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McCambridge, C., Dick, J., & Elwood, R. (2016). 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. *Journal of Shellfish Research*, 35(4), 1037-1044. <https://doi.org/10.2983/035.035.0426>

Published in:
Journal of Shellfish Research

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
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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 \underline{v} autotomy n=34; intact \underline{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

436 **Acknowledgments**

437 This work was funded by the Department of Agriculture and Rural Development
438 Northern Ireland (DARDNI) under their PhD Studentship Scheme.

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	<i>Activity</i>	<i>Description</i>
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		
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609		
610	<i>Defensive behaviour</i>	
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

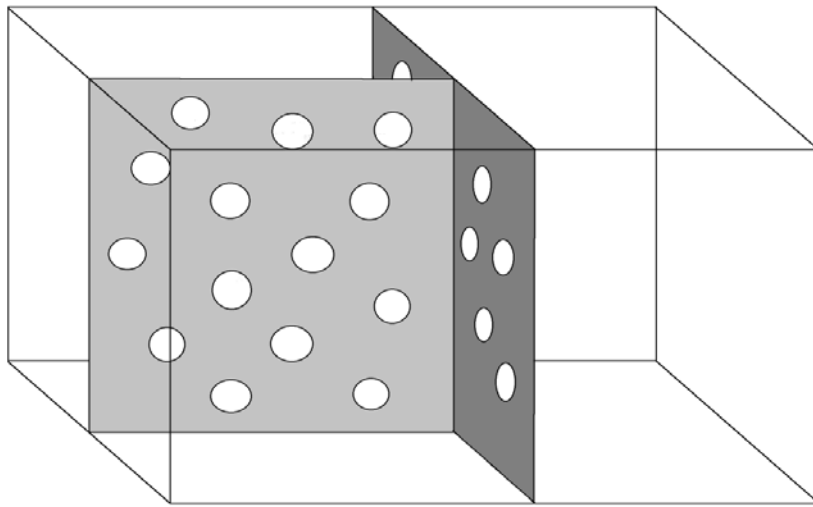


Fig 2

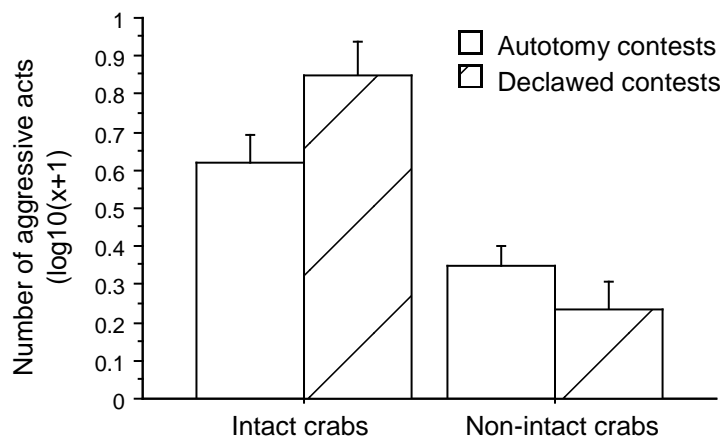


Fig 3

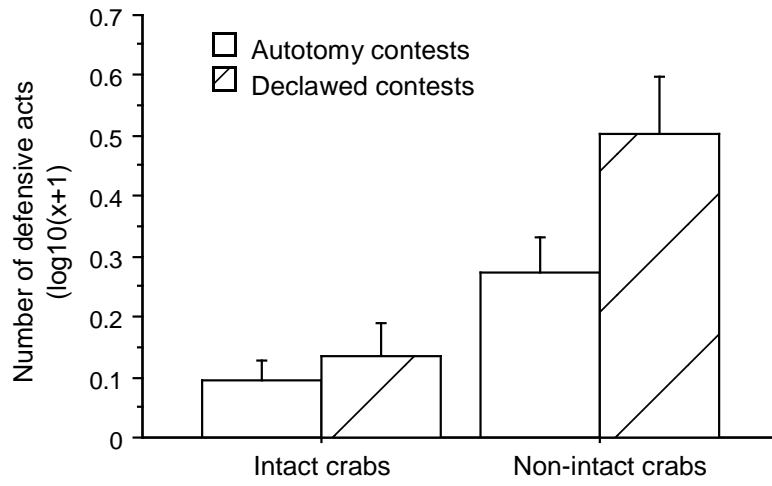


Fig 4

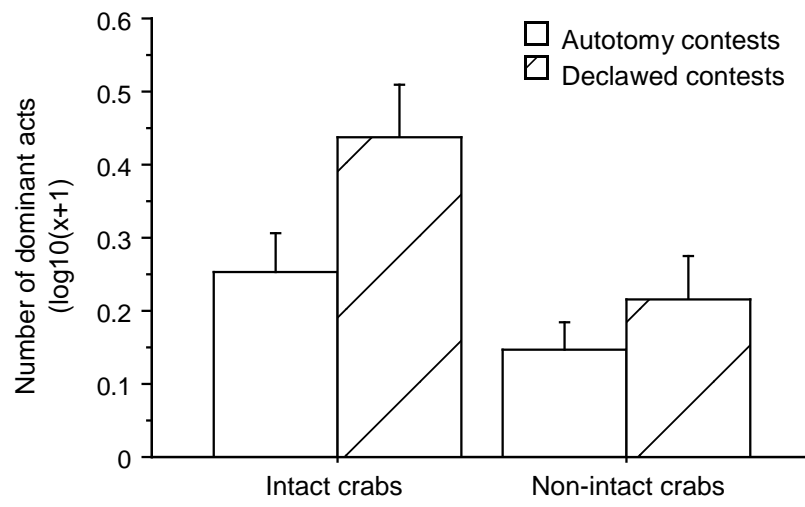


Fig 5

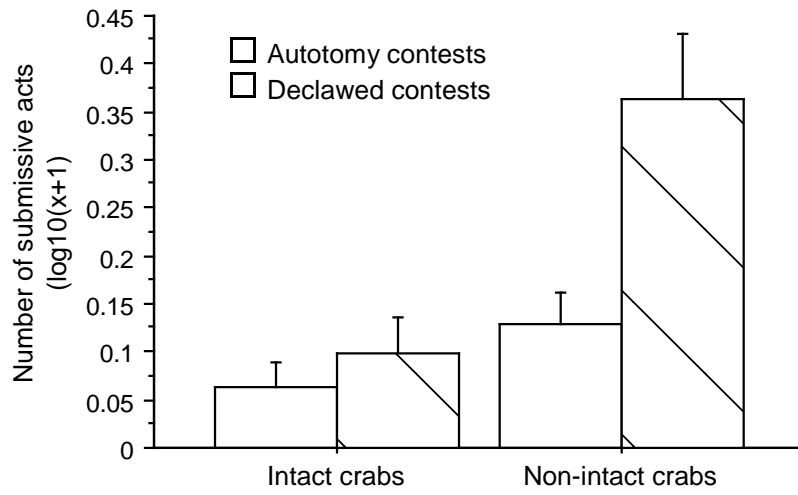


Figure legends

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.