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**Effects of autotomy compared to manual declawing on contests between males for females in the edible crab, *Cancer pagurus*: implications for fishery practice and animal welfare.**

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27

28 **Abstract**

29 In many decapod fisheries, claws are removed and the animal returned to the sea with  
30 the assumption that there is little impact on the fitness and welfare of the animal, or on  
31 the productivity of the population. Here, the impact of claw loss, by two methods of claw  
32 removal, is examined during competition between males for access to females in the  
33 crab, *Cancer pagurus*. Males induced to autotomize a claw showed little reduction in  
34 their competitive ability, however, those subject to the fishery practice of manual  
35 declawing showed a marked decrease in their competitive ability. Compared to  
36 autotomized males, these declawed crabs displayed activities that suggest an  
37 awareness of the wound caused by the appendage being twisted off and the data are  
38 consistent with an impaired welfare for these animals. They were also less likely to  
39 display to their opponent compared to autotomized crabs. Intact males showed high  
40 aggression towards declawed males, which showed low aggression in return. Further,  
41 declawed crabs showed particularly high levels of submissive acts. The declawed crabs  
42 thus rarely gained the female compared to autotomized crabs. The present study  
43 demonstrates that manual declawing has a major detrimental impact on fitness and  
44 welfare of edible crabs and we suggest that this method of harvesting should be  
45 replaced with induced autotomy of a single claw.

46 **Key words:** autotomy, *Cancer pagurus*, manual declawing, contests, welfare.

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## 55 1. Introduction

56 Manual declawing of crabs is practiced in many fisheries, including the Southern  
57 Florida stone crab, *Menippe mercenari*, (Ehrhardt 1990), the North East Atlantic deep-  
58 water red crab, *Chaceon affinis*, the Southern Iberian fiddler crab, *Uca tangeri*, (Oliveira  
59 et al. 2000) and in Northern Europe, the edible crab, *Cancer pagurus* (Patterson et al.  
60 2009). After declawing, the animal is released and the practice of manual declawing is  
61 defended because crabs may naturally autotomize a claw or walking leg, for example  
62 when grasped by a potential predator, and then regenerate the lost limb (Juanes and  
63 Smith 1995). It has thus been argued that manual declawing offers a sustainable resource  
64 within the fishery (Carroll and Winn 1989).

65 The fishery practice of manual declawing by twisting and breaking the limb from  
66 the body in the edible crab, however, typically breaks some of the exoskeleton of the main  
67 body around the point of articulation of the limb (Patterson et al. 2007). This causes a  
68 stress response that includes a marked elevation of glucose within 10 minutes and  
69 increased lactate within 1 minute. The ratio of glucose to glycogen altered significantly  
70 after 10 minutes, indicating mobilisation of glycogen energy stores typical of the  
71 crustacean stress response (Patterson et al., 2007). Claw ablation of the freshwater  
72 prawn, *Macrobrachium rosenbergii*, produced a similar increase in glucose (Manush et  
73 al. 2005). In the edible crab, however, induced autotomy, which results in a clean  
74 severance of the limb without damage to the adjacent exoskeleton, does not cause  
75 physiological stress (Patterson et al., 2007).

76 Manual declawing under experimental conditions also results in high mortality. In  
77 the stone crab, *Menippe mercenari*, 47% of individuals that had both claws removed died  
78 within 24hr and 28% died after a single claw removal (Davis et al. 1978). Patterson et al.  
79 (2007) found that wound sizes of manually declawed *C. pagurus* that died were larger  
80 than those that survived, suggesting that the extent of wounding is a major factor in crab  
81 mortality. Those that had claws removed by induced autotomy, had significantly lower  
82 mortality than did those manually declawed. A lower mortality rate was noted when claws  
83 were broken along the natural fracture plane in *M. mercenaria* (Simonson and Hochberg  
84 1986) and mortality depended on the severity of the wound, and how the claw was broken  
85 off (Juanes and Smith 1995).

86 Further, the loss of one or both claws by either method places crabs at a distinct  
87 disadvantage in terms of feeding. For example, although loss of one claw does not alter  
88 the feeding motivation of *C. pagurus*, it does decrease ability to feed on bivalves  
89 (Patterson et al. 2009). This reduced food choice due to claw loss is also seen in *Cancer*  
90 *productus* and *Carcinus maenas*, which are constrained to handling smaller prey (Elner  
91 1980; Brock and Smith 1998) and growth and regeneration may be reduced (Savage and  
92 Sullivan 1978; Elner 1980; Juanes and Smith 1995; Seed and Hughes 1995; Brock and  
93 Smith 1998). Thus, claw loss can affect the long term fitness of these animals  
94 (Smallegange and Van Der Meer 2003).

95 In keeping with many other decapods, the claws of *C. pagurus* are sexually  
96 dimorphic, being larger in males, and are used during competition between males for  
97 access to females (Lee 1995). This dimorphism is even greater in fiddler crabs, *Uca*  
98 *tangeri*, in which the major claws of males are used for signalling to females to attract  
99 them to their breeding burrows and to defend their burrows from other males. The removal  
100 of this vital appendage biases the operational sex ratio towards females, as clawless  
101 males are treated as females by other males and females (Oliveira et al. 2000). Thus,  
102 removing the major claw of male fiddler crabs has potential consequences at the  
103 population level. In hermit crabs, *Pagurus minutus* and *P. nigrofascia*, males show  
104 precopular guarding of females and often fight intruder males to retain the female.  
105 Intruders with a naturally missing, presumably autotomized, major cheliped were as likely  
106 as intact intruders to escalate a contest but were less successful in gaining the female  
107 compared to intact males (Yasuda and Koga 2016, Yasuda et al. 2011). Deficits in  
108 contests for females have also been noted in other decapods that have missing chelae  
109 (Smith 1992; Daleo 2009). These studies, however, have only examined how claw loss  
110 affects contest behaviour and outcome and have not examined how the nature of claw  
111 loss might mediate contest behaviour, outcome and fitness.

112 It is expected that the loss of a major weapon will adversely affect contest  
113 performance in that damaged male when fighting an intact male (Arnott and Elwood  
114 2009). This could be due to a decrease in how that damaged male assesses its own  
115 fighting ability, often called resource holding potential, RHP (Parker and Stuart 1976). In  
116 addition, it might reduce the intact opponent's estimation of the damaged male's RHP. It

117 is likely, however, that there is a greater loss of RHP to the damaged male if the claw is  
118 removed by manual declawing rather than by induced autotomy, because the former  
119 causes considerably more injury and physiological stress (Patterson et al. 2007). It is  
120 possible that the intact opponent could detect the greater injury caused by manual  
121 removal of its opponent's claw. Alternatively, it is possible that the intact male may simply  
122 detect the loss of the claw in its opponent and not the manner of that loss. By comparing  
123 the contests involving either manually declawed or autotomized males competing against  
124 intact males insights into the assessment processes during contests may be gained.

125 Two major practical concerns associated with claw harvesting in *C. pagurus* and  
126 other decapods are addressed. First, the practice might not be as benign to the population  
127 as previously suggested and thus future productivity may be compromised (Carroll and  
128 Winn 1989). Here, the fitness consequences of having a missing claw and on the nature  
129 of the claw loss of males competing for females is examined. If claw loss and the nature  
130 of claw loss impact fitness it would be expected that there would be differences in the  
131 ability to compete for key resources. Second, some methods of claw removal may affect  
132 the welfare of individual crabs more than others (Sherwin 2001; Patterson et al., 2007;  
133 Elwood et al. 2009). Thus, activities indicating an awareness (not necessarily conscious)  
134 of the wounds arising from declawing are recorded.

## 135 **2. Material and Methods**

### 136 *2.1 Collection, maintenance and experimental procedure*

137 Male and female *C. pagurus* of 140mm-180mm carapace width were collected by  
138 commercial fishermen in April and May 2012, using baited pots, in the Irish Sea, off the  
139 Ards Penisular of County Down, and maintained on deck in fish trays and baskets. Crabs  
140 were transported from the harbour slip at Portaferry, Co Down, Northern Ireland to the  
141 adjacent Queen's University Marine Laboratory (QML) in storage boxes.

142 Morphometric data were collected from each animal; sex, wet weight (g) and  
143 carapace width (cm), and the crab was tagged with 'Queen Bee' tags (Thorne, UK), small  
144 coloured plastic dots numbered 1-100, attached to the carapace with non-toxic, water  
145 proof hypox glue. Crabs were then maintained for 5 days to recover from the stress of  
146 capture (Patterson et al. 2007; Barrento et al. 2011) in outdoor 5500 litre circular, low

147 profile water tanks (76cm depth, 175cm diameter), with a continual supply of sand-filtered  
148 water piped directly from the sea (8-9°C). Tanks were equipped with overflow outlets to  
149 allow for water circulation, and an air diffuser was used to aerate the water. To control  
150 feeding and provide shelter and protection crabs were kept in individual lidded storage  
151 boxes (71cm(L) x 44cm(W) x 38cm(H)), with approximately 20 x 3cm diameter ventilation  
152 holes for water and oxygen circulation. Approximately 10-13 boxes were kept in each  
153 outdoor tank. The outdoor tanks were kept covered and secured with blue/green coated  
154 woven polyethylene tarpaulins, to ensure minimum light intensity/disturbance. The crabs  
155 were not fed during this period.

156 Observations of contests were made in a tank (Figure 1) of 9.5mm thick plate  
157 glass measuring 80cm(L) x 50cm(W) x 50cm(H). It comprised three chambers separated  
158 by removable rigid Perspex partitions (3mm thick), blackened using marine paint (Krylon  
159 Fusion). These tank dividers were perforated (3cm diameter holes) to allow the movement  
160 of water and any chemical cues released by the crabs, including haemolymph leaking  
161 from wounds, throughout the tank. A continuous supply of Strangford Lough sea water at  
162 approximately 9.5°C and air (via an Airstone (BiOrb)) was pumped into the tank.

163 Sand and small pebble substrate, collected from the Strangford Lough tidal area,  
164 was provided (approx. 3-4cm deep). The exterior rear and sides of the tank were also  
165 blackened using black marine paint. The area surrounding the tank was cordoned off  
166 using black plastic sheeting to control for light interference during the observation period.  
167 Red light (OSRAM Fireglow Effect 60W, 170 Lumen) was used to enable observations  
168 without natural and/or artificial light intrusion, and to obscure the observer. At the end of  
169 each observation, the sea water was drained from the tank, and refilled for the next  
170 subjects to eliminate chemical cues and leaked haemolymph.

171 For each replicate, two male crabs and one female crab were randomly selected  
172 for each contest. From these, one of the males was randomly selected (by drawing tokens  
173 from a cup) to have either the right or the left claw forcibly removed (manually declawed),  
174 or the male crab was induced to autotomize a claw. The other male crab and the female  
175 crab remained intact. The experimental replication was: intact  $\bar{v}$  autotomy n=34; intact  $\bar{v}$   
176 manually declawed n=26 and animals were used only once. Manual declawing involved

177 holding the body of the crab in one hand and grasping and sharply twisting the claw with  
178 the other (Patterson et al. 2007). Autotomy involved making a small cut at the joint at the  
179 top of the merus, the claw is then cast off by the crab at the joint that attaches to the body  
180 (Patterson et al. 2007). Males were individually placed in the two small chambers and the  
181 female in the large chamber (Figure 1), for one hour to acclimatise in red light. The tank  
182 partitions were then removed and all three crabs were free to move throughout the tank.  
183 Continuous recording, using a mounted digital camera above the tank, was used to  
184 capture all occurrences of behaviour during the 60 minute observational period. The  
185 winner was the male in physical contact with the female at the end of the contest. Some  
186 were on top of the female in the typical guarding posture. Others remained next to the  
187 female, using a claw to hold her by the carapace or a leg, or the male placed a claw or  
188 walking legs on the female. Other winners simply stayed next to or in front of the female,  
189 but remained in physical contact. Females did not show resistance to the presence of the  
190 male. The contest losers were not in close proximity to the winning male or the female at  
191 the end of the contest. From preliminary observations, a number of activities were  
192 identified. These were classified into five broad categories, to avoid excessive analyses  
193 (Table 1). In addition, 'frothing' from the mouth parts was recorded as occurring or not  
194 immediately after the claw treatments were performed, before the crab was placed into  
195 the water. It was characterized by a bubbly foam coming out of the mouth parts. Further,  
196 when the non-intact males were first put into the individual sections of the observation  
197 arena, it was noted whether or not haemolymph was visible in the water. Finally, touching  
198 the wound by the non-intact crab, with its remaining claw and/or walking legs, was  
199 recorded during the 60 minute observational period.

## 200 *2.2 Ethical consideration*

201 No licence was required for this experiment because invertebrates other than  
202 cephalopods are not regulated under the UK Scientific Procedures Act. Nevertheless,  
203 sample sizes were kept as low as possible for contingency analyses, and fewer replicates  
204 were used in the treatment considered to be the more extreme, as recommended (Elwood  
205 1991). Manual claw removal is an extreme procedure but one that is used in many  
206 fisheries on very large numbers of animals. It is possible that the data from the present



207 study might guide future fisheries practice. On this basis the procedures used in the  
208 experiment were considered justified.

### 209 *2.3 Data Analyses*

210 Effects of claw loss and the nature of that loss on which animal initiated the contests,  
211 produced the first display, success in obtaining the female, and self-directed behaviour  
212 towards the wound of non-intact males, were analysed using contingency tests and/or  
213 binomial tests. Logistic regression was used to analyse the effect of relative size of  
214 contestants that were successful in obtaining the female. For the categories aggression,  
215 defensive, dominant and submission, the occurrence of each activity for each category  
216 was noted without respect to duration and totalled as the number of such acts in each  
217 category. An activity was deemed to have occurred twice (or more) if separated by the  
218 occurrence of another activity.

219 We used a one between and one within repeated measures ANOVA to determine the  
220 effects of claw removal procedure (between observations factor: declawed or  
221 autotomized) and claw removal status (within observations factor: missing claw or intact)  
222 on the agonistic behaviours. We also included the interaction term between these factors.  
223 Repeated measures are used because two animals within one contest do not act  
224 independently of each other (see Briffa and Elwood 2010 for statistical rationale). All data  
225 in the ANOVAs were  $\log_{10}(x+1)$  transformed to improve normality. Multiple tests were not  
226 adjusted by Bonferroni correction because that has been criticized for too easily rejecting  
227 real effects (Nakagawa 2004). All statistical analyses used the Statview package.

228

## 229 **3. Results**

### 230 *3.1 Initiation, display and success.*

231 Of the 60 staged encounters, 57 resulted in one male obtaining the female but in  
232 6 of these there was no overt interaction between the males. In the other 51 cases the  
233 males interacted before one obtained the female and, of these replicates, intact crabs  
234 were more likely than non-intact crabs to win the contest (binomial 35  $\geq$  16,  $P=0.003$ ).

235 Autotomized males were as likely to get the female as intact males (binomial 14 v 17,  
 236  $P=0.72$ ), but manually declawed crabs were less likely to obtain females compared to  
 237 intact crabs (binomial 2 v 18,  $P=0.0004$ ). Further, autotomized crabs were more likely to  
 238 win the contest compared to manually declawed crabs (autotomized 14/31  $\underline{v}$  manually  
 239 declawed 2/20,  $G=7.76$ ,  $P=0.005$ ). Logistic regression showed that relative size of  
 240 competing crabs did not affect whether or not the intact crab won the female ( $\chi^2=0.008$ ,  
 241  $df_{1,50}$ ,  $P=0.93$ ).

242 Of the 51 contests, 44 involved cheliped displays by one or both opponents. Intact  
 243 crabs were more likely than non-intact crabs to be the first to display (binomial 33 v 11  
 244  $P=0.0013$ ). Nevertheless, intact crabs did not differ from autotomized crabs in displaying  
 245 first (binomial 17 v 10,  $P=0.24$ ), but were more likely to display first if placed with a  
 246 manually declawed male (binomial 16 v 1). Further, autotomized crabs were significantly  
 247 more likely than declawed crabs to initiate displays (autotomized 10/27  $v$  manually  
 248 declawed 1/17,  $\chi^2_1=5.5$ ,  $P=0.02$ ).

249 There was no difference between autotomized crabs and manually declawed crabs  
 250 in the probability of initiating the contest (autotomized 14/31  $\underline{v}$  manually declawed 7/20,  
 251  $G=0.52$ ,  $P=0.47$ ). Contest initiators were more likely to win than were non-initiators  
 252 (binomial 35  $\underline{v}$  16,  $P=0.003$ ). Further, intact initiators were more likely than non-intact  
 253 initiators to win the contest (intact 25/31  $\underline{v}$  non-intact 10/20,  $G= 5.26$ ,  $P=0.022$ ).  
 254 Autotomized crabs that initiated the contest against their intact opponent were more likely  
 255 to win compared to manually declawed crabs that initiated the contest against their intact  
 256 opponent (autotomized 9/14  $\underline{v}$  manually declawed 1/7,  $G=5.07$ ,  $P=0.024$ ).

257

### 258 *3.2 Aggression*

259 There was no overall difference between contests involving autotomized or  
 260 manually declawed crabs in the number of aggressive activities ( $F_{1,49}=0.42$ ,  $P=0.5$ ; Figure  
 261 2). Intact crabs exhibited more aggressive behaviour than did the non-intact crabs  
 262 ( $F_{2,49}=65.13$ ,  $P<0.0001$ ; Figure 2). Importantly, there was a significant interaction effect  
 263 between type of contest (involving autotomized or manually declawed), and the  
 264 intact/non-intact status of the contestants ( $F_{2,49}=9.80$ ,  $P=0.003$ ; Figure 2). This is because  
 265 intact crabs competing against manually declawed crabs showed a particularly high

266 number of aggressive activities, whereas the manually declawed crab showed the least  
267 number (Fig 2).

268

### 269 *3.3 Defence*

270 More defensive activities occurred in contests involving manually declawed crabs  
271 than those with autotomized crabs ( $F_{1,49}=4.22$ ,  $P=0.045$ ; Figure 3) and non-intact crabs  
272 displayed considerably more defensive behaviour compared to intact crabs ( $F_{2,49}=24.62$ ,  
273  $P<0.0001$ ; Figure 3), but there was no significant interaction effect between these factors  
274 ( $F_{2,49}=2.87$ ,  $P=0.096$ ).

275

### 276 *3.4 Dominance*

277 Contests involving autotomized or manually declawed crabs did not differ in the  
278 overall number of dominance activities ( $F_{1,49}=3.70$ ,  $P=0.06$ ; Figure 4) and intact crabs  
279 exhibited more dominance activities than did non-intact crabs ( $F_{2,49}=14.53$ ,  $P=0.0004$ ;  
280 Figure 4), but there was no significant interaction effect ( $F_{2,49}=1.77$ ,  $P=0.19$ ).

281

### 282 *3.5 Submissive*

283 A higher number of submissive activities occurred in contests involving manually  
284 declawed crabs than those involving autotomized crabs ( $F_{1,49}=9.32$ ,  $P=0.004$ ; Figure 5).  
285 Non-intact crabs exhibited more submissive behaviour than did intact crabs ( $F_{2,49}=22.47$ ,  
286  $P<0.0001$ ; Figure 5). Importantly, there was a significant interaction effect ( $F_{2,49}=8.19$ ,  
287  $P=0.006$ ; Figure 5). This arose because of the exceptionally high number of submissive  
288 activities performed by the manually declawed crabs compared to the other groups.

### 289 *3.6 Other observations*

290 Crabs that were manually declawed were more likely to froth at the mouth than  
291 autotomized crabs (manually declawed 17/23  $\underline{v}$  autotomized 9/34,  $G=12.88$ ,  $P<0.001$ ),

292 haemolymph from the wound was visible in the water in more replicates with manually  
293 declawed crabs than autotomized crabs (manually declawed 16/23  $\underline{v}$  6/34,  $G=16.07$ ,  
294  $P<0.0001$ ), and manually declawed crabs were more likely to touch the wound with its  
295 remaining claw or front walking legs than did autotomized crabs (manually declawed  
296 15/23  $\underline{v}$  autotomized 7/34,  $G=15.93$ ,  $P<0.0001$ ).

297

#### 298 **4. Discussion**

299 Although intact crabs were more successful than were non-intact crabs in competing  
300 for females, those induced to autotomize a claw were considerably more successful than  
301 crabs that were manually declawed. Indeed, autotomized crabs fared no worse than intact  
302 crabs when just those contests were examined. That is, it is not the absence of a claw  
303 that reduces the ability of a male to obtain a female, at least under the present conditions,  
304 rather it is the manner of claw loss. Manual declawing clearly places males under a severe  
305 intra-specific competitive disadvantage. Negative effects of claw loss have been noted in  
306 other studies (Sekkelsten, 1988; Abello et al., 1994), but the manner of claw loss has  
307 received little or no attention with regard to such competition. To understand how the  
308 outcome of contests is influenced by the nature of the claw loss, the activities used in the  
309 competitive process are considered.

310 Activities that occur early in the encounter should indicate how the males assess  
311 themselves in terms of RHP rather than indicating how the opponent perceives them  
312 (Elwood and Arnott 2012). Intact crabs were more likely than non-intact crabs to initiate  
313 the contest by moving towards the opponent, however, manually declawed and  
314 autotomized crabs did not differ in the probability of initiation of contests. Initiating the  
315 contest gives an advantage to that crab because those that initiated were more likely to  
316 obtain the female. Autotomized crabs that initiated, however, were more likely to win  
317 access to the female than were manually declawed crabs, suggesting that the latter did  
318 particularly poorly in the ensuing fight.

319 Intact males were also more likely than non-intact males to be the first to display.  
320 Here, there was a marked effect of the nature of claw loss because, while the autotomized  
321 crabs were as likely as the intact to display first, the manually declawed crabs very rarely

322 displayed first. This suggests that it is not the lack of a claw that is dissuading the crab to  
323 engage in display but, rather, it was due to the poor condition of the declawed crabs  
324 (Patterson et al. 2007). Further, the raising up and stretching out of the claw or claws is  
325 likely to be energetically expensive (Doake et al. 2010) and perhaps beyond the capability  
326 of a manually declawed crab.

327         Manually declawed crabs were more likely than autotomized crabs to lose  
328 haemolymph in amounts that could be seen in the water. Frothing at the mouth was also  
329 more common in declawed crabs than in autotomized crabs, such frothing in crabs having  
330 been attributed to stress (Deshai 2012). Manual declawing also results in elevated  
331 concentrations of lactate compared to intact and autotomized crabs (Patterson et al.  
332 2007). High lactate concentrations during contests causes fatigue (Briffa and Elwood  
333 2005) and alters behaviour such as defensive actions (Stoner 2012). Manually declawed  
334 crabs may therefore be unable to engage in fighting, and may withdraw from the contest  
335 based on assessment of their internal state.

336         Manually declawed crabs appeared to be aware of their wound, as indicated by  
337 their much higher incidence of touching the wound compared to autotomized crabs.  
338 Although not part of the recording protocol, a number of manually declawed crabs showed  
339 a 'shudder' response when touching the wound. The remaining claw or a leg was brought  
340 to the wound site and either inserted directly into the wound or probed the edges of the  
341 wound site. The 'shudder' response was only observed when the wound was being  
342 touched and the crab's body was seen to give a little shake or tremble. Touching at the  
343 site of the application of a noxious stimulus has been noted in glass prawns (Barr et al.  
344 2008) and hermit crabs (Appel and Elwood 2009) and is considered to indicate an  
345 awareness of the location of a wound. Shaking of a claw has been noted following  
346 injection of formalin into that appendage (Dyuzen et al. 2012), but the present study is  
347 the first to note shaking/shuddering of the entire body.

348         Some manually declawed crabs shielded their wound by positioning the remaining  
349 claw in front of the wounded area. This protected the wound from contact by the intact  
350 opponent, but impeded the ability of wounded crabs to engage in the normal activities  
351 seen in crab fights. These observations indicate that declawed crabs were aware (not  
352 necessarily conscious) of their wound and that the wound resulted in marked changes in

353 behaviour that are not merely reflexive but consistent with the idea of pain (Elwood 2011;  
354 Sneddon et al. 2014). These crabs also appeared to be in poor condition and incapable  
355 of effective competition. How this resulted in losing the encounter may be determined by  
356 examining the specific groups of activities that comprise the competitive interaction i.e.  
357 aggression, defence, dominance and submission.

358 Intact crabs were more aggressive than non-intact crabs and they were particularly  
359 aggressive when encountering a manually declawed crab rather than one that had  
360 autotomized. In return, the manually declawed crabs showed very few aggressive acts. It  
361 is possible that the intact crab was responding to either the wound or the behaviour of  
362 declawed opponents and increasing aggression above that normal for crab fights.  
363 Alternatively, the intact crab might be fighting normally without information being gathered  
364 about the wound or behaviour of the non-intact crab. It is clear, however, these contests  
365 are highly asymmetric with respect to the number of aggressive acts shown. Intact crabs  
366 also showed more acts of dominance than did the non-intact crabs, but the lack of a  
367 significant statistical interaction shows that, in contrast to aggressive acts, this was not  
368 affected by the nature of claw loss. With dominance activities, there is no evidence that  
369 the intact male can discriminate between the two types of claw loss in an opponent. Thus,  
370 the behaviour of the intact crab does not distinguish whether or not these contests are  
371 based on self-assessment, where each contestant acts according to its own abilities, or  
372 by mutual assessment, where each incorporates information about the ability of the  
373 opponent (Elwood and Arnott 2012).

374 Defensive acts were shown less often by the intact crabs compared to non-intact  
375 crabs. Both types of claw loss resulted in high numbers of defensive acts in the affected  
376 males and the lack of a significant statistical interaction indicates that the nature of claw  
377 loss did not have a marked effect in defensive behaviour. Crabs with a missing claw also  
378 showed more submissive acts than did those with both claws. In this case, submissive  
379 acts were much more frequent by manually declawed compared to autotomized crabs.  
380 This is evidence that the declawed crabs are attempting to avoid the agonistic encounter,  
381 presumably because they are aware of their poor condition. Thus, judging from the  
382 observation on submission, manually declawed crabs are not attempting to fight but rather

383 are attempting to limit damage. Thus, the data on the non-intact crabs indicates self-  
384 assessment is affecting how they compete (sensu Taylor and Elwood 2003).

385 It is clear that intact crabs were more motivated to fight compared to those missing  
386 a claw. Further, autotomized crabs were more motivated to engage in a fight than  
387 manually declawed crabs. This is evidenced by crabs that were autotomized showing  
388 fewer submissive acts and winning more contests than manually declawed crabs. It is  
389 possible that autotomized crabs engaged in dishonest signalling to convey a greater  
390 aggressive intent and fighting ability, a common trait among crustaceans (Steger and  
391 Caldwell 1983; Backwell et al. 2000; Elwood et al. 2006; Laidre 2009). Indeed, male  
392 hermit crabs that lack the major claw (presumably by autotomy) are just as likely to  
393 escalate contests for females, but were much less likely to win than intact intruders  
394 (Yasuda and Koga 2016). In the mud crab, *Cyrtograpsus angulatus* Dana, crabs missing  
395 claws by induced autotomy were also able to win contests when competing against intact  
396 crabs (Daleo 2009).

397 One surprise in the current study was that body size did not have a significant  
398 effect of the outcome of contests because body size has been shown to be important in  
399 numerous other taxa (Arnott and Elwood 2009). In the present study, however, a narrow  
400 range of crab sizes was employed as no crab below the minimum legal landing size of  
401 140mm carapace width was included in the experiment. With a wider size range of  
402 opponents those crabs with a missing claw might effectively compete against much  
403 smaller opponents. Thus, if autotomized animals are released in the sea they would  
404 encounter a broader range of crabs than in the experiment and might have an increased  
405 chance of winning a contest for females, as well as other resources, when facing much  
406 smaller opponents. Further, it is possible that manually declawed crabs might also fare  
407 better with much smaller opponents. That is not to suggest that these crabs might do well  
408 if released because previous studies have shown a high mortality of manually declawed  
409 crabs (Patterson et al. 2007). It is important to note that in this experiment a maximum  
410 of one claw was removed whereas in some fisheries two may be removed. The  
411 consequences of losing both claws by manual declawing would be severe from the point  
412 of view of survival (Davis et al. 1978) and even if lost by autotomy, there would be major

413 detrimental effects on ability to feed (Juanes and Smith 1995) and undoubtedly on  
414 competitive ability.

415

## 416 **5. Conclusion.**

417 It is clear that the ability to compete against intact crabs is severely affected by the  
418 nature of claw removal. Crabs that have a single claw manually removed by twisting have  
419 very poor success in male-male contests compared to those that lose a claw by induced  
420 autotomy. This major fitness impact is likely due to the haemolymph loss seen  
421 immediately after manual claw removal but much less after induced autotomy. Wounds  
422 are much larger after manual declawing (Patterson et al. 2007) and these crabs showed  
423 the stress response of frothing from the mouth (Deshai 2012). Manual declawing rather  
424 than autotomy also results in rapid increases in haemolymph lactate and glucose that is  
425 typical of a marked physiological stress response (Patterson et al. 2007). Further, the  
426 observation of repeated touching and picking at the wound after manual declawing, as  
427 well as guarding of wounds, suggests an awareness of the wound. Thus, there are  
428 concerns for the welfare of crabs subject to manual declawing (Elwood 2011). There must  
429 also be concerns that returning crabs to the sea after manual declawing will not enhance  
430 population sustainability, because of the loss in competitive ability, the loss of feeding  
431 ability (Patterson et al. 2009) and the substantial mortality (Patterson et al. 2007) seen in  
432 these animals. It is suggested that manual declawing is discontinued in those fisheries in  
433 which it still occurs. An alternative would be training fishermen to induce autotomy in one  
434 claw, followed by return of the crab to the sea.

435

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439

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560 **Table 1** Male competitive activities grouped into broad categories.

561 ***Initiate contest***

562 This is characterized by one crab decreasing the distance between it and its opponent  
563 and one of four other activities follows.

564 <u>Activity</u>	<u>Description</u>
565 Approach	One opponent approaches the other opponent, decreasing the distance between the contestants. This is followed by:
566 Mutual Alignment	Opponents face each other; no contact,
567 Contact	One opponent makes contact with other opponent,
568 Contact Alignment	Opponents face each other, claws in contact, or
569 Claw Stroke	One opponent uses claw(s) to stroke other opponent.
570	
571	

572 ***Aggressive behaviour***

573 Aggressive activities include 'displays', incurring low costs, followed by an 'attack', and  
574 finally a 'fight', that presumably incurs the highest costs with the potential for injury to both  
575 crabs.

576	<b><i>Activity</i></b>	<b><i>Description</i></b>
577		
578	Display	One opponent extends claws out towards other opponent, pinchers open; no contact.
579		
580	Threat Display	One opponent raises body high on walking legs, extends claws, directed towards other opponent.
581		
582		
583		
584	Extend	One opponent swipes claw towards other opponent; no contact.
585		
586	Lunge	One opponent, claw open and extended, thrusts body forward at opponent; brief contact.
587		
588	Manus Contact	Opponents face each other in threat display; claws in contact, pinchers open.
589		
590	Pull In	One opponent uses claws to pull opponent, decreasing distance between individuals.
591		
592	Mutual Push	One opponent uses claw(s) to push against other opponent, other opponent pushes back.
593		
594		
595	Carapace Grasp	One opponent grasps and holds other opponents carapace.
596	Grip	One opponent uses claw(s) to grip other opponent, pinching/crushing observed.
597		
598	Anterior Strike	One opponent uses claw(s) to grip anterior region of carapace of other opponent.
599		
600	Wound Grasp	One opponent uses claw(s) to grasp other opponents wound site.
601		
602	Repeated Grasp	One opponent repeatedly grabs and grips opponent; vigorous pushing and pinching/crushing observed.
603		
604	Grip Back	One opponent uses claw(s) to return the grip of other opponents' claw(s), pinching/crushing observed.
605		
606	Flip	With interlocked claws or by grasp of carapace, one opponent is lifted from the substrate and held above opponent.
607		
608		
609		
610	<b><i>Defensive behaviour</i></b>	
611	Defensive activities include one crab attempting to repel and/or escape from its opponent.	
612	<u><i>Activity</i></u>	<u><i>Description</i></u>
613	Retreat	One opponent retreats rapidly from the other opponent.
614	Withdraw	One opponent leaves the area of the other opponent, increasing the distance between the contestants.
615		

616	Struggle	One opponent struggles to free itself from other opponents grasp.
617		
618	Push Away	One opponent uses claw(s) to push other opponent away, creating distance between the opponents.
619		
620	Dismount	One opponent climbs off other opponent.

621

622 ***Dominant behaviour***

623 Dominant behaviour was observed when one crab appeared to exert control over its  
624 opponent, typically with its opponent engaging in subordinate behaviour (below).

625	<u>Activity</u>	<u>Description</u>
626	Rise up	One opponent rises up on legs.
627	Pushdown	One opponent uses claw(s) to push down on other opponent's carapace.
628		
629	Tap	One opponent uses claw(s) to 'tap' on other opponent's carapace.
630		
631	Mount	One opponent crawls on top of the other opponent.
632	Push	One opponent uses claws and/or body to push against other opponent; contact.
633		
634	Free	One opponent releases other contestant from grasp.

635

636 ***Submissive behaviour***

637 This was observed by crabs typically in response to dominant behaviour by the opposing  
638 crab.

639	<u>Activity</u>	<u>Description</u>
640	Motionless	One opponent freezes body position; no overt sign of movement or response.
641		
642	Submission	Opponent draws claws and walking legs in and under body, lowers body.
643		
644	Crawl under	One opponent attempts to position itself under other opponent's body.
645		

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Fig 1

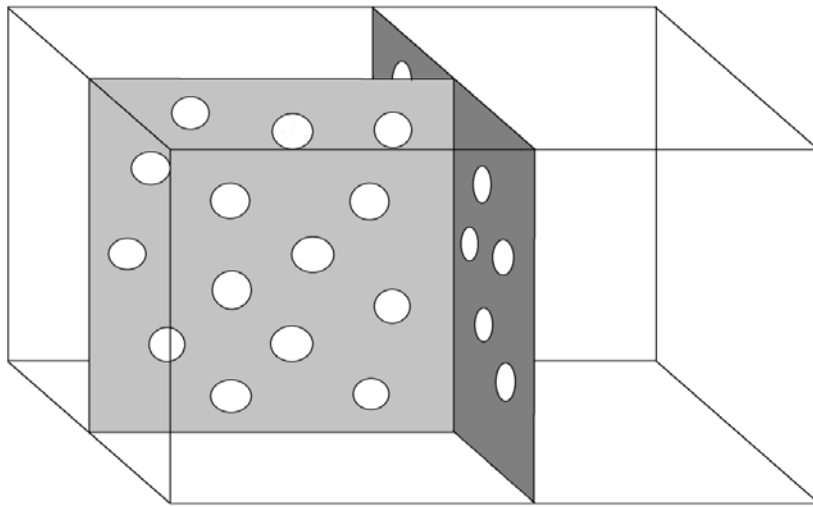


Fig 2

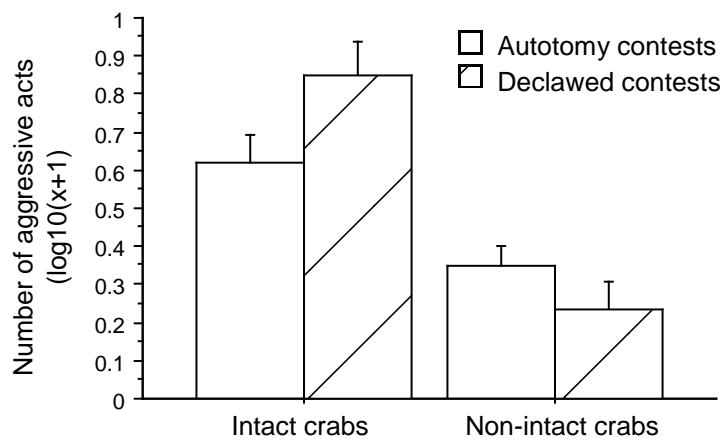


Fig 3

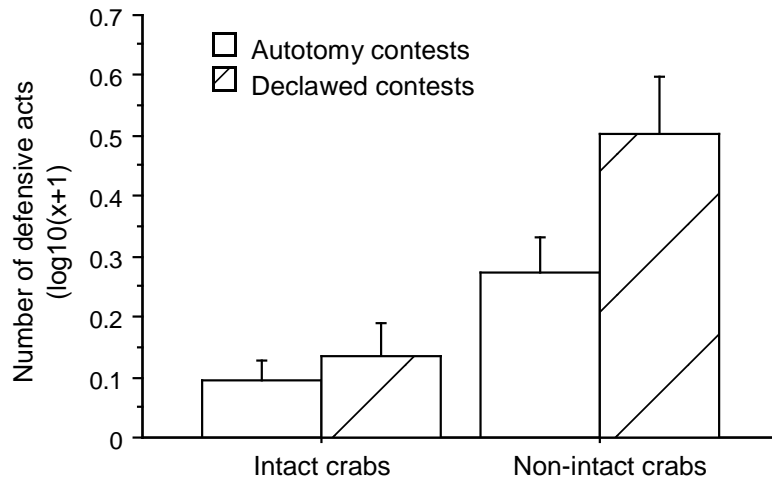


Fig 4

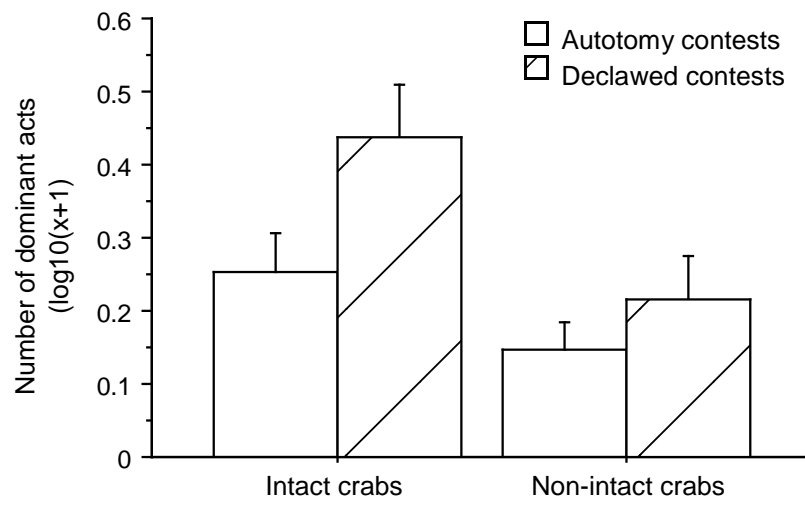
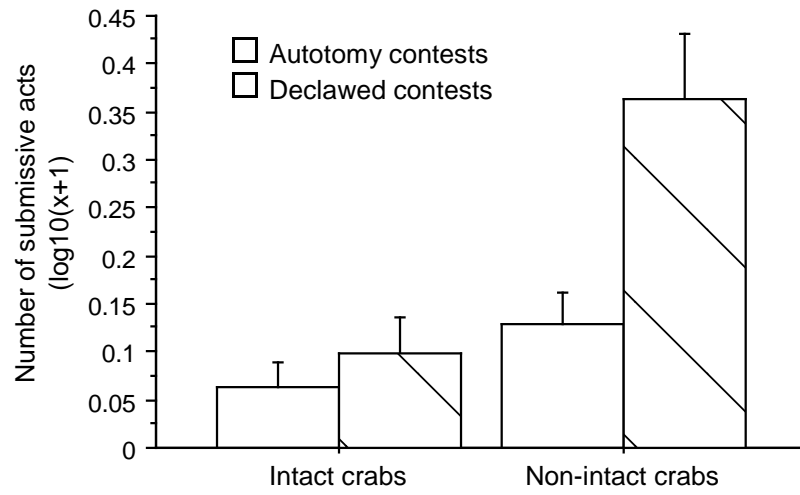


Fig 5



## Figure legends

Figure 1 Schematic of observational tank, showing removable partitions that creates three temporary holding chambers.

Figure 2 Mean (+S.E) number of aggressive acts displayed by intact and non-intact crabs involving contests of autotomized and manually declawed crabs.

Figure 3 Mean (+S.E) number of defensive acts displayed by intact and non-intact crabs involving contests of autotomized and manually declawed crabs.

Figure 4 Mean (+S.E) number of dominant acts displayed by intact and non-intact crabs involving contests of autotomized and manually declawed crabs.

Figure 5 Mean (+S.E) number of submissive acts displayed by intact and non-intact crabs involving contests of autotomized and manually declawed crabs.