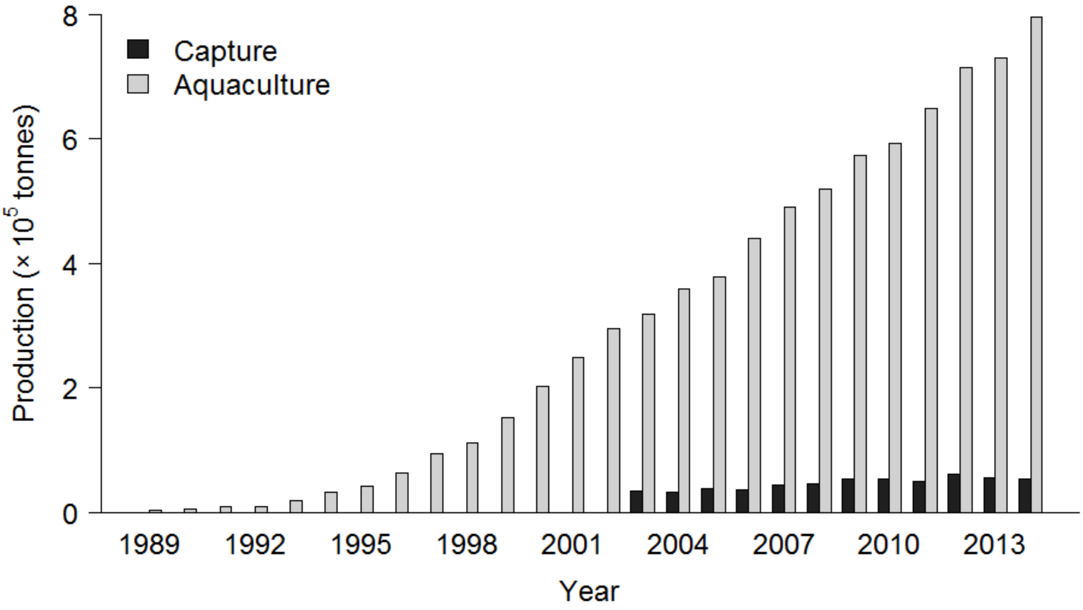


Fig. 1.2 Global aquaculture and capture production of the Chinese mitten crab *Eriocheir sinensis* (data source: http://www.fao.org/fishery/species/3466/en).

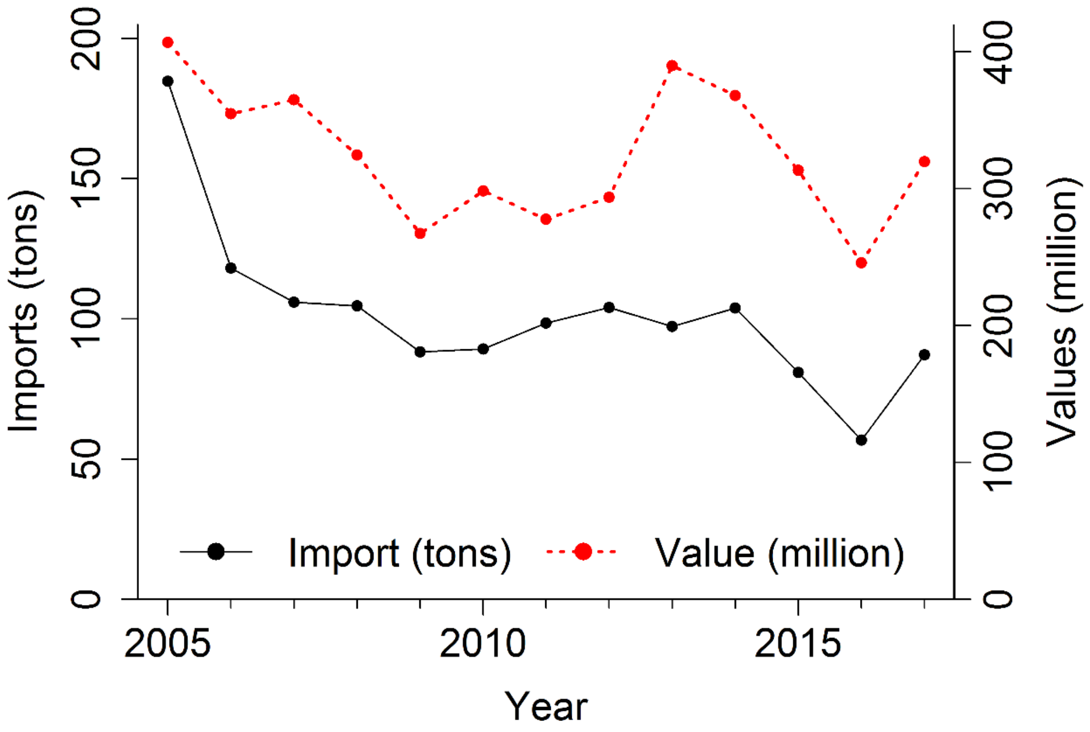


Fig. 1.3 Trade of the Chinese mitten crab *Eriocheir sinensis* in Japan (data source: http://www.maff.go.jp/j/tokei/kouhyou/kokusai/houkoku_gaikyou.html#r26).

Tables

Table 1.1 Similarities between the invasive Chinese mitten crab *Eriocheir sinensis* and the native Japanese mitten crab *Eriocheir japonica*.

Name	Chinese mitten crab *Eriocheir sinensis*	Japanese mitten crab *Eriocheir japonica*
Photograph		
Life cycle	Catadromous	Catadromous
Feeding habit	Omnivorous & opportunistic	Omnivorous & opportunistic
Chromosome number	2n = 146	2n = 146

Chapter 2

A periodic matrix population model of the invasive Chinese mitten crab, *Eriocheir sinensis*

2.1 Introduction

The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards, 1853), is a widespread aquatic species that is native to eastern Asia (Zhao et al., 1988; Sui et al., 2011). Because of its delicate flavor and high commercial value, this crab has become an important aquaculture species, especially in China (Zhao et al., 1988; Wang et al., 2006; Cheng et al., 2008; Sui et al., 2011; Wang et al., 2016); its aquaculture production has increased rapidly in recent years and reached nearly 800 thousand tonnes in 2014 (FAO, 2016).

Despite its commercial importance within its native range, *E. sinensis* has been recognized as a problematic invasive species in many regions of the world, especially North America and Europe (Veldhuizen and Stanish, 1999; Rudnick et al., 2000; Herborg et al., 2003; Dittel and Epifanio, 2009; Drotz et al., 2012; McLay, 2015). It is widely accepted that the invasion of this species is mainly caused by human activities such as ballast water discharge and live importation (Cohen and Carlton, 1997; Herborg et al., 2007a, b; Dittel and Epifanio, 2009; Tilburg et al., 2011). This species is catadromous, growing in freshwater ecosystems and migrating to brackish waters for reproduction after reaching sexual maturity (Zhao et al., 1988; Veldhuizen and Stanish, 1999; Rudnick et al., 2005; Dittel and Epifanio, 2009; McLay, 2015). Therefore, it could have negative impacts on both freshwater and estuarine ecosystems. For example, as an omnivorous and opportunistic feeder this crab can consume a variety of food materials and exert detrimental impacts on native aquatic communities (Veldhuizen and Stanish, 1999; Rudnick and Resh, 2005; Czerniejewski et al., 2010; Rosewarne et al., 2016). Previous studies confirmed that under laboratory conditions *E. sinensis* could predate on fish eggs and the blue mussel *Mytilus edulis trossulus* (Webster et al., 2015; Wójcik et al., 2015). In addition, this invasive crab could disturb indigenous biodiversity by competing with native species: Gilbey et al. (2008) demonstrated that juvenile *E. sinensis* outcompeted the similar–sized indigenous crab *Carcinus maenas* in the Thames estuary. *E. sinensis* has also caused considerable economic loss by damaging fishing facilities as a result of its burrowing activity (Rudnick et al., 2000; Dittel and Epifanio, 2009). In addition to predation and competition, Schrimpf and colleagues (2014) confirmed that this pest can transmit the crayfish plague pathogen *Aphanomyces astaci* to native European crayfish species. Given the substantial adverse impacts of *E. sinensis* on invaded ecosystems, this species was registered in the list of “100 of the world’s worst invasive alien species” (Lowe et al., 2000). To effectively control this invasive species, it is of great importance to understand its population dynamics and life history. Moreover, systematic consideration of this specific catadromous life history makes both estimating invasion ability and developing effective control measures significant challenges.

Matrix models are a powerful tool for understanding population dynamics, and can combine important life–history information to allow detailed simultaneous analysis of several vital rates (Caswell, 2001; Roff, 2010). Life–history information plays a significant role in matrix model construction: depending on the variables, matrix models can be divided into age–based matrix models and stage/size–based matrix models (Caswell, 2001; Roff, 2010). Matrix models have been extensively applied to design effective management strategies for initial population growth or spread of target species (Federico and Canziani, 2005; Govindarajulu et al., 2005; Morris et al., 2011; Dunham et al., 2014; Cuddington et al., 2014; Beston et al., 2016). For example, Govindarajulu et al. (2005) constructed a matrix model for the invasive American bullfrog *Rana catesbeiana* and suggested that removing metamorphs was the most effective strategy for decreasing bullfrog population growth rates. Morris et al. (2011) developed a matrix population model for the invasive lionfish and evaluated the effectiveness of possible removal efforts.

In this study, we constructed a matrix population model based on larval stage, body size and reproductive seasonality for *E. sinensis* using published information about its life history. The most critical parameters in regulating mitten crab population dynamics were identified by an elasticity analysis. The efficacy of possible removal efforts was also estimated by numerical simulation.

2.2 Materials and Methods

2.2.1 Life cycle description

The Chinese mitten crab is catadromous, meaning that it grows in freshwater ecosystems in summer and migrates to brackish waters for reproduction in winter (Zhao et al., 1988; Veldhuizen and Stanish, 1999; Rudnick et al., 2005; Dittel and Epifanio, 2009). In aquaculture, it is a common practice to release *E. sinensis* megalopae into freshwater habitats (such as ponds and lakes). Under aquaculture conditions, its life cycle duration is normally two years, which consists of three main stages, i.e., hatchery stage, nursery stage, and adult grow–out culture stage (Wang et al., 2006; Cheng et al., 2008; Wang et al., 2016). In this study, we used juvenile or larval developmental stage (j–stage) and adult body size classes as the basic variable describing the life history of *E. sinensis*, as with a previous model for the blue crab (Miller, 2001). The life cycle of this species was divided into two seasons: summer (June to November) and winter (December to May) and each season contained three classes or stages (Fig. 2.1). In summer, j–stage individuals move to freshwater habitats and grow into small crab (s–class: crablets, coin–sized crabs) at winter (as_{11}). A small proportion of s–class become precocious and participate in reproduction (aw_{11}) while others survive winter (the overwinter crablets) and develop into middle crab (m–class: smaller than 5 cm carapace width: CW) at the first of next summer (aw_{21}). After m–class crabs survive during summer (as_{22}), some m–class crabs develop into large crabs (l–class: larger than 5cm CW) (aw_{32}), other crabs migrate to estuary mouths for reproduction (aw_{12}) and rest remain in the same class (aw_{22}). The l–crabs who survive during summer remain in this class (as_{33}). In winter, some l–class crabs move to the estuary to reproduce (aw_{13})and others stay in the river and wait until next reproductive season (aw_{33}).

2.2.2 Model development

Based on above life–history information, a periodic matrix population model was developed and a one–year time step (also called projection interval) from December to December was used. We assume that sex ratio of the population is always even and focus on female population in this study. The annual transition matrix ($\boldsymbol{A}$) was calculated as the product of two seasonal matrices ($\boldsymbol{A}_{summer} \times \boldsymbol{A}_{winter}$) as follows:

$$\boldsymbol{A} = \begin{bmatrix} as_{11} & 0 & 0 \\ 0 & as_{22} & 0 \\ 0 & as_{32} & as_{33} \end{bmatrix} \times \begin{bmatrix} aw_{11} & aw_{12} & aw_{13} \\ aw_{21} & aw_{22} & 0 \\ 0 & aw_{32} & aw_{33} \end{bmatrix},$$

where as_{ij} and aw_{ij} of *i* row and *j* column in the matrixes represent transition probabilities during summer and winter, respectively. Detailed biological meanings of these transition probabilities have been described in the previous paragraph and these estimates are presented in next subsection.

The matrix equation projecting *E. sinensis* population from year *t* to *t* + 1 was:

$$\boldsymbol{N}_{t+1} = \boldsymbol{A}\boldsymbol{N}_t,$$

where column vectors $\boldsymbol{N}_t$ and $\boldsymbol{N}_{t+1}$ represent December abundance by life stage at year *t* and *t* + 1, respectively; the matrix $\boldsymbol{A}$ is the annual population projection matrix, where its dominant eigenvalue measures the population growth rate λ, and its right and left eigenvectors are the stable class distribution and the class–specific reproductive values, respectively (Caswell, 2001).

2.2.3 Parameter estimation

Fifteen parameters are needed to describe transition probabilities in the annual transition matrix (Table 2.1). *E. sinensis* farming has developed rapidly in China in recent decades and information on this species is well known; therefore, several vital parameters of this species were mainly estimated based on published information. Sexual precocity has been observed in crablets (s–class) of *E. sinensis* (Zhu et al., 2012; Chang et al., 2017); based on the culture results of Zhu et al. (2012), we assumed that the precocity rate of s–class (R_1) is 0.044. In this study, we assumed that, except for body weight, there is no difference in vital rates between m–class and l–class. For m–crabs in winter, we assumed that they have two equal choices: either migrate to an estuary for reproduction or grow into the l–class. Thus, we ignored the possibility that a m–class crab survives winter and remains in the same class; $aw_{22} = 0$. The reproduction probability of both m–class (R_2) and l–class (R_3) is assumed to be 0.5.

Chang et al. (2017) compared the reproductive performance of precocious and normal female *E. sinensis*; they found that body weight, fecundity, spawning rate, percentage of berried females successfully hatching larvae, egg hatching rate, and egg fertilization rate of normal females were higher than those of the precocious crabs (Table 2.1 in Chang et al., 2017). According to their study, the body weights of precocious and normal crabs are 21.4 g and 97.1 g, respectively; we assumed that the body weights of s– and l– class crabs correspond to precocious and normal crabs, respectively, and the body weight of a m–class crab is 60 g. Based on the above information, the effective fecundity of a l–class crab was calculated as:

$$F_3 = 97.1 \times 5{,}234 \times 0.85 \times 0.853 \times 0.938 \times 0.747 \times \frac{1}{2} = 129{,}096 \ .$$

For adjusting to female population, we divided by 2 as an even sex ratio. Similarly, the effective fecundity of a precocious s–class crab (F_1) and a m–class crab (F_2) were calculated to be 807 and 79,771, respectively.

Larvae of *E. sinensis* include five zoeal stages and a megalopa stage (Zhao et al., 1988; Anger, 1991; Cheng et al., 2008; Dittel and Epifanio, 2009; Wang et al., 2016). The survival rate during j–stage (σ_j) was expressed as follows:

$$\sigma_j = e^{-MD},$$

where *M* is the instantaneous mortality rate and *D* the developmental duration. Information on the larval biology of *E. sinensis* is limited, therefore, *M* was adopted from the estimation by White et al. (2014), who calculated that $M \leq 0.14$ larvae per day; hence, we assumed $M = 0.14$ larvae per day. Anger (1991) described *D*, the duration of the zoea and megalopa stages in larvae of *E. sinensis*, was mainly affected by water temperature (*T*), and the relationship between developmental duration and water temperature was expressed as follows:

$$D = 58.4e^{-0.131T} + 36.7 * e^{-0.120T} + 55.0e^{-0.144T} + 61.7e^{-0.139T} + 82.1e^{-0.136T} + 100e^{-0.095T}.$$

The first five terms on the right side of above equation represent the periods of the zoea, and the last term is the megalopa period. All periods depend on water temperature. The Changjiang (Yangtze River) estuary is the most notable area where wild *E. sinensis* larvae are captured (Zhao et al., 1988; Sui et al., 2011), and its mean water temperature from April to May, when the larvae occur, is about 15.65 °C (Lin et al., 2016). Therefore, *D* was calculated to be about 58.29 days and σ_j was estimated as about 0.0002855. The average number of j–stage produced by a crab in body class i (aw_{1i}, $i = 1$: s–crab, $i = 2$:

m–crab, $i = 3$: l–crab) was calculated as the product of R_i, F_i, and σ_j:

$aw_{1i} = R_i F_i \sigma_j$.

The overwinter survival rates of s–class (σ_{W1}) and l–class (σ_{W3}) were 0.8750 and 0.7637, respectively (Wu et al. 2007, 2009; Li et al. 2011). As indicated above, for the sake of simplicity we assumed no difference in vital rates between m–class and l–class; thus, the overwinter survival rate of m–class (σ_{W2}) was also 0.7637. The probability that s–class crab survive winter and grow into m–class was calculated as $aw_{21} = \sigma_{W1} \times (1 - R_1)$. In the same way, the probability that m–class crabs survive winter and grow into l–class was as $aw_{32} = \sigma_{W2} \times (1 - R_2)$. The l–class crabs do not grow, but stay in the river and wait until next reproductive season. So, $aw_{33} = \sigma_{W3} \times (1 - R_3)$.

Based on field culture experiments, during summer the survival rates of j–stage (σ_{S1}, which equals as_{11}) and m–class (σ_{S2}) were 0.1106 and 0.8488, respectively (Zhu et al., 2012). We assume that a m–class in summer has two equal choices: either grow into l–class or stay in the class. If the probability of a m–class crab growing into l–class ($\gamma_{m \to l}$) is assumed to be 0.5. The transition (growth) to l–class and stay probabilities of m–class in summer are expressed as $as_{22} = \sigma_{S2} \times (1 - \gamma_{m \to l})$ and $as_{32} = \sigma_{S2} \times \gamma_{m \to l}$, respectively. The survival rate of l–crabs during summer (σ_{S3}, which equals as_{33}) is unknown, but a positive correlation between survival rate and body size has been found in crustaceans (Chockley and Mary, 2003); therefore, as_{33} is assumed to be 0.9.

2.2.4 Elasticity analysis

As shown in Table 2.1, a number of parameters that are measured at different scales (e.g., survival rate and effective fecundity) are required for the determination of the matrix model and parameters; therefore, an elasticity analysis (change in λ due to a proportional change in a vital rate) rather than a sensitivity analysis (change in λ due to an absolute change in a vital rate) was carried out to identify the key factors that influence mitten crab population dynamics (Caswell, 2001; Stubben and Milligan, 2007).

2.2.5 Inclusion of removal efforts

The matrix model was used to explore the efficacy of possible control strategies for reducing numbers of invasive *E. sinensis*. Harvest strategies in summer and winter are represented by diagonal matrices $\boldsymbol{H}_S$ and $\boldsymbol{H}_W$ respectively as follows (Caswell, 2001; Federico and Canziani, 2005):

$$\boldsymbol{H}_S = \begin{bmatrix} 1-S_1 & 0 & 0 \\ 0 & 1-S_2 & 0 \\ 0 & 0 & 1-S_3 \end{bmatrix},$$

$$\boldsymbol{H}_W = \begin{bmatrix} 1-W_1 & 0 & 0 \\ 0 & 1-W_2 & 0 \\ 0 & 0 & 1-W_3 \end{bmatrix},$$

where S_1, S_2 and S_3 represent the proportion of j–stage, m–class, and l–class removed from the population during summer, respectively; W_1, W_2 and W_3 represent the proportion of s–class, m–class, and l–class removed before reproduction during winter, respectively. The number of crabs at each class in December including harvest was therefore expressed as follows:

$$\boldsymbol{N}_{t+1} = \boldsymbol{A}_{summer}\boldsymbol{H}_S\boldsymbol{A}_{winter}\boldsymbol{H}_W\boldsymbol{N}_t.$$

Numerical simulations were performed to assess the efficacy of possible management activities. All statistical analyses and simulations were performed using R version 3.1.0 (R Development Core Team, 2014).

2.3 Results

2.3.1 Model calculation

The matrix population model demonstrated that the population growth rate λ of *E. sinensis* in a suitable habitat was 1.301. Although deterministic equation like this model must be described exponential population growth for any trivial and small initial population size, we confirmed that at least six l–class female crabs are needed for population growth by numerical simulation (Fig. 2.2). For simplicity, we henceforth focused on an initial population of eight l–class females being introduced to a suitable habitat where this species did not exist previously. The results of stable stage distribution indicated that j–stage and s–class dominated the population during summer and winter, respectively (Table 2.2). The model also suggested that reproductive values of *E. sinensis* increased with body growth (Table 2.2).

2.3.2 Elasticity analysis results

The results of elasticity analysis suggest that parameters in the matrix population model contributed differently to λ (Table 2.1). Two parameters, including R_1 and M, had negative effects on λ, while all the other parameters had positive effects. The absolute values of the elasticity analysis results suggested that the water temperature and mortality rate during larval development contribute most to population growth. As a consequence, the larval stage is the most critical in the life history of *E. sinensis*. The effects of these two variables on population growth rate were examined by numerical simulations. Consistent with the elasticity analysis results, simulations showed that the water temperature had a positive effect on λ while the effect of larval mortality rate was negative; in addition, either a greater than 4.2% decrease in temperature or a greater than 8.1% increase in mortality rate would result in negative population growth (Figure 2.3a). The combined effects of the water temperature and larval mortality rate on population growth rate are presented in Figure 2.3b.

2.3.3 Effects of removal efforts

The effects of summer and winter removal efforts on population growth rate are shown in Figure 2.4. Despite the simulation results suggested that it is effective to reduce population growth by removing larva in summer and s–class in winter (Figure 2.4), removal efforts were only focused on m–class and l–class because of the difficulty in capturing abundant small and invisible individuals. In winter, removing l–class crabs is effective in controlling *E. sinensis* population size but at least 52.6% of l–class must be removed from the population to achieve a negative population growth (Figure 2.4a). In summer, it is effective to reduce population size by removing m–class crabs and at least 48.3% of m–class are required to be captured to get a negative population growth (Figure 2.4b). A combination of summer removal of m–class and winter removal of l–class would be most effective in reducing the population size (Figure 2.5). Removal efforts were assumed to be commenced after 20 years of invasion and the results of the combined removal efforts on population size suggested that higher removal rates for a long time were required to totally eradicate this pest (Figure 2.6).

2.4 Discussion

2.4.1 Model validity and important parameters

In this study, we constructed a periodic body size based matrix population model for *E. sinensis*, which provides an initial step toward a better understanding of the specific life history of this crab. The body size specific reproductive values and stable size distribution results were consistent with the biology of this crab. A positive correlation between fecundity and body size has been reported for *E. sinensis* (Przemysław and Marcello, 2013; Chang et al., 2017); the high fecundity of this species certainly results in a high proportion of larvae in summer. Miller (2001) developed a four–stage matrix model for the blue crab *Callinectes sapidus* in Chesapeake Bay. According to his interpretation, the probability of transition from larvae to overwintering juveniles included survival of zoea, megalopae, and newly settled crabs (Miller, 2001), meaning that the larval (megalopae) stage in his analysis actually represents eggs; hence, he explained the high reproductive values of matured *C. sapidus* in summer by a high larval mortality rate (Miller, 2001). Our present results for much higher reproductive value and lower stable ratios of m–class and l–class in summer (Table 2) were comparable to those reported by Miller (2001).

The elasticity analysis results of our matrix model demonstrated that larval mortality rate and precocity rate had negative effects on population growth. It is easy to understand the negative effect of larval mortality on λ. Compared with normal crabs, the precocious crabs have poorer reproductive performance (Chang et al., 2017); therefore, an increase in the precocity rate means juvenile crabs have less opportunity to grow large, hence the number of large crabs would decrease, leading to a decrease in mitten crab population recruitment. The elasticity analysis also indicated that the water temperature and mortality during the larval stage are the most critical parameters in the mitten crab life history. This result supports the assumption in previous studies that the larval stage is critical for the establishment of this crab (Anger, 2006; Tilburg et al., 2011; Blumenshine et al., 2012). The dynamics of mitten crab larvae are strongly influenced by various environmental factors such as water temperature, salinity, and hydrodynamic conditions (Anger, 1991; Tilburg et al., 2011; Blumenshine et al., 2012). The water temperature and salinity during larval development could directly influence the larval survival rate (Anger, 1991). In addition, water temperature positively influences the duration of larval development (Anger, 1991): a lower temperature leads to a longer planktonic larval development period, which would increase the susceptibility of larvae to natural enemies or their risk of being transported out of the habitat. The larval swimming behavior of *E. sinensis* is unknown (Dittel and Epifanio, 2009; Tilburg et al., 2011), but it is generally accepted that planktonic larvae are at the whim of the currents, and their retention and settlement mainly rely on local hydrodynamic features, such as tides, river discharge, and winds (Tilburg et al., 2011). In this process, large numbers of larvae are carried away and lost.

2.4.2 Invasion risk from biological aspects

Currently, the most prevalent methods of evaluating *E. sinensis* invasion risk are the ecological niche–modeling approach and the habitat–matching approach. For instance, Herborg et al. (2007a, b) developed ecological niche models for this invasive species, based on species occurrence records and selected environmental variables, to predict its potential suitable habitat in Europe and North America. Capinha and Anastácio (2011) predicted the potential distribution of this invasive crab in the Iberian peninsula by an ensemble modeling approach. Although previous approaches are mainly used statistical relations between environment and invasion success, our matrix population model focuses on biological structure of *E. sinensis* and identifies that the larval stage strongly influences the population growth. Therefore, the estuarine environments deserve more attention when evaluating the future invasion risk of this species, because they are the habitat where mitten crab reproduction and recruitment occur.

2.4.3 Effectivity of control efforts

In attempts to reduce the population size of this invasive crab, several control methods have been suggested, including commercial exploitation and a “catch as many as you can” strategy, but these have not proved to be effective (Clark, 2011; Global Invasive Species Database, 2018). Our simulation results indicate that a large proportion of large size crabs (l–class) in winter and middle size crabs (m–class) in summer need to be removed to achieve negative population growth, and that an extended period of time is required to totally eradicate this pest. These results may partially explain the unsuccessful eradication efforts, and suggest that it is difficult and costly to totally eradicate this invasive species once it becomes established (Hänfling et al., 2011). Therefore, it is of great importance to take control measures at the early stages of invasion to prevent the introduction and spread of this invasive crab. For example, in Japan, *E. sinensis* has been designated as an invasive alien species according to the Japanese “Invasive Alien Species Act” (Ministry of the Environment, Government of Japan, 2004), but approximately 100 tons of live crabs are imported as edible delicacies every year, and two adult females were discovered in Tokyo Bay in 2004 (Takeda and Koizumi, 2005). It is possible that invasive *E. sinensis* will become established in Japan (Kobayashi, 2012); once established, this invasive crab could have negative consequences for native Japanese species, especially for its congener the Japanese mitten crab *E. japonica*, which is an important fisheries species widely distributed in Japan (Zhang et al., 2016, 2017, 2018). Ishiguro et al. (2015) confirmed that *E. sinensis* has similar ability to survive in dry conditions as *E. japonica*. To prevent the invasion of *E. sinensis*, the Japanese government has taken strict preventive measures. For example, special permission is needed for importation, sale, or study of live *E. sinensis*. We should note that in addition to live importation of adult crabs, larvae of the Chinese mitten crab can be transported via ballast water (Cohen and Carlton, 1997; Dittel and Epifanio, 2009). Therefore, appropriate ballast water management strategies should be developed to prevent the further introduction of this pest via ballast water discharge.

2.4.4 Further prospects

We developed a periodic body size based matrix population model for *E. sinensis*. The model demonstrated that the larval stage is most critical in the mitten crab life history, and that estuarine environments warrant greater attention in the development of economically and biologically efficient management strategies. Despite its potential importance, our model has some limitations: it does not include density dependence because of the lack of information about density–dependent effects on vital rates in *E. sinensis*. Although the motivation of this study is invasion impact on region with competitor *E. japonica*, the present model does not consider its the interdependence for simplify. In addition, there is limited knowledge about the larval biology of this species, and general planktonic larval mortality rate was estimated based on previous studies. Therefore, further studies are needed to address these aspects.

Figures

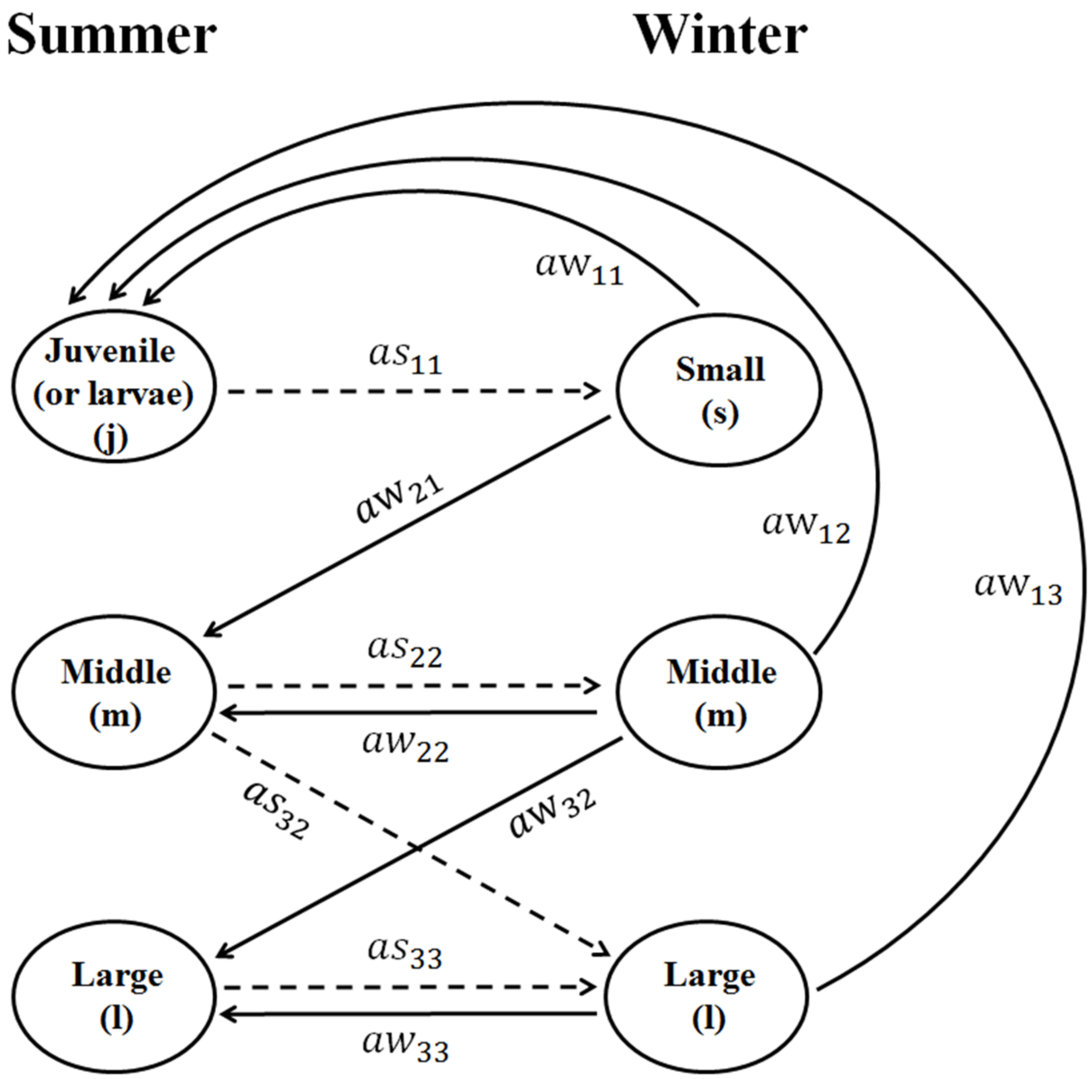


Fig. 2.1 Life cycle chart of the Chinese mitten crab *Eriocheir sinensis* used to construct the periodic matrix population model based on stage (j: juvenile or larvae) and body size (s: small, m: middle, l: large). The life cycle was divided into two seasons and three classes. Thin arrows represent transitions among classes. Thick arrows indicate reproduction from classes in winter. The relationships among parameters of the arrow and vital rates in Table 2.1 are as follows: $as_{11} = \sigma_{S1}$, $as_{22} = \sigma_{S2} \times (1 - \gamma_{m \to l})$, $as_{32} = \sigma_{S2} \times \gamma_{m \to l}$, $as_{33} = \sigma_{S3}$, $aw_{11} = R_1 F_1 e^{-MD}$, $aw_{12} = R_2 F_2 e^{-MD}$, $aw_{13} = R_3 F_3 e^{-MD}$, $aw_{21} = \sigma_{W1} \times (1 - R_1)$, $aw_{22} = 0$, $aw_{32} = \sigma_{W2} \times (1 - R_2)$, $aw_{33} = \sigma_{W3} \times (1 - R_3)$.

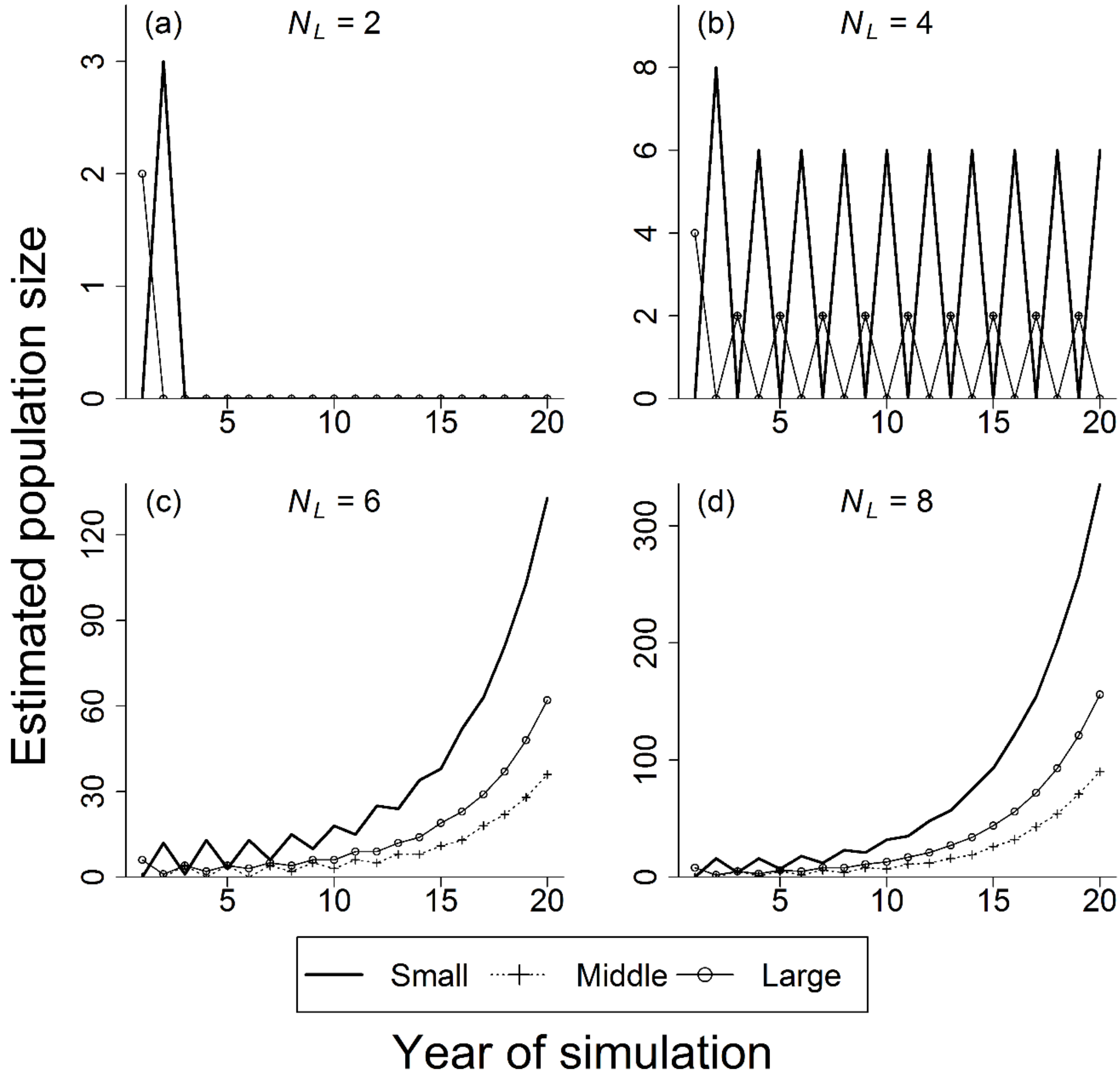


Fig. 2.2 Number of Chinese mitten crab *Eriocheir sinensis* in December starting with different initial population sizes in the stage–based matrix population model. N_L means the number of initial introduced large sized crabs. (a) $N_L = 2$, (b) $N_L = 4$, (c) $N_L = 6$, (d) $N_L = 8$.

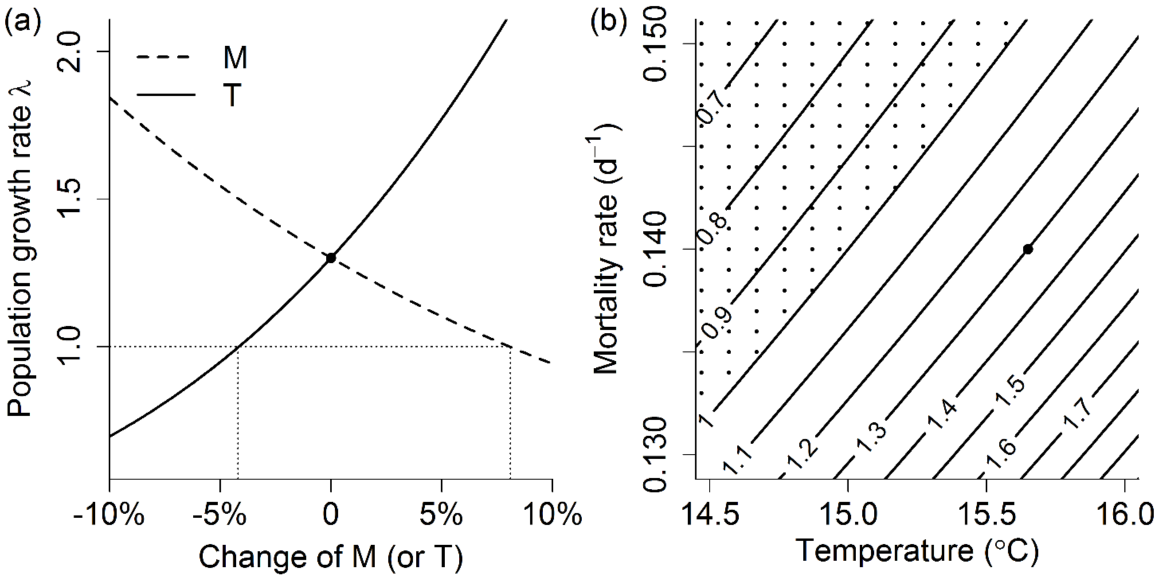


Fig. 2.3 (a) Separate effects on the population growth rate of the Chinese mitten crab *Eriocheir sinensis* of water temperature (*T*) and larval mortality rate (*M*) during larval development. Intersection of the two curves represents the population growth rate when no change occurs in water temperature or larval mortality rate. Dashed lines indicate where the population growth rate is 1. (b) The combined effects of water temperature and larval mortality rate on population growth rate. The solid circle represents the population growth rate when no change occurs in water temperature and larval mortality rate. The dotted area indicates that the population growth rate is < 1

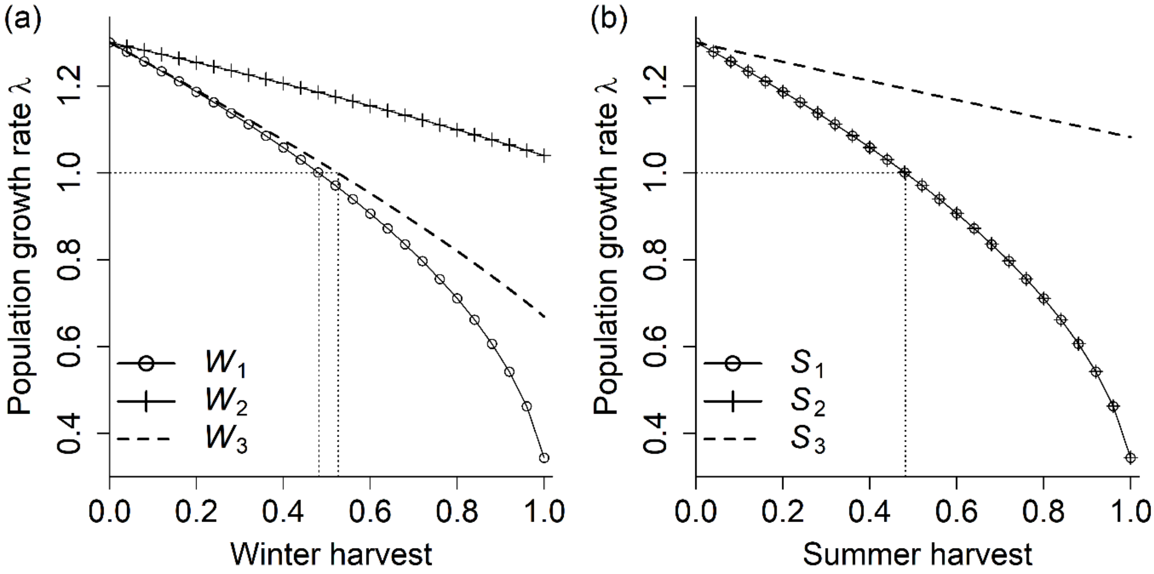


Fig. 2.4 Effects of winter (a) and summer (b) removal efforts on the population growth rate of the Chinese mitten crab *Eriocheir sinensis*. W_1, W_2, and W_3 represent the proportion of small, middle, and large sized crabs removed from the population before reproduction during winter; S_1, S_2, and S_3 mean the proportion of larvae, middle sized crabs, and large sized crabs removed before growth during summer. Dashed lines indicate where the population growth rate is 1

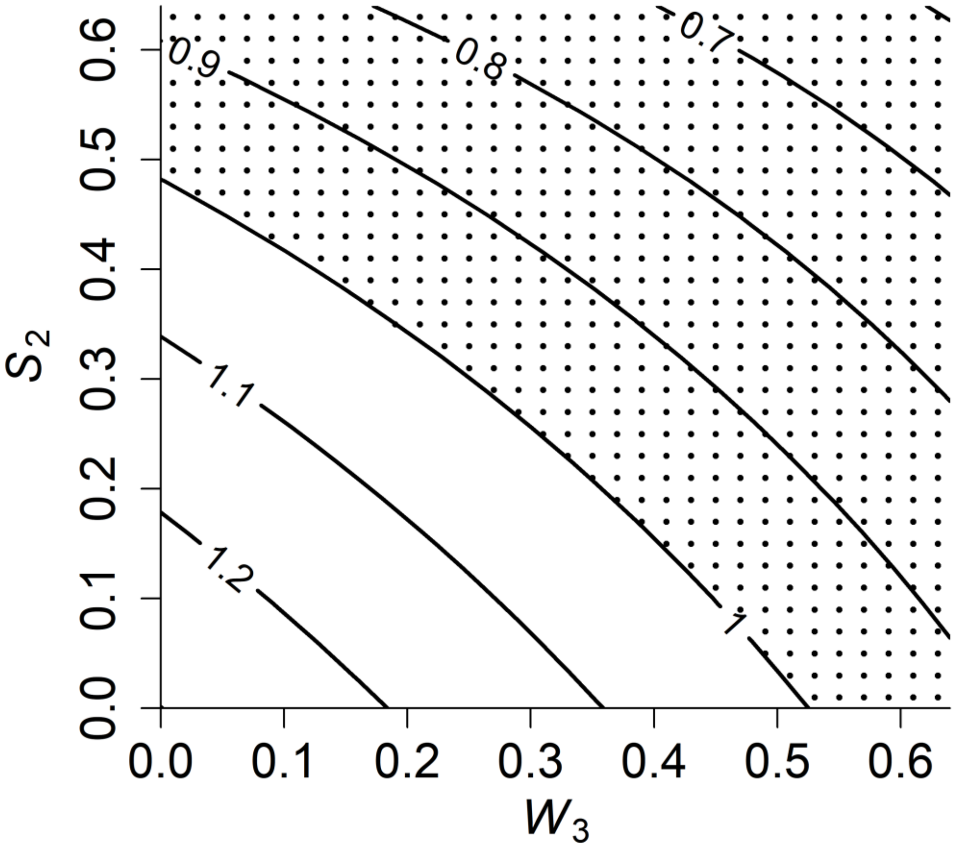


Fig. 2.5 The combined effects of summer and winter removal efforts on population growth rate of the Chinese mitten crab *Eriocheir sinensis*. W_3 represents the proportion of large sized crabs removed during winter. S_2 indicates the proportion of middle sized crabs removed during summer. The dotted area indicates that the population growth rate is < 1

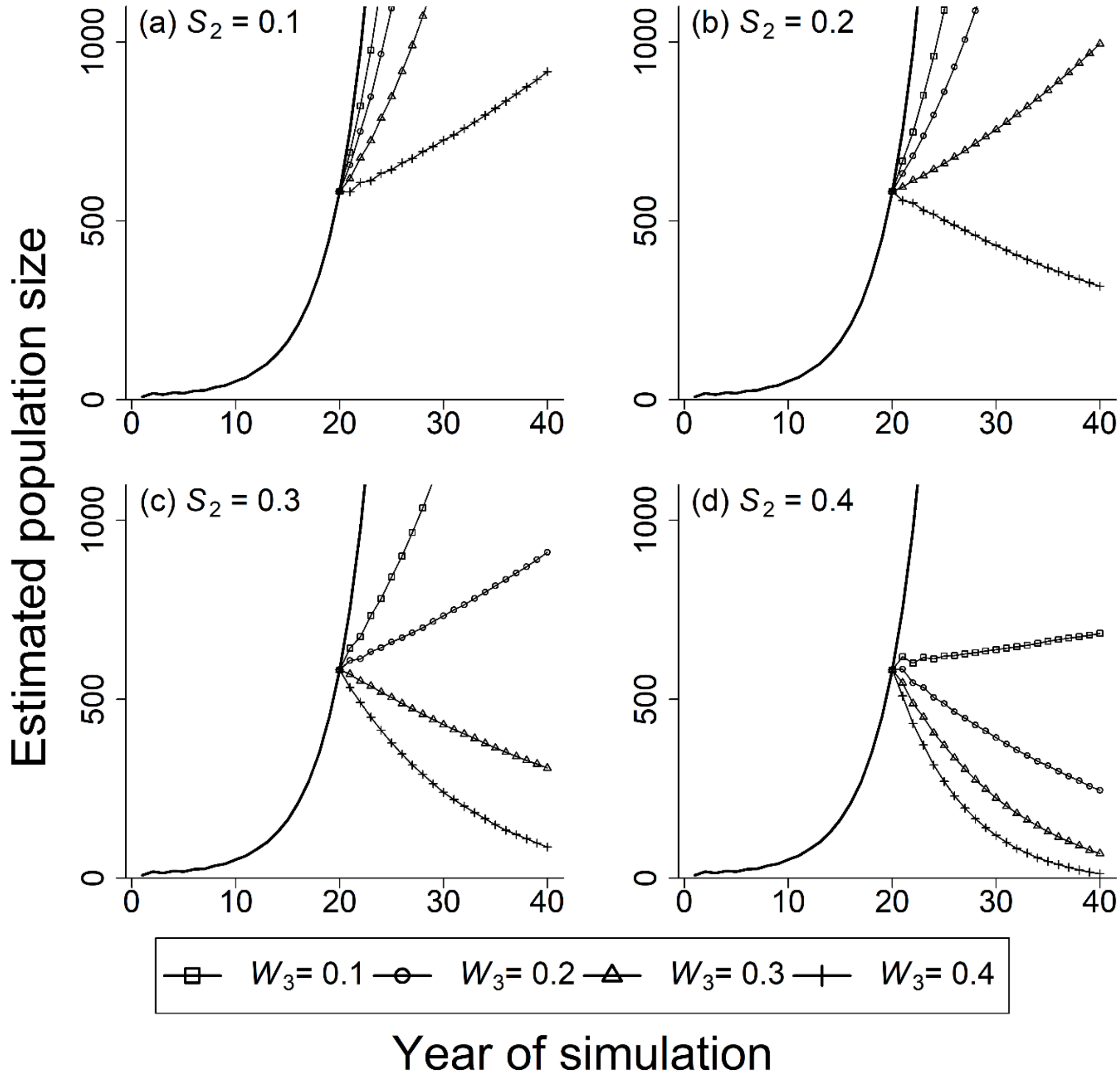


Fig. 2.6 Effects of summer and winter removal efforts on the abundance (sum of small, middle, and large crabs) of Chinese mitten crab *Eriocheir sinensis* in December. (a) S_2 = 0.1, (b) S_2 = 0.2, (c) S_2 = 0.3, (d) S_2 = 0.4. Removal efforts were assumed to be taken after 20 years of invasion. S_2 represents the proportion of middle sized crabs removed during summer and W_3 represents the proportion of large sized crabs removed before reproduction during winter. Solid lines without any symbol represent the population size without any removal efforts.

Tables

Table 2.1 The definition, estimates, and elasticities of vital parameters for the Chinese mitten crab *Eriocheir sinensis*

Symbol	Definition	Estimate	Elasticity
R_1	Precocity rate of s–class	0.044[a]	–0.01867
R_2	Reproduction probability of m–class	0.50	0.04581
R_3	Reproduction probability of l–class	0.50	0.1949
F_1	Effective fecundity of a precocious s–crab	807[b]	0.0003567
F_2	Effective fecundity of a m–crab	79,771[b]	0.1094
F_3	Effective fecundity of a l–crab	129,096[b]	0.3041
M	Instantaneous larval mortality rate	0.14[c]	–3.377
T	Water temperature during larval stage	15.65[d]	6.293
σ_{W1}	Overwinter survival rate of s–class	0.8750[e]	0.4134
σ_{W2}	Overwinter survival rate of m–class	0.7637	0.06355
σ_{W3}	Overwinter survival rate of l–class	0.7637[f]	0.1092
σ_{S1}	Survival rate of j–stage during summer	0.1106[a]	0.4138
σ_{S2}	Survival rate of m–class during summer	0.8488[a]	0.4134
σ_{S3}	Survival rate of l–class during summer	0.9000	0.1727
$\gamma_{m \to l}$	Probability of m–class growing into l–class	0.50	0.06762

[a] Zhu et al. 2012; [b] Chang et al. 2017; [c] White et al. 2014; [d] Lin et al. 2016; [e] Li et al. 2011; [f] Wu et al. 2007, 2009

Table 2.2 The stable stage distribution and reproductive values of the Chinese mitten crab *Eriocheir sinensis* during summer and winter

Summer			Winter		
Stage or class	Stable ratio	Reproductive value	Stage or class	Stable ratio	Reproductive value
j–stage	0.9131	1	s–class	0.5741	1
m–class	0.0649	14.05	m–class	0.1567	1.531
l–class	0.0220	17.33	l–class	0.2692	2.130

Chapter 3

Potential competitive impacts of the invasive Chinese mitten crab on native Japanese mitten crab

3.1 Introduction

Invasive alien species have caused substantial ecological and economic costs in many ecosystems; once established, they are extremely difficult and cost–intensive to eradicate (Pimentel et al., 2000; Genovesi, 2005; Davis, 2009; Brockerhoff & McLay, 2011; Hänfling et al., 2011). The Chinese mitten crab *Eriocheir sinensis* (H. Milne Edwards, 1853), which is a catadromous species native to eastern Asia, has been regarded as a notorious invasive alien species outside native range and is included in the list of “100 of the world’s worst invasive alien species” (Lowe et al., 2000; Herborg et al., 2003; Dittel & Epifanio, 2009; Brockerhoff & McLay, 2011). Invasion by this crustacean may be facilitated through various pathways, including ballast water discharges, live import, and even religious practices of animal release (Cohen & Carlton, 1997; Shiu & Stokes, 2008; Dittel & Epifanio, 2009; Low et al., 2013; Fialho et al., 2016). *E. sinensis* has been introduced to many regions and successfully established self–sustaining populations in some European and North American countries (Cohen & Carlton, 1997; Herborg et al., 2003; Dittel & Epifanio, 2009).

Invasive *E. sinensis* has caused considerable adverse impacts on invaded ecosystems. Chinese mitten crab is an opportunistic omnivore that may consume a variety of prey and therefore it is considered to have negative impacts on native food web dynamics (Rudnick & Resh, 2005; Webster et al., 2015; Wójcik et al., 2015; Mills et al., 2016; Rosewarne et al., 2016). In addition to predatory impacts, *E. sinensis* was found to compete for limited resource with native species. Gilbey et al. (2008) examined competitive interactions between invasive *E. sinensis* and native *Carcinus maenas* in the Thames estuary; their results suggested that *E. sinensis* are competitively superior to similarly sized individuals of the native crab because they successfully evict the native species from shelters. In addition, this pest has caused severe economic loss due to its burrowing activities and resulting river bank erosion (Dittel & Epifanio, 2009). Moreover, *E. sinensis* was recently found to be a carrier of the crayfish plague pathogen (*Aphanomyces astaci*) and might infect native European crayfish species (Schrimpf et al., 2014). Considering these negative impacts, control strategies are required to eradicate this species and prevent its further introduction. In Japan, *E. sinensis* has also been designated as an invasive species (Ministry of the Environment, Government of Japan, 2004). Despite this fact, live Chinese mitten crabs are imported from China to Japan for human consumption every year. In 2017, about 87 tons of Chinese mitten crab were imported to Japan with a value of approximately 320 million JPY (Ministry of Agriculture, Forestry and Fisheries, Japan). In 2004, two female adult *E. sinensis* were found in Tokyo Bay (Takeda & Koizumi, 2005). Given the effects that *E. sinensis* has had on other ecosystems around the world, it could become established and have also a negative impact on Japanese ecosystems through mechanisms such as competition with or predation on native species. Thus far, however, no study has been performed to explore the potential ecological impact of *E. sinensis* on native Japanese species, especially on its congener Japanese mitten crab *Eriocheir japonica*. The native crab is an important benthic crustacean widely distributed in Japan and has been extensively studied (Kobayashi & Matsuura, 1999; Zhang et al., 2016, 2017, 2018).

Up to now, eradication of established *E. sinensis* populations has turned out to be extremely difficult and unsuccessful (Gollasch, 2006; Schrimpf et al., 2014; Global

Invasive Species Database, 2018). Therefore, it is of great importance to understand the potential impacts of this species on native ecosystems and take precautionary control measures at the early stage of invasion (Genovesi, 2005; Hänfling et al., 2011; Schrimpf et al., 2014; Rosewarne et al., 2016). Given the fact that native *E. japonica* and invasive *E. sinensis* share similar life–history characteristics, habitat use and food habits (Jin et al., 2003; Dittel & Epifanio, 2009; Kobayashi, 2009), we hypothesize that this two species might compete for limited resources. Therefore, in this study, we performed laboratory competition experiments to address the following questions: (1) whether native *E. japonica* and invasive *E. sinensis* compete for shelter or not, and if so, (2) whether the two species display the same agonistic behavioural patterns or not, and (3) which species is more aggressive.

3.2 Materials and methods

3.2.1 Animal collection and maintenance

Only intact, healthy, adult intermoult crabs were used in this study. Native *E. japonica* were collected from the Agano River, Niigata Prefecture, Japan. Invasive *E. sinensis* from Yangcheng Lake, Jiangsu Province, China, were purchased from a local dealer in Ueno, Tokyo, Japan. The purchase and experiments with the invasive *E. sinensis* received a special permission from the Ministry of the Environment, Government of Japan. The carapace width (CW) and the height of the right chela propodus (CPH) of each crab were measured as described by Zhang et al. (2017). Preliminary experiments showed that male crabs were more aggressive than females (Zhang et al., unpublished data); therefore, as with previous studies (Gherardi & Daniels, 2004; Savvides et al., 2015), only male individuals were used in shelter competition trials to eliminate the effect of sex differences. Prior to competition experiments, crabs were reared in isolation for at least 1 week as described by Zhang et al. (2018). Most crabs were used in only one trial; if the same crab was used more than once, it was kept for at least 7 days of isolation between consecutive trials to remove any prior social effects (Zulandt Schneider et al., 2001; Gherardi & Daniels, 2004). All competition trials were conducted at the Tokyo University of Marine Science and Technology, Tokyo.

3.2.2 Shelter competition experiment

Competition experiments were conducted in a rectangular tank filled with dechlorinated tap water with a depth of approximately 12 cm (Fig. 3.1). The bottom of the experimental tank was covered by a layer of sand. The shelter was built using bricks and its size was adjusted to fit the size of an average adult crab, so as to be occupied by only one crab at a time. Preliminary observations showed that both species have nocturnal habits, foraging at night and hiding in the shelter during the day. Therefore, we decided to conduct competition trials during daytime. The room temperature was constant at 27°C and 15 W white fluorescent light tubes were used as the light source. A 10L:14D light cycle was maintained during the experiment. Crabs were fed prior to the experiment. No food or aeration was provided during the experiment. The observation area was kept free from any kind of external disturbance.

A resident–intruder model was used to examine the shelter competition between the two species (Figler et al., 1999). Native *E. japonica* was considered as a resident and was introduced to the experimental tank first, to acclimate to conditions for about 30 min. The experiment was initiated by releasing the intruder, invasive *E. sinensis*, in the far corner from the shelter inside the experimental tank. Interactions between the two opponents were registered by a drive recorder (CL–706DV–D, Guangdong, China) placed above the tank without any additional illumination. Results of preliminary experiments in which crab behaviour was recorded for 180 min suggested that crabs always finished their competition and established the dominance–subordinance relationship within 30 min; therefore, we only observed the interactions of the two species for the first 30 min. The experimental tank, sand, and shelter were thoroughly washed after each trial to remove any scent cues left by the previous test animals.

In total 42 trials were run and the shelter competition outcome (i.e. which species wins the shelter; 0 and 1 for a win by the native *E. japonica* or the invasive *E. sinensis*, respectively) was recorded for each trial. The relative size difference (RSD) between two opponents was calculated as described by Briffa & Elwood (2001) and Zhang et al. (2018). For instance, the RSDCW (i.e. relative size difference of carapace width) was calculated as follows:

$$RSDCW = 1 - \frac{CW\ of\ E.\ japonica}{CW\ of\ E.\ sinensis}.$$

The RSDCPH (i.e. relative size difference of chela propodus height) was calculated in a similar way. A logistic regression was used to examine the relationship between the binary competition outcome and RSD as below:

$$p = \frac{e^{a+bx}}{1+e^{a+bx}},$$

where p is the probability of winning the competition, x means the RSD, and a and b are the parameters to be estimated.

To examine the differences in behavioural patterns between *E. japonica* and *E. sinensis*, we selected seven fighting ability–matched pairs instead of size–matched pairs. Observations were made in the same tanks with shelter used in the previous experiments as the interactions typically occurred outside the shelter. Crab behaviour was divided into four categories: (1) approach; (2) weak contact by walking legs; (3) chela contact; and (4) retreat (Fig. 3.2) and the frequency of each behaviour type was recorded. Differences in behaviour frequency between both species were examined by a nonparametric permutation test with 10,000 permutations (Good, 1994). A fighting bout was defined as both crabs striking each other using their chela and was considered as finished when one crab retreated for at least 10 s. For trials consisting of more than one fighting bout, the fight duration of the first three bouts was recorded (Ayres–Peres et al., 2015). A generalized additive model (GAM) with an identity link function and Gaussian error distribution was used to analyse the effects of RSDCW and bout order (i.e. the first, second, and third bout) on fight duration. All analyses were performed in R version 3.1.3 (R Development Core Team, 2014). GAM analysis was performed by using the function called “gam” in the “mgcv” R package (Wood, 2001).

3.3 Results

3.3.1 Competition outcome

Invasive *E. sinensis* won 22 (52%) of the 42 competition trials performed. The

RSDCW between the two opponents ranged from –0.368 to 0.489, and the RSDCPH values varied from –0.499 to 0.573 (Fig. 3.3). The competition outcome in relation to RSDs (both RSDCW and RSDCPH) suggested that competition between the two species was strongly size–dependent: *E. japonica* always successfully defended shelter when competing with size–matched or slightly larger *E. sinensis*; *E. sinensis* always evicted *E. japonica* from shelter when its carapace or chela were at least 10 or 7% larger, respectively, than those of *E. japonica* (Fig. 3.3). Results of logistic regressions showed that *E. sinensis* had a 50% probability of taking over the shelter when the RSDCW and RSDCPH values reached 0.084 and 0.031, respectively (Table 3.1).

3.3.2 Competition behaviour

All trials began with the native *E. japonica* hidden under the shelter. The competition behaviour was initiated by a frontal approach toward the shelter by the intruder. The intruder touched the resident using their walking legs. Analysis of the video recordings indicated that RSDCW also influenced the competition behaviour of the two opponents: if the size difference between two crabs was large, the smaller one would retreat without further agonistic behaviour; native *E. japonica* possessed competitive advantages over similarly sized invasive *E. sinensis* and escalated interactions occurred only when the intruder was larger than the resident. Once a dominance–subordinance relationship was established, the loser moved away from its opponent rapidly and avoided further agonistic interactions. There was a degree of overlap in the relationships between binary competition outcomes and RSDCW (Fig. 3.3a), and the seven pairs of crabs (RSDCW ranged from

0.077 to 0.096; *E. sinensis* won three out of the seven trials) in the overlap area were selected to examine the behavioural patterns between both species. Our results showed that the two species displayed different behavioural patterns during the experimental period. *E. japonica* exhibited more frequent approach behaviour (permutation test, $p = 0.006$) and chela contact behaviour (permutation test, $p = 0.040$), while *E. sinensis* displayed more frequent retreat behaviour (permutation test, $p < 0.001$) (Fig. 3.4). No significant differences were found in weak contact by walking legs (permutation test, $p = 0.511$) between both species (Fig. 3.4). In the present study, approach, weak contact by walking legs and chela contact were classified as positive behaviour and retreat was regarded as negative behaviour. Compared with *E. sinensis*, *E. japonica* frequently displayed positive behaviour (permutation test, $p = 0.021$) and seldom displayed negative behaviour.

3.3.3 Fight duration

Our results showed that fights between *E. japonica* and *E. sinensis* only occurred when the RSDCW ranged from –0.032 to 0.201 (Fig. 3.5a). Fights were observed in 23 of the 42 pairs tested and of these, 18 pairs consisted of more than one fighting bout. A total of 53 fighting bouts were recorded and the fight duration varied from 3 to 44 s with a mean duration (± standard error) of 18.0 s (± 1.4; Fig. 3.5a). The results of GAM analysis indicated that bout and RSDCW had significant effects on fight duration, and the total deviance explained was 39.9% (Table 3.2). There was no significant difference in fight duration between the first and second bouts but the first bout was significantly longer than the third (Table 3.2). Fight duration between *E. sinensis* and *E. japonica* as a function of

RSDCW followed an inverted U–shaped curve (Fig. 3.5b). When one competitor was obviously larger than the other, the smaller crab rarely exhibited agonistic behaviour towards the larger and the fight duration was always short; when the two opponents had a similar fight ability (i.e. similar possibility to win the shelter), the fight escalated. Not surprisingly, the fight duration reached maximum level at approximately $RSDCW_{50}$ (Fig. 3.5b).

3.4 Discussion

3.4.1 Competitive asymmetry

In the present study, we examined competitive interactions between the invasive *E. sinensis* and native *E. japonica* under laboratory conditions. Our results indicate that the two species readily fight for access to shelter, which is an important limiting resource for crustaceans. For example, shelter provides protection against predators and reduces the risk of predation, especially during the moult period (Figler et al., 1999; Gherardi & Daniels, 2004; Zhang et al., 2018). Our results indicate that relative differences in carapace size (RSDCW) and chela size (RSDCPH) are reliable predictors of competition outcome between crab species. This finding is consistent with previous studies (Richards & Cobb, 1986; Sneddon et al., 1997; Nakata & Goshima, 2003; Painting & Holwell, 2014). For instance, Sneddon and colleagues (1997) reported that chela length is a reliable predictor of fight outcome for male shore crab *Carcinus maenas* (L.). Body size and chela size are always regarded as indicators of resource holding potential (RHP) (Sneddon et al., 1997; Hardy & Briffa, 2013; Painting & Holwell, 2014). Therefore, our present study suggests that native crab *E. japonica* has larger RHP than similarly sized invasive crab *E. sinensis*. In addition to differences in RHP, the present study found that the two species displayed different behavioural repertoires: the invasive *E. sinensis* exhibited more submissive and less aggressive behaviour than the native *E. japonica*. Previous studies have pointed out that *E. sinensis* has been introduced into new regions mainly by ballast waters of ships and live transportation (Herborg et al., 2003; Dittel & Epifanio, 2009; Global Invasive Species Database, 2018). These introduction patterns also exist in Japan (Takeda & Koizumi, 2005). However, up to now, this invasive crab has not become established in Japan despite repeated introductions. The results of our current competition experiments suggest that the widely distributed native *E. japonica* is competitively superior and this may act as a form of biotic resistance impeding the establishment of invasive *E. sinensis* in Japan. In contrast, in Europe and North America, the absence of strong native competitors may favour the successful establishment of *E. sinensis*. The important role of strong native species in preventing invasive species has been demonstrated. For instance, Paini and colleagues (2008) found that native *Frankliniella tritici* have a higher competitive ability than invasive *Frankliniella occidentalis*, which might account for the failure of *F. occidentalis* to establish in the eastern states of the USA. DeRivera et al. (2005) reported that native blue crab *Callinectes sapidus* predated intensively on invasive European green crab *Carcinus maenas*, which may limit the distribution of this invasive crab in eastern North America. Besides, a previous model study also indicated that invasion success of invaders negatively correlated with the strength of interspecific interactions and the existence of strongly interacting species would reduce the invasion success of alien species (Case, 1990).

Contrary to our present findings, many invasive species are considered to have competitive superiority over native species, and this competitive asymmetry can lead to the reduction or displacement of native species (Usio et al., 2001; Holway et al., 2002; Nakata & Goshima, 2003; Gherardi & Daniels, 2004; Paini et al., 2008). For instance, Gherardi and Daniels (2004) revealed that the invasive crayfish *Procambarus clarkii* might reduce or eliminate the native crayfish *Procambarus acutus acutus* since the invader showed competitive superiority and performed more aggressive and less submissive behaviour. Usio et al. (2001) examined the interactions between the native crayfish *Cambaroides japonicus* and the invasive crayfish *Pacifastacus leniusculus*. They showed that the invasive *P. leniusculus* frequently performed aggressive attacks whereas native *C. japonicus* exhibited more defensive behaviour, and suggested an association between this differential behaviour and the species displacement between both species.

3.4.2 Fight duration

In the present study, the interactions between both species were always initiated by walking leg contacts. If the size of an intruder was much smaller than that of a resident, the intruder would retreat without further agonistic interactions. On the contrary, if the intruder was much larger, the resident would give up defending and leave the shelter soon. Previous studies have reported that the setae on the walking legs of crustaceans are important sensory organs (Derby, 1982; Garm & Watling, 2013), and we assume the setae on the walking legs of *E. sinensis* and *E. japonica* may be used to gather information about the opponent's RHP. Such information gathering activities have been verified in hermit crabs, which use their appendages to assess the shell quality of their opponent and their opponent's RHP during a shell fight (Dowds & Elwood, 1983; Briffa & Elwood, 2001).

When fights occurred between the two species, fight duration decreased with the fighting bout sequence. Fights are always costly, and this de–escalation pattern can reduce not only the costs of time and energy, but also the risk of injury during agonistic interactions (Hardy & Briffa, 2013). A similar de–escalation pattern has been confirmed in crayfish and *Aegla* sp. (crab) (Zulandt Schneider et al., 2001; Ayres–Peres et al., 2015). Game theory models have frequently been applied in the study of animal contests, and these suggest that escalated fights are expected to occur when competitors have a similar RHP; a large asymmetry in RHP results in a short fight duration because the inferior individual always exhibits avoidance behaviour to reduce costs such as time, energy and injury risk (Pavey & Fielder, 1996; Sneddon et al., 1997; Vorburger & Ribi, 1999; Andersen et al., 2000; Morrell et al., 2005; Smallegange & Van der Meer, 2007). The inverted U–shaped relationship between fight duration and RSDCW in the present study supports the game theory predictions.

3.4.3 Further studies

Our present study represents the initial attempt to understand the potential impacts of invasive *E. sinensis* in Japan, however, further studies are necessary. We cannot conclude that the invasion of *E. sinensis* in Japan is impossible based solely on our present competition study because in addition to direct competition, this invasive crab is capable of negatively influencing native species population dynamics through other mechanisms such as predation and parasitism (Rudnick & Resh, 2005; Schrimpf et al., 2014; Webster et al., 2015; Wójcik et al., 2015; Rosewarne et al., 2016). A spatially segregated distribution pattern in rivers has been found in *E. japonica*: juvenile crabs concentrate in the lower reaches of a river, while adult individuals live upstream (Kobayashi & Matsuura, 1999). This distribution pattern was considered a type of evolutionary adaptation to reduce the risk of cannibalism in *E. japonica* (Zhang et al., 2018) but ironically could render the smaller individuals susceptible to predation in case of invasion by *E. sinensis*. Future studies are needed to investigate this hypothesis. In this experiment, native *E. japonica* was always introduced first to the tank but the reverse scenario should be investigated in future studies. Besides, further studies are required to examine the competition between the two species for other resources, such as food items.

Figures

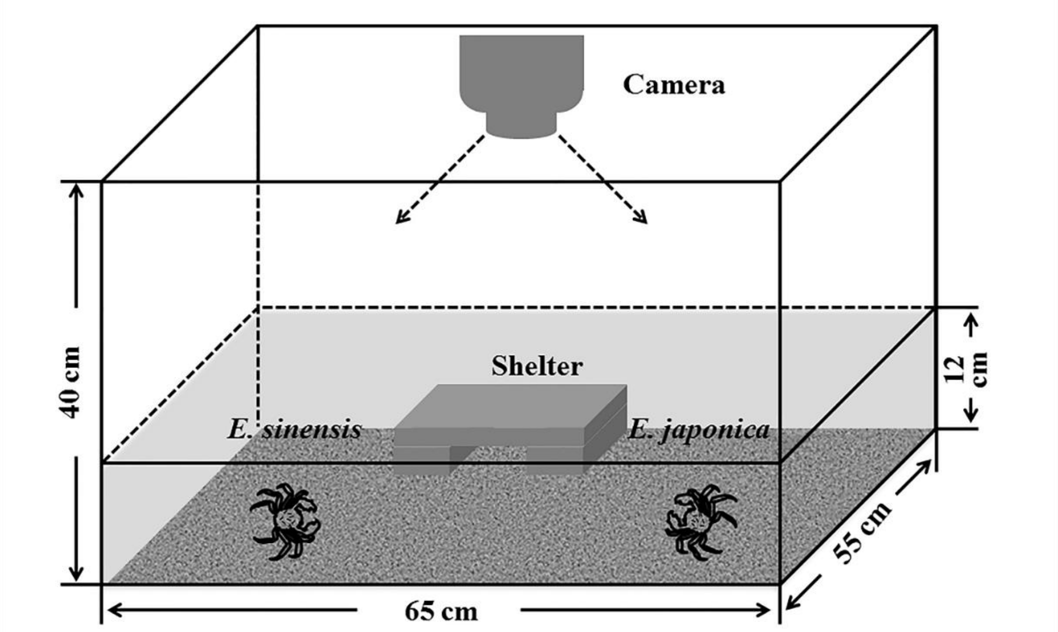
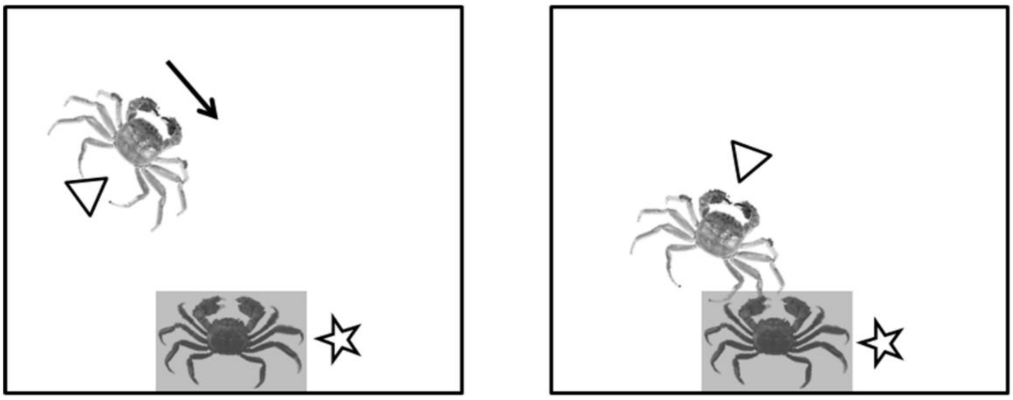
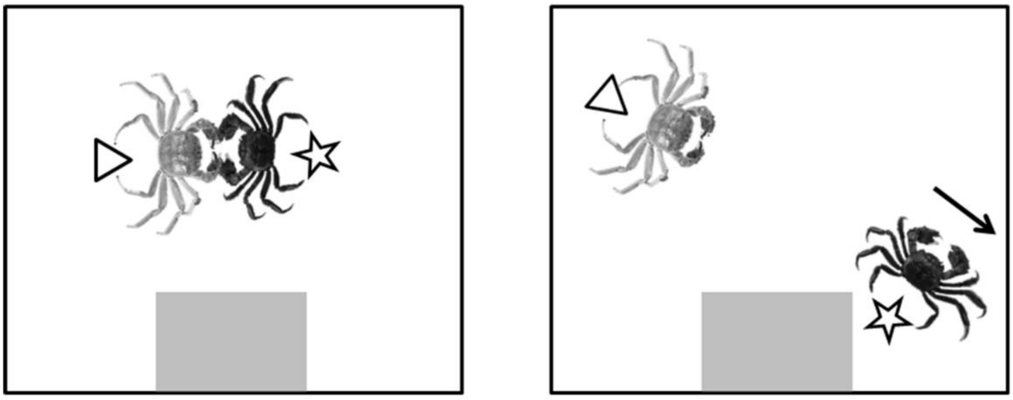


Fig. 3.1 Schematic diagram of the experimental tank. The tank bottom was covered by a layer of fine sand and the shelter was built out of bricks. A drive recorder was placed on the top of the tank to record interactions between the two opponents.



Approach **Weak contact by walking legs**



Chela contact **Retreat**

Fig. 3.2 Competition behaviour between the invasive Chinese mitten crab *Eriocheir sinensis* and the native Japanese mitten crab *Eriocheir japonica*. The shaded area indicates the shelter, arrows represent movement directions and triangles and stars indicate *E. sinensis* and *E. japonica*, respectively.

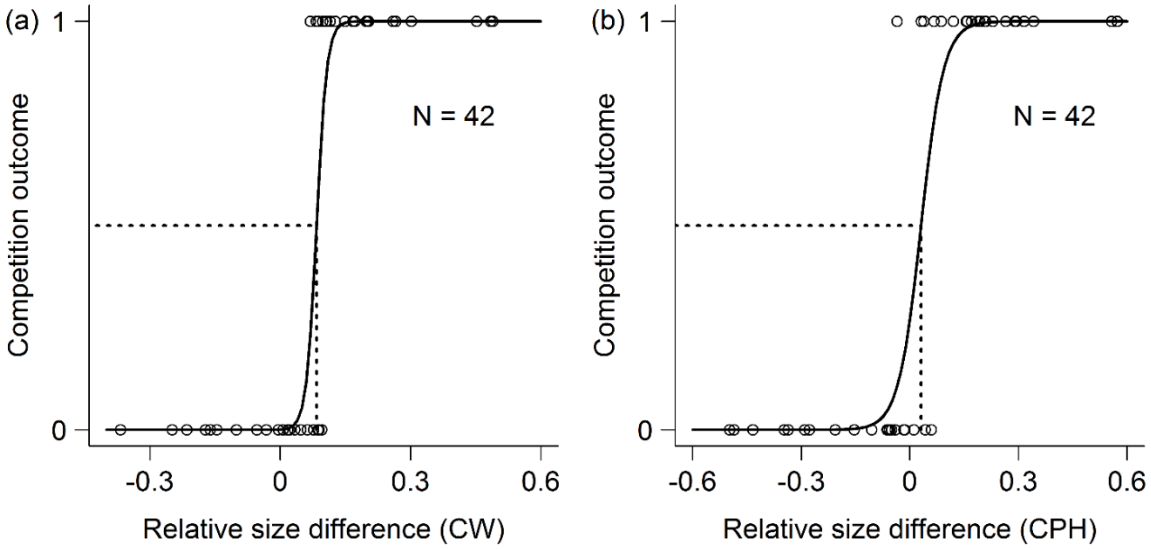


Fig. 3.3 Relationships between shelter competition outcome (0 if the native Japanese mitten crab *Eriocheir japonica* won the shelter, and 1 if the invasive Chinese mitten crab *Eriocheir sinensis* won the shelter) and relative size difference. Results are shown separately for: (**a**) relative size difference of carapace width (RSDCW) and (**b**) relative size difference of chela propodus height (RSDCPHP). Dotted lines indicate the relative size difference at which the two opponents had the same winning possibility.

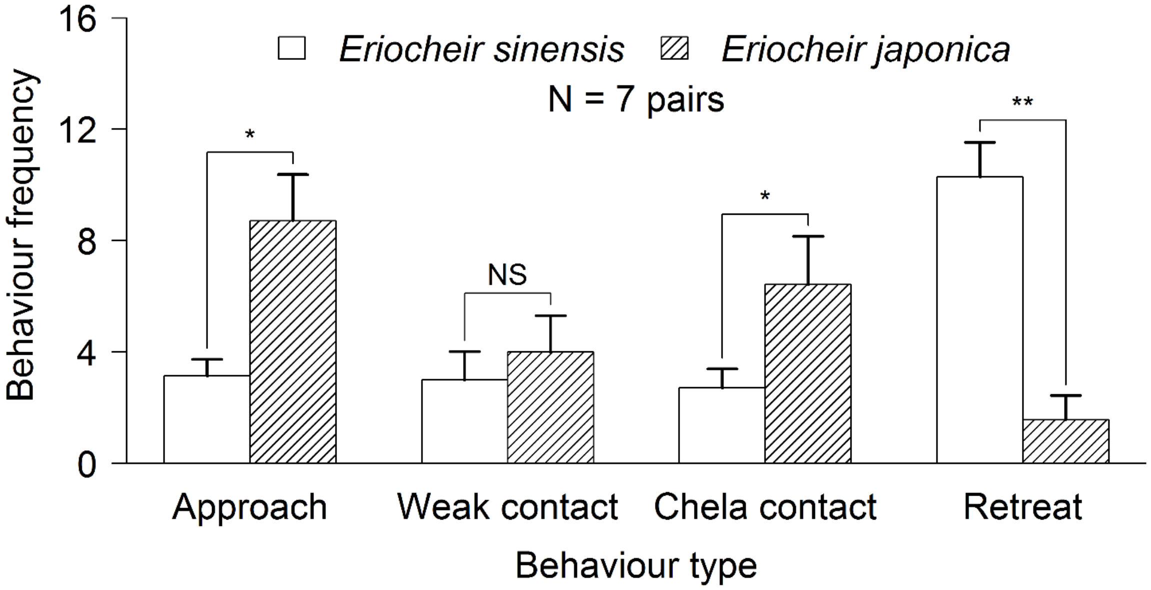


Fig. 3.4 Frequency (mean ± standard error) of the four types of competition behaviour (approach, weak contact by walking legs, chela contact, and retreat) performed by the native Japanese mitten crab *Eriocheir japonica* and the invasive Chinese mitten crab *Eriocheir sinensis* within 30 min. Difference in behaviour frequency was tested by the nonparametric permutation test with 10,000 permutations (* $p < 0.05$, ** $p < 0.01$, NS = not significant).

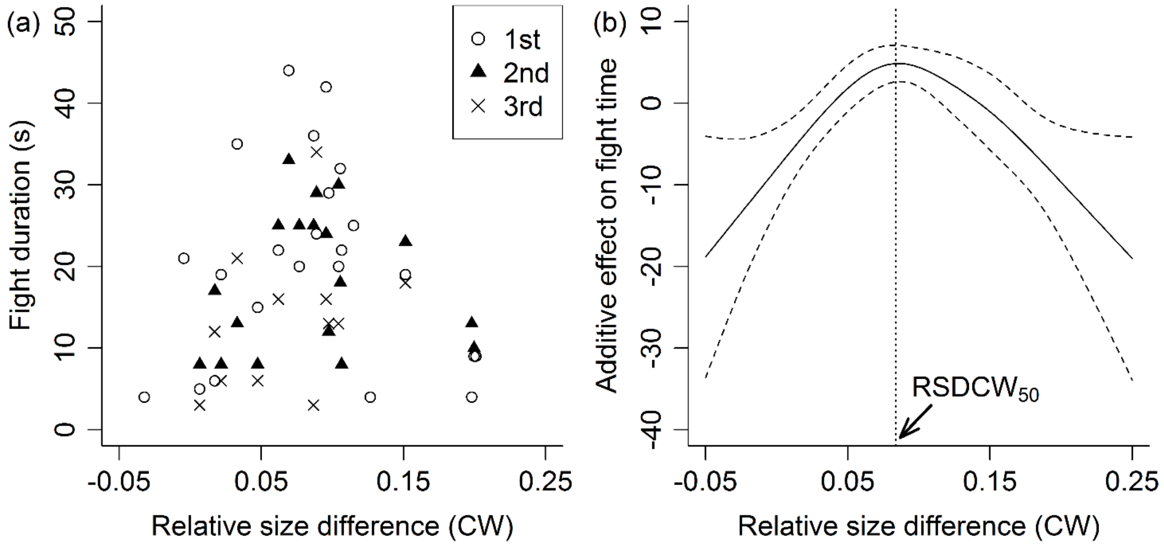


Fig. 3.5 Relationship between: (**a**) relative size difference of carapace width (RSDCW) and fight duration (in seconds), and (**b**) the additive effect of RSDCW on fight duration examined by a generalized additive model. Positive values in RSDCW indicate that the invasive Chinese mitten crab *Eriocheir sinensis* was larger than the native Japanese mitten crab *Eriocheir japonica*, and vice versa. The solid line represents the estimated additive effect of RSDCW on fight duration, and the dashed lines represent 95% confidence intervals. The relative wide confidence intervals at both ends were due to the few fight events with large RSDCWs. The vertical dotted line indicates the $RSDCW_{50}$ at which two opponents have the same winning possibility.

Tables

Table 3.1 Results of logistic regressions between competition outcome (0 if the native Japanese mitten crab *E. japonica* won the shelter, and 1 if the invasive Chinese mitten crab *Eriocheir sinensis* won the shelter) and relative size difference (RSD)

RSD	Logistic regression	RSD_{50}
RSDCW	$P = \frac{e^{-7.118+85.10x}}{1+e^{-7.118+85.10x}}$	0.084
RSDCPH	$P = \frac{e^{-0.9925+32.22x}}{1+e^{-0.9925+32.22x}}$	0.031

RSDCW: relative size difference of carapace width; RSDCPH: relative size difference of chela propodus height. P is the winning probability of *E. sinensis*, and RSD_{50} indicates the RSD value at which *E. sinensis* has a 50% probability of winning.

Table 3.2 Results of the generalized additive model (GAM) analysis in terms of fight duration in relation to bout order and relative size difference of carapace width (RSDCW)

Estimation of parametric coefficients				
Variable	Estimate	Standard error	*t* value	Pr (> |t|)
Intercept	21.126	1.796	11.762	< 0.0001 ***
2nd fighting bout	–3.342	2.711	–1.233	0.224
3rd fighting bout	–8.629	3.101	–2.782	0.008 **
Approximate significance of smooth terms (Nonparametric)				
Smooth variable	edf	Ref.df	*F*	*p*–value
RSDCW	2.666	3.311	6.922	0.0004***

The GAM model explained 39.9% of the deviance with an adjusted *R*–square of 0.34. The number of observed fight events was 53. edf: estimated degrees of freedom; Ref.df: reference degrees of freedom. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Chapter 4

Potential predatory impacts of the invasive Chinese mitten crab on native Japanese mitten crab

4.1 Cannibalism in the Japanese mitten crab, Eriocheir japonica

4.1.1 Introduction

Cannibalism, also referred to as intraspecific predation, is defined as killing and eating conspecific individuals (Fox, 1975; Polis, 1981). This behaviour is a ubiquitous phenomenon in nature and has been confirmed in over 1,300 species of both invertebrates and vertebrates (Fox, 1975; Polis, 1981). Cannibalism is an especially common phenomenon in decapod crustaceans and has been studied extensively (Dutil et al., 1997; Amaral et al., 2009; Romano & Zeng, 2016). A variety of factors can influence the occurrence and degree of cannibalism, such as relative size of the cannibal and victim, hunger level, and habitat complexity (Polis, 1981; Hecht & Pienaar, 1993; Dutil et al., 1997; Göçmen et al., 2008; Amaral et al., 2009; Mateo & Pleguezuelos, 2015; Romano & Zeng, 2016).

Cannibalism has been considered as an important mechanism in population structuring and regulation (Fox, 1975; Polis, 1981; Polis & Holt, 1992; Claessen et al., 2004; Moksnes, 2004). It has been suggested that in some species with complex life cycles, small individuals exhibit avoidance behaviour towards large conspecifics to reduce intraspecific predation risk, and that this avoidance behaviour may be partly responsible for the habitat/spatial segregation among different–sized individuals in many stage–structured species (Leonardsson, 1991; Jormalainen & Shuster, 1997; Robertson & Cushing, 2011). Cannibalism can also reduce the number of potential competitors and provide nutritional benefits, especially when there is a limitation in either quantity or quality of food (Polis, 1981).

The Japanese mitten crab, *Eriocheir japonica* (De Haan, 1835), is widely distributed in Japan, Korea, and the Russian island of Sakhalin (Kobayashi & Matsuura, 1999; Zhang et al., 2016). As a catadromous species, this crab grows in river and migrates to the sea for reproduction after reaching sexual maturity (Kobayashi & Matsuura, 1999). This species has been studied extensively and a longitudinal distribution pattern in river has been confirmed: juveniles are concentrated in the lower reaches of a river while larger adults live further upstream (Kobayashi & Matsuura, 1991; Kobayashi, 1995). Previous stomach content analysis suggests this crab is an omnivore and a deposit feeder, which can consume a variety of materials (Kobayashi, 2009). Although the presence of exoskeleton fragments of conspecifics was confirmed in stomach contents, *E. japonica* was considered as a scavenger rather than a cannibal because muscle or inner parts were rarely attached to the fragments (Kobayashi, 2009). Up to now, no study has examined cannibalism in *E. japonica*, and relatively little information is known about the degree of cannibalism in this species.

Considering the prevalence of cannibalism among decapod crustaceans and the omnivorous feeding habit of *E. japonica*, we hypothesize that *E. japonica* might also be a cannibalistic species and exhibit cannibalistic behaviours. In this study, we performed several laboratory experiments to examine (1) whether *E. japonica* presents cannibalistic behaviour or not and, if it does, (2) what are the effects of predator sex, predator–prey size difference, prey density, and presence of alternative food and shelter on cannibalism. We also discuss the possible implications of cannibalism on the population dynamics of this species.

4.1.2 Materials and Methods

4.1.2.1 Animal collection and maintenance

Crabs were collected with hand–held nets (mesh size = 1.0 mm) by turning over stones from a small river in Tateyama, Chiba Prefecture, Japan (34.975°N to 34.974°N, 139.776°E to 139.775°E) in 2016. In the laboratory, specimens were graded by size, and maintained in tanks with dechlorinated tap water and stones. Crabs were fed with krill every day. Only active, intact, and intermolt crabs were used in this study. All experiments were conducted at Tokyo University of Marine Science and Technology, Tokyo.

4.1.2.2 Experimental procedures

All experiments were conducted in cylindrical tanks (diameter 40 cm, height 30 cm) provided with a constant flow of dechlorinated tap water (renewal rate of 200% per day). The tanks were placed on shelves in the laboratory and illuminated with 15W white fluorescent light tubes between 8:00 and 18:00. The tank bottom was evenly covered with a thin layer of sand and the water depth was adjusted to 8 cm. Temperature was kept constant at 27°C and no aeration was provided during the experimental period.

The experiments were carried out from August 19 to October 21, 2016 and crabs were used only once throughout this period. The larger individuals are considered as cannibals; they were reared separately and starved for 48 h prior to use to standardize the hunger level; prey crabs (smaller individuals) were not starved (Luppi et al., 2001; Long et al., 2012;

Daly & Long, 2014). On the morning of each trial, prey crabs were introduced to the experimental tank first to acclimate for 20 min; the predation experiment was initiated by adding the predator crab at 9: 30 am. The predation trials lasted for 24 h and the tanks were observed again at 9:30 on the next morning. Cannibalism was defined as the proportion of all prey crabs that were injured or killed during the trials as in earlier studies (Luppi et al., 2001; Sotelano et al., 2012, 2016). In addition, the number and position of lost appendages (chelipeds, first to fourth walking legs, right or left side of the body) per surviving, injured crab were recorded. In case the prey survived, its position in the tank and that of the predator were also noted. Tank and sand were thoroughly washed after each trial to remove any scent cue left by the previous crabs.

In the first experiment, we tested whether *E. japonica* is a cannibalistic species or not. Two different–sized crabs were placed in the experimental tank. In this experiment, the effects of predator sex and relative size difference (RSD) between cannibal and victim on cannibalism outcome were studied. The RSD was calculated as per a previous study (Briffa & Elwood, 2001):

$$RSD = 1 - \frac{size\ of\ prey}{size\ of\ predator}.$$

In addition, the relationship between the binary outcomes of cannibalism (0 if cannibalism is absent, and 1 if cannibalism is present) and RSD was analysed by a logistic regression as follows:

$$p = \frac{e^{a+bx}}{1+e^{a+bx}},$$

where p is the probability of cannibalism, and x represents the RSD between two different–sized crabs, a and b are the parameters of the logistic regression model. A chi–square test was performed to test the differences between observed and predicted values. Differences in the probability of cannibalism between male and female predators were evaluated using the multiple logistic regression analysis.

In the second experiment, we studied the effects of the presence of alternative food and shelter on cannibalism rate. Three treatments were performed: sand control group (five replicates), food group (with two dead shrimp) (six replicates), and shelter group (with three stones) (five replicates). Each trial contained one predator and four prey crabs. In addition, we conducted another trial without a predator (five replicates). Based on the results of the first experiment as to whether male predators are more cannibalistic than females (see Results), only male predators were used in the second experiment. In order to exclude the effect of size difference on cannibalism results, the mean (± SD) RSD between predator and prey animals was 0.669 (± 0.046) (the size of prey crabs was 11.30 ± 1.92 mm carapace width (CW), and the size of predators was 34.03 ± 2.40 mm CW); there was no significant difference in the RSD among treatments (Kruskal–Wallis test, $p = 0.351$). Kruskal–Wallis test followed by Dunn's multiple comparison analysis was performed to determine the differences in cannibalism rate among treatments.

In the third experiment, we studied the functional response of predator to prey density. In this experiment, four prey densities were used: 1 (five replicates), 2 (three replicates), 4 (five replicates), and 8 (three replicates) prey crabs per tank. Control trials without a predator were performed at each prey density (three replicates). Similar to settings in the second experiment, only male predators were used; the RSD was 0.671 ± 0.045 (the size of prey animals was 11.53 ± 1.95 mm CW, and the size of predators was 34.91 ± 2.41 mm

CW), and no significant difference was detected in RSD among prey density treatments (Kruskal–Wallis tests, p = 0.543). Male *E. japonica* exhibit a type II functional response (see Results). The Holling's disc equation and the Rogers random predator equation have been frequently used to describe the type II functional response (Haddaway et al., 2012). The Holling's disc equation is expressed as follows:

$$N = \frac{aN_0T}{1+ahN_0};$$

and the Rogers random predator equation has the following form:

$$N = N_0(1 - e^{a(hN-T)});$$

where N is the number of consumed prey animals, N_0 is the number of initial prey animals, a is the attack rate, h is the handling time, and T is the experiment duration (a fixed variable, and $T = 1$ in this study).

Parameters in the Holling's type II functional response and the Rogers random predator equation were estimated by the maximum likelihood method (Bolker, 2008). Akaike's information criterion (AIC) values were used to select the best model. All statistical analyses were performed using R version 3.1.3 (R Development Core Team, 2014).

4.1.3 Results

4.1.3.1 Effects of predator sex and size difference

Cannibalism was observed in *E. japonica* (Fig. 4.1.1) and found to be dependent on both size and sex. First, in both sexes of *E. japonica*, cannibalism only occurred when the RSD between cannibal and victim was large (Fig. 4.1.2). Second, predator sex had significant effects on the probability of cannibalism (multiple logistic regression analysis, $p < 0.05$). Male *E. japonica* showed a strong tendency to cannibalism (Fig. 4.1.2a), while in females, cannibalism was a rare event, even when the RSD was large (Fig. 4.1.2b). Results of logistic regressions between the presence/absence of cannibalism and RSD are presented in Table 4.1.1. Chi–square tests suggested logistic regression for both male and female predators fitted the data well (male: $\chi^2 = 1.602$, $p = 0.991$; female: $\chi^2 = 3.239$, $p = 0.919$). During encounters with a male intraspecific predator, the probability of cannibalism was 50% if the RSD between the opponents reached 0.430 (or predator–prey size ratio = 1.754). However, when the intraspecific predator was female, the RSD value increased to 0.790 before the probability of cannibalism was 50% (or predator–prey size ratio = 4.762) (Table 4.1.1).

In the male predator treatment, nine prey crabs were consumed and 10 prey animals were injured (Fig. 4.1.2a). The mean (± SD) RSD value between predators and injured prey crabs ($RSD_{injured}$) was 0.511 (± 0.109), and the mean (± SD) RSD value between predators and consumed prey animals (RSD_{killed}) was 0.633 (± 0.118) (Fig. 4.1.3). The RSD_{killed} was significantly larger than the $RSD_{injured}$ (Student's t test, $t = 2.327$, $p = 0.033$) (Fig. 4.1.3). Thus, we conclude that the probability of the prey being killed in a cannibalistic encounter increases with the RSD.

4.1.3.2 Effects of alternative food and shelter

Considering the effect of size difference on cannibalism (Fig. 4.1.2a), it was not surprising that no cannibalism event was observed in trials without predators in the second experiment. Therefore, the death of prey crabs was due to predation by large crabs. The cannibalism rate was high in the sand control group, approximately 0.850 ± 0.224 (Fig. 4.1.4). Significant differences among treatments were detected (Kruskal–Wallis tests, $p = 0.014$), and the presence of alternative food and shelter significantly reduced the cannibalism rate (Dunn's test, $p < 0.05$, Fig. 4.1.4). Pairwise comparisons suggested there was no significant difference in cannibalism rate between food and shelter treatments (Dunn's test, $p = 0.159$) (Fig. 4.1.4).

4.1.3.3 Effects of prey density: the predator functional response

In the third experiment, intra–size cannibalism was not observed in all control trials. Male *E. japonica* exhibited a typical type II functional response: the number of consumed prey crabs by male *E. japonica* increased with increasing prey density, and predators became satiated as prey abundance increased (Fig. 4.1.5). The estimation results of two functional response models are summarized in Table 4.1.2. The Rogers random predator equation and Holling's disc equation produced very similar AIC values.

4.1.3.4 Pattern of lost appendages in injured crabs

Injured crabs accounted for approximately half (58.7%) of the cases of cannibalism without a clear trend among the treatments. A total of 44 injured prey crabs lost 111 appendages during the trials (Fig. 4.1.6a) and single appendage loss was most common among injured prey crabs (Fig. 4.1.6b). No significant difference was observed in the frequencies of lost appendages between the left and right sides ($\chi^2 = 0.441$, $p = 0.506$). The probability of loss varied among appendages (χ^2 = 19.541, p = 0.021) and the 2nd and 3rd walking legs were lost most often (Fig. 4.1.6a).

4.1.3.5 Size–specific behavioural response

Observation of the position of the surviving crabs at the end of each trial, 1.5 hours after the onset of the light period, revealed a clear size–specific location within the tanks. The largest crabs always hided in the shade provided by the protruding inflow water pipe. When two crabs had similar size, they shared this position (Fig. 4.1.7a). In contrast, smaller (prey) crabs characteristically stayed against the wall in the opposite side of the tank, away from the predator (Fig. 4.1.7b).

4.1.4 Discussion

4.1.4.1 Cannibalism patterns in E. japonica

This study provides direct evidence that intermolt *E. japonica* individuals cannibalize conspecifics in the laboratory under the following conditions.

First, cannibalism in *E. japonica* was size–dependent and directional: large crabs successfully consumed small ones only when the size difference between opponents was large. This is because under this scenario, the cannibals would be at less risk of injury (Polis, 1981; Mateo & Pleguezuelos, 2015). The effect of size difference on cannibalism has been confirmed in many crustaceans (Dutil et al., 1997; Luppi et al., 2001; Sotelano et al., 2012; Long & Whitefleet–Smith, 2013; Daly & Long, 2014). For instance, Daly & Long (2014) demonstrated that in the blue king crab *Paralithodes platypus*, the number of consumed prey crabs was positively correlated with predator size in sand habitat.

Second, sexual differences occur in cannibalism patterns of *E. japonica*: males show a stronger cannibalistic tendency than females. As reviewed by Romano & Zeng (2016), among crustaceans, sexual difference in cannibalism has been confirmed in only a few decapod species, such as the blue swimmer crab *Portunus pelagicus* and West Indian spider crab *Mithrax spinosissiumus*. Generally, male crabs tend to have a higher propensity to behave aggressively than do female crabs because of their enlarged chelipeds, which is exactly the case with *E. japonica* (Zhang et al., 2017). In particular, after reaching morphological sexual maturity, the enlarged chelipeds enable males to attack conspecifics and successfully defend themselves.

Third, both alternative food and shelters could reduce the cannibalism rate. Our results suggest that alternative food seems to be a more effective method than shelters in mitigating cannibalism in *E. japonica* (Fig. 4.1.4); this might be because alternative food and shelters work in different ways in reducing cannibalism. Alternative food lowers cannibalism in several ways, such as directly reducing predators' hunger levels and influencing predators' foraging strategies; while shelters work by reducing the encounter rate of different–sized individuals or increasing predator handling time (Janssen et al., 2007; Amaral et al., 2009; Hill & Weissburg, 2013). Cannibalism is always a hunger–driven behaviour and has been regarded as an alternative feeding strategy (Fox, 1975; Hecht & Pienaar, 1993) so starving crabs to standardize hunger levels as in this study may have potentiated to some extent the cannibalistic response of *E. japonica* (see further discussion below).

Fourth, male *E. japonica* exhibited a classic type II functional response under the present set of experimental conditions. Similar functional responses have been reported in other crustaceans, including the red king crab *P. camtschaticus* and the blue king crab *P. platypus* (Long et al., 2012; Long & Whitefleet–Smith, 2013; Daly & Long, 2014). But we should notice that the functional response of predators can be influenced by different factors, such as habitat type and predator size (Long et al., 2012; Long & Whitefleet–Smith, 2013; Daly & Long, 2014). Our results demonstrated that the Rogers random predator equation and the Holling's disc equation provided similar fit to the data, but the former model was preferred as it could account for prey depletion during the experiment (Bolker, 2008). In the experiment, we adopted a prey depletion functional response design and the consumed prey crabs were not replaced; the Holling's type II functional response fails to consider the depletion of prey crabs over the course of the experiment (Haddaway et al., 2012).

4.1.4.2 Appendage loss in E. japonica

Our results suggest that *E. japonica* may autotomize appendages under predation by larger conspecifics as noted also in the southern king crab *Lithodes santolla* (Sotelano et al., 2012) and many other crustaceans. We previously studied the patterns of limb loss in field specimens of *E. japonica*, and considered this behaviour as a bet–hedging strategy to increase the chance of survival during predator attack (Zhang et al., 2016). Consistent with the results of that study, no difference was found in the frequency of limb loss between left and right sides of the body, a fact that may reflect the unpredictable and random direction of predator attack. Also, in this study, *E. japonica* lost the 2nd and 3rd walking legs more often than other appendages. This is not surprising considering that the 2nd and 3rd walking legs of *E. japonica* are longer than other appendages (Zhang et al., 2016) and that appendage length in crustaceans is positively correlated with the chance of it being grabbed by predators (Edwards, 1972; Smith, 1990). An alternative explanation may be that chelipeds have multiple functions such as foraging and competition, and the loss of a cheliped may be a greater loss than the loss of a walking leg; in this situation, crabs may preferentially autotomize their walking legs. Interestingly, careful inspection of the limb loss data in the *E. japonica* field specimens examined by Zhang et al. (2016) suggests a relation between body size and the probability of a particular limb of being lost/autotomized. Thus, the relative frequency of walking leg loss was higher in small crabs and decreased with increased body size whereas that of cheliped loss showed reciprocal variation (Zhang et al., unpublished observations).

4.1.4.3 Cannibalism in the field

It is not possible at this stage to easily relate the high incidence of cannibalism observed in these laboratory experiments to natural populations of *E. japonica*. Based on a stomach content analysis of a large number of wild *E. japonica*, Kobayashi (2009) suggested that the incidence of cannibalism in this species may be low, although he did notice the presence of conspecific exoskeleton fragments among the stomach contents. He interpreted those fragments as exuviae because soft tissues were rarely observed and concluded that "*E. japonica* may be a scavenger rather than a cannibal" (Kobayashi, 2009).

While this may or not be true, the absence of soft tissues in the stomach could be caused by their faster digestion rate compared with the exoskeleton as shown in a digestion study with the snow crab *Chionoecetes opilio* (Lovrich & Sainte–Marie, 1997). Moreover, we would like to point to the fact that in many experiments we observed that predators ate predominantly the soft tissues of victims, leaving the empty exoskeleton behind. So rather than the lack of cannibalistic behaviour per se, the low incidence of cannibalism in the field could be related to other factors such as abundant alternative food resources (from plants to insects) and complex physical structures that provide shelter in the field, two factors that we found to mitigate predation in the laboratory (e.g. Luppi et al., 2001; Amaral et al., 2009; Romano & Zeng, 2016). In addition, the longitudinal distribution pattern of developmental stages of *E. japonica* along rivers might also reduce the possibility for cannibalism to occur. This size–dependent segregation reduces the encounter rate of different–sized crabs and therefore reduces the possibility of intraspecific predation and guarantees stable recruitment. Spatial/habitat segregation has been frequently observed in stage–structured species and is regarded as an effective mechanism to mitigate conspecific predation risk (Leonardsson, 1991; Jormalainen & Shuster, 1997; Nielsen et al., 2007; Amaral et al., 2009; Robertson & Cushing, 2011; Braccini & Taylor, 2016). Interestingly, we noted that small crabs tend to stay away from their larger conspecifics during daytime. Further studies are needed to determine the importance of cannibalism in shaping the segregated distribution of developmental stages in *E. japonica*.

Our results provide an initial step toward understanding the cannibalism in *E. japonica*. Despite its potential importance, the present study has some limitations. Here, we explored the cannibalism patterns of *E. japonica* under laboratory conditions and when potential predators were starved. Starving predators not only standardizes hunger levels, but also artificially enhances their motivation to feed (Luppi et al., 2001); as a consequence, the degree of cannibalism intensity in *E. japonica* determined in this study may be over–estimated in comparison to natural environments. The fate and reproductive potential of injured crabs, which accounted for half of the cases in cannibalistic encounters in the current experiments, also needs to be determined in the field. On the other hand, we used only intermolt crabs in the experiments whereas other authors have shown that cannibalism can be enhanced during molting periods when soft–state crabs are extremely vulnerable to attacks (Luppi et al., 2001; Sotelano et al., 2012; Romano & Zeng, 2016). Therefore, further studies are needed to examine cannibalism in *E. japonica* during molting periods and under field conditions.

Figures

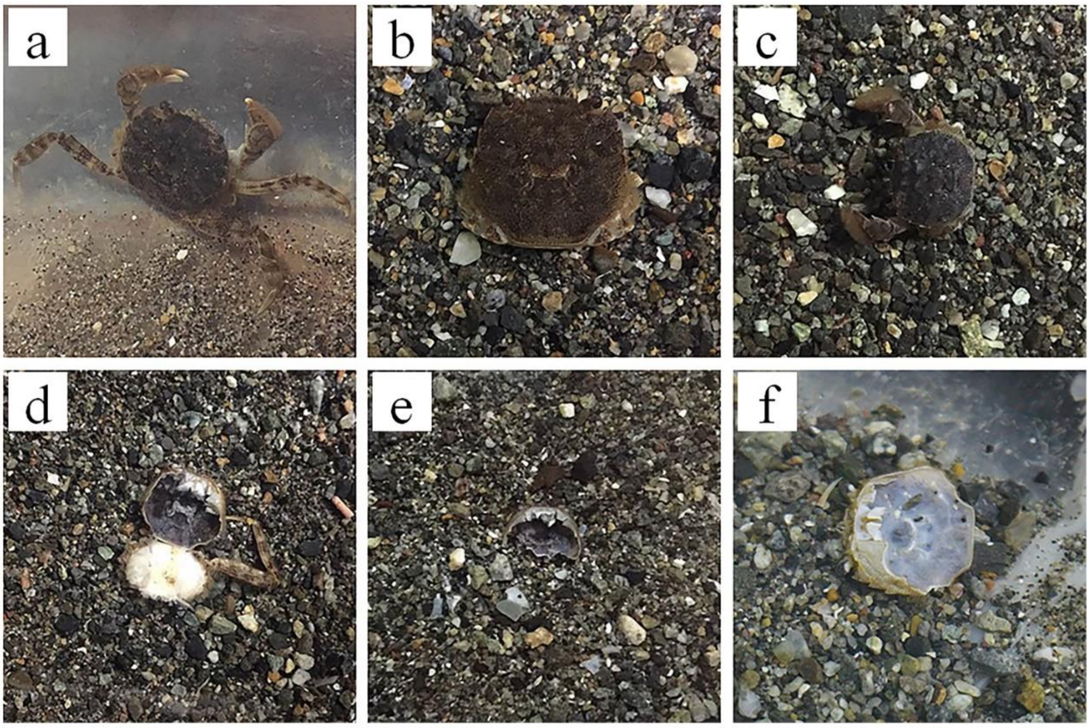


Fig. 4.1.1 Photographs of injured (a, b, c) and remains of consumed (d, e, f) prey crabs. Injured crabs had from minor to complete loss of appendages but little or no damage to the body (a, b, c). Soft tissue of killed prey crabs was consumed by the cannibals, while hard exoskeleton was left (d, e, f)

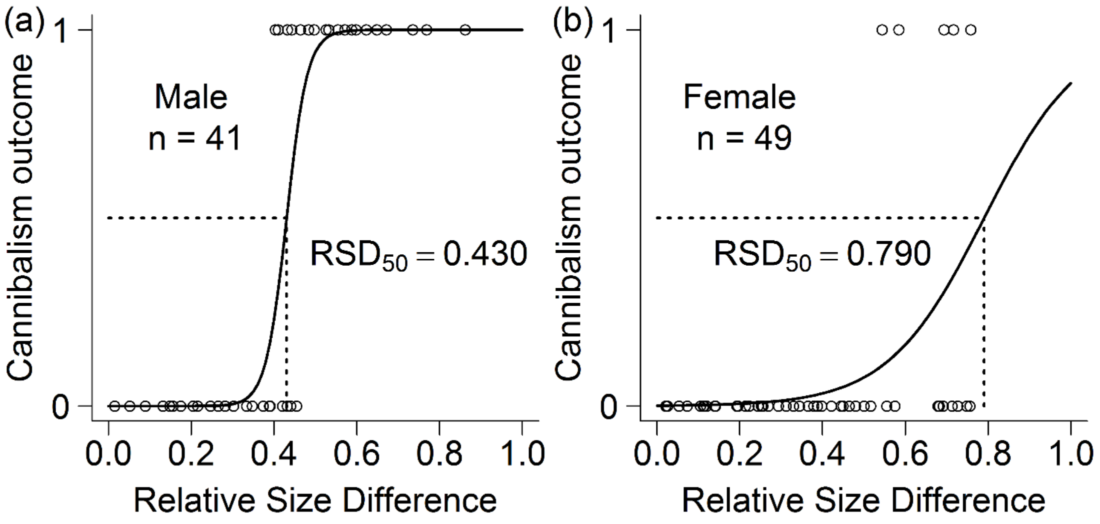


Fig. 4.1.2 Cannibalism outcome in relation to the relative size difference (RSD) between two different–sized *Eriocheir japonica* (0 if cannibalism is absent, and 1 if cannibalism is present). Results are shown separately for male (a) and female (b) predators. Solid lines are logistic regression fits; dashed lines indicate the relative size difference (RSD) values at which cannibalism has a 50% probability of occurring

Fig. 4.1.3 Mean (± SD) relative size difference (RSD) between male cannibals and injured victims. *Killed* indicates prey crabs that were killed and consumed by male predators, and *Injured* represents prey crabs that lost their appendages. Values designated by different superscript letters are significantly different (Student's *t* test, $p < 0.05$)

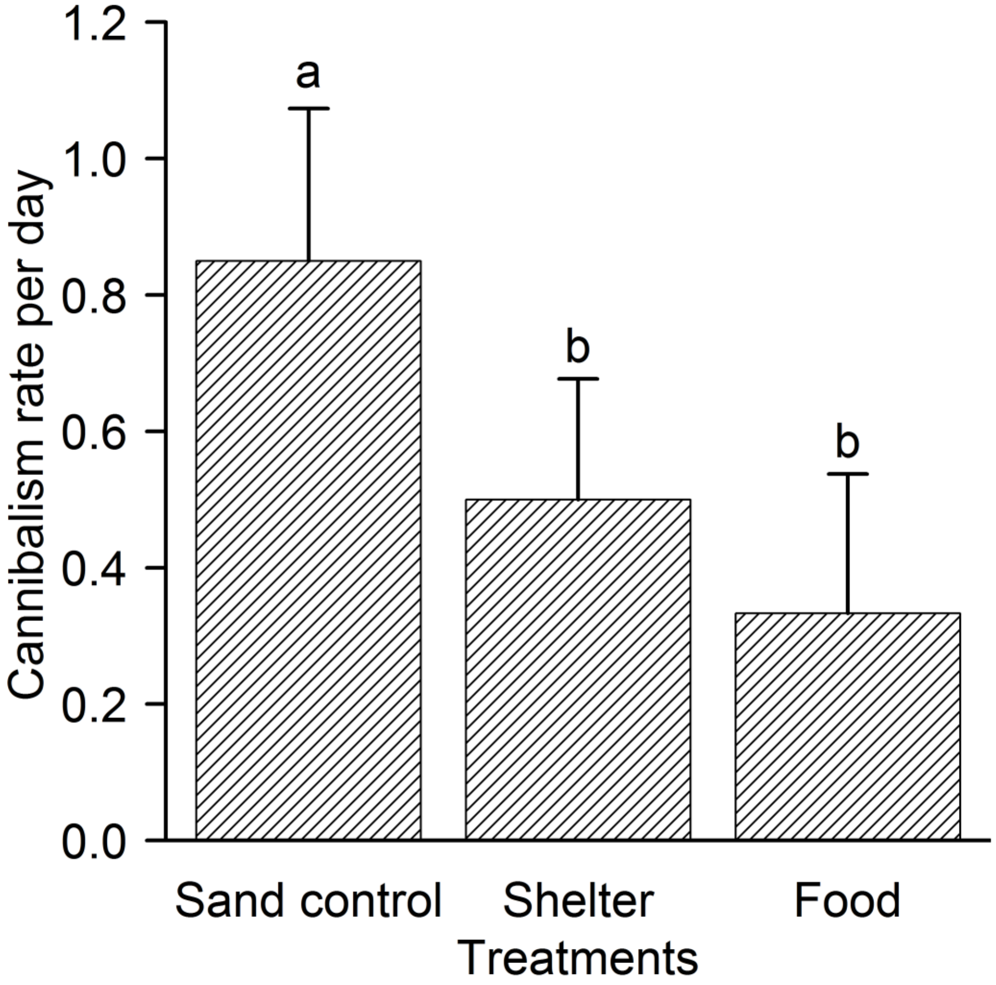


Fig. 4.1.4 Mean (± SD) cannibalism rate of *Eriocheir japonica* in three treatments (sand control, shelter, and food groups). Each trial was conducted with one predator and four prey. Significant differences in the cannibalism rate among treatments were found (Kruskal–Wallis tests, $p < 0.05$). Values with different superscript letters are significantly different (Dunn's test, $p < 0.05$)

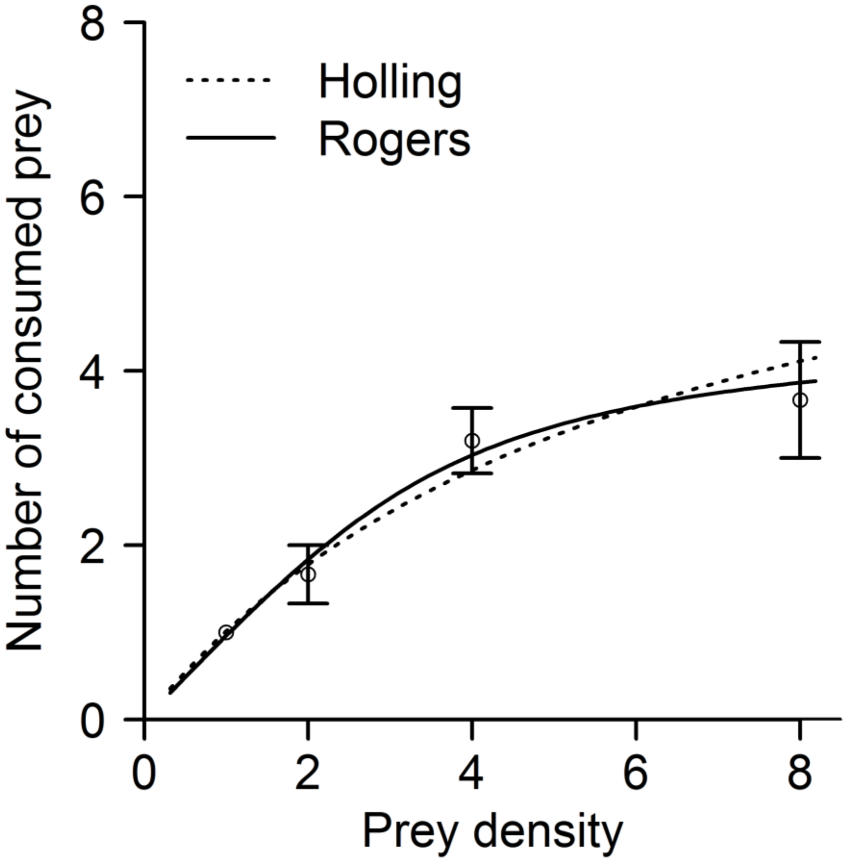


Fig. 4.1.5 The predator functional response of male *Eriocheir japonica* preying on small conspecifics. Symbols represent the mean ± standard error. The dashed line indicates the fit of Holling's type II functional response; the solid line represents the results of Rogers random predator functional response

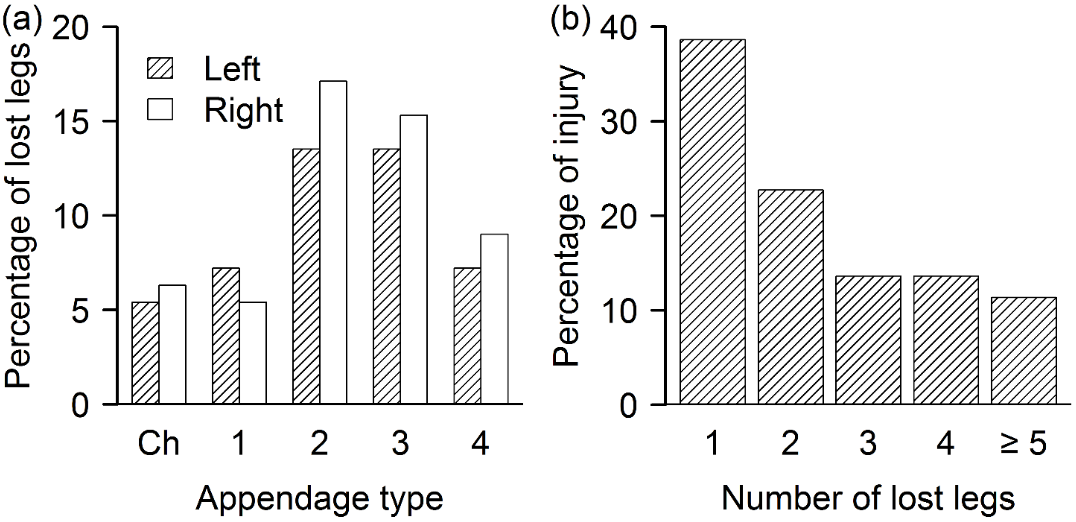


Fig. 4.1.6 (a) The relationship between percentage of lost appendages and appendage types among injured *Eriocheir japonica* (Ch: chelipeds; 1–4: walking legs). Not all appendages had an equal probability of loss, and the 2nd and 3rd walking legs were lost most often. (b) The observed percentages of injured *E. japonica* losing 1, 2, 3, 4, and ≥ 5 appendages. Single–appendage loss was most common among injured crabs

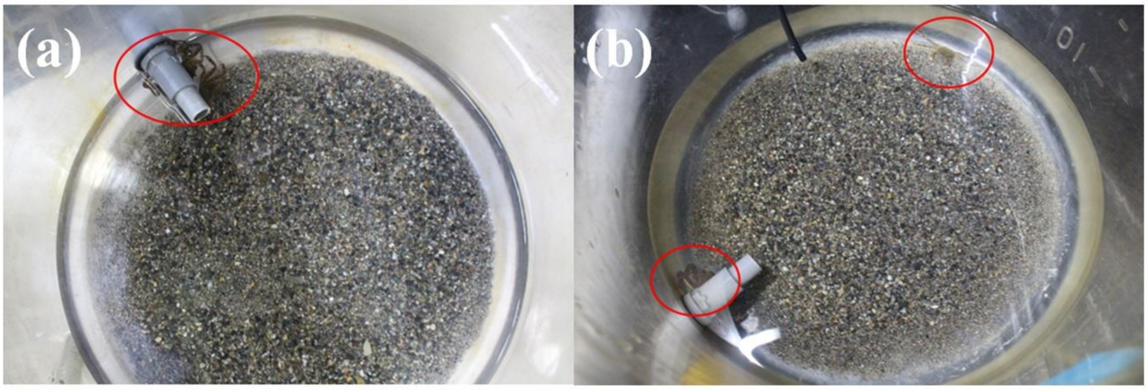


Fig. 4.1.7 (a) The position of predator and prey crabs at the end of trial. The RSD was 0.148, and cannibalism did not happen. (b) The position of predator and prey crabs at the end of trial. The RSD was 0.443, and prey crab lost several appendages (R1 + R4 + L1+ L2).

Tables

Table 4.1.1 Results of logistic regressions between cannibalism outcome (0 if cannibalism is absent, and 1 if cannibalism is present) and relative size difference (RSD) in the Japanese mitten crab *Eriocheir japonica*. p is the probability of cannibalism, and RSD_{50} indicates the RSD value at which cannibalism has a 50% probability of occurring.

Predator sex	Logistic regression	RSD_{50}
Male	$p = \frac{e^{-17.17+39.90x}}{1+e^{-17.17+39.90x}}$	0.430
Female	$p = \frac{e^{-6.784+8.585x}}{1+e^{-6.784+8.585x}}$	0.790

Table 4.1.2 Estimation results of two different kinds of type II functional response models (Holling's type II functional response and Rogers random predator functional response) of male *Eriocheir japonica* preying on smaller conspecifics. The standard errors of parameters are in parentheses. AIC means the Akaike's information criterion

Model	Attack rate (*a*)	Handling time (*h*)	AIC
Holling's type II	1.179 (± 0.286)	0.137 (± 0.060)	29.083
Rogers random predator	4.213 (± 2.066)	0.218 (± 0.059)	28.952

4.2 Comparison of cannibalism and interspecific predation

4.2.1 Introduction

Invasive species have been regarded as a serious global environmental problem posing substantial threats to native species and ecosystems (Lodge, 1993; Brockerhoff and McLay, 2011; Lockwood et al., 2013). The Chinese mitten crab, *Eriocheir sinensis* (H. Milne Edwards, 1853), is natively distributed in eastern Asia (Zhao et al., 1988; Dittel and Epifanio, 2009). Outside its native range, this crab becomes an annoying invasive alien species and has successfully invaded North America and Europe (Herborg et al., 2003; Dittel and Epifanio, 2009). This species can be transported to new habitat in various pathways including live import, ballast water discharge and Buddhist animal release practice (Cohen and Carlton, 1997; Rudnick et al., 2000; Dittel and Epifanio, 2009; Low et al., 2013; Yeomans and Clark, 2016).

The rapid spread of invasive *E. sinensis* in Europe and North America is partially due to the fact that this pest has enlarged chelipeds, which make them a strong competitor and thus outcompete native species (Gilbey et al., 2008; Wójcik et al., 2015). In addition to competitive superiority, a wide prey choice ranging from algae to fish may also favour the survival and further spread of this invasive crab in invasive range (Jin et al., 2003). Previous laboratory studies found that invasive *E. sinensis* is capable of consuming various native prey items, such as amphipod, gastropod molluscs, blue mussel, fish egg, chironomids and isopods (Webster et al., 2015; Wójcik et al., 2015; Rosewarne et al., 2016; Mills et al., 2016).

In Japan, *E. sinensis* has also been regarded as an invasive species and two female adult crabs were discovered in Tokyo Bay in 2004 (Takeda and Koizumi, 2005). Up to now, the predatory impacts of *E. sinensis* on native Japanese species, particularly the Japanese mitten crab *E. japonica*, still remains unstudied. *E. japonica* is an important fisheries species widely distributed in Japan (Kobayashi and Matsuura, 1999; Zhang et al., 2016, 2017, 2018). Segregated distribution pattern of *E. japonica* along river course has been found by field investigations: large crabs live in upstream and juveniles inhabit downstream areas. Such a longitudinal distribution pattern along river course might be an evolutionary adaptation to reduce the risk of intraspecific predation, therefore ensure a stable recruitment (Chapter 4.1). Results of the competition experiments (Chapter 3) suggest that compared with invasive *E. sinensis*, native *E. japonica* is a stronger competitor. Accordingly, I hypothesize that if *E. sinensis* invaded Japanese ecosystems, they would not occupy the upstream areas because competitively superior native *E. japonica* inhabit there; the defeated *E. sinensis* might move to downstream locations, where they would outcompete or consume small natives. In order to verify the predatory impacts of invasive *E. sinensis* on native *E. japonica*, I carried out laboratory experiments to compare the strength of intra– and interspecific predation on juvenile *E. japonica*.

4.2.2 Materials and Methods

4.2.2.1 Animal collection and maintenance

Adult *E. japonica* were bought from the Agano river, Niigata prefecture, Japan. Juvenile *E. japonica* were collected from a small in Tateyama, Chiba prefecture, Japan

(34.975°N to 34.974°N, 139.776°E to 139.775°E). Adult *E. sinensis* were purchased from a Ueno market in Tokyo, which were imported from Yangcheng Lake, Jiangsu province, China. Special permission was obtained from the Ministry of the Environment, Government of Japan to rear the invasive *E. sinensis*. The carapace width (CW) of each crab was measured to the nearest 0.01 mm with digital calipers. Prior to experiments, crabs were separated by species, sex, and size and maintained in tanks for at least one week. Experiments were conducted in Tokyo University of Marine Science and Technology, Tokyo.

4.2.2.2 Predation experiment

Predation experiments were conducted in cylindrical tanks (diameter: 40 cm, height: 30 cm) (water level: about 10 cm), whose bottom was covered with a layer of sand. Adult *E. sinensis* and *E. japonica* (both male and female) were regarded as predators and reared individually. Size of predators was summarized in Table 4.2.1. Results of cannibalism experiments (Chapter 4.1) suggest that relative size difference between predators and prey crabs greatly influences the predation results. Therefore, for the purpose of removing the effect of relative size difference, the mean (± standard deviation) relative size difference between four types of predators and juvenile *E. japonica* was controlled to be 0.7699 (± 0.0133), and there was no significant difference in the relative size difference between predator and prey crabs among treatments (Fig. 4.2.1, Kruskal–Wallis test, $p = 0.449$). In cannibalism experiments (Chapter 4.1), predators were starved for 48 hours. We noticed that starving predators not only standardizes hunger levels but also increases predators' motivation to feed; therefore, cannibalism rate might be over–estimated. In order to get rid of the artificially predator voracity, in this experiment, predator crabs were not starved.

Juvenile *E. japonica* were considered as prey and introduced to experimental tank first to acclimate for about 20 minutes. The predation experiment was initiated by introducing the predator crab. Each trial contains one predator and five prey crabs, no food and aeration was provided during experimental period. Consistent with cannibalism experiments (Chapter 4.1), the number of consumed prey crabs, both injured and dead prey crabs, was recorded after 24 h. In addition, trials without a predator were performed as control groups (five replicates). Replicates for each treatment were shown in Table 4.2.1. Kruskal–Wallis test and Mann–Whitney's *U*–rank sum test were performed to determine the differences in predation rate among treatments.

4.2.3 Results

The survival rate of prey crabs in control groups (without a predator) was 100% in all replicates, thus the experimental deaths of prey crabs were attributed to consumption by adult predators. Results of the predation experiments indicate that both invasive *E. sinensis* and native *E. japonica* are capable of consuming juvenile *E. japonica*. Under present confined laboratory conditions, no significant difference was found in predation rate among treatments (Fig. 4.2.2, Kruskal–Wallis test, $p = 0.9708$). All predators showed high predation rate (45.83%) on juvenile *E. japonica* (Fig. 4.2.2). When experiments finished, juvenile *E. japonica* gathered together in control groups; since the relative size difference between predator and prey crabs was large in this experiment, prey crabs were always found to stay away from their predators.

4.2.4 Discussion

The invasion of *E. sinensis* has posed various negative impacts in invaded ecosystems; among these adverse impacts, predatory impacts have received considerable attention (Webster et al., 2015; Wójcik et al., 2015; Rosewarne et al., 2016; Mills et al., 2016). My present study represents the first attempt to compare the intensity of cannibalism and predation by adult *E. japonica* and *E. sinensis* on juvenile *E. japonica*. Current results suggest in both sexes, adults of both native *E. japonica* and invasive *E. sinensis* predated intensively on native juvenile *E. japonica*. This result was unlike the expectation of previous studies, which suggest invasive species are more effective predators than native species and would consume more native prey (Salo et al., 2007; Howard et al., 2017). For instance, Griffen and Riley (2015) examined the potential impacts of invasive European green crabs *Carcinus maenas* and Asian shore crabs *Hemigrapsus sanguineus* on native rock crab *Cancer irroratus* and their results elucidated that predation by invasive crabs exceeded cannibalism. In addition, in the previous cannibalism studies (Chapter 4.1), male *E. japonica* were found to be more cannibalistic than females. These two discrepancies might be mainly due to the large relative size difference between predator and prey crabs. Intraspecific predation in *E. japonica* is strongly size–dependent in both sexes and is prone to occur when the size difference becomes large (Chapter 4.1). In present experiments, the

RSD values were large (about 0.77); which would ensure both native and invasive predators easily to consume smaller *E. japonica* even the predators were not starved.

In Japanese rivers, abundant alternative food, physical shelter and the segregated distribution patterns along river courses are believed to play a significant role in mitigating cannibalism and thus guaranteeing stable recruitment in *E. japonica* (Zhang et al., 2018). Indeed, the longitudinal distribution pattern of *E. japonica* along river course was considered as an evolutionary adaptation to reduce cannibalism risk (Chapter 4.1). Previous studies have pointed it out that invasive species could expand rapidly in new habitats due to the lack of coevolutionary history with native species (Facon et al., 2006; Lankau et al., 2012). Invasive *E. sinensis* lack co–evolutionary history with native Japanese species and thus might have great predation pressure on juvenile *E. japonica* when they invaded Japanese ecosystems.

Present study has some limitations. I only examined the strength of intra– and interspecific predation by adult *E. japonica* and *E. sinensis* on juvenile *E. japonica* due to the lack of juvenile *E. sinensis*. Previous studies have elucidated that asymmetry in mutual predation between invasive and native species plays an important role in species displacement (Nakata and Goshima, 2006). Further studies are required to investigate the asymmetry in mutual predation between invasive *E. sinensis* and native *E. japonica*.

Figures

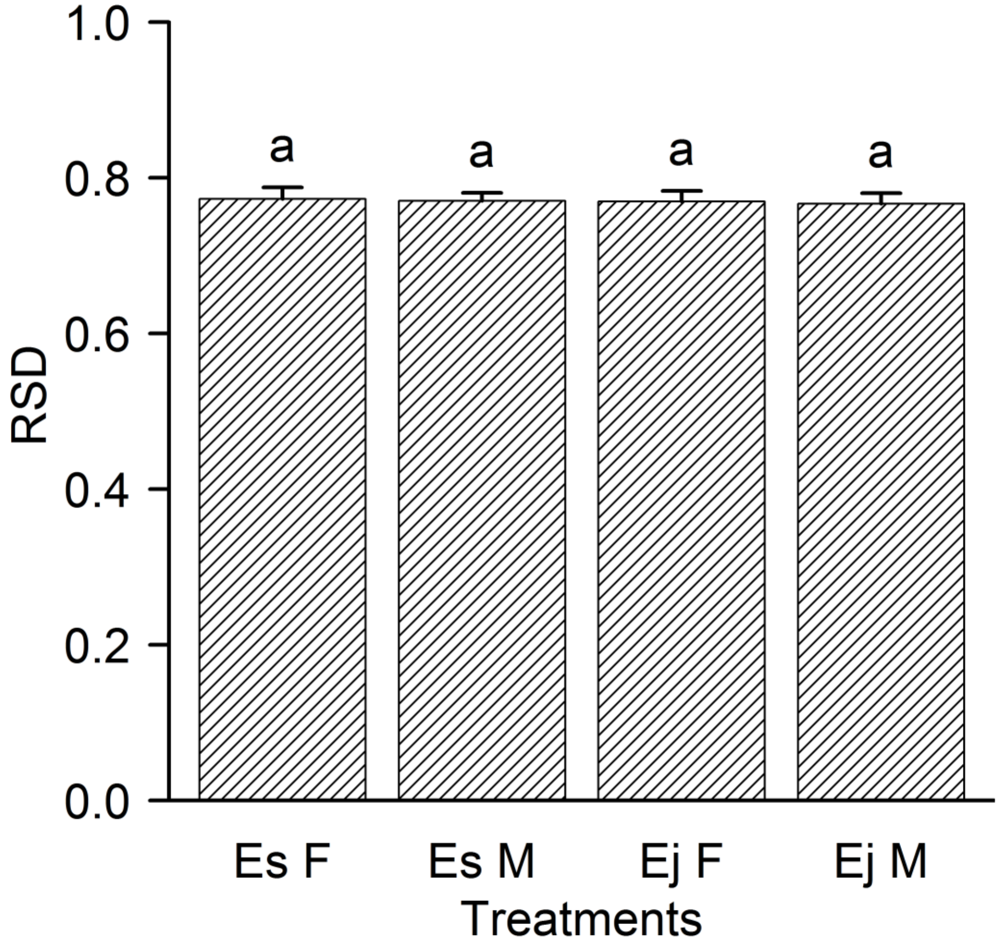


Fig. 4.2.1 Relative size difference (RSD) between predator crabs and juvenile Japanese mitten crab *Eriocheir japonica*. Es: *Eriocheir sinensis*, Ej: *Eriocheir japonica*, F: female, M: male. No significant difference was detected among treatments.

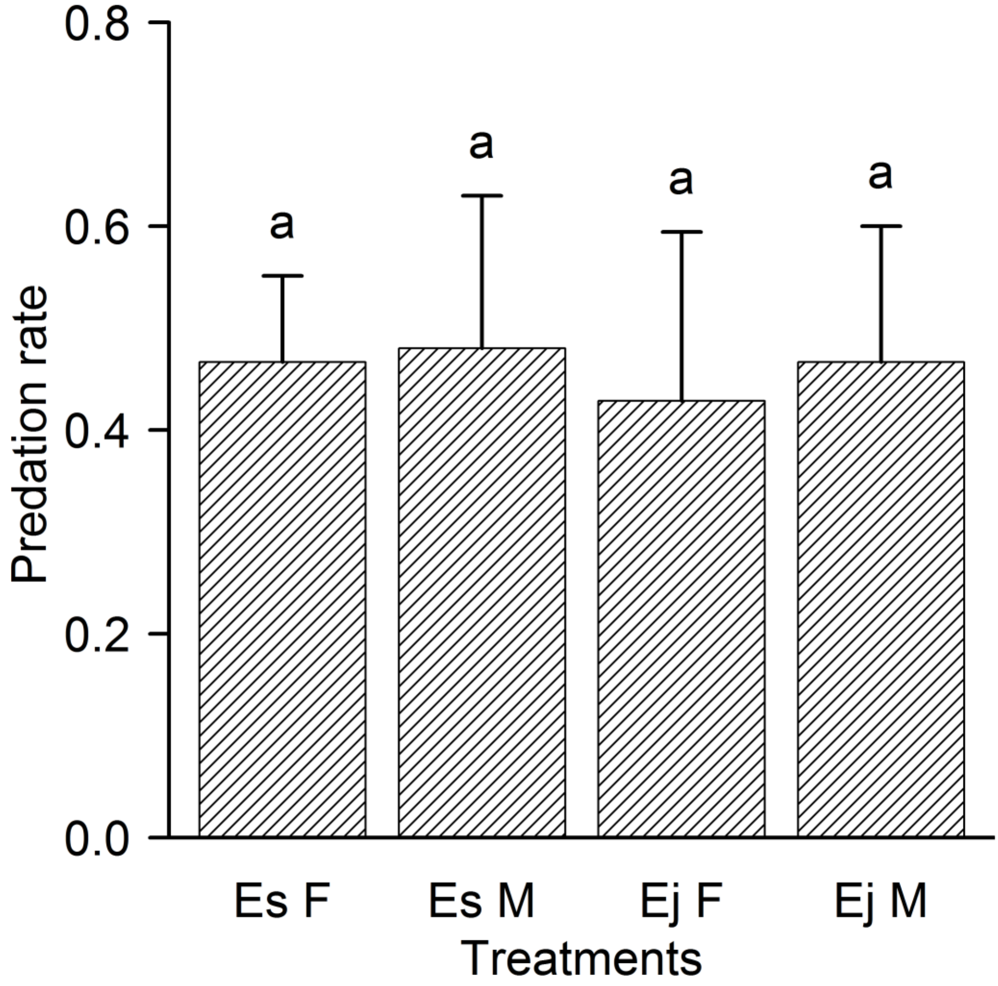


Fig. 4.2.2 The mean predation rate (± standard error) on juvenile *Eriocheir japonica* among different treatments. Es: *Eriocheir sinensis*, Ej: *Eriocheir japonica*, F: female, M: male. Each trial contained one predator and five prey crabs. No significant difference was observed among treatments.

Tables

Table 4.2.1 Carapace width (CW in mm) of adult Chinese mitten crab *Eriocheir sinensis* and Japanese mitten crab *Eriocheir japonica* used in this experiment.

Species	Sex	Replicates	Mean CW	Standard error
Eriocheir sinensis	Male	5	65.95	0.304
	Female	6	59.90	0.411
Eriocheir japonica	Male	6	54.43	0.846
	Female	7	56.37	0.969

Chapter 5

General Discussion

5.1 Invasion risk of *E. sinensis* in Japan

In summary, in this study, I developed a periodic matrix population model for the invasive Chinese mitten crab, which helps us understand its population growth and develop effective control strategies. In addition, I studied the potential competitive and predatory impacts of invasive *E. sinensis* on native *E. japonica* under laboratory conditions, which represent the first study of potential impact of this invasive species on native Japanese species.

If Chinese mitten crab successfully establishes self–sustaining populations in Japan, it might disturb population dynamics of native *E. japonica*. The distribution pattern of *E. japonica* along river course has been previously studied and large crabs live in the upstream while small individuals gather in the downstream (Kobayashi and Matsuura, 1999). This distribution pattern is suggested to be an evolutionary adaptation to reduce cannibalism probability (Zhang et al., 2018). As suggested by the competition results, the native *E. japonica* is more aggressive than similar sized invasive *E. sinensis*; therefore, the large *E. japonica* in the upstream may force the invasive *E. sinensis* to move to the middle stream or downstream, where invasive *E. sinensis* would outcompete and predate intensively on juvenile *E. japonica*. As a consequence, the recruitment and stability of native *E. japonica* populations would be adversely affected. In addition to *E. japonica*, the invasion of Chinese mitten crab would also negatively influence other Japanese species through mechanisms such as predation or competition.

The invasion of Chinese mitten crab in some European and North American countries was believed to be caused by ballast waters and live import (Cohen and Carlton, 1997;

Rudnick et al., 2000; Dittel and Epifanio, 2009). These two introduction pathways also exist in Japan. Up to now, however, *E. sinensis* population has not been found in Japanese ecosystem. On the basis of my present results, I propose the following two hypothetical explanations.

First, Japanese ecosystem may be unsuitable for the establishment of Chinese mitten crab. As suggested by the periodic matrix population model, larval stage is critical in the initial population growth of invasive *E. sinensis* estuarine environment should be considered seriously when evaluating the future invasion risk of this invasive species. Kobayashi (2012) qualitatively compared the estuarine environment between China–Korea (where native *E. sinensis* populations exist) and Japan. If his results were correct, most of Japanese estuarine environments are different from those of China–Korea, and only the Ariake sea area in Japan is similar to the estuaries where *E. sinensis* larvae occur (Kobayashi, 2012). This finding suggests that the Ariake sea area is susceptible to the future invasion of *E. sinensis*. More recently, Zhang et al. (in press) constructed an ensemble species distribution model for the Chinese mitten crab by using worldwide occurrence records and related environmental variables to predict its global potential distribution in freshwater habitats. Their ensemble model had high predictive performance and successfully predicted the known distribution of Chinese mitten crab in its native range and invasive ranges. In addition, their model predicted that part of Japan is under the risk of invasion by *E. sinensis* (Fig. 5.1). Although the Ariake sea area might be suitable for the survival of Chinese mitten crab larvae, freshwater habitats around Ariake sea are suitable for this species (Fig. 5.1). This mismatch of suitable estuarine and freshwater habitats may partially lead to the absence of Chinese mitten crab population in Japan.

Second, native strong species may prevent the invasion of Chinese mitten crab in Japan. From Fig. 5.1, we can see a very small freshwater habitat around Ariake sea is suitable for *E. sinensis*. Native Japanese mitten crab is widely distributed in Japan and populations of *E. japonica* also exist around Ariake sea area (Fig. 5.2). The results of competition experiments (Chapter 3) indicate that native *E. japonica* are competitively superior to similarly sized invasive *E. sinensis*. Therefore, the native strong competitor may act as a form of biotic resistance and prevent the invasion of invasive *E. sinensis*.

From above results, I still cannot confidentially conclude that invasive Chinese mitten crab would not establish a population in Japan. There are mainly two reasons. Firstly, there is limited knowledge about the larval biology of Chinese mitten crab and the environmental requirement of Chinese mitten crab larvae is still largely unknown (Dittel and Epifanio, 2009; Blumenshine et al., 2012). The results of Kobayashi (2012) were derived from a habitat–matching approach, which was first proposed by Hanson and Sytsma (2008). Hanson and Sytsma (2008) stated in their study that "The evaluation of invasion potential is based on the premise that mitten crab populations will become established in estuary–river systems that match ecological conditions that define the native and introduced range." It is unclear whether this premise is true or not. In addition, they selected variables including watershed area, estuary area, salinity intrusion, tidal influence, salinity intrusion, and flushing time to predict the invasion ranges of *E. sinensis* in the Pacific Northwest and Alaskan estuaries (Hanson and Sytsma, 2008). How can the prediction accuracy be guaranteed if selected diagnostic variables are unimportant or even irrelevant? Therefore, a more robust quantitative technique should be developed to evaluate the suitable estuarine habitats for *E. sinensis* larvae. Secondly, in addition to competitive and predatory impacts, invasive Chinese mitten crab may adversely influence native Japanese mitten crab populations in many other ways, such as pathogen transmission and hybridization. Chinese mitten crab has been identified as a competent vector of the crayfish plague pathogen *Aphanomyces astaci* (Schrimpf et al., 2014), a disease fatal to native European crayfish species. Further studies are needed to evaluate the potential parasitic impact of invasive *E. sinensis* on native *E. japonica*. In addition, native *E. japonica* and invasive *E. sinensis* belong to the same genus and have the same chromosome number. There is a possibility that interspecific hybrid between the two species may occur. Huxel (1999) suggested that hybridization between native and invasive species could lead to the rapid displacement of native species. Further studies should be performed to evaluate the hybridization probability between native *E. japonica* and invasive *E. sinensis*.

5.2 Management strategies

Considering the fact that the role of invasive *E. sinensis* on native *E. japonica* population dynamics is not fully understood, it is of great importance to take effective control measures to prevent the invasion of Chinese mitten crab in Japan. Here, I propose several management strategies to control this invasive species in Japan.

First, early monitoring programmes should be developed for the invasive Chinese mitten crab. Due to the similar morphological features, it is kind of difficult to distinguish between native *E. japonica* and invasive *E. sinensis*. Therefore, advanced technique, such as Environmental DNA, should be adopted to detect the existence of Chinese mitten crab in Japan. Second, strict management measures should be taken to prevent the escape of live *E. sinensis* from food market. The Japanese government has established strict regulations to avoid the escape of *E. sinensis* into Japanese ecosystems. For instance, a special permission from the Ministry of the Environment, Government of Japan is required to import, sale or study the invasive Chinese mitten crab. Third, appropriate ballast water management strategies should be developed to prevent the further introduction of larvae of Chinese mitten crab via ballast water discharge.

5.3 Further studies

My current study represents the first study to investigate the invasion risk of Chinese mitten crab in Japan. Despite its potential importance, the present study has some limitations and further studies are required.

Up to now, the information on larval biology of *E. sinensis* is limited; therefore, larval mortality rate in the present matrix population model was assumed based on previous studies. Further studies are required to improve the model by including more accurate parameters. In addition, the present matrix population model density independent and focuses on only one species. Further studies are needed to consider the density–dependent effects on vital rates and include the competition into the model.

In this study, I only investigated the potential competitive and predatory impact of invasive *E. sinensis* on native Japanese mitten crab. As I mentioned above, further studies are needed to evaluate the parasitic impact of invasive *E. sinensis* on native *E. japonica*. In addition, hybridization probability between the two species should be studied in future. The potential impact of Chinese mitten crab on other Japanese species should also be studied in further studies.

Up to now, the Ariake sea area is considered to be susceptible to the invasion of *E. sinensis* by a qualitative habitat comparison method. A more robust quantitative method should be used to evaluate the potential suitable estuarine environment for *E. sinensis*, such as species distribution model. Species distribution model requires both species occurrence records and related environmental layers. There are many kinds of marine environmental variables available such as Bio–ORACLE (Tyberghein et al. 2012). The challenge to develop a species distribution model for *E. sinensis* larvae is lack of larvae distribution data. Further studies should be conducted to collect accurate distribution data for *E. sinensis* larvae.

Figures

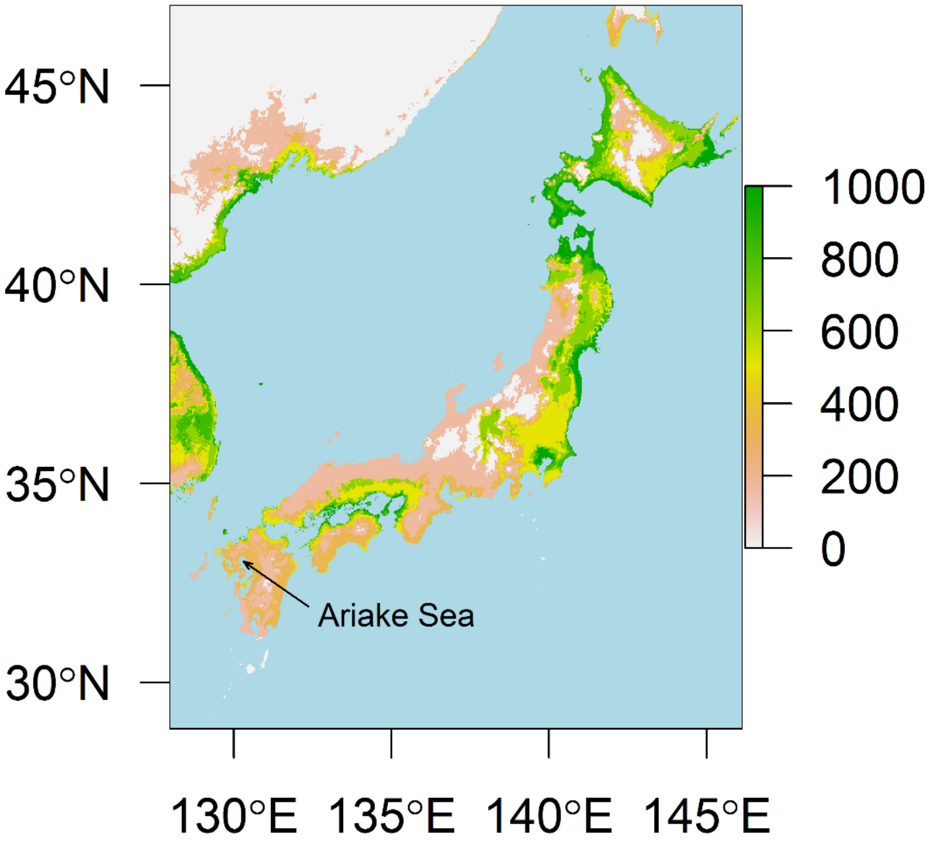


Fig. 5.1 The potential distribution of Chinese mitten crab *Eriocheir sinensis* in Japan predicted by an ensemble species distribution model. Habitat suitability map ranges from 0 to 1000. Values on X and Y axes represent degrees of longitude and latitude, respectively.

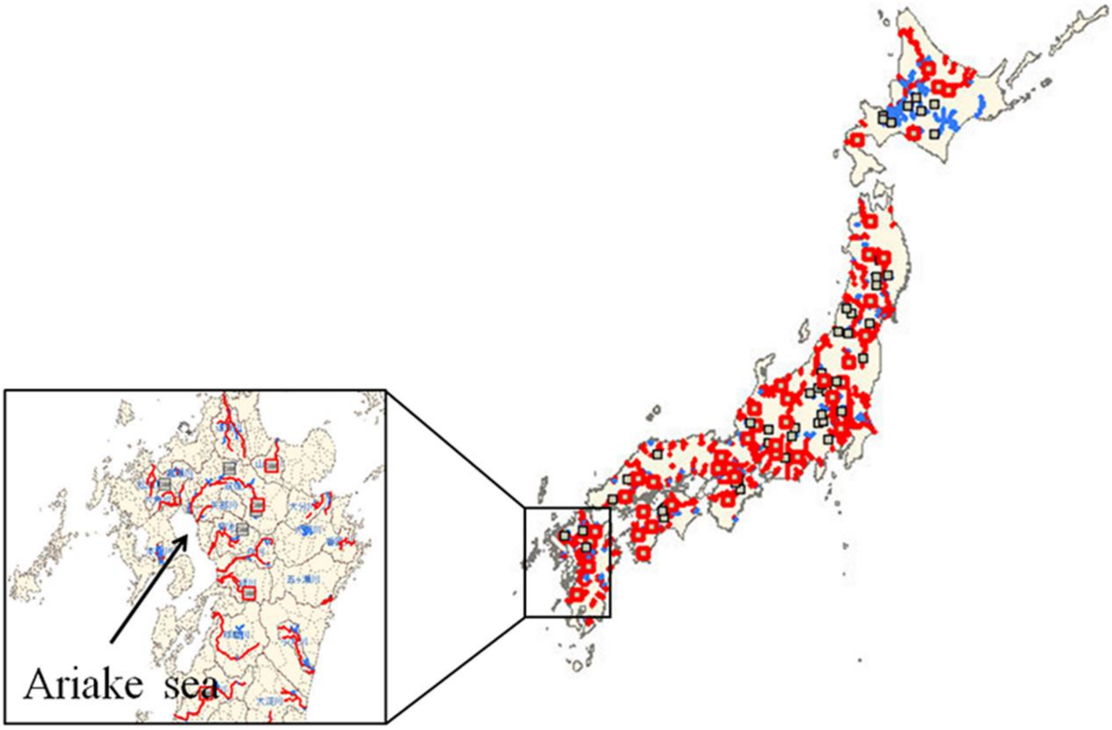


Fig. 5.2 The distribution of Japanese mitten crab *Eriocheir japonica* in Japan. Red area represents the distribution of *E. japonica* in Japan, blue area indicates freshwater habitats. (Data source: The Ministry of Land, Infrastructure, Transport and Tourism: http://mizukoku.nilim.go.jp/ksnkankyo/).

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