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1 **Relative growth and size at onset of sexual maturity of the brown crab,**
2 ***Cancer pagurus* in the Isle of Man, Irish Sea**

3

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11 **Running head:** Relative growth and size at maturity of *Cancer pagurus*

12

13 **ABSTRACT**

14 In this study, the relative growth, size-weight relationships and size at onset of maturity of the
15 brown crab *Cancer pagurus* were investigated in the Isle of Man. For the analyses of relative
16 growth and size at onset of maturity, the samples were collected seasonally between autumn
17 2012 and spring 2013 using several methods: pot surveys, dredge and trawl surveys, market
18 surveys and shore surveys. Results showed that allometric growth occurred in the chelipeds of
19 males (n = 87) and in the abdomen of females (n = 222). Four different measures of maturity
20 (behavioural, functional, morphometrical and physiological) were examined. With respect to
21 the behavioural maturity, the smallest female crab found with a sperm plug measured 110 mm
22 CW, whereas in terms of functional maturity the smallest ovigerous female had a CW of 134
23 mm. Based on direct observations of gonad maturity, 50% of females were mature at 108 mm
24 CW, whereas 50% of males were mature at 89 mm CW. The size at the onset of maturity
25 measurements of female and male *C. pagurus* based on gonad development is smaller than the
26 current minimum landing size (130 mm), and therefore this suggests that the current
27 minimum landing size is an adequate management measure.

28 **KEYWORDS**

29 *Cancer pagurus*; relative growth; size at maturity; minimum landing size; Isle of Man

30 **Introduction**

31 Crustacean growth is discontinuous and different body parts of males and females often
32 exhibit different growth rates. This phenomenon is commonly known as “relative growth” or
33 “allometric growth” (Hartnoll 1978; Frigotto et al. 2013). In particular, the changes in size of
34 secondary sexual characters (e.g. abdomen, chelipeds) with growth have been used to estimate
35 the size at maturity of aquatic animals (Hartnoll 1974; Farias et al. 2014; Williner et al. 2014).

36 These changes in growth rate of secondary sexual characteristics often occur after what is
37 termed the 'puberty' moult.

38 Age and size at the onset of sexual maturity are commonly used by fisheries managers
39 as biological proxies to establish the appropriate minimum landing size (MLS) of exploited
40 marine species (Bianchini et al. 1998). For the Crustacea, body size is generally used to
41 access maturity data because the determination of age is expensive and time consuming and
42 not particularly accurate (Sheehy & Prior 2008; Murray et al. 2009). Consistent and accurate
43 estimates of size at the onset of maturity (SOM) are needed to determine the appropriate MLS
44 to avoid growth-overfishing and recruitment-overfishing (Ungfors 2007; Pardo et al. 2009).
45 However, some authors have reported that SOM of decapod crustaceans vary both spatially
46 and temporally, depending upon environmental factors (water temperature, depth, habitat) and
47 population density (Tuck et al. 2000; Landers et al. 2001; Lizarraga-Cobedo et al. 2003;
48 Melville-Smith & de Lestang 2006; Zheng 2008). Thus for widely distributed species it is
49 important to have regional measures of SOM that reflect the responses of the animals to local
50 environmental conditions.

51 For crustacean fisheries, the carapace width (or length) at which 50% of the sampled
52 animals are mature is often reported as size at maturity (CW_{50}). In order to determine the
53 SOM in decapod crustaceans, four types of criteria can be applied (Waddy & Aiken 2005;
54 Pardo et al. 2009): (1) physiological sexual maturity; (2) behavioural sexual maturity; (3)
55 morphometrical sexual maturity and (4) functional sexual maturity. Physiological maturity is
56 generally difficult to determine as it is estimated based on microscopic investigation of the
57 gonads or histological observations of ovaries, testes and the vas deferens (Claverie & Smith
58 2009; Pardo et al. 2009). Behavioural maturity can be inferred from the presence of sperm
59 plugs and direct observations of mating behaviour (Tallack 2007; Ungfors 2007; Pardo et al.
60 2009). Morphometric maturity in many decapod species is indicated by positive allometry in

61 characteristics such as chelal length, height and/or width for males and in abdomen width for
62 females (Hartnoll 1974; Zheng 2008). These defined positive allometries in relative growth
63 indicate the passage from the juvenile stage to adulthood and prepares the males for
64 intrasexual competition for mates and carrying eggs in females (Hartnoll 1974; Claverie &
65 Smith 2009). However, morphometric maturity does not always indicate functional maturity
66 (Oh & Hartnoll 1999; Marochi et al. 2013). The presence of eggs externally is evidence of
67 functional maturity in females, however the determination of functional maturity in males is
68 more difficult (McQuaid et al. 2006; Claverie & Smith 2009) and has not been sufficiently or
69 accurately identified to date for many species.

70 *Cancer pagurus* Linnaeus 1758, is commonly known as the brown crab or European
71 edible crab, and is found along the NE Atlantic Coast from Norway to the North Coast of
72 Africa and Mediterranean Sea (Ungfors 2008; FAO 2014). The brown crab is one of the most
73 important commercial fishery species in terms of economic value (nearly £ 31 m in 2011) in
74 the United Kingdom (MMO 2014). The MLS used in brown crab fisheries varies considerably
75 across northern Europe, ranging from 110 mm to 160 mm carapace width (CW) (ICES 2014).
76 Around the Irish Sea, the MLS of both female and male crabs varies between 130 mm and
77 140 mm CW depending on local management regimes (ICES 2014). The present study
78 focused on the Isle of Man (Irish Sea) brown crab fishery, which is primarily a small-scale
79 fishery worth approximately £0.5 M per annum and supports between 20 – 30 fishermen. At
80 present the MLS for brown crab is 130 mm CW in the Isle of Man, but there has been little
81 research to understand whether this is the appropriate size at which to set this limit. The
82 current MLS was identified by reference to other *C. pagurus* populations in the United
83 Kingdom.

84 The first objective of the present study was to estimate the SOM of female and male
85 *C. pagurus* in the Isle of Man by determining sexual dimorphism from allometric

86 relationships and then using morphometric and reproductive characteristics as indicators to
87 identify when crabs begin to become sexually mature. The second objective was to determine
88 the timing of mating and spawning periods to understand better the biology of brown crab in
89 the Isle of Man fishery. Understanding these relationships would help managers understand
90 whether the current MLS is appropriate and to understand in which periods of the year the
91 brown crab population is most vulnerable to potential negative interactions with other
92 fisheries (e.g. the scallop dredge fishery).

93 **Materials and methods**

94 *Data collection*

95 To determine the relative growth and size at maturity of brown crabs, male and female
96 specimens were collected seasonally from commercial baited pots in the Isle of Man from
97 autumn 2012 to spring 2013. Crabs under and over the MLS were collected. Pots tend to
98 under sample small body-sized animals due to the use of escape gaps used in the Isle of Man
99 fishery. In order to supplement the sample of immature specimens more were collected during
100 shore surveys between autumn 2012 and spring 2013. Juvenile crabs (< 74 mm CW) were
101 hand collected from Fleshwick Bay and Niarbyl Bay at extreme low water spring tide line. In
102 addition, ovigerous females rarely enter baited pots because these crabs have reduced feeding
103 activity during this egg-carrying period and the large egg mass on the abdomen also restricts
104 their movement (Bennett & Brown 1983). Therefore, in order to gather trap independent data,
105 crabs were also collected from the otter trawl surveys conducted in autumn 2012 and scallop
106 dredge surveys conducted monthly between November 2012 and May 2013. Subsamples of
107 the catch were brought to the laboratory for further analysis.

108 *Size – wet weight relationships*

109 To determine the relationship between the carapace width (CW) and body wet weight of
110 female and male crabs, the data (n = 2181) was collected during pot surveys on the boat. In
111 order to measure the weight of crabs, a mechanical scale (the nearest 25 g) was used.

112 *Laboratory procedures*

113 *Morphometric measurements*

114 Changes in body morphometry have been shown previously to indicate the onset of maturity
115 in decapod crustaceans (Hartnoll 1974; Farias et al. 2014; Williner et al. 2014), for this
116 reason, cheliped propodus length and abdomen width were measured because these are strong
117 indicators of the presence of allometric growth. In addition, the relationship between carapace
118 width and carapace length was determined because this relationship provides information on
119 allometry. Measurements of the following body parts were recorded using vernier calipers (to
120 the nearest 0.1 mm): carapace width (CW); carapace length (CL); right cheliped propodus
121 length (RChL) and abdomen width (AW).

122 *Size at onset of maturity*

123 In order to understand the timing of mating and spawning seasons, the presence of sperm
124 plugs were noted and extrusion of eggs in the samples collected throughout the year (Tallack
125 2007). Based on microscopic observations of dissected crabs, the ovarian and testes
126 development stages were classified into 5 and 3 classes respectively (Table I).

127 Table I.

128 *Data analysis*

129 The relationships between CW versus CL, CW versus AW and CW versus ChL were
130 compared and the allometric growth defined by the equation $Y = aX^b$. CW was used as

131 predictor variable and other body measurements were selected as the dependent variables
132 (Hartnoll 1978, 1982; Baeza et al. 2012). The allometric growth constant or relative growth
133 rate is given by the constant b. The data were log-transformed to give the formula:

134 $\log y = \log a + b \cdot \log x$ (Hartnoll 1982).

135 If $b > 1$, then positive allometry exists, with the variable growing faster than a standard
136 measure of body size (in this case carapace width). If $b < 1$ then there is a negative allometry,
137 and when $b = 1$ this indicates isometry (Hartnoll 1982).

138 The standard power function $W = a \cdot L^b$ was used in order to determine carapace width
139 (CW) weight relationships for female and male crabs. Where W is total body wet weight (g);
140 L is carapace width (CW) (mm); the a (intercept) and b (slope) are constants (Ricker 1975).
141 The ANCOVA was used to compare size-weight relationships of female and male crabs.

142 In order to calculate the expected size at maturity values of the crabs, the maturity
143 stage data was converted to binary data (immature = 0, mature = 1). Stage 1 was considered
144 immature, whilst all other stages were considered mature. The mature individuals and the
145 immature were proportioned for the each size group. In order to determine the size at maturity
146 of the population (CW_{50}), the the logistic regression equation was used (Perera-García et al.
147 2011):

148 $M = 1/(1 + e^{(S1 - S2 \cdot CW)})$

149 Where M is the accumulated relative frequency of mature individuals, and S1 and S2
150 are the constants and CW_{50} was given by $S1/S2$.

151 In order to calculate the inflection points, data were analysed with “Solver” in MS-
152 Excel (Tokai 1997) and the software of Sigmaplot (version 12.3) was used to draw sigmoid

153 graphs and show inflection points related to the size at maturity. The SPSS (version 22) was
154 used for statistical analyses.

155 **Results**

156 *Relative growth and size at onset of sexual maturity*

157 The CL - CW relationship revealed that negative allometric growth occurred for both males (n
158 = 87) and females (n =222) (Table II; Figure 1a). There was a significant relationship between
159 chela length and CW in both sexes (Table II). Males exhibited stronger allometry with respect
160 to the growth pattern of chela in comparison with females (Table II). Male chelipeds size
161 began to increment more rapidly after a carapace width of 107 mm was achieved (Figure 1b).
162 Female abdomen width became significantly larger at a carapace width of 155 mm (Figure
163 1c).

164 A total of 80 female crabs observed with sperm plugs; ranged in size from 110 to 200
165 mm CW. Sperm plugs were found in the autumn (September, October, and November). Based
166 on these observations, the main mating season was estimated to be the autumn. The observed
167 ovigerous females varied in size from 134 to 215 mm CW (Figure 2a). Based on dredge
168 surveys ovigerous crabs were found from November to end of May. However, the peak
169 occurrence of egg bearing females occurred in November in dredge surveys (Figure 2b). A
170 total of 16 berried females were found in pot surveys in autumn and late winter-early spring.

171 Table II.

172 Figure 1.

173 Figure 2.

174 Based on direct observations of gonad development, the CW_{50} of females was
175 estimated as 108 mm CW, while CW_{50} was determined as 89 mm CW for males (Figure 3).

176 Figure 3.

177 *Size - wet weight relationships*

178 Figure 4 shows the equations of CW-weight relationship for females and males *C. pagurus*;
179 males were significantly heavier in comparison to females of the same size and/or weight
180 (ANCOVA $F_{44, 2067} = 2.03, P < 0.001$).

181 Figure 4.

182 **Discussion**

183 A full understanding of the reproductive ecology, relative growth and size at maturity
184 contribute the determination of MLS and understand whether the necessity of the catch-effort
185 restrictions, a ban of landings of berried crabs, closed seasons and protected areas and play an
186 important role for sustainable fisheries management (Jennings et al. 2001; Mente, 2008).

187 Numerous studies have indicated that the relative growth rate of crustacean body parts
188 can be used to determine the morphological size of maturity, in particular the chelipeds in
189 males and the abdomen width in females (Hartnoll 1974, 1982; Claverie & Smith 2009;
190 Marochi et al. 2013; Williner et al. 2014). In the present study, positive allometry in cheliped
191 length was found in males and females; however this allometry is stronger in males than
192 females. Hartnoll (1974, 1982) suggested that an increase in cheliped length of male
193 specimens of crustaceans occurs after puberty. In the present study, females exhibited positive
194 allometry in abdomen width. Similar findings were recorded for the female *Cancer pagurus*
195 in Scotland (Tallack 2007) and Sweden (Ungfors 2008). Sexual dimorphism in chelipeds in
196 males can be related to the feeding, mate-guarding and fighting (Hartnoll 1969; Lizarraga-

197 Cubedo et al. 2003), while in females wider abdomens can accommodate larger clutch size
198 (Crawford & De Smidt 1922; Baeza et al. 2012).

199 Depending on the technique used, the estimate of SOM was found to be extremely
200 variable. In the present study, with respect to behavioural sexual maturity, the smallest female
201 crab found with sperm plugs was 110 mm CW. In contrast, when the morphometric sexual
202 maturity method was used, the estimated SOM was 155 mm and 107 mm CW for females and
203 males respectively. However, in terms of functional maturity, the smallest ovigerous female
204 crab was 134 mm CW (although it should be noted that this is based on a limited range of
205 observations that are area, season or gear specific). Based on gonad maturity, 50% of females
206 were mature at 108 mm CW, whereas 50% of males were mature at 89 mm CW. The latter
207 figures seem to be reasonably consistent across the U.K. (Haig et al. unpublished data) which
208 may indicate that this is the most reliable method.

209 Geographic variation in SOM has been recorded for many crustacean species
210 (Lizarraga-Cubedo et al. 2003). Similarly, the current study evaluated published observations
211 of the SOM of *C. pagurus* from different regions based on behavioural, functional and
212 morphometric criteria (Supplementary material, Table SI). Across six different sampling
213 regions, based on gonad development, CW_{50} varied between 108 and 139 mm in females,
214 whilst this character varied between 89 and 105 mm in males (Figure 5). Population density,
215 the availability of mates and environmental factors may account for the observed differences
216 in values of crustaceans in different regions (Landers et al. 2001; Lizarraga-Cubedo et al.
217 2003). In particular, water temperature may influence the size at maturity such that maturity
218 occurs at a larger size in warmer waters (Ungfors 2008). For example, Le Foll (1984) reported
219 that based on gonad development the CW_{50} of female *C. pagurus* is 110 mm CW around Bay
220 of Biscay. Earlier maturation results in shorter generation times and higher survival to
221 maturity due to less time spent in the juvenile stage (McQuaid et al. 2006).

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222 There was a significant difference between the CW_{50} of female and male crabs
223 according to pooled data (results of this study and literature) (Figure 5). The sexes generally
224 exhibit different growth rates after the puberty moult as females divert more energy to
225 reproduction than males (Hartnoll 1982, 1985; Abello et al. 1990).

226 Figure 5.

227 Tallack (2007) suggested that more conservative MLS should be estimated based on
228 not only behavioural maturity but also functional maturity; hence, immature individuals will
229 be protected until they reach the size at which they can contribute to the reproductive capacity
230 of the stock. MLS of *C. pagurus* varied from 110 mm to 160 mm carapace width (CW) in
231 different fishing areas (Table III; ICES 2014). Due to the difference in size at maturity of
232 male and female crabs, MLS values of sexes are different for some regions such as Western
233 Channel and Celtic Sea (Table III).

234 Table III.

235 The results from the present study show that both female and male *C. pagurus*
236 specimens are maturing at a smaller size than the current MLS (130 mm) in the Isle of Man,
237 therefore crabs reproduce at least once prior to capture. Though the current MLS (130 mm
238 CW) of brown crab is available in the Isle of Man according to results of this study, the Data
239 Collection Framework (DCF) (European Commission) suggests that SOM data should be
240 collected at least every three years to determine temporal variations.

241

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247 **Disclosure statement**

248 No potential conflict of interest was reported by the authors.

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253 **References**

- 254 Abelló P, Pertierra P, Reid DG. 1990. Sexual size dimorphism, relative growth and
255 handedness in *Liocarcinus depurator* and *Macropipus tuberculatus* (Brachyura:
256 Portunidae). *Scientia Marina* 54:195-202.
- 257 Baeza JA, Anderson JR, Spadaro JA, Behringer DC. 2012. Sexual dimorphism,
258 allometry and size at first maturity of the caribbean king crab, *Mithrax*
259 *spinosissimus*, in the Florida Keys, USA. *Journal of Shellfish Research* 31:909-16.
- 260 Bennett DB, Brown CG. 1983. Crab (*Cancer pagurus*) migrations in the English
261 Channel. *Journal of Marine Biological Association of the United Kingdom* 63:371-
262 98.
- 263 Bianchini M, Di Stefano L, Ragonese S. 1998. Size and age at onset of sexual maturity of
264 female Norway lobster *Nephrops norvegicus* L. (Crustacea: Nephropidae) in the
265 Strait of Sicily (Central Mediterranean Sea). *Scientia Marina* 62:151-9.

- 266 Brown CG, Bennett DB. 1980. Population and catch structure of the edible crab (*Cancer*
267 *pagurus*) in the English Channel. Journal du Conseil International pour
268 l'Exploration de la Mer 39:88-100.
- 269 Claverie T, Smith IP. 2009. Morphological maturity and allometric growth in the squat
270 lobster *Munida rugosa*. Journal of Marine Biological Association of the United
271 Kingdom 89:1189-94.
- 272 Crawford DR, De Smidt WJJ. 1922. The spiny lobster, *Panulirus argus*, of southern
273 Florida: its natural history and utilization. Fishery Bulletin 38:281-310.
- 274 Edwards E. 1979. The edible crab and its fishery in British waters. 1st ed. Surrey,
275 England: Fishing News Books Ltd. 142 pages.
- 276 FAO. 2014. Food and agriculture organization of the United Nations. Available from
277 <<http://www.fao.org/fishery/species/2627/en>> (accessed 22.10.14).
- 278 Farias EN, Luppi T, Spivak ED. 2014. Habitat use, relative growth and size at maturity
279 of the purple stone crab *Platyxanthus crenulatus* (Decapoda: Brachyura), calculated
280 under different models. Scientia Marina 78:567-78.
- 281 Frigotto SF, Marochi MZ, Masunari S. 2013. Relative growth of *Acantholobulus schmitti*
282 (Rathbun, 1930) (Crustacea, Brachyura, Panopeidae) at Guaratuba Bay, southern
283 Brazil. Brazilian Journal of Biology 73:863-70.
- 284 Hartnoll RG. 1969. Mating in the Brachyura. Crustaceana 16:161-81.
- 285 Hartnoll RG. 1974. Variation in Growth Pattern Between Some Secondary Sexual
286 Characters in Crabs (Decapoda Brachyura). Crustaceana 27:131-6.
- 287 Hartnoll RG. 1978. The determination of relative growth in Crustacea. Crustaceana
288 34:281-93.

- 289 Hartnoll RG. 1982. Growth. In: Abele LG, editor. The biology of Crustacea. Volume II.
290 Embryology, morphology and genetics. New York, USA: Academic Press, p 111-
291 96.
- 292 Hartnoll RG. 1985. Growth, sexual maturity and reproductive output. In: Wenner AM,
293 editor. Factors in Adult Growth. 1st ed. Rotterdam, Netherlands: Balkema, p 101-
294 29.
- 295 Hines AH. 1991. Fecundity and reproductive output in nine species of Cancer crabs
296 (Crustacea, Brachyura, Cancridae). Canadian Journal Fisheries and Aquatic
297 Sciences 48:267–75.
- 298 ICES. 2014. Interim Report of the Working Group on the Biology and Life History of
299 Crabs (WGCRAb). 22-24 April 2014; Tromsø, Norway. ICES CM
300 2014/SSGEF:12. 35 pages.
- 301 Jennings S, Kaiser MJ, Reynolds JD. 2001. Marine Fisheries Ecology. Oxford, Blackwell
302 Science Ltd. 432 pages.
- 303 Landers DF, Keser M, Saila SB. 2001. Changes in female lobster (*Homarus americanus*)
304 size at maturity and implications for the lobster resource in Long Island Sound,
305 Connecticut. Marine and Freshwater Research 52:1283-90.
- 306 Le Foll A. 1984. Contribution a l'étude de la biologie du crabe-tourteau *Cancer pagurus*
307 sur les cotes de Bretagne Sud. Revue des Travaux de l'Institut des Pêches
308 Maritimes 48:5-22. (in French)
- 309 Lizarraga-Cubedo HA, Tuck I, Bailey N, Pierce GJ, Kinnear JAM. 2003. Comparisons of
310 size at maturity and fecundity of two Scottish populations of the European lobster,
311 *Homarus gammarus*. Fisheries Research 65:137-52.

- 312 Marochi MZ, Moreto TF, Lacerda MB, Trevisan A, Masunari S. 2013. Sexual maturity
313 and reproductive period of the swimming blue crab *Callinectes danae* Smith, 1869
314 (Brachyura: Portunidae) from Guaratuba Bay, Paraná State, southern Brazil.
315 *Nauplius* 21:43-52.
- 316 McQuaid N, Briggs RP, Roberts D. 2006. Estimation of the size of onset of sexual
317 maturity in *Nephrops norvegicus* (L.). *Fisheries Research* 81:26-36.
- 318 Melville-Smith R, de Lestang S. 2006. Spatial and temporal variation in the size at
319 maturity of the western rock lobster *Panulirus cygnus* George. *Marine Biology*
320 150:183-95.
- 321 Mente E. 2008. Reproductive biology of crustaceans: case studies of decapod
322 crustaceans. Enfield, NH: Science Publishers. 549 pages.
- 323 MMO. 2014. UK Sea Fisheries Statistics 2013. London, England. 178 pages.
- 324 Murray LG, Hinz H, Kaiser MJ. 2009. Marine fisheries research report to DAFF
325 2007/2008. Fisheries & Conservation report No. 7, Bangor University. 60 pages.
- 326 Oh CW, Hartnoll RG. 1999. Size at sexual maturity, reproductive output, and seasonal
327 reproduction of *Philocheirus trispinosus* (Decapoda) in Port Erin Bay, Isle of Man.
328 *Journal of Crustacean Biology* 19:252-9.
- 329 Pardo LM, Fuentes JP, Olguin A, Orensanz JM. 2009. Reproductive maturity in the
330 edible Chilean crab *Cancer edwardsii*, methodological and management
331 considerations. *Journal of Marine Biological Association of the United Kingdom*
332 89:1627-34.

- 333 Pearson J. 1908. Cancer (the edible crab). Liverpool Marine Biology Committee
334 Memoirs, 16, 263 pages.
- 335 Perera-García MA, Mendoza-Carranza M, Contreras-Sanchez WM, Huerta-Ortíz M,
336 Perez-Sanchez E. 2011. Reproductive biology of common snook *Centropomus*
337 *undecimalis* (Perciformes: Centropomidae) in two tropical habitats. Revista de
338 Biología Tropical 59:669-81.
- 339 Ricker WE. 1975. Computation and interpretation of the biological statistics of fish
340 populations. Bulletin of the Fisheries Research Board of Canada 191:1-382.
- 341 Sheehy MRJ, Prior AE. 2008. Progress on an old question for stock assessment of the
342 edible crab *Cancer pagurus*. Marine Ecology Progress Series 353:191-202.
- 343 Smith MT, Lawler A, Laurans M. 2007. Case Study 2 -- Edible crab (*Cancer pagurus*)
344 fisheries in the English Channel/La Manche, Western Approaches, Celtic Sea and
345 Bay of Biscay. Report. 38 pages.
- 346 Tallack SML. 2002. The biology and exploitation of three crab species in the
347 Shetland Islands, Scotland: *Cancer pagurus*, *Necora puber* and *Carcinus maenas*.
348 PhD thesis. The North Atlantic Fisheries College, Shetland, and the University
349 of the Highlands and Islands, Inverness, UK. 390 pages.
- 350 Tallack SML. 2007. The reproductive cycle and size at maturity observed in *Cancer*
351 *pagurus* in the Shetland Islands, Scotland. Journal of Marine Biological
352 Association of the United Kingdom 87:1181-9.
- 353 Tokai T. 1997. Maximum likelihood parameter estimates of a mesh selectivity logistic
354 model through SOLVER on MS-Excel. Bulletin of Japanese Society of Fisheries
355 Oceanography 61:288-98.

- 356 Tuck ID, Atkinson RJA, Chapman CJ. 2000. Population biology of the Norway lobster,
357 *Nephrops norvegicus* (L.) in the Firth of Clyde, Scotland. II. Fecundity and size at
358 onset of sexual maturity. ICES Journal of Marine Science 57:1227-39.
- 359 Tully O, Robinson M, Cosgrove R, O’Keeffe E, Doyle O, Lehane B. 2006. The brown
360 crab (*Cancer pagurus* L.) fishery: analysis of the resource in 2004-2005. Fisheries
361 Resource Series, No. 4. 51pages.
- 362 Ungfors A. 2007. Sexual maturity of the edible crab (*Cancer pagurus*) in the Skagerrak
363 and the Kattegat, based on reproductive and morphometric characters. ICES
364 Journal of Marine Science 64:318-27.
- 365 Ungfors A. 2008. Fisheries biology of the edible crab (*Cancer pagurus*) in the Kattegat
366 and the Skagerrak - implications for sustainable management. PhD thesis,
367 University of Gothenburg, Gothenburg, Sweden. 55 pages + published papers.
- 368 Waddy SL, Aiken DE. 2005. Impact of invalid biological assumptions and
369 misapplication of maturity criteria on size at maturity estimates for American
370 lobster. Transactions of the American Fisheries Society 134:1075-90.
- 371 Williner V, Torres MV, Carvalho DA, König N. 2014. Relative growth and
372 morphological sexual maturity size of the freshwater crab *Trichodactylus*
373 *borellianus* (Crustacea, Decapoda, Trichodactylidae) in the Middle Paraná River,
374 Argentina. ZooKeys 457:159-70.
- 375 Woll A. 2003. In situ observations of ovigerous *Cancer pagurus* Linnaeus, 1758 in
376 Norwegian waters (Brachyura, Cancridae). Crustaceana 76:469-78.

377 Zheng J. 2008. Temporal changes in size at maturity and their implications for fisheries
 378 management for eastern Bering Sea Tanner crab. Journal of the Northwest Atlantic
 379 Fishery Science 41:137-49.

Tables

Table I. Female (1-5) and male (1-3) visually determined gonad development stages for *Cancer pagurus* modified from the literature (Edwards 1979; Ungfors 2008).

| Female | 1 | 2 | 3 | 4 | 5 |
|---------------|--|-----------------------------|---|--|---|
| Description | Immature | Undeveloped | Developing | Mature | Resting / Recovery |
| Stage | No egg cells present | Pre-vitellogenesis | Early secondary vitellogenesis | Late secondary vitellogenesis | Post reproductive |
| Visual | Thin translucent gonad. White and pale | Lobes present, greyish pink | Slight Pink appearance, covering <50% of cavity | Orange, red obvious ovaries. Covers >50% of cavity | Whitish ovary with loose appearance. Easily separable eggs, in pleopodal setae of abdomen |
| Male | 1 | 2 | 3 | | |
| Description | Immature | Developing | Mature | | |
| Stage | Spermatids | Spermatozoa | Spermatophore | | |

| | | | |
|--------|--|-----------------------------|--|
| Visual | Testes small and transparent or undetectable | Testes obvious and white | Testes and vas deferens swollen and white |
|--------|--|-----------------------------|--|

Table II. The summary of the log-transformed regression analyses of the relationships between morphometric parameters (carapace length (CL), right cheliped propodus length (RChL) and abdomen width (AW)) and carapace width (CW) in *Cancer pagurus* using the equation for allometry. The abbreviations are: negatively (- ve), positively (+ ve).

| Variable | Sex | Equation | R^2 | P -value | Allometry |
|------------------------------------|--------|--------------------------------------|-------|------------|-----------|
| $\log y = \log a + b \cdot \log x$ | | | | | |
| CL | Female | $\log CL = -0.163 + 0.977 \log CW$ | 0.99 | < 0.001 | - ve |
| | Male | $\log CL = -0.065 + 0.927 \log CW$ | 0.99 | < 0.001 | - ve |
| RChL | Female | $\log RChL = -0.410 + 1.023 \log CW$ | 0.95 | < 0.001 | + ve |
| | Male | $\log RChL = -0.841 + 1.279 \log CW$ | 0.99 | < 0.001 | + ve |
| AW | Female | $\log AW = -1.712 + 1.531 \log CW$ | 0.97 | < 0.001 | + ve |

Table III. Minimum landing size (MLS) of *Cancer pagurus* in different fishing regions (Source: ICES 2014). CRH: Crab hens (females and small males), CRC: cocks (large males).

| Area | Irish Sea | Central North Sea | Southern North Sea | Eastern Channel | Western Channel | Celtic Sea |
|-----------------------------------|--|---|----------------------|---|--|--|
| Management measure | UK | UK | UK | UK | UK | UK |
| Minimum Landing Size (MLS) | Various/ regional 130 mm – 140 mm (CRH) 130-140 mm (CRC) | 130 mm CW (140 mm North of 56N) | 115 and 130 mm CW | 130 mm in Southern Bight and 140 mm CW | Various/ regional 140 mm – 150 mm (CRH) 140-160 mm (CRC) | Various/ regional 130 mm – 150 mm (CRH) 130- 160 mm (CRC) |

Table III continue. Minimum landing size (MLS) of *Cancer pagurus* in different fishing regions (Source: ICES 2014). CRH: Crab hens (females and small males), CRC: cocks (large males).

| Area | Norway | Scotland | Eastern Channel | Western Channel | Celtic Sea | Bay of Biscay |
|-----------------------------------|--|---------------------------------|-----------------|-----------------|------------|---------------------|
| Management measure | | UK | FR | FR | FR | |
| Minimum Landing Size (MLS) | 110 mm Swedish border-59 30 N, 130 mm Northwards | 130 mm CW (140 mm North of 56N) | 140 mm CW | 140 mm CW | 140 mm CW | 130 mm South of 48° |

Figure legends

Figure 1. A) Morphometric relationship between the carapace width (log-CW) and carapace length (log-CL); B) sexual dimorphism for females and males in the relationship between right cheliped length (log-RCHL) and carapace width (log-CW); C) morphometric relationship between the carapace width (log-CW) and abdomen width (log-AbW) of female specimens of *Cancer pagurus*. The dash dots show inflection points (the values of inflection points based on non-transformed data were showed in the parenthesis).

Figure 2. A) Proportion of the observed ovigerous crabs in size classes; B) Monthly variation in berried crabs catch rate (mean number of berried females captured per 1000 m² swept by scallop dredge).

Figure 3. A) Predicted size at maturity based on ovary development in female *Cancer pagurus* (n = 215); B) Predicted size at maturity based on testes development in male *Cancer pagurus* (n = 82).

Figure 4. The relationship between carapace width (CW) and body wet weight of female (n = 1091) and male (n = 1090) specimens of *Cancer pagurus*.

Figure 5. Male versus female size at maturity, estimated from gonad development and size at 50% maturity for *Cancer pagurus* in different studies. References of studies across Europe: Scotland (Tallack 2007), Skagerrak and Kattegat (Ungfors 2008), Eastern Channel, Western Channel, North Sea (Smith et al. 2007 (Cefas Lawler 2006; unpubl)) and the Isle of Man (Current study).

Supplementary material:

S I. Size at maturity of *Cancer pagurus* in the published literature and current study. Table shows the methods used, sex (females in bold), location and year of study. CW mature is when the smallest mature individual is reported in the range of sampled crabs (and no CW50 was reported).

| Maturity | CW ₅₀ (mm) | CW mature (mm) | Method | Country | Year | n | Sex | Reference |
|--------------------|--------------------------|----------------------|---------------------------|--------------------|------------------|------------|----------|------------------------|
| Behavioural | 106.6 | | Sperm in spermathaeca | Sweden | 2002 | 399 | F | (Ungfors 2008) |
| Behavioural | 118.5 | | Sperm plug present | Sweden | 2002 | 399 | F | (Ungfors 2008) |
| Behavioural | 116 | | Sperm plug present | England | | | F | (Edwards 1979) |
| Behavioural | | 105-211 | Sperm plug present | England | | | F | (Brown & Bennett 1980) |
| Behavioural | 122.9 | | Sperm plug present | Scotland | 1999-2001 | 812 | F | (Tallack 2007) |
| Behavioural | | 110-200 | Sperm plug present | Isle of Man | 2012-2013 | 215 | F | This study |
| Physiological | 127-139 | | Gonad development | SW Ireland | | | F | (Edwards 1979) |
| Physiological | 110 | | Gonad development | Bay of Biscay | | | F | (Le Foll 1984) |

| | | | | | | | | |
|---------------|-----|-------------------|-----------------|--|--|--|---|-------------------------------|
| Physiological | 126 | Gonad development | Eastern Channel | | | | F | *(Cefas Lawler 2006; unpubl.) |
| Physiological | 112 | Gonad development | Western Channel | | | | F | *(Cefas Lawler 2006; unpubl.) |

SI continued. Size at maturity of *Cancer pagurus* in the published literature and current study. Table shows the methods used, sex (females in bold), location and year of study. CW mature is when the smallest mature individual is reported in the range of sampled crabs (and no CW50 was reported).

| Maturity | CW ₅₀ (mm) | CW mature (mm) | Method | Country | Year | n | Sex | Reference |
|----------------------|--------------------------|-------------------|--------------------------|--------------------|------------------|------------|----------|-------------------------------|
| Physiological | 109 | | Gonad development | North Sea | | | F | *(Cefas Lawler 2006; unpubl.) |
| Physiological | 131.8 | | Gonad development | Sweden | 2002 | 399 | F | (Ungfors 2008) |
| Physiological | 133.5 | | Gonad development | Scotland | 1999-2001 | 114 | F | (Tallack 2007) |
| Physiological | 120 | | Gonad development | Ireland | 1998 | | F | (Tully et al. 2006) |
| Physiological | 108 | | Gonad development | Isle of Man | 2012-2013 | 215 | F | This study |
| Physiological | 105 | | Gonad development | Eastern Channel | | | M | *(Cefas Lawler 2006; |

| | | | | | | | | |
|---------------|-------|------|-------------------|-----------------|-----------|-----|---|--|
| Physiological | 90 | | Gonad development | Western Channel | | | M | unpubl.) *Cefas Lawler 2006; unpubl.) |
| Physiological | 89 | | Gonad development | North Sea | | | M | *Cefas Lawler 2006; unpubl.) |
| Physiological | 100.9 | | Gonad development | Sweden | 2002 | 271 | M | (Ungfors 2008) |
| Physiological | | >110 | Gonad development | England | 1961-1966 | | M | (Edwards 1979) |

SI continued. Size at maturity of *Cancer pagurus* in the published literature and current study. Table shows the methods used, sex (females in bold), location and year of study. CW mature is when the smallest mature individual is reported in the range of sampled crabs (and no CW50 was reported). *This unpublished data (Cefas, Lawler 2006; unpubl.) were obtained from Smith et al. 2007.

| Maturity | CW ₅₀ (mm) | CW mature (mm) | Method | Country | Year | n | Sex | Reference |
|----------------------|--------------------------|----------------------|--------------------------|--------------------|------------------|-----------|----------|------------------------|
| Physiological | 104.3 | | Gonad development | Scotland | 1999-2001 | 73 | M | (Tallack 2002, 2007) |
| Physiological | 89 | | Gonad development | Isle of Man | 2012-2013 | 82 | M | This study |
| Functional | | 111 | Ovigerous | France | | | F | (Le Foll 1984) |
| Functional | | 122-159 | Ovigerous | Norway | | | F | (Woll 2003) |
| Functional | | 115 | Ovigerous | England | | | F | (Pearson 1908) |
| Functional | | 133-205 | Ovigerous | England | 1968-1972 | 35 | F | (Brown & Bennett 1980) |
| Functional | | 140-184 | Ovigerous | Scotland | 1985 | | F | (Hines, 1991) |
| Functional | | 118 | Ovigerous | Scotland | 1999- | 1396 | F | (Tallack |

| | | | | | | | | |
|-------------------|-------|----------------|------------------|--------------------|------------------|------------|----------|----------------------|
| | | | | | 2001 | | | 2007) |
| Functional | | 127-216 | Ovigerous | England | 1961-1966 | | F | (Edwards 1979) |
| Functional | 143.7 | 100 | Ovigerous | Scotland | 1999-2001 | 1025 | F | (Tallack 2002, 2007) |
| Functional | | 134-215 | Ovigerous | Isle of Man | 2012-2013 | 108 | F | This study |
| Morphometric | 103.7 | | Abdomen | Sweden | 2002 | 399 | F | (Ungfors 2008) |

S I continued. Size at maturity of *Cancer pagurus* in the published literature and current study. Table shows the methods used, sex (females in bold), location and year of study. CW mature is when the smallest mature individual is reported in the range of sampled crabs (and no CW50 was reported). *This unpublished data (Cefas, Lawler 2006; unpubl.) were obtained from Smith et al. 2007.

| Maturity | CW₅₀ (mm) | CW mature (mm) | Method | Country | Year | n | Sex | Reference |
|---------------------|---------------------------------|-------------------------------|----------------------|--------------------|------------------|------------|------------|-------------------|
| Morphometric | 155 | | Abdomen | Isle of Man | 2012-2013 | 222 | F | This study |
| Morphometric | 115.9 | | Abdomen | Scotland | 1999-2001 | 412 | F | (Tallack 2007) |
| Morphometric | | 110 | Chelae | England | 1961-1966 | | M | (Edwards 1979) |
| Morphometric | 101.6-109.5 | | Chelae | Scotland | 1999-2001 | 402 | M | (Tallack 2007) |
| Morphometric | 107 | | Chelae length | Isle of Man | 2012-2013 | 87 | M | This study |
| Morphometric | 147.3 | | Pleopod | Scotland | 1999-2001 | 131 | F | (Tallack 2007) |
| Morphometric | 119.5 | | Chelae width | Sweden | 2002 | 271 | M | (Ungfors 2008) |
| Morphometric | 122.3 | | Chelae height | Sweden | 2002 | 271 | M | (Ungfors 2008) |

| | | | | | | | |
|--------------|-------|--------------|--------|------|-----|---|-------------------|
| Morphometric | 122.5 | Chelae depth | Sweden | 2002 | 271 | M | (Ungfors 2008) |
|--------------|-------|--------------|--------|------|-----|---|-------------------|
