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

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

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

KEYWORDS

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

Introduction

Crustacean growth is discontinuous and different body parts of males and females often exhibit different growth rates. This phenomenon is commonly known as “relative growth” or “allometric growth” (Hartnoll 1978; Frigotto et al. 2013). In particular, the changes in size of secondary sexual characters (e.g. abdomen, chelipeds) with growth have been used to estimate the size at maturity of aquatic animals (Hartnoll 1974; Farias et al. 2014; Williner et al. 2014).
These changes in growth rate of secondary sexual characteristics often occur after what is termed the ‘puberty’ moult.

Age and size at the onset of sexual maturity are commonly used by fisheries managers as biological proxies to establish the appropriate minimum landing size (MLS) of exploited marine species (Bianchini et al. 1998). For the Crustacea, body size is generally used to access maturity data because the determination of age is expensive and time consuming and not particularly accurate (Sheehy & Prior 2008; Murray et al. 2009). Consistent and accurate estimates of size at the onset of maturity (SOM) are needed to determine the appropriate MLS to avoid growth-overfishing and recruitment-overfishing (Ungfors 2007; Pardo et al. 2009).

However, some authors have reported that SOM of decapod crustaceans vary both spatially and temporally, depending upon environmental factors (water temperature, depth, habitat) and population density (Tuck et al. 2000; Landers et al. 2001; Lizarraga-Cobedo et al. 2003; Melville-Smith & de Lestang 2006; Zheng 2008). Thus for widely distributed species it is important to have regional measures of SOM that reflect the responses of the animals to local environmental conditions.

For crustacean fisheries, the carapace width (or length) at which 50% of the sampled animals are mature is often reported as size at maturity (CW₅₀). In order to determine the SOM in decapod crustaceans, four types of criteria can be applied (Waddy & Aiken 2005; Pardo et al. 2009): (1) physiological sexual maturity; (2) behavioural sexual maturity; (3) morphometrical sexual maturity and (4) functional sexual maturity. Physiological maturity is generally difficult to determine as it is estimated based on microscopic investigation of the gonads or histological observations of ovaries, testes and the vas deferens (Claverie & Smith 2009; Pardo et al. 2009). Behavioural maturity can be inferred from the presence of sperm plugs and direct observations of mating behaviour (Tallack 2007; Ungfors 2007; Pardo et al. 2009). Morphometric maturity in many decapod species is indicated by positive allometry in
characteristics such as chelal length, height and/or width for males and in abdomen width for females (Hartnoll 1974; Zheng 2008). These defined positive allometries in relative growth indicate the passage from the juvenile stage to adulthood and prepares the males for intrasexual competition for mates and carrying eggs in females (Hartnoll 1974; Claverie & Smith 2009). However, morphometric maturity does not always indicate functional maturity (Oh & Hartnoll 1999; Marochi et al. 2013). The presence of eggs externally is evidence of functional maturity in females, however the determination of functional maturity in males is more difficult (McQuaid et al. 2006; Claverie & Smith 2009) and has not been sufficiently or accurately identified to date for many species.

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

The first objective of the present study was to estimate the SOM of female and male * C. pagurus * in the Isle of Man by determining sexual dimorphism from allometric
relationships and then using morphometric and reproductive characteristics as indicators to identify when crabs begin to become sexually mature. The second objective was to determine the timing of mating and spawning periods to understand better the biology of brown crab in the Isle of Man fishery. Understanding these relationships would help managers understand whether the current MLS is appropriate and to understand in which periods of the year the brown crab population is most vulnerable to potential negative interactions with other fisheries (e.g. the scallop dredge fishery).

**Materials and methods**

**Data collection**

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

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

**Laboratory procedures**

**Morphometric measurements**

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

**Size at onset of maturity**

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

<table>
<thead>
<tr>
<th>Table I</th>
</tr>
</thead>
</table>

**Data analysis**

The relationships between CW versus CL, CW versus AW and CW versus ChL were compared and the allometric growth defined by the equation $Y = aX^b$. CW was used as
predictor variable and other body measurements were selected as the dependent variables (Hartnoll 1978, 1982; Baeza et al. 2012). The allometric growth constant or relative growth rate is given by the constant b. The data were log-transformed to give the formula:

$$\log y = \log a + b \log x \text{ (Hartnoll 1982).}$$

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

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

The ANCOVA was used to compare size-weight relationships of female and male crabs.

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

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

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

In order to calculate the inflection points, data were analysed with “Solver” in MS-Excel (Tokai 1997) and the software of Sigmaplot (version 12.3) was used to draw sigmoid
graphs and show inflection points related to the size at maturity. The SPSS (version 22) was used for statistical analyses.

Results

Relative growth and size at onset of sexual maturity

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

A total of 80 female crabs observed with sperm plugs; ranged in size from 110 to 200 mm CW. Sperm plugs were found in the autumn (September, October, and November). Based on these observations, the main mating season was estimated to be the autumn. The observed ovigerous females varied in size from 134 to 215 mm CW (Figure 2a). Based on dredge surveys ovigerous crabs were found from November to end of May. However, the peak occurrence of egg bearing females occurred in November in dredge surveys (Figure 2b). A total of 16 berried females were found in pot surveys in autumn and late winter-early spring.
Based on direct observations of gonad development, the CW50 of females was estimated as 108 mm CW, while CW50 was determined as 89 mm CW for males (Figure 3).

Figure 3.

**Size - wet weight relationships**

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

Figure 4.

**Discussion**

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

Numerous studies have indicated that the relative growth rate of crustacean body parts can be used to determine the morphological size of maturity, in particular the chelipeds in males and the abdomen width in females (Hartnoll 1974, 1982; Claverie & Smith 2009; Marochi et al. 2013; Williner et al. 2014). In the present study, positive allometry in cheliped length was found in males and females; however this allometry is stronger in males than females. Hartnoll (1974, 1982) suggested that an increase in cheliped length of male specimens of crustaceans occurs after puberty. In the present study, females exhibited positive allometry in abdomen width. Similar findings were recorded for the female *Cancer pagurus* in Scotland (Tallack 2007) and Sweden (Ungfors 2008). Sexual dimorphism in chelipeds in males can be related to the feeding, mate-guarding and fighting (Hartnoll 1969; Lizarraga-
Cubedo et al. 2003), while in females wider abdomens can accommodate larger clutch size (Crawford & De Smidt 1922; Baeza et al. 2012).

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

Geographic variation in SOM has been recorded for many crustacean species (Lizarraga-Cubedo et al. 2003). Similarly, the current study evaluated published observations of the SOM of *C. pagurus* from different regions based on behavioural, functional and morphometric criteria (Supplementary material, Table SI). Across six different sampling regions, based on gonad development, CW50 varied between 108 and 139 mm in females, whilst this character varied between 89 and 105 mm in males (Figure 5). Population density, the availability of mates and environmental factors may account for the observed differences in values of crustaceans in different regions (Landers et al. 2001; Lizarraga-Cubedo et al. 2003). In particular, water temperature may influence the size at maturity such that maturity occurs at a larger size in warmer waters (Ungfors 2008). For example, Le Foll (1984) reported that based on gonad development the CW50 of female *C. pagurus* is 110 mm CW around Bay of Biscay. Earlier maturation results in shorter generation times and higher survival to maturity due to less time spent in the juvenile stage (McQuaid et al. 2006).
There was a significant difference between the $CW_{50}$ of female and male crabs according to pooled data (results of this study and literature) (Figure 5). The sexes generally exhibit different growth rates after the puberty moult as females divert more energy to reproduction than males (Hartnoll 1982, 1985; Abello et al. 1990).

Figure 5.

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

Table III.

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

Acknowledgements

We are grateful to Manx crab and scallop fishermen for making the study possible. We gratefully acknowledge Dr. Richard Hartnoll, Prof. Lewis LeVay and Dr. Luis Gimenez for
their suggestions related to the data analyses. The comments of anonymous reviews improved an earlier version of this manuscript.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

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**References**


Farias EN, Luppi T, Spivak ED. 2014. Habitat use, relative growth and size at maturity of the purple stone crab Platyxanthus crenulatus (Decapoda: Brachyura), calculated under different models. Scientia Marina 78:567-78.


**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).

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

<table>
<thead>
<tr>
<th>Male</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Description</strong></td>
<td><strong>Immature</strong></td>
<td><strong>Developing</strong></td>
<td><strong>Mature</strong></td>
</tr>
<tr>
<td>Stage</td>
<td>Spermatids</td>
<td>Spermatozoa</td>
<td>Spermatophore</td>
</tr>
</tbody>
</table>
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).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Sex</th>
<th>Equation</th>
<th>$R^2$</th>
<th>P-value</th>
<th>Allometry</th>
</tr>
</thead>
<tbody>
<tr>
<td>CL</td>
<td>Female</td>
<td>logCL = -0.163 + 0.977 logCW</td>
<td>0.99</td>
<td>&lt; 0.001</td>
<td>- ve</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>logCL = -0.065 + 0.927 logCW</td>
<td>0.99</td>
<td>&lt; 0.001</td>
<td>- ve</td>
</tr>
<tr>
<td>RChL</td>
<td>Female</td>
<td>logRChL = -0.410 + 1.023 logCW</td>
<td>0.95</td>
<td>&lt; 0.001</td>
<td>+ ve</td>
</tr>
<tr>
<td></td>
<td>Male</td>
<td>logRChL = -0.841 + 1.279 logCW</td>
<td>0.99</td>
<td>&lt; 0.001</td>
<td>+ ve</td>
</tr>
<tr>
<td>AW</td>
<td>Female</td>
<td>logAW = -1.712 + 1.531 logCW</td>
<td>0.97</td>
<td>&lt; 0.001</td>
<td>+ ve</td>
</tr>
</tbody>
</table>
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).

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

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).
<table>
<thead>
<tr>
<th>Area</th>
<th>Norway</th>
<th>Scotland</th>
<th>Eastern Channel</th>
<th>Western Channel</th>
<th>Celtic Sea</th>
<th>Bay of Biscay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Management measure</td>
<td>UK</td>
<td>FR</td>
<td>FR</td>
<td>FR</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Minimum Landing Size (MLS)</td>
<td>110 mm Swedish border-59 30 N, 130 mm Northwards</td>
<td>130 mm CW</td>
<td>140 mm CW</td>
<td>140 mm CW</td>
<td>130 mm South of 48°</td>
<td></td>
</tr>
</tbody>
</table>

**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).

<table>
<thead>
<tr>
<th>Maturity</th>
<th>CW50 (mm)</th>
<th>CW mature (mm)</th>
<th>Method</th>
<th>Country</th>
<th>Year</th>
<th>n</th>
<th>Sex</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Behavioural</td>
<td>106.6</td>
<td></td>
<td>Sperm in spermatoeca</td>
<td>Sweden</td>
<td>2002</td>
<td>399</td>
<td>F</td>
<td>(Ungfors 2008)</td>
</tr>
<tr>
<td>Behavioural</td>
<td>118.5</td>
<td></td>
<td>Sperm plug present</td>
<td>Sweden</td>
<td>2002</td>
<td>399</td>
<td>F</td>
<td>(Ungfors 2008)</td>
</tr>
<tr>
<td>Behavioural</td>
<td>116</td>
<td></td>
<td>Sperm plug present</td>
<td>England</td>
<td></td>
<td></td>
<td>F</td>
<td>(Edwards 1979)</td>
</tr>
<tr>
<td>Behavioural</td>
<td>105-211</td>
<td></td>
<td>Sperm plug present</td>
<td>England</td>
<td></td>
<td></td>
<td>F</td>
<td>(Brown &amp; Bennett 1980)</td>
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<tr>
<td>Behavioural</td>
<td>122.9</td>
<td></td>
<td>Sperm plug present</td>
<td>Scotland</td>
<td>1999-2001</td>
<td>812</td>
<td>F</td>
<td>(Tallack 2007)</td>
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<tr>
<td>Behavioural</td>
<td>110-200</td>
<td></td>
<td>Sperm plug present</td>
<td>Isle of Man</td>
<td>2012-2013</td>
<td>215</td>
<td>F</td>
<td>This study</td>
</tr>
<tr>
<td>Physiological</td>
<td>127-139</td>
<td></td>
<td>Gonad development</td>
<td>SW Ireland</td>
<td></td>
<td></td>
<td>F</td>
<td>(Edwards 1979)</td>
</tr>
<tr>
<td>Physiological</td>
<td>110</td>
<td></td>
<td>Gonad development</td>
<td>Bay of Biscay</td>
<td></td>
<td></td>
<td>F</td>
<td>(Le Foll 1984)</td>
</tr>
</tbody>
</table>
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).

<table>
<thead>
<tr>
<th>Maturity</th>
<th>CW50 (mm)</th>
<th>CW mature (mm)</th>
<th>Method</th>
<th>Country</th>
<th>Year</th>
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### S1 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.*

<table>
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<th>Maturity</th>
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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.

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