



ORIGINAL RESEARCH ARTICLE

# Impact of Chinese mitten crab *Eriocheir sinensis* on blue mussel *Mytilus edulis trossulus* – laboratory studies of claw strength, handling behavior, consumption rate, and size selective predation<sup>☆</sup>

Dagmara Wójcik<sup>a,\*</sup>, Monika Normant<sup>a</sup>, Barbara Dmochowska<sup>a</sup>, Amy Fowler<sup>b</sup>

<sup>a</sup> Department of Experimental Ecology of Marine Organisms, Institute of Oceanography, University of Gdańsk, Gdynia, Poland

<sup>b</sup> Marine Resources Research Institute, South Carolina Department of Natural Resources, Charleston, USA

Received 19 May 2014; accepted 25 March 2015

Available online 9 April 2015

## KEYWORDS

Non-indigenous species;  
Invasive;  
Introduced;  
Native;  
Mortality

**Summary** We examined the claw strength, handling behavior, consumption rate, and size selective predation of the invasive Chinese mitten crab *Eriocheir sinensis* feeding on native Baltic Sea blue mussels *Mytilus edulis trossulus* during 24 h laboratory experiments. Single starved crabs were offered 15 mussels (five mussels in three length classes) at a time. The total number of mussels consumed by a single crab increased significantly ( $P < 0.05$ ) with the experimental time from  $1.7 \pm 0.7$  # mussels crab<sup>-1</sup> h<sup>-1</sup> after 4 h to  $0.2 \pm 0.7$  # mussels crab<sup>-1</sup> h<sup>-1</sup> after 24 h. The highest consumption rate was observed within the first 4 h, and it decreased significantly ( $P < 0.05$ ) during the experiment. This was most likely due to the crabs being starved before the start of the experiment.

*E. sinensis* can also harm blue mussel shells by crushing them without further consumption. The mean daily damage, and not consumption, by a single crab was  $0.9 \pm 1.4$  of 11–40 mm mussels. The claw strength of *E. sinensis* ranged from 1.50 to 20.43 N (mean  $8.51 \pm 5.93$  N) and was significantly correlated ( $P < 0.05$ ) with sex and both claw size and carapace size. The study showed that *E. sinensis* may be able to impact the native *M. edulis trossulus* population

<sup>☆</sup> This research was supported by DS/G220-4-0150-11 from the University of Gdańsk, Poland.

\* Corresponding author at: Department of Experimental Ecology of Marine Organisms, Institute of Oceanography, University of Gdańsk, Al. Marszałka J. Piłsudskiego 46, 81-378 Gdynia, Poland. Tel.: +48 58 523 68 66; fax: +48 58 523 66 78.

E-mail address: [d.wojcik@ug.edu.pl](mailto:d.wojcik@ug.edu.pl) (D. Wójcik).

Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.



Production and hosting by Elsevier

abundance in the coastal Baltic waters either through direct predation or indirect mortality by damaging (crushing) the shell.

© 2015 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier Sp. z o.o. All rights reserved.

## 1. Introduction

It is well known that crabs choose their diet to maximize the net energy intake per unit foraging time (i.e. optimal foraging theory; Charnov, 1976; Elner and Hughes, 1978; Emlen, 1968; Hughes, 1979; Pulliam, 1974), and that the energy uptake from particular sized prey changes with crab size and species (Elner and Hughes, 1978; Hughes and Seed, 1981; Jubb et al., 1983). The optimal foraging theory (Hughes, 1979) predicts that a large crab predator would prey upon smaller prey, such as bivalves, as they afford a high energy return per unit foraging time. Larger bivalves with thicker shells would require more energy to break into and may result in chelae damage to the crab (Floyd and Williams, 2004), while thinner shells of same sized prey would have more flesh for the predator to consume and would be easier to open. However, although simple foraging behavior predictions assume that handling times and profitability remain constant over time, other studies have shown that these values are influenced by numerous factors including prey encounter rates, hunger, experience, and perception of prey items (e.g. Cornell, 1976; Cunningham and Hughes, 1984; Hughes, 1979; McNair, 1981; Palmer, 1981; Pyke, 1984). The influence of these factors can reduce the profitability of certain prey items, allowing them to be outranked by previously lower ranked prey (Hughes, 1979).

Previous experimental work has shown that predatory crabs prefer smaller prey items, down to a critical size, when there is a range of sizes available (e.g. Brousseau et al., 2001; Floyd and Williams, 2004; Hughes and Seed, 1981; Rheinallt, 1986; Seed, 1982). This may be due to larger sized prey having immunity related to their shell properties, including size, thickness, degree of inflation, and the presence or absence of a gap (Brousseau et al., 2001; Mascaro and Seed, 2000a, 2000b; Seed and Brown, 1978; Whetstone and Eversole, 1978). While small prey items may be actively chosen by the predator, the limitations of the predator's claw morphology and biomechanics may also influence their food choice. For example, bivalves with highly inflated and/or thicker shells require increased shell-breaking time and, thus, decrease the overall profitability of the prey (Boulding, 1984).

While most of the previous work has been in systems where both the predator and prey have long co-evolutionary relationships, we wanted to document the bivalve prey choices of a novel predator to examine if the behavior of the predator shifts when encountering a new prey species. We chose the invasive Chinese mitten crab *Eriocheir sinensis* (H. Milne-Edwards, 1853; Decapoda: Brachyura: Varunidae) as our novel predator model as this species was accidentally introduced into European waters at the beginning of the last century (Panning, 1938). Due to the environmental conditions for larval survival (i.e. higher salinity and temperature

than in the Baltic Sea), *E. sinensis* is unable to reproduce in the southern Baltic Sea (Anger, 1991; Herborg et al., 2003, 2007). Only adults are found throughout the year (Normant et al., 2002; Ojaveer et al., 2007) as part of the population living in German rivers (Czerniejewski et al., 2012; Drotz et al., 2010).

*E. sinensis* was listed by the International Union for the Conservation of Nature and Natural Resources among the world's worst 100 alien invasive species (ISSG, 2006; Lowe et al., 2000; Veldhuizen, 2001) partly because of its negative impact on other aquatic organisms and on resource users. Globally, the diet of the *E. sinensis* frequently consists of algae and vascular plants (Czerniejewski et al., 2010; Fladung, 2000; Jakubowska et al., 2011; Jin et al., 2003; Rogers, 2000), but its strong claws enable this species to prey on less mobile calcareous organisms, such as bivalves and snails (Mariappan et al., 2000). Large numbers of *E. sinensis* have also been reported to significantly reduce the abundance of potential prey in other locations (Dittel and Epifanio, 2009; Gollash, 2006; Herborg et al., 2003; Normant et al., 2002; Veilleux and de Lafontaine, 2007), especially when large numbers of crabs are migrating from rivers to the sea (Rudnick and Resh, 2005). However, little is known about how *E. sinensis* impacts populations of its prey or its behavior while feeding along the Baltic coast, but previous reports from this area document the preference of *E. sinensis* for the blue mussel *Mytilus edulis trossulus* (Wójcik and Normant, 2012; Wójcik et al., unpublished data).

While other bivalve species have energy values related to the size of the individual (Stoeckmann and Garton, 1997; Szaniawska et al., 1986), *M. edulis trossulus* from the Gulf of Gdańsk (southern Baltic Sea) does not share this trait (Pazikowska and Szaniawska, 1988; Szaniawska, 1991) even though larger individuals have harder and more mineralized shells (Barnes et al., 2007). Therefore, we hypothesize that *E. sinensis*, similar to other crab species (Aronhime and Brown, 2009; Ray-Culp et al., 1999), would preferably consume smaller *M. edulis trossulus* to maximize the net energy intake per unit foraging time. This potential preference for smaller juveniles has important implications for the maintenance of *M. edulis trossulus* populations and the entire ecosystem of the Baltic Sea, as they are a key component of Baltic benthic communities, contributing up to 95% of the fauna in some areas (Havenhand, 2012; Kautsky, 1982).

In order to test this hypothesis, we designed experiments using the blue mussel *M. edulis trossulus* as prey to determine and describe *E. sinensis*: (1) claw strength, (2) handling behavior, (3) consumption rate, and (4) prey size preference.

## 2. Material and methods

Specimens of the Chinese mitten crab, *E. sinensis* (male  $n = 7$ ; female  $n = 6$ ), and blue mussel, *M. edulis trossulus*,

**Table 1** Summary of morphological measurements of individual male and female *Eriocheir sinensis* ( $n = 13$ ) collected from the Gulf of Gdańsk in April–June 2010. M, male; F, female; L, left; R, right.

Crab no.	Carapace width [mm]	Carapace length [mm]	Sex	Claw length [mm]		Claw width [mm]		Claw height [mm]		Claw strength [N]	
				L	R	L	R	L	R	L	R
1	58.84	51.87	M	37.53	37.09	12.2	12.04	22.08	19.82	8.24	7.20
2	53.88	49.39	M	37.17	33.95	11	11.37	18.84	17.5	8.88	5.72
3	53.63	49.39	M	—	35.82	—	10.27	—	19.64	—	5.14
4	63.96	57.45	M	45.14	44.54	15.52	14.75	23.91	24.17	12.64	9.38
5	72.48	64.16	M	53.59	52.1	16.67	16.37	28.2	28.1	20.38	19.80
6*	79.29	72.19	M	57.48	54.58	19.22	18.89	30.76	30.72	20.43	18.87
7*	58	51.67	M	39.07	37.82	13.14	12.53	22.11	21.32	13.97	8.37
Mean M	62.87	56.59		45.00	42.27	14.63	13.75	24.32	23.04	14.09	10.64
±SD	9.74	8.68		8.74	8.27	3.08	3.07	4.40	4.86	5.35	6.12
8*	70.36	62.2	F	39.25	37.65	10.89	10.51	21.27	20.46	4.70	4.63
9*	62.2	54.8	F	32.95	32.26	9.53	7.97	17.59	16.38	6.33	6.78
10*	61.35	57.12	F	33.88	34.38	9.33	8.01	18.07	17.38	8.03	2.20
11*	55.69	51.12	F	24.08	30.59	6.37	7.71	13.71	9.35	3.23	1.93
12*	58.18	52.22	F	31.76	31.93	8.55	6.61	15.57	14.81	3.80	2.40
13*	55.65	51.31	F	30.42	31.29	8.5	8.78	15.77	16.14	8.13	1.50
Mean F	60.57	54.80		32.06	33.02	8.86	8.27	17.00	15.75	5.70	3.24
±SD	5.53	4.30		4.94	2.61	1.50	1.30	2.61	3.67	2.12	2.05
Mean	61.81	55.76		38.53	38	11.74	11.22	20.66	19.68	9.89	7.22
±SD	7.85	6.8		9.56	7.75	3.79	3.67	5.15	5.63	5.85	5.93

\* Individual was also used in the feeding experiments.

were collected by local fishermen in fyke-nets between April and June 2010 from the Gulf of Gdańsk (southern Baltic Sea). Epibionts were removed from the mussels, and shell length, width, and height were determined ( $\pm 0.01$  mm). Undamaged mussels in good condition were then divided into three shell length classes: (1) 11–20 mm, (2) 21–30 mm, and (3) 31–40 mm and frozen at  $-20^{\circ}\text{C}$ . Crabs were sexed and measurements of the carapace width and length and claw length, width, and height were taken ( $\pm 0.01$  mm). All crabs used in experiment had intact, fully grown claws, except crab no. 3 (Table 1), which had only one intact claw.

## 2.1. Claw strength

Claw strength of each individual *E. sinensis* (male  $n = 7$ ; female  $n = 6$ ) was measured five times (every second day), and the arithmetic mean was calculated. Strength was measured by a device constructed on the basis of a calibrated force resistive sensor type CP9 150 ns (IEE, Poland) with a ATMEGA8535L microcontroller (Atmel, USA) and an internal 10-bit A/C sensor (measuring range 0.2–100.0 N) connected to a measuring bridge supplied with a voltage source. A shift in the measured claw force activated a change in the resistance of the sensor, which was proportional to the registered voltage signal. The voltage signal was amplified ( $3\times$ ) and converted to a digital signal by using an AD620 amplifier (Analog Devices, USA).

Differences between sexes and claws were tested with the Wilcoxon paired test and multiple regressions at the 5% level using Statistica 10.0.

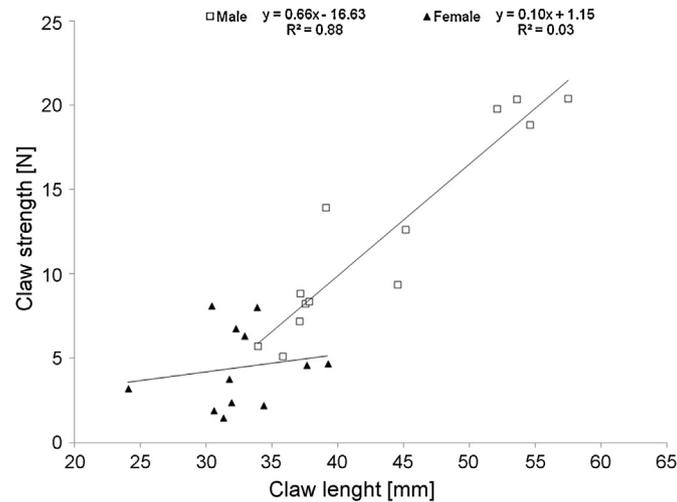
## 2.2. Prey handling behavior and effect of time on consumption rate

From the original 13 individuals, a subset of eight *E. sinensis* (male  $n = 2$ ; female  $n = 6$ ; some individuals died before this experiment) were used in further experiments. To observe *E. sinensis* prey handling behavior, a camera was installed above each experimental tank, where male ( $n = 7$ ) and female ( $n = 6$ ) *E. sinensis* were fed with dead, intact blue mussels. *E. sinensis* were placed singly in plastic aquaria (25 cm  $\times$  35 cm  $\times$  15 cm) filled with aerated water ( $15^{\circ}\text{C}$ , salinity 7), without any substratum, to acclimate for two weeks. Water was exchanged once before the start of experiment.

The consumption rate of mussels ( $n = 15$ , 11–40 mm) in consecutive time intervals by *E. sinensis* ( $n = 13$ ) was expressed as a mean with standard deviation (mean + SD). The consumption rate was standardized to 1 h to enable comparison between specimens. Differences between sexes and consumption rates were tested with Student *t*-tests and multiple regressions at the 5% level using Statistica 10.0.

## 2.3. Prey size preferences

Individuals of *E. sinensis* (male  $n = 2$ ; female  $n = 6$ ) were held in tanks as described above. They were fed ad libitum with dead, intact blue mussels *M. edulis trossulus* but were starved for four days before the start of the experiment to standardize hunger levels. Dead *M. edulis trossulus* ( $n = 15$ ;  $n = 5$  from each length class) were thawed and given to each crab, and the number of eaten, crushed, and uncrushed



**Figure 1** Linear regression analysis of both claw strength [N] and length [mm] of male ( $n = 13$ ) and female ( $n = 12$ ) *Eriocheir sinensis* collected from the Gulf of Gdańsk in April–June 2010.

mussels in each length class was determined after 4, 8, and 24 h.

Results were expressed as the mean ( $\pm$ SD), and the relationship between measured parameters was determined by a linear regression analysis with a coefficient of determination  $R^2$  for a significance level  $P < 0.05$ . The differences between the groups of results were tested with Student  $t$ -test and multiple regression at the 5% level using Statistica 10.0.

### 3. Results

#### 3.1. Crab characteristics and claw strength

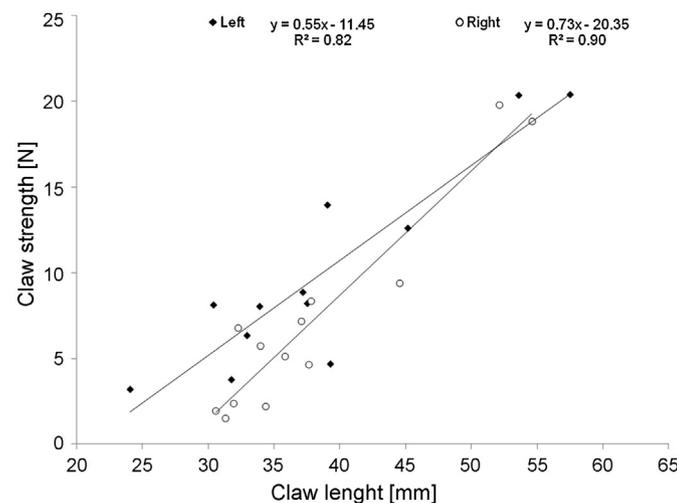
The claw strength of the left claw of both male and female *E. sinensis* was significantly greater than that of the right one ( $P = 0.0037$ ; Table 1), but females, on average, had significantly less claw strength for both claws than males

( $P = 0.0029$ ) (Table 1 and Fig. 1). Combining data for both males and females, claw strength of both claws was significantly correlated with claw length ( $P = 0.000$ ), width ( $P = 0.000$ ), and height ( $P = 0.000$ ) as well as with the carapace width ( $P = 0.000$ ; Fig. 2). There were no significant differences between slopes or intercepts of claw strength in the linear regression analysis.

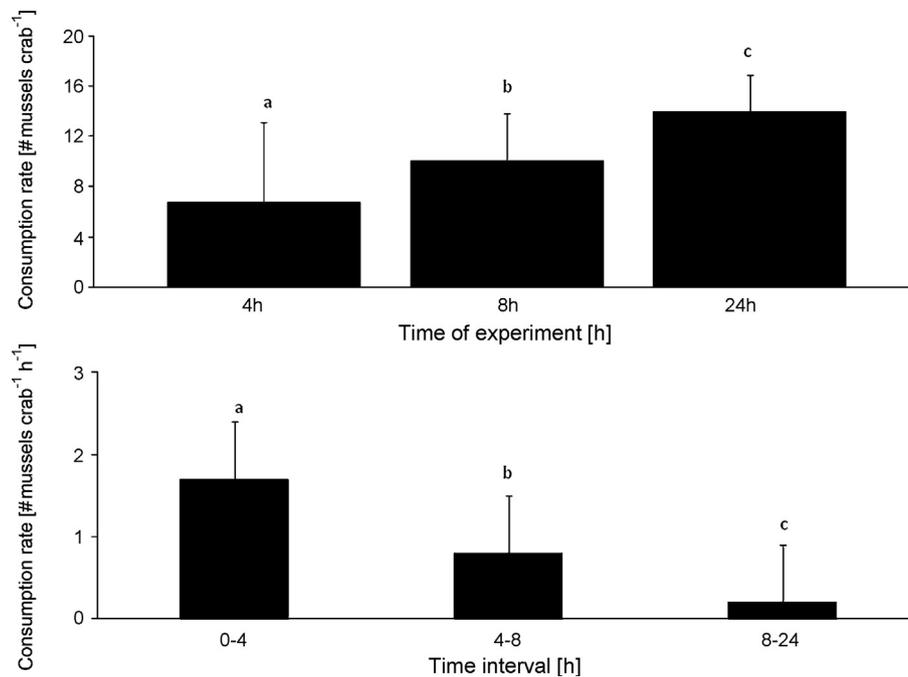
*E. sinensis* tightened strain gauge in pulses. The first measurement of claw strength was always greater, compared to the following pulses; however, the differences were not statistically significant.

#### 3.2. Prey handling behavior and effect of time on consumption rate

To consume a mussel, *E. sinensis* held it with one claw and used the other claw to either crush mussel into little pieces or break off small pieces of the shell to consume the soft tissue.



**Figure 2** Linear regression analysis of strength [N] and length [mm] of left ( $n = 12$ ) and right ( $n = 13$ ) claws of male and female *Eriocheir sinensis* collected from the Gulf of Gdańsk in April–June 2010.



**Figure 3** Mean (+SD) consumption rate of mussels (*Mytilus edulis trossulus*) by male ( $n = 2$ ) and female ( $n = 6$ ) *Eriocheir sinensis* collected from the Gulf of Gdańsk in April–June 2010. (A) Consumption rate [# mussels crab<sup>-1</sup>] after 4, 8 and 24 h; (B) consumption rate [# mussels crab<sup>-1</sup> h<sup>-1</sup>] separated by consecutive time intervals. Different letters indicate significant differences ( $P < 0.05$ ).

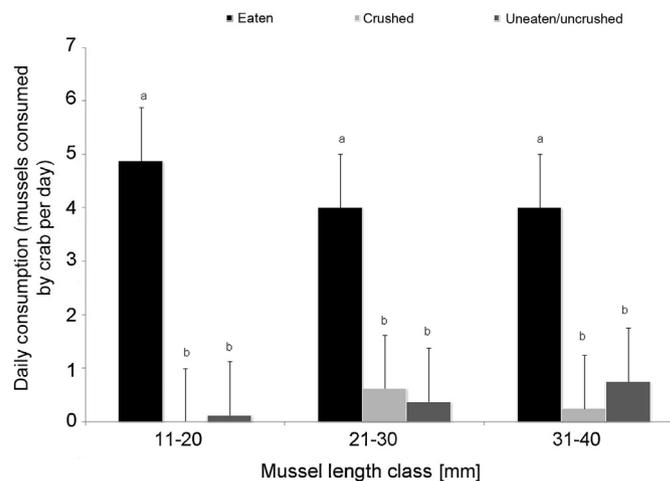
There was no preferred claw for each activity (either right or left) among all the crabs, but each crab, both males and females, favored the same claw for each purpose each time. The one crab with only one claw (no. 3 in Table 1) held the mussel with walking legs during consumption.

There was significant inter-individual variability in the number of consumed mussels, with the number of mussels consumed by a single crab increasing significantly with time from  $1.7 \pm 0.7$  # mussels crab<sup>-1</sup> h<sup>-1</sup> after 4 h to  $0.2 \pm 0.7$  # mussels crab<sup>-1</sup> h<sup>-1</sup> after 24 h (Fig. 3A). The highest consumption rate was observed within the first 4 h, and it decreased significantly during the last 16 h (Fig. 3B).

### 3.3. Prey size preferences

Overall, individual male and female *E. sinensis* (male  $n = 2$ ; female  $n = 6$ ) consumed between 5 and 15 mussels over the 24 h period, but the individual daily consumption did not differ significantly. While there were no statistically significant differences in consumption rate of the different mussel size classes, the smallest mussels (11–20 mm) were consumed at a higher rate ( $4.9 \pm 0.4$  mussel day<sup>-1</sup>) than the largest mussels (31–40 mm;  $4.0 \pm 1.8$  mussel day<sup>-1</sup>; Fig. 4).

*E. sinensis* was also observed crushing mussel shells ( $n = 2$ , 31–40 mm;  $n = 5$ , 21–30 mm) without later consumption



**Figure 4** Mean (+SD) daily rates of mussels (*Mytilus edulis trossulus*), separated by size class that were eaten, crushed, and uncrushed by male ( $n = 2$ ) and female ( $n = 6$ ) *Eriocheir sinensis* collected from the Gulf of Gdańsk in April–June 2010. Different letters indicate significant differences ( $P < 0.05$ ).

(avg.  $0.9 \pm 1.4$  mussel day<sup>-1</sup>), but this occurred after 4 and 8 h. The number of crushed and uncrushed mussels did not significantly differ between individuals after 24 h.

#### 4. Discussion

The results of this laboratory study show that *E. sinensis* may negatively impact the *M. edulis trossulus* population abundance in coastal Baltic waters either through predation of juveniles or indirect mortality from damage (crushing) to the shell. This species' average claw strength of  $8.51 \pm 5.93$  N enables a high consumption rate of *M. edulis trossulus*.

The stronger claw strength of males (mean  $12.23 \pm 5.82$  N) compared to females (mean  $4.47 \pm 2.37$  N) is a clear example of sexual dimorphism in this species (Czerniejewski et al., 2003; Flores and Negreiros-Fransozo, 1999). The claw length of *E. sinensis* is ~60% of the carapace width, and they are able to generate closing forces greater than those measured in other species (e.g. *Uca pugnax* and *Carcinus maenas* claw strength ranges between 2 and 6 N; Levinton and Judge, 1993). While the claw strength for *E. sinensis* in this study was significantly correlated with claw length, other crabs have shown significant correlations of claw strength with claw height (e.g. *Cancer productus* and *Lophopenopeus bellus*; Behrens Yamada and Boulding, 1998). However, these differences may result from inherently species-specific overall shapes of the claws and the muscle mass needed to close them (Levinton and Judge, 1993). Also, claw strength increased with crab size (i.e. carapace width) in both sexes of *E. sinensis* (Behrens Yamada and Boulding, 1998), but females have shorter claws than males of the same carapace width and are characterized by lesser claw strength.

Claw strength also depends on the condition of the individual and can change over time. Crabs which are ill or old are less vigorous and aggressive, and they crush prey with less force; this was observed in individuals that stay in the laboratory for a longer period of time (i.e. months; Wójcik, personal observation). However, decapods have the ability to learn crushing techniques which may influence their behavior during long-term experiments (Elwood, 2011; Gherardi, 2009). We also observed that the first measurement of claw strength of *E. sinensis* was always the strongest. Seed and Hughes (1995) showed that this initial attack is based on a strong crush, followed by a series of weaker ones. The number of crushing movements is related to the thickness of the material being crushed (Juanes, 1992).

*E. sinensis* exhibited handling behavior similar to other crabs families, with the number of mussels consumed by a single crab increasing with time (Davidson, 1986; Ray-Culp et al., 1999; Rheinallt and Hughes, 1985). In the case of small-sized mussels, crabs are able to hold more than one prey individual in their claws, but they still need a second claw for consumption (Rheinallt, 1986). In one case, an *E. sinensis* that was missing a left claw used walking legs to support the feeding behavior. Several individual *E. sinensis* crushed mussels but did not consume them, which may reflect a need to strengthen the claws, especially after regeneration (Hughes and Seed, 1995).

Adult *E. sinensis* (carapace width  $61.81 \pm 7.85$  mm) can consume up to 15 blue mussels (*M. edulis trossulus*; 11–40 mm) in 24 h at 15°C, but there were no significant differences in number of prey consumed between males

and females. Other crab species have been reported to consume similar, or even higher amounts of prey items (e.g. Aronhime and Brown, 2009; Dudas et al., 2005; Fowler, unpublished data; Lohrer and Whitlatch, 2002; Ray-Culp et al., 1999). However, the number of consumed mussels can be impacted by various factors such as food availability and density, the period of starvation prior to consumption, or temperature (Ray-Culp, 1999).

There was significant inter-individual variability in the number of consumed mussels, with the number of mussels consumed by a single crab increasing significantly with time. The relationship of the consumption rate of mussels (*M. edulis trossulus*) and time in *E. sinensis* reflects the predation functional response curve type 1 described by Holling (1959), which assumes a linear increase in intake rate with food density, either for all food densities or only for food densities up to a maximum, beyond which the intake rate is constant. This linear increase indicates that the time needed by the consumer to process a food item is negligible, or that consuming food does not interfere with searching for food. This could be an important factor to consider for natural field populations of *M. edulis trossulus* that aggregate on rocky coasts in that *E. sinensis* is able to consume large numbers of mussels, without having to spend time searching for them.

Many factors play a role in crabs' prey size selection, including: the size relationship between crab and prey, degree of satiation, claw gape, dentition, strength, and total prey handling (Behrens Yamada and Boulding, 1998). In this study, *E. sinensis* did not show any size preference of *M. edulis trossulus* prey, although there was a trend for higher consumption of the smallest size class (11–20 mm). While *E. sinensis* has the ability to crush mussels >45 mm (Wójcik et al., unpublished data), smaller mussels would be easier and quicker to crush and consume, thus optimizing energy profits (Aronhime and Brown, 2009; Kulp et al., 2011; Ray-Culp et al., 1999; Sih and Christenses, 2001). This is especially true for *M. edulis trossulus*, as its energy value is not related to individual size (Pazikowska and Szaniawska, 1988). In several individual cases, the depletion of the smallest mussels in the aquarium caused an increase in the consumption of larger mussels. While the encounter rates with larger mussels would increase due to experimental densities in the tank, *E. sinensis* could also easily overlook the medium sized *M. edulis trossulus* in favor for larger prey (Hughes and Seed, 1995). However, as *E. sinensis* were fed with dead, intact *M. edulis trossulus*, the mussels were not attached to any substrate due to lack of byssal threads. Therefore, *E. sinensis* did not have to bear any additional energy costs separating individuals from the colony, which made access to the largest mussels easier than it would be in the natural environment.

While *E. sinensis* can directly prey on *M. edulis trossulus*, they can also cause indirect mortality of the mussels without consuming them. The obtained results provided new information on the feeding ecology of *E. sinensis* and may be useful to estimate the predation pressure by this species on blue mussels in the coastal Baltic waters, where the crab abundance has steadily increased over time (Jakubowska and Normant, 2011; Normant et al., 2012; Ojaveer et al., 2007). However, prey species selection in the field is highly dependent on prey availability, density, and the probability of

encountering a prey species. The small size of the experimental aquariums virtually eliminated the search time of these predatory crabs, and therefore these results represent idealized foraging conditions and possible satiation levels rather than the actual functional response of the species. However, in areas where the natural recruitment of bivalves is substantial or where there are large populations of juvenile bivalves, these laboratory feeding rates provide a reasonable estimate of the predatory potential of *E. sinensis* in coastal Baltic waters.

## Acknowledgement

We would like to thank Mr. Romuald Jachimowicz from the Sea Fisheries Inspectorate in Frombork for his assistance in collecting the material for this study.

## References

- Anger, K., 1991. Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae). *Mar. Ecol. Prog. Ser.* 72, 103–110.
- Aronhime, B.R., Brown, K.M., 2009. The roles of profit and claw strength in determining mussel size selection by crabs. *J. Exp. Mar. Biol. Ecol.* 379, 28–33.
- Barnes, R.S.K., Calow, P., Olive, P.J.W., Golding, D.W., Spicer, J.I., 2007. *The Invertebrates: a synthesis*. Blackwell Publishing, 302–316.
- Behrens Yamada, S., Boulding, E., 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *J. Exp. Mar. Biol. Ecol.* 220, 191–211.
- Boulding, E., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* 16, 201–223.
- Brousseau, D., Filipowicz, A., Baglivo, J., 2001. Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. *J. Exp. Mar. Biol. Ecol.* 262, 199–210.
- Charnov, E., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.
- Cornell, H., 1976. Search strategies and the adaptive significance of switching in some general predators. *Am. Nat.* 110, 317–320.
- Cunningham, P., Hughes, R., 1984. Learning of predatory skills by shorecrabs *Carcinus maenas* feeding on mussels and dogwhelks. *Mar. Ecol. Prog. Ser.* 16, 21–26.
- Czerniejewski, P., Filipiak, J., Radziejewska, T., 2003. Body weight and morphometry of the Chinese mitten crab (*Eriocheir sinensis* H. Milne-Edwards 1853) in the River Odra/Oder Estuary (North-Western Poland). *Acta Sci. Pol. Ser. Piscaria* 2, 29–39.
- Czerniejewski, P., Rybczyk, A., Wawrzyniak, W., 2010. Diet of the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853, and potential effects of the crab on the aquatic community in the River Odra/Oder estuary (N.-W. Poland). *Crustaceana* 83, 195–205.
- Czerniejewski, P., Skuza, L., Drotz, M., Berggren, M., 2012. Molecular connectedness between self and none self-sustainable populations of Chinese mitten crab (*Eriocheir sinensis*, H. Milne Edwards, 1853) with focus to the Swedish Lake Vänern and the Oder and Vistula River in Poland. *Hereditas* 149, 55–61.
- Davidson, R., 1986. Mussel selection by the paddle crab *Ovalipes catharus* (White): evidence of flexible foraging behaviour. *J. Exp. Mar. Biol. Ecol.* 102, 281–299.
- Dittel, A., Epifanio, C., 2009. Invasion biology of the Chinese mitten crab *Eriocheir sinensis*: a brief review. *J. Exp. Mar. Biol. Ecol.* 374, 79–92.
- Drotz, M.K., Berggren, M., Lundberg, S., Lundin, K., von Proschwitz, T., 2010. Invasion routes, current and historical distribution of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards, 1853) in Sweden. *Aquat. Inv.* 5, 387–396.
- Dudas, S.E., McGraw, I.J., Dower, J.F., 2005. Selective crab predation on native and introduced bivalves in British Columbia. *J. Exp. Mar. Biol. Ecol.* 325, 8–17.
- Elner, R., Hughes, R., 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.* 47, 103–116.
- Elwood, R., 2011. Pain and suffering in invertebrates? *ILAR J.* 52, 175–184.
- Emlen, J., 1968. Optimal choice in animals. *Am. Nat.* 102, 385–389.
- Fladung, E., 2000. Untersuchungen zur Bestandsregulierung und Verwertung der Chinesischen Wollhandkrabbe (*Eriocheir sinensis*) unter besonderer Berücksichtigung der Fischereiverhältnisse im Elbe/Havel-Gebiet. *Schriften des Instituts für Binnenfischerei e.V. Potsdam-Sacrow. Band 5*, 1–82.
- Flores, A., Negreiros-Fransozo, M., 1999. Allometry of the secondary sexual characters of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). *Crustaceana* 72, 1051–1066.
- Floyd, T., Williams, J., 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of softshell clams (*Mya arenaria* L.) in the Southern Gulf of St. Lawrence. *J. Shellfish Res.* 23, 457–462.
- Gherardi, F., 2009. Behavioural indicators of pain in crustacean decapods. *Ann. Ist. Super. Sanita* 45, 432–438.
- Gollash, S., 2006. NOBANIS – Invasive Alien Species Fact Sheet – *Eriocheir sinensis*. Online Database of the North European and Baltic Network on Invasive Alien Species – NOBANIS, [www.nobanis.org](http://www.nobanis.org) (download: 10.12.2012 r).
- Havenhand, J.N., 2012. How will ocean acidification affect Baltic Sea ecosystems? An assessment of plausible impacts on key functional groups. *AMBIO* 41 (6), 637–644.
- Herborg, L.M., Rushton, S.P., Clare, A.S., Bentley, M.G., 2003. Spread of the Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) in Continental Europe: analysis of a historical data set. *Hydrobiologia* 503, 21–28.
- Herborg, L.M., Weetman, D., van Oosterhout, C., Hänfling, B., 2007. Genetic structure and contemporary dispersal patterns of a recent European invader the Chinese mitten crab, *Eriocheir sinensis*. *Mol. Ecol.* 16, 231–242.
- Holling, C., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Hughes, R., 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *Am. Nat.* 113, 209–221.
- Hughes, R., Seed, R., 1981. Size selection of mussels by the Blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Mar. Ecol. Prog. Ser.* 6, 83–89.
- Hughes, R.N., Seed, R., 1995. Behavioural mechanisms of prey selection in crabs. *J. Exp. Mar. Biol. Ecol.* 193, 225–238.
- Invasive Species Specialist Group (ISSG), 2006. Web database application, <http://www.issg.org/database/species/ecology.asp?si=38> (accessed December 2011).
- Jakubowska, M., Normant, M., 2011. Effect of temperature on the physiology and bioenergetics of adults of the Chinese mitten crab *Eriocheir sinensis*: considerations for a species invading cooler waters. *Mar. Freshw. Behav. Physiol.* 44 (3), 171–183.
- Jakubowska, M., Wójcik, D., Kolasa, A., Krzak, J., Normant, M., 2011. Feeding of an invasive crab *Eriocheir sinensis* in the coastal Baltic waters. In: 8th Baltic Sea Science Congress. St. Petersburg, Russia, 22–26 August 2011 Book of Abstracts, 289.
- Jin, G., Xie, P., Li, Z., 2003. Food habits of two-year-old Chinese mitten crab (*Eriocheir sinensis*) stocked in Lake Bao'an, China. *J. Freshw. Ecol.* 18, 369–375.
- Juanes, F., 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Mar. Ecol. Prog. Ser.* 87, 239–249.

- Jubb, C., Hughes, R., Rheinallt, T., 1983. Behavioural mechanisms of size-selection by crabs *Carcinus maenas* (L.) feeding on mussels *Mytilus edulis* (L.). *J. Exp. Mar. Biol. Ecol.* 66, 81–87.
- Kautsky, N., 1982. Growth and size structure in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68 (2), 117–133.
- Kulp, R.E., Politano, V., Lane, H.A., Lombardi, S.A., Paynter, K.T., 2011. Predation of juvenile *Crassostera virginica* by two species of Mud crabs found in the Chesapeake Bay. *J. Shellfish Res.* 30, 261–266.
- Levinton, J.S., Judge, M.L., 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Funct. Ecol.* 7, 339–345.
- Lohrer, A., Whitlatch, R., 2002. Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Mar. Ecol. Prog. Ser.* 227, 135–144.
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000. 100 of the World's Worst Invasive Alien Species A Selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union, 12, First published a special lift-out in Aliens 12, December 2000, Updated and reprinted version: November 2004.
- Mariappan, P., Balasundaram, C., Schmitz, B., 2000. Decapod crustacean chelipeds: an overview. *J. Biosci.* 25, 301–313.
- Mascaro, M., Seed, R., 2000a. Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. *J. Shellfish Res.* 19, 283–291.
- Mascaro, M., Seed, R., 2000b. Foraging behavior of *Carcinus maenas* (L.): species-selective predation among four bivalve prey. *J. Shellfish Res.* 19, 293–300.
- McNair, J., 1981. A stochastic foraging model with predator training effects. II. Optimal diets. *Theor. Popul. Biol.* 19, 147–162.
- Normant, M., Chrobak, M., Skóra, K.E., 2002. The Chinese mitten crab *Eriocheir sinensis* – an immigrant from Asia in the Gulf of Gdańsk. *Oceanologia* 44, 124–126.
- Normant, M., Król, M., Jakubowska, M., 2012. Effect of salinity on the physiology and bioenergetics of adult Chinese mitten crabs *Eriocheir sinensis*. *J. Exp. Mar. Biol. Ecol.* 416/417, 215–220.
- Ojaveer, H., Gollash, S., Jaanus, A., Kotta, J., Laine, A.O., Minde, A., Normant, M., Panov, V.E., 2007. Chinese mitten crab *Eriocheir sinensis* in the Baltic Sea – a supply-side invader? *Biol. Invasions* 9, 409–418.
- Palmer, A., 1981. Do carbonate skeletons limit the rate of body growth? *Nature* 292, 150–152.
- Panning, A., 1938. The Chinese mitten crab. Report of the Board of Regents of the Smithsonian Institution (Washington) 3508. 409–418.
- Pazikowska, G., Szaniawska, A., 1988. Variations in energy and lipid content of *Mytilus edulis* from the Gulf of Gdansk. *Oceanologia* 25, 99–107.
- Pulliam, H., 1974. On the theory of optimal diets. *Am. Nat.* 108, 59–74.
- Pyke, G., 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15, 523–575.
- Ray-Culp, M., Davis, M., Stoner, A.W., 1999. Predation by xanthid crabs early post-settlement gastropods: the role of prey size, prey density and habitat complexity. *J. Exp. Mar. Biol. Ecol.* 240, 303–321.
- Rheinallt, T., 1986. Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Mar. Ecol. Prog. Ser.* 29, 45–53.
- Rheinallt, T., Hughes, R., 1985. Handling methods used by the velvet swimming crab *Liocarcinus puber* when feeding on mollusks and shore crabs. *Mar. Ecol. Prog. Ser.* 25, 63–70.
- Rogers, L., 2000. The feeding ecology of the invasive Chinese mitten crab, *Eriocheir sinensis*: implications for California's freshwater communities. In: Senior Research Seminar, Environmental Science Group Major. University of California, Berkeley, p. 18.
- Rudnick, D., Resh, V., 2005. Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacea. *Freshw. Biol.* 50, 1323–1336.
- Seed, R., 1982. Predation of the ribbed mussel *Geukensia demissa* by the blue crab *Callinectes sapidus*. *Neth. J. Sea Res.* 16, 163–172.
- Seed, R., Brown, R., 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J. Anim. Ecol.* 47, 283–292.
- Seed, R., Hughes, R.N., 1995. Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *J. Exp. Mar. Biol. Ecol.* 193, 177–195.
- Sih, A., Christensen, B., 2001. Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.* 61, 379–390.
- Stoeckmann, A., Garton, D., 1997. A seasonal energy budget for zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Can. J. Fish. Aquat. Sci.* 54, 2743–2751.
- Szaniawska, A., 1991. Gospodarka energetyczna bezkręgowców bentosowych występujących w Zatoce Gdańskiej. University of Gdańsk, 118, (in Polish).
- Szaniawska, A., Wołowicz, M., Wenne, R., 1986. Energetic values of the body of *Macoma balthica* L. from the Gulf of Gdańsk. *Oceanologia* 24, 55–62.
- Veilleux, E., de Lafontaine, Y., 2007. Biological synopsis of the Chinese mitten crab (*Eriocheir sinensis*). *Can. Manuscr. Rep. Fish. Aquat. Sci.* 2812 vi + 45.
- Veldhuizen, T., 2001. Life history, distribution, and impacts of the Chinese mitten crab, *Eriocheir sinensis*. *Aquat. Inv.* 12, 1–9.
- Whetstone, J., Eversole, A., 1978. Predation on hard clams, *Merccenaria mercenaria* by mud crabs, *Panopeus herbstii*. *Proc. Natl. Shellfish. Assoc.* 68, 42–48.
- Wójcik, D., Normant, M., 2012. Claw strength and blue mussel *Mytilus edulis trossulus* size selection by Chinese mitten crab *Eriocheir sinensis*. In: VII European Conference on Biological Invasions, Neobiota 2012. Pontevedra, Spain, 12–14 September 2012 Book of Abstracts, 223.