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Flexible prey handling, preference and a novel capture technique in invasive, sub-adult Chinese mitten crabs

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Running header: Prey handling and preference of *Eriocheir sinensis*

Eriocheir sinensis (Crustacea: Brachyura: Varunidae) is one of only two crabs on the world's list of 100 most invasive aquatic invertebrates. This crab has successfully invaded NE Europe as well as well as the United States, eastern Canada, southern Iraq and Tokyo Bay, Japan. In England, the River Thames population of *E. sinensis* continues to increase in numbers and disperse westward upstream, although little is known about foraging. The present study undertook a preference and prey handling study of sub-adult mitten crabs collected from the Thames. A digital camcorder, capable of detecting infrared light, was used in the laboratory overnight to identify crab food preference, document prey handling times and record behaviour. The test prey species, namely the amphipod *Gammarus zaddachi*, and two species of gastropod molluscs, *Theodoxus fluviatilis* and *Radix peregra*, were collected in the same

26 habitat as the crabs and all were consumed under laboratory conditions. *Eriocheir* were able
27 to capture mobile *G. zaddachi* using a novel prey capture technique not previously described
28 in brachyurans and use different skills for handling each prey species. This flexibility in prey
29 handling may be an important contributory factor in their freshwater invasive capacity.
30 Results indicated that the crabs had a preference for *G. zaddachi* which were consumed most
31 frequently and preferentially over both mollusc species. Prey choice may be based on
32 maximising net energy gain as consuming *G. zaddachi* was shown to provide the highest rate
33 of potential energy consumption by the crab due, in part, to a much shorter handling time
34 than both species of snails.

35

36 Keywords

37 *Eriocheir sinensis* – predation – prey handling – *Gammarus zaddachi* – *Theodoxus fluviatilis*
38 – *Radix peregra* – video recording

39

40 Introduction

41

42 Invasive species can have considerable effects on their colonized habitats such as displacing
43 native species (Dick et al., 1995; Kiesecker et al., 2001; Sanders et al., 2003), habitat
44 modification (Cuddington & Hastings, 2004) and hybridising with native species (Daehler &
45 Strong, 1997). Non-native decapod crustaceans are highly prevalent in all types of aquatic
46 habitats and, in Europe, invasive species make up 46% of all Decapoda within freshwater
47 habitats (Ranasinghe et al., 2005; Galil, 2008; Karatayev et al., 2009). Due to their
48 prevalence, they have a wide range of effects within their invaded habitats. These include
49 competition for resources e.g., *Hemigrapsus sanguineus* (de Haan, 1853) being able to
50 displace juvenile *Carcinus maenas* (Linnaeus, 1758) from shelter (Landschoff et al, 2013)

51 and as vectors for disease e.g., *Pacifastacus leniusculus* (Dana, 1852) a known carrier of
52 crayfish plague which has caused rapid decline in populations of *Austropotamobius pallipes*
53 (Lereboullet, 1858) within the UK (Lilley et al., 1997).

54

55 One important effect invasive species can have is on trophic interactions since these are key
56 in determining the structure of ecosystems. To determine the potential impacts, different
57 aspects of trophic interactions can be used such as preference, feeding frequency and mutual
58 predation. Invasive species can have vastly different trophic impacts in invaded habitats when
59 compared to their native range. Invasives can have an impact on prey at twice the intensity
60 than that of native predators (Salo et al., 2007). Following this they can have the potential to
61 extirpate or severely reduce the population size of prey species such as the brown tree snake
62 causing large declines in avifauna in Guam (Wiles et al., 2003). There are a number of
63 examples where invasive decapod crustaceans have impacted trophic relationships in their
64 invaded habitat. For example *Procambarus clarkii* (Girard, 1852) has become a common
65 prey item for several native predators in the Mediterranean (Geiger et al., 2005), whereas in
66 Japan the invasive *P. leniusculus* consumes a potential competitor, the native *Cambaroides*
67 *japonicus* (de Haan, 1841), which could contribute to species replacement (Nakata &
68 Goshima, 2006). Other trophic effects of invasive decapods have also been observed in *C.*
69 *maenas*. Predation by this species in non-native regions can induce shell thickening in
70 populations of mussels (Freeman & Byers, 2006), reduce the presence of juvenile cockles
71 (Walton et al., 2002) and the species is also capable of displacing native species from their
72 prey (McDonald et al., 2001; Rossong et al., 2006). Understanding flexibility in feeding
73 behaviour and feeding preferences could be useful for assessing the potential impacts that
74 they can have on their new habitat. Predators do not consume prey following their
75 distribution or density, but usually show preference for certain prey items over others

76 (Jackson & Underwood, 2007; Grason & Miner, 2012). Preference can be defined as an
77 individual choosing to eat its most favoured prey item before others and, as such, the last prey
78 item eaten would be the least desired. When there is no preference, selection of prey would
79 be random.

80

81 An invasive decapod which has spread globally is the Chinese mitten crab, *Eriocheir sinensis*
82 H. Milne Edwards, 1853. This species is native to China and Korea and is listed as one of
83 only two brachyuran crab species in the top 100 most invasive species (Lowe et al., 2000)
84 based on their serious impact on biological diversity and/or human activities. Unlike native
85 crab species in the UK, it spends most of its lifespan in freshwater and has a catadromous life
86 history. This species has been present within the UK since 1935, introduced either through
87 ballast water or intentional introduction, and had become well established by 1973 (Herborg
88 et al., 2005). Subsequently *E. sinensis* numbers have increased greatly within the Thames
89 (Clark et al., 1998; Gilbey et al. 2008).

90

91 Considering its global distribution, little is known about the feeding strategy of mitten crabs
92 in invaded habitats other than being described as opportunistic omnivores, based on two
93 analyses of gut contents using morphological evidence and stable isotopes (Rudnick & Resh,
94 2005; Czerniejewski et al. 2010). In both of these studies chironomids were shown to be most
95 prevalent invertebrate in their diet, although much of what was in the gut was
96 morphologically unidentifiable; a common problem when examining the diet of decapod
97 crustaceans due to the effectiveness of the gastric mill. The evidence for this species of crab
98 to utilise other potential prey species is limited, although recent work has demonstrated
99 consumption of fish eggs in laboratory conditions (Webster et al. 2015). Despite the lack of
100 prey preference studies for *E. sinensis*, such data are available for other species of decapod

101 crustaceans using a variety of different methods (e.g., Ashton, 2002; Buck et al., 2003;
102 Jackson & Underwood, 2007; Erickson et al. 2008; Grason & Miner, 2012; Haddaway et al.,
103 2012; Laitano et al., 2013). For the present study methods devised by Taplin (2007) were
104 used and observations on handling times of the different prey species were also made.
105 Handling time observations have been undertaken on several species of decapod crustaceans
106 (e.g., Elner & Hughes, 1978; Hughes & Seed, 1981; ap Rheinallt, 1986; Hudson & Wigham,
107 2003) feeding primarily on bivalves.

108

109 Sub-adult *E. sinensis* (10–40mm) collected from the River Thames were used to establish
110 prey preference for the most abundant species found at the same locations as the mitten crabs.
111 As sub-adult *E. sinensis* are captured upstream in great numbers, they have a great potential
112 to cause disruption to native habitat hence the use of this size range in the current study. The
113 main hypothesis is that there will be a difference in preference between different potential
114 prey species and it is predicted that sub-adult crabs will exhibit a preference for prey which
115 are more profitable as defined by the rate of energy acquisition by the crab. Handling times
116 were also observed and further detailed observations allow for description of the handling
117 methods used for different prey species.

118

119 Materials and methods

120

121 *Study Organisms*

122

123 Sub-adult crabs were collected during low spring tides at Chelsea Bridge (51.4847°N,
124 0.1500°W) 22nd October 2013 and Kew Bridge (51.4869°N, 0.2875°W), England, at low
125 spring tide 31st March 2014. A total of 33 and 22 crabs were collected from each site

126 respectively. Another 54 crabs were also made available from previous collections made in
127 Summer, 2013, also from Chelsea Bridge and Kew Bridge. All crabs were housed in groups
128 in large tanks of aerated, dechlorinated tap water within the aquarium and fed regularly with
129 defrosted fish (perch, *Perca fluviatilis*) up until use in experiments.

130

131 Potential prey species were also collected at low tide on the foreshore in the vicinity of
132 Chelsea Bridge. Three of the most abundant species were the amphipod *Gammarus zaddachi*
133 Sexton, 1912 and two species of molluscs, the river nerite, *Theodoxus fluviatilis* (Linnaeus,
134 1758), and the wandering snail, *Radix peregra* (O.F. Müller, 1774). All are native to the UK
135 and were selected as they represent different morphologies and habits and thus different
136 challenges when it comes to prey handling. The amphipod, *G. zaddachi* is a fast-swimming
137 species; *T. fluviatilis* is an operculate gastropod with a non-spiral shell which is usually
138 closely attached to the substrate; *R. peregra* lacks an operculum and has a spiral shell.
139 Preliminary experiments, in which aquaria were set up with individual mitten crabs with four
140 specimens of each potential prey species and left for seven days, showed that all three species
141 were consumed.

142

143 *Preference Experiments*

144

145 To determine the preference of crabs for the three prey species, trials were completed using
146 the method described by Taplin (2007). This method assumes that an individual consumes
147 prey in the order of preference. Therefore each prey item is assigned a rank depending on
148 order of consumption i.e. the first prey eaten will be assigned rank 1, the second prey 2 and
149 so on until all prey have been assigned a rank. When a prey item is not consumed it is
150 considered last or if there are multiple prey left unconsumed they are considered tied for last

151 and given an average rank. In this way unconsumed prey items are considered as the predator
152 having the least preference for them (Taplin, 2007). The total number of prey items
153 consumed in each trial was recorded.

154
155 Fifty crabs were starved for 7 days prior to the preference trials to assure maximum prey
156 consumption. Furthermore, only crabs which had both chelae present were used so they
157 would be feeding at optimum efficiency. Each crab was only trialled once. The prey species
158 used for these trials were *G. zaddachi*, *T. fluviatilis* and *R. peregra*.

159
160 During preference trials crabs were placed individually in each aquarium and given six hours
161 to acclimate. After acclimation two of each prey species ranging from 7–10mm in length (six
162 prey items in total) were placed randomly in the aquaria to help reduce any initial bias
163 towards nearby prey. Crabs were then left for a period of sixteen hours over night with the
164 prey; three hours light followed by twelve hours dark then one more hour of light to record
165 the predominantly nocturnal feeding activity. During this period three aquaria were recorded
166 simultaneously from underneath by being positioned on top a glass panel supported by a
167 frame.

168
169 A JVC HZ-300 digital camcorder converted to full spectrum detection and set to time lapse,
170 capturing frames at 1-s intervals, was used to record feeding behaviour. All recorded footage
171 was slowed down using MPC-HC 1.7.6 software during review. The camcorder was
172 equipped with two darkness activated infrared emitters directed at the aquaria so recording
173 could be captured in darkness. After the trial the crabs were removed, the aquaria were
174 cleaned and the water replaced for the next trial. Footage was reviewed taking note of the
175 order in which prey were consumed. Gender, carapace width and chela height was noted to

176 0.1mm using a dial calliper after the trial so not to cause any unnecessary stress prior to trials.
177 Controls with six prey items and no crab showed no natural mortality in prey species over the
178 same period of time.

179

180 All feeding experiments were undertaken in clear aquaria measuring 255mm × 150mm × 190
181 mm (L × W × D). These were filled with 1500ml of dechlorinated tap water and were aerated
182 with an air stone attached to an air pump. The aquaria were set up within the marine
183 aquarium at RHUL with a constant temperature of 11°C ± 1°C and a L:D 12:12 cycle using
184 fluorescent lighting.

185

186 *Prey Handling*

187

188 In a separate series of experiments, twenty mitten crabs were fed *G. zaddachi*, ten *T.*
189 *fluviatilis* and eleven *R. peregra* in the preference trials. Some crabs were used for multiple
190 species due to the limited availability. Despite this each crab was only used once for each
191 prey species.

192

193 The crabs were offered a prey species within the same 7–10mm size range as used above. For
194 *G. zaddachi* two individuals were offered to the crabs because this increased the likelihood of
195 capture to allow behavioural observations. For both mollusc species individuals were placed
196 directly in front of the crabs. If a crab did not consume any prey item, no data were collected
197 and it was removed from the aquarium and replaced with another specimen. Crabs were
198 recorded whilst feeding to allow description of handling methods and to provide accurate
199 handling times.

200

201 Handling time was defined as the period starting from when the crab captured the prey until
202 the point at which the crab was no longer interacting with it. As the morphology of *G.*
203 *zaddachi* and the two snail species differs the end point of handling time was defined
204 differently. For *G. zaddachi* the end of handling time was defined as the point at which the
205 entire prey item was consumed and for the two snail species as the point at which the crab
206 abandoned the empty shell for a period of one minute; this time was subtracted from the total
207 handling time.

208

209 The total handling time for the two snail species was also divided into several periods. In the
210 case of *T. fluviatilis* it was divided into three periods as follows: time to remove operculum,
211 time to remove the flesh and time spent picking at the empty shell. The first period started
212 once the crab picked up the shell with its chelae and finished when it had completely
213 removed the operculum from the foot of the snail. The next period started once the operculum
214 had been detached and continued until the flesh was removed from the shell and had finished
215 consuming the flesh. The final period started once the flesh had been consumed and the crab
216 began to pick at the shell with its chelae. This period finished once the crab had dropped the
217 shell and left it for one minute. For *R. peregra* handling was divided into two periods, the
218 first started once the crab picked up the shell and ended once all flesh had been consumed.
219 The final period was the same as *T. fluviatilis*; it started once the flesh had been removed and
220 finished once the crab had abandoned the shell for one minute.

221

222 To determine the rate of energy consumption during prey manipulation the handling time was
223 combined with the energy content for each prey species which was gathered from relevant
224 literature. This was calculated by converting the length of the prey item used in the sample to
225 wet weight using a regression equation for each prey species (Appendix 1); wet weight was

226 changed to shell free dry weight using relevant conversion factors from Rumohr et al. (1987).
227 This was then combined with the handling time of each sample and the average energy
228 content of the relevant species (or related species) to provide the rate of energy consumption
229 for the crab during manipulation and ingestion.

230

231 *Statistical Analysis*

232

233 All statistical analyses were completed using SPSS software. Data were checked for
234 normality and homogeneity of variance using Shapiro-Wilk and Levene's test respectively.
235 As data for prey preference scores, average handling times and energy acquisition rates did
236 not meet the assumptions for parametric tests, Kruskal-Wallis tests followed by *post hoc*
237 Mann-Whitney U tests were used to determine differences between treatments. Linear
238 regression analysis was used to explore the relationships between size of crabs and handling
239 times for the different prey species.

240

241 Results

242

243 *Preference*

244

245 During preference trials *G. zaddachi* was the most frequently consumed species, with both
246 mollusc species being consumed far less frequently during the experimental period (Table 1).
247 At least one *G. zaddachi* was eaten in every trial and both specimens were eaten in 80% of
248 studies. Snails were eaten far less frequently, with one *T. fluviatilis* consumed in 40% of trials
249 and one *R. peregra* in 18%. Occasions where the crabs consumed both the *T. fluviatilis*
250 happened more frequently than instances where a single *R. peregra* was consumed (e.g., 20%

251 of trials). There was a significant difference in preference for different prey species
252 ($\chi^2=107.554$, $P<0.001$). It was found that crabs have the strongest preference for *G. zaddachi*
253 over *T. fluviatilis* ($U=14$, $Z=-8.74$, $P<0.001$) and *R. peregra* ($U=1.5$, $Z=-8.81$, $P<0.001$) with
254 a preference score of 1.9. Between the two snails there was a smaller preference for *T.*
255 *fluviatilis* over *R. peregra* ($U=782$, $Z=-3.43$, $p=0.001$) with preference scores of 4.1 and 4.5
256 respectively (Fig. 1). It was also shown that male crabs that have a preference for *T. fluviatilis*
257 over *R. peregra* ($U=113$, $p<0.001$), whereas for female crabs there was no preference
258 between the two mollusc species (Fig. 2).

259

260 *Handling Methods*

261

262 Mitten crabs displayed three different methods of prey capture for the amphipod *G. zaddachi*.
263 For two capture methods (see Appendix 2 for examples), the crab exhibited minimal
264 movement or remained stationary. In the first method it stayed in this position until the prey
265 swam underneath its sternum and between the merus and the propodus of the chela. At this
266 point the propodus was snapped shut against the merus trapping the amphipod. The amphipod
267 was effectively speared between a row of spines on the inner surface on the propodus (see
268 Fig. 3) and held firmly against a row of spines on the inner margin of the merus (see Fig. 4).
269 This adaptation potentially allows capture of smaller, faster moving prey items than if using
270 the pincers alone which almost certainly involves a finer degree of motor control of the dactyl
271 and propodus. Indeed this could be said of all three methods used when capturing amphipods.
272 The head of the amphipod was then sometimes crushed by the pincers (propodus and
273 dactylus) of the other chela. For the second method the crabs would also stay in a stationary
274 position until the prey swam underneath its sternum at which point the crab trapped the prey
275 against the ventral surface of the body using the pereopods nearest to the prey and then used

276 its nearest chela to either trap the prey against its body using the row of spines on the merus
277 or to grasp the prey. When the prey was securely trapped against the sternal plates, the crab
278 then grasped the amphipod using the free chela. The pereopods that were holding the prey in
279 place would then release the prey. In cases where one chela was used to trap the prey against
280 the ventral surface of the body, this chela would subsequently be manoeuvred to also hold on
281 to the prey. In both cases once grasped with the chelae the crab would then manipulate the
282 prey towards the mouthparts where the third maxillipeds were used to aid in holding the prey
283 in place. The prey was then guided through the mouthparts to the mandibles which were used
284 to shred the prey before being passed through the mouth into the gastric mill. Once the main
285 prey portion was consumed, the crab then picked up any soft fragments remaining and these
286 were consumed.

287

288 The third method of capture involved the crab actively trying to catch the prey. Here the crab
289 pounced towards the nearby prey and used its chelae to scoop and trap the prey against the
290 ventral surface of the body similarly to previous description. The prey was then carefully
291 manoeuvred by the chelae, these being used in turn to grip onto the prey and, if necessary, the
292 second pereopods were also used to help hold the prey. From this point onwards prey was
293 processed as described for the first capture method.

294

295 As molluscs are slow moving the capture of these prey items was simple, though in the case
296 of *T. fluviatilis* it took a short period of time to remove the individual from the surface of the
297 aquarium. The handling method for *T. fluviatilis* initially involved picking up the individual
298 with the chelae. Next the crab positioned the chelae on both sides of the aperture lip with the
299 second pereopods used to support the shell. In this position the crab pulled at both sides of
300 the shell aperture using the chelae. During this process the crab would pause occasionally to

301 use one chela to pinch at the rear of the operculum where it is attached to columellar muscle
302 at the dorsal end of the foot. After a period of time the operculum was released and, at this
303 point, the chela was used to remove the operculum with the majority flesh. The flesh was
304 then moved towards the mouth parts where the third and second maxillipeds were used to
305 guide the flesh through the mouth. Once the majority of flesh was removed the crab
306 continued to pick at the empty shell removing any remnants of flesh inside. The crab
307 occasionally held the shell with its third maxillipeds as well as the chelae to allow scraping of
308 the outside of the shell with the second maxillipeds. Eventually the crab abandoned the empty
309 shell.

310

311 The handling method for *R. peregra* started with the crab picking up the snail with the chelae
312 and then manipulating it into a position where it could begin removing the flesh from the
313 shell. The crab then removed pieces of flesh through the aperture of the shell using one chela
314 whilst the other chela held on to the lip of the shell aperture. These pieces of flesh were then
315 passed to the mouthparts where the third and second maxillipeds were used to guide it
316 through the mouth. On occasions when all the flesh could not be removed through the
317 aperture, the crab would begin to break the shell of the snail along the lip of the aperture
318 using the chelae. Once sufficient shell had been detached the crab resumed removing the
319 flesh from the shell. When the majority of flesh had been separated, the crab continued to
320 pick at the empty shell remains removing any remnants of flesh. During handling when small
321 chunks of flesh were removed the flagellum-like extension of the exopod on the third and
322 second maxillipeds were flicked constantly. Sample footage of handling methods for all three
323 prey species can be viewed at <http://tinyurl.com/kqox89j>

324

325 *Handling Times*

326

327 Handling time for of *G. zaddachi* prey was shown to be best related to crab carapace width
328 with a significant negative linear regression ($R^2=0.381$, $P=0.004$) compared to the relation
329 with average chela height ($R^2=0.315$, $P=0.01$; see Fig. 5). Handling time for *T. fluviatilis* prey
330 was best related to average chela height with a significant linear regression ($R^2=0.653$,
331 $P=0.005$) compared to the relation with average carapace width ($R^2=0.332$, $P=0.081$; see Fig.
332 6). Similarly with *R. peregra* handling time was best related to average chela height
333 ($R^2=0.397$, $P=0.038$) compared to the relation with carapace width ($R^2=0.274$, $P=0.098$; see
334 Fig. 7).

335

336 There was a significant difference in handling times between the three prey species ($\chi^2=29.663$,
337 $P<0.001$). The handling time of *G. zaddachi* was significantly shorter (< 300 secs) than *T.*
338 *fluviatilis* ($U=0$, $Z=-4.40$, $P<0.001$, > 3000 secs) and *R. peregra* ($U=6$, $Z=-4.29$, $P=0.003$, ca.
339 2000 secs). It was also found that the handling time for *R. peregra* was significantly shorter
340 than that of *T. fluviatilis* ($U=26$, $Z=-2.04$, $P=0.041$; see Fig. 8).

341

342 When combining energy values of each prey species (Table 2) with handling time a
343 difference was found between prey species ($\chi^2=30.030$, $P<0.001$). *Gammarus zaddachi*
344 provided the highest rate of energy consumption being significantly higher than both *T.*
345 *fluviatilis* ($U=0$, $Z=-4.38$, $P<0.001$) and *R. peregra* ($U=0$, $Z=-4.52$, $P<0.001$). There was no
346 difference in the calculated rate of energy consumption between the two mollusc species
347 ($U=38$, $Z=-0.317$, $P=0.749$; see Fig. 9).

348

349 Discussion

350

351 This present study demonstrated that the amphipod *Gammarus zaddachi* and the molluscs
352 *Theodoxus fluviatilis* and *Radix peregra* are consumed by sub-adult Chinese mitten crabs
353 under laboratory conditions. All three species are similar to prey items consumed in their SE
354 Asian native habitat where *Eriocheir* feed on snails and freshwater shrimp (Hymanson et al.,
355 1999). Out of the three native UK species consumed, mitten crabs demonstrated a clear
356 preference for *G. zaddachi* and demonstrated considerable flexibility in handling strategies
357 between different types of prey. Similar flexibility in feeding behaviour for different types of
358 molluscan prey, linked to maximising feeding efficiency, has been demonstrated for *Cancer*
359 *novaezelandiae* (Creswell & McLay, 1990).

360

361 The results of this study showed that handling times for each of these prey species decreased
362 as crab sized increased. For the handling time of *G. zaddachi* it was shown crab carapace
363 width, as an indication of mouth aperture size, provided the best fit as this was the most likely
364 limiting factor in prey handling. This is because *G. zaddachi* is relatively soft-bodied and of
365 relatively small size, so the chelae were not required beyond manipulating the prey towards
366 the mouthparts where it is dismembered and guided into the mouth. In comparison, for the
367 molluscs it was shown that chela height provided a better indicator of handling time as these
368 were used extensively in prey handling; either breaking through the operculum for *T.*
369 *fluviatilis* or the shell for *R. peregra*. The average handling time for each prey species showed
370 that *G. zaddachi* took a significantly shorter amount of time to handle compared to the two
371 snail species. Between the two snail species handling time for *T. fluviatilis* was significantly
372 longer than *R. peregra* due to two factors; namely the presence of an operculum and having a
373 relatively thicker shell. This was shown during handling of *T. fluviatilis* where crabs were
374 unable to break through the shell and had to resort to breaking through the operculum which
375 required more time. In comparison, when handling snails, other crab species primarily crush

376 the shell rather than pull the flesh from the aperture which shortens handling time (Zipser &
377 Vermeji, 1978; Bertness & Cunningham, 1981; Schindler et al., 1994; Shigemiy, 2003;
378 Rochette et al., 2007). This behaviour of crushing a molluscan shell may not be possible in
379 sub-adult *E. sinensis* as they do not possess a distinct crushing chela and also, in the present
380 study, the crabs were relatively small individuals (10–40mm carapace width). *Carcinus*
381 *maenas* and *Callinectes sapidus* Rathbun, 1896 can use a similar technique to that described
382 for *E. sinensis* given *R. peregra* when handling other species of snails. Both these species use
383 their chelae to pull the flesh directly from the species of snail given though the aperture or
384 use their chelae to chip around the aperture to gain better access (Schindler et al., 1994;
385 Rochette et al., 2007). *Eriocheir sinensis* showed unique methods for handling *T. fluviatilis*
386 compared to other species of crabs handling related species from the Family Neritidae. *Ozius*
387 *verreauxii* Saussure, 1853 and *Eriphia squamata* Stimpson, 1860 when failing to crush the
388 snail shell, break only the shelf of the shell allowing them to remove the operculum and then
389 remove the flesh from the shell (Bertness & Cunningham, 1981). Another technique is used
390 by *E. smithii* MacLeay, 1838 and here the crab would break away the shell from the lip of the
391 aperture until it could remove the flesh (Shigemiy, 2003). A possible explanation for why
392 *Eriocheir sinensis* did not display any of these techniques whilst handling *T. fluviatilis* is that
393 the individuals used were all sub-adults and consequently were not strong enough to break
394 the shell using their chelae.

395

396 Of the three prey species studied, mitten crabs preferred *G. zaddachi* which had shorter
397 handling time and higher potential energy consumption rates. Furthermore these preference
398 results suggest that despite the high abundance of both snail species in the habitat, crabs have
399 little interest in consuming them, especially *R. peregra*. It is possible that the sub-adult crabs
400 in this study chose prey based primarily on energy maximisation similar to what is found in

401 other species of decapods (Elner & Hughes, 1978; Hughes, & Seed, 1981; Gherardi et al.,
402 1989; Weissburg, 1993). For example, when given equal amounts of both optimum prey
403 (providing the highest rate of energy acquisition) and suboptimum prey, *C. maenas* would
404 preferentially consume optimum prey at a frequency of 72% (Elner & Hughes, 1978). Of the
405 two snail species used here, the mitten crabs slightly preferred *T. fluviatilis* even though this
406 involved a significantly longer handling time. A possible explanation for this is that *T.*
407 *fluviatilis* could have higher energy content than *R. peregra* as the latter has a lower energy
408 content of 12.33Jmg⁻¹ (Lien, 1978) which is below the average for three nerite species (*Nerita*
409 *tessellata*, *N. versicolor* and *N. peloronta*) of 20.48 Jmg⁻¹ (Hughes, 1971). However, there
410 was no difference in the rate of energy consumption between the two species of snails despite
411 *R. peregra* being easier to handle.

412

413 Feeding on the amphipod, *G. zaddachi*, involved the use of novel prey capture techniques,
414 utilising well-developed spination on certain elements of the chelipeds (see Figs 3, 4). To our
415 knowledge this is the first description of the function of this ornamentation in this group of
416 decapods. Even though there was a high preference *G. zaddachi* during these laboratory trials
417 it is possible that this prey would be difficult for sub-adult mitten crabs to catch in the wild as
418 they are highly mobile and are clearly not limited to the confines of an aquarium. During this
419 study, however, the sub-adults appeared to be competent at catching *G. zaddachi*. Another
420 factor that could increase the likelihood of capture in the wild is that *G. zaddachi* appeared in
421 high numbers under rocks in exactly the same habitat where small mitten crabs were usually
422 encountered. It is also possible that *G. zaddachi* do not recognise the crabs as a potential
423 predator making them easier to catch, as it was noted in this study that individuals would
424 swim under crabs often leading to their capture. This suggestion is based on findings for
425 another invasive decapod, the signal crayfish, *Pacifastacus leniusculus*, where the presence of

426 chemical cues from this species did not lower locomotory activity in gammarid prey whereas
427 chemical cues from fish did (Åbjörnsson et al, 2000). As the crabs are able to catch *G.*
428 *zaddachi* it is entirely possible they are capable of catching other highly mobile prey. There
429 are reports that other species of crab do consume mobile amphipods (Williams, 1982; Stehlik,
430 1993; Buck et al., 2003; Griffen & Byers, 2006).

431

432 Whilst these trials were carried out under laboratory conditions, with a limited size range of
433 crabs, the results do demonstrate that this invasive species has the capacity for considerable
434 flexibility in its prey handling techniques. This may be linked to their considerable success in
435 invading new habitats and exploiting new food resources (see Bentley, 2011). Furthermore in
436 the trials less obvious, fast-moving, targets were preferred and their capture utilised a
437 previously undescribed technique and, in the process, provide an explanation for the function
438 of cheliped spines. The present laboratory results also demonstrate the potential for this
439 species to consume these prey types in the field and a flexibility in feeding behaviour, both of
440 which may be of concern when considering the potential impact on native biota.

441

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443

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447

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650

651 **Appendix 1.** Regression equations used to estimate wet weight (y) in grams for each prey

652 species from *G. zaddachi* body length or from shell length for snails (x) in millimetres ($n=50$)

653

Species	Regression equation	r^2
<i>G. zaddachi</i>	$y = 0.0164x - 0.0594$	0.863
<i>T. fluviatilis</i>	$y = 0.0468x - 0.2417$	0.894
<i>R. peregra</i>	$y = 0.0337x - 0.1773$	0.856

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Table 1

Percentage of occasions during preference trials where one or both of each prey were consumed

Prey consumed	Percentage of occurrence
<i>G. zaddachi</i>	100
<i>T. fluviatilis</i>	40
<i>R. peregra</i>	18
Both <i>G. zaddachi</i>	80
Both <i>T. fluviatilis</i>	20
Both <i>R. peregra</i>	6

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Table 2

Dry weight energy content for the prey species (shell free dry weight for snail)

Species	Energy Content (Jmg ⁻¹)	Author
<i>G. zaddachi</i>	15.16	Rumohr et al. (1987)
<i>T. fluviatilis</i> *	20.48	Hughes (1971)
<i>R. peregra</i>	12.33	Lien (1978)

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*Average energy content for *Nerita sp.* (data for the most closely related species available in literature).

677
678 Captions

679
680 **Fig. 1**

681
682 Average preference score \pm SE for three prey species in sub-adult *Eriocheir sinensis*.

683
684 **Fig. 2**

685
686 Average preference score \pm SE for male and female *Eriocheir sinensis* preying on *T.*
687 *fluviatilis* and *R. peregra*.

688
689 **Fig. 3**

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691
692 *Eriocheir sinensis* H. Milne Edwards, 1853; NHM 1993:1, River Cray, Hall Place near
693 Crayford, Kent, collected B. Martin, 20 August 1992, right chela showing spines on internal
694 surface of propodus (circled). These spines are normally obscured by the mittens in male
695 crabs. Taken by Harry Taylor, NHM Photo Unit. Scale bar in mm divisions of 1 cm.

696
697 **Fig. 4**

698
699 *Eriocheir sinensis* H. Milne Edwards, 1853; NHM 1993:1, River Cray, Hall Place near
700 Crayford, Kent, collected B. Martin, 20 August 1992, showing the prey grasping co-
701 adaptation between spines on internal surface of the right chela propodus and those on the
702 merus (circled). These spines are normally obscured by the mittens in male crabs. Taken by
703 Harry Taylor, NHM Photo Unit. Scale bar in mm divisions of 1 cm.

704

705

Fig. 5

706

707 Handling time of *G. zaddachi* prey against **A** carapace width and **B** average chela height for

708

E. sinensis.

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Fig. 6

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712 Handling time of *T. fluviatilis* prey against **A** carapace width and **B** average chela height for

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E. sinensis.

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715

Fig. 7

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717 Handling time of *R. peregra* prey against **A** carapace width and **B** average chela height for *E.*

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sinensis.

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720

Fig. 8

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722 Average handling time: for *G. zaddachi* = total time to complete ingestion; for *T. fluviatilis*

723 time to complete ingestion comprising operculum removal (dark), handling empty shell

724 (white) and ingestion (light); and for *R. peregra* time to complete ingestion comprising

725 handling empty shell (white) and ingestion/shell removal (hatched).

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728

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Fig. 9

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731 Average rate of energy consumption \pm SE by sub-adult *Eriocheir sinensis* for three prey

732

species.

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