Sexual maturity of the edible crab (*Cancer pagurus*) in the Skagerrak and the Kattegat, based on reproductive and morphometric characters

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The size at the onset of sexual maturity of female and male edible crab (*Cancer pagurus*) from the Skagerrak and the Kattegat and the fecundity of females were estimated. Physiological maturity of females, i.e. ovary development, was at a larger size than behavioural maturity (indications of successful copulation). The carapace width (CW) at which 50% of females were mature (CW50), based on development of the gonads, was 132 mm, sperm presence gave a CW50 of 107 mm, and the presence of sperm plugs a CW50 of 118 mm. Changes in relative abdominal width were found at approximately 100 and 130 mm, and CW50 was 104 mm. A smaller fraction (25%) of the females is functionally mature at sizes < 140 mm. However, male physiological and functional maturity was more synchronized: CW50s based on advanced sperm production and allometric changes in the chelae were within 5 mm (117–122 mm). Size-specific fecundity increases with CW (0.5–2.5 million eggs). Recommendations for a minimum landing size (MLS) of 140 mm CW for females and males will reduce future potential landings more in the Skagerrak than in the Kattegat.

**Keywords:** allometry, Cancridae, fecundity, gonad development, management, minimum landing size, size at maturity.

Received 23 May 2005; accepted 24 November 2006; advance access publication 16 January 2007.

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**Introduction**

To avoid recruitment-overfishing of brachyurans, recruits to the fishery should be able to reproduce at least once. To meet this requirement, management actions can restrict the size of landed crabs by minimum landing size (MLS), by restrictions on the gear deployed, or by a one-sex harvesting strategy. Additional regulations can protect the pre-recruits and recruits at vulnerable stages of their life, e.g. by decreasing handling mortality during moulting periods by seasonal closures (Hankin et al., 1997; Siddeek et al., 2004). The size at the onset of sexual maturity (SOM) needs to be considered in the implementing process of a MLS, and signs of mating activities, gonad development, or allometric changes in growth of the body parts have been used to discriminate between juveniles and adult Brachyura, e.g. Cancridae (Weymouth and MacKay, 1936; Edwards, 1979; Brown and Bennett, 1980; Campbell and Eagles, 1983; Orensanz and Gallucci, 1988; Orensanz et al., 1995; Hankin et al., 1997; Pinho et al., 2001), Portunidae (González-Gurriarán and Freire, 1994; Muino et al., 1999; de Lestang et al., 2003; Hall et al., 2006), Majidae (Alunno-Bruscia and Sainte-Marie, 1998; Sampedro et al., 1999), and Xanthidae (Flores and Paula, 2002). Stock assessment can use egg production (S) of mature individuals and stock-recruitment relationships of commercial species (Addison and Bennett, 1992), so for management purposes the relationship between size and egg production (fecundity) is important.

The edible crab (*Cancer pagurus*) is distributed along the Northeast Atlantic coast (Christiansen, 1969); in Swedish waters, it is limited to the Skagerrak and the Kattegat, where there is a small commercial fishery. The total landings in 2005 in Europe were 46 280 t, most in the UK, Ireland, and France. In 2002, the Swedish landings in fisheries targeting crabs were 105 t, 57% of the total taken by crab pots, and of this, 68% (57 t) was caught by boats < 10 m (ICES, 2003). In Sweden, the main landing season is July–November. In most parts of its distribution a MLS is implemented, either of national (UK, Addison and Bennett, 1992; Norway, J-102-2004) or international status (Anon., 1998). However, the crab fishery in Swedish waters in the Skagerrak and Kattegat is not regulated by implementation of a MLS, but by obligatory 75 mm escape gaps in pots fished shallower than 30 m and in fykenets fished deeper than 10 m (Anon., 1998, 2004a). These escape gaps allow crabs of carapace width (CW) < 110–120 mm to escape (Dybern, 1983). In the northern part of Skagerrak, from the Swedish border to the Norwegian southwest coast (Rogaland), the commercial landing of crabs < 110 mm is prohibited (Anon., 2004b).

The aim of this study is to investigate whether the current management actions in the Skagerrak and the Kattegat preclude recruitment-overfishing. The SOM is defined as the CW at which 50% of the population is mature, and both physiological and functional sexual maturity are considered by evaluating the gonad development in both sexes, the presence of sperm plugs and filled spermathecae in females, and by measuring male chelae and female abdomens. I did not sample ovigerous females for maturity because of their low catchability (Howard, 1982).
However, I did conduct fecundity analyses, so that they can be considered in the process of MLS recommendation and in stock modelling. In addition, I experimentally evaluated the potential for crabs to escape from creels with gaps of different diameter and forecast the potential commercial landings under an MLS based on the SOM.

**Material and methods**

**Sampling and classification**

From July to December of 2001 and 2002, edible crabs of both sex were collected from fishing vessels (potters) operating in the archipelagos along the Swedish Skagerrak coast and on coastal and offshore banks in the Kattegat (Figure 1). Subsamples of the catch were brought to the laboratory. As reproduction of *Cancer* spp. has a temporal component (Charniaux-Cotton and Payen, 1988; Shields, 1991) females for ovary classification were sampled from September to December, when a large proportion of *Cancer pagurus* females have ripe or ripening ovaries (Edwards, 1979). Ovaries were classified as immature (previtellogenesis), undeveloped (primary vitellogenesis), developing (early secondary vitellogenesis), ripe/mature (late secondary vitellogenesis), or resting (primary vitellogenesis, loose appearance), and testes were classified as immature (no visual indication of, or just tiny 5 mm coiled, testes), developing (production of spermatozoa has started, testes and vas deferens are thin but partly filled), or mature (vas deferens is extended and filled by a white mass of spermatophores). Observations were made on the presence of spermatophores in the spermathecae and the presence of sperm plugs in the oviducts of early post-moult females. CW, female fifth abdominal segment at the broadest part (AW), and the length, height, and width of the male right propodus (RPL, RPH, and RPW, respectively) (Figure 2) were measured to the nearest millimetre. If the right chela was missing or regenerating, the left propodus was used (a pairwise *t*-test showed no significant difference between right and left measurements of RPL, RPH, or RPW; *p* = 0.07–0.41, *n* = 34). Moult stage was determined according to four classes: (i) crabs at early post-moult, having a soft carapace, a whitish appearance and sharp toe tips; (ii) crabs with indications of recent moulting, i.e. a clean appearance but not fully hardened shell (late post-moult); (iii) inter-moult crabs had some fouling organisms, worn toe tips, and a presumed high meat yield; (iv) crabs with shell necrosis and many fouling organisms were classified as degrading. This classification is not based on Drach’s (1939) setal definition of moult stage (A–D₄), but rather on a modification of macroscopic characters, e.g. as used by Edwards (1979).

**Analysis of size at sexual maturity**

SOM was estimated by fitting the percentage of mature crabs per 5 mm size interval to the logistic equation Proportion mature = 1/(1 + Ae^(-BCW)) by non-linear least squares regression (Somerton, 1980). The CW at which 50% of crabs are mature (CW₅₀), i.e. the mature proportion *P* = 0.5, is calculated as CW₅₀ = −log A B⁻¹. Females were defined as mature if the ovary was in a developing or mature stage during autumn, or if there were indications of mating (e.g. the presence of sperm in spermathecae or a sperm plug in early post-moult females). For males, two alternative scenarios for gonad classification were applied in the calculations: gonads classified as developing were defined either as immature (scenario 1) or as mature (scenario 2), because there were definition difficulties with this stage. Chi-squared tests were used to analyse differences in the mature proportion of inter-moult and post-moult females and males and the mature proportion of females in autumn and summer. The allometric relationship between size (CW) and organ dimension (AW, RPL, RPH, and RPW) was analysed in three ways: (i) a one- or two-phase model (Gaertner and Laloe, 1986), (ii) minimum sum of squared residuals (SSR) in the transition zone (Lovett and Felder, 1989), and (iii) iterative assignment of adolescent individuals (Somerton, 1980). Data were divided into two data sets, juveniles or adults, on an *a priori* basis. For (i), the lower *a priori* limit for

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**Figure 1.** Sampling areas for the edible crab *Cancer pagurus* for analyses of SOM (black circles) and for ovigerous females for fecundity analyses (crosses).

**Figure 2.** Claw of the edible crab (*Cancer pagurus*) and morphometric measurements. RPL is the right propodus length, and RPH is the right propodus height. The right propodus width (RPW) is not shown but is measured at the widest part of propodus. Modified from an illustration by H. Samuelsson, Göteborg University, Sweden.
female adults (LA) was set to 150 mm because 75% of large females have developed or resting ovaries (this study). Further, three limits for juveniles (LJ) were used, namely <104 mm (100% immature), <109 mm (75% immature), and 124 mm (75% undeveloped). Most males >110 mm CW are mature in the UK (Edwards, 1979), so an a priori higher LJ males was set at 109 mm, and for adults at ≥110 mm. A priori limits for (ii) and (iii) are provided graphically.

Ovigerous females for fecundity analyses were collected in April and May 2002. Samples (n = 29) were collected as bycatch in nets deployed for lumpfish (Cyclopterus lumpus) west of Måseskär (58°04′N 11°18′E) at depths of 40–50 m, or in crab creels at Kummel Bank (57°28′N 11°23′E) (n = 10) in the Kattegat (Figure 1). After fixation for 1 month in Davidson solution (Lightner, 1996), the egg mass was washed in water, separated from pleopods, and dried to constant weight at 60°C. A sample (n = 10 per crab) of fixed but not dried eggs was measured for oocyte diameter (µm). Three subsamples of 2–10 mg (0.1 mg accuracy) of approximately 200–650 eggs were chosen randomly for exact enumeration and calculating egg weight per subsample. The whole crab was dried to constant weight in four main pieces, and the total body weight was recorded. The weight of the missing claw (or claws) was calculated from the regression equation

\[ y = 0.342x - 31.23 \]  

\[ (n = 39, r^2 = 0.86, p < 0.0001; \text{model with best fit of data}) \]

where \( y \) is the dry weight per claw and \( x \) is the CW. Losses of walking legs were considered by additions of a mean walking leg weight or by the regression equation

\[ y = 0.4886x - 43.5 \]  

\[ (n = 35, r^2 = 0.91, p < 0.0001) \]

where \( y \) is the dry weight of four pairs of walking legs and \( x \) is again the CW. Fecundity (the number of fertilized eggs per crab) was calculated by dividing the total dry weight of the egg by the mean weight of each egg (the standard deviation was calculated by triplicates of egg weight). Relative fecundity was calculated as a proportion of the dry weight of eggs and body. Fecundity and relative fecundity were analysed statistically by linear regression (untransformed and logged data) and by testing the curve fit to logarithmic, quadratic, power, exponential, and logistic relationships, respectively (using the computer program SPSS), with CW used as a measure of body size. The relation between oocyte diameter and the number of eggs per batch and with CW was tested by linear regression.

A manipulative laboratory experiment was set up in October 2005 to determine how the diameter of the escape gap in creels affects the size of potential escapers. Four escape gap sizes (75, 80, 85, and 90 mm) were tested against six different size classes of crabs (115–119, 120–124, 125–129, 130–134, 135–139, and 140–144 mm CW). Four females and four males per size class were arranged within a creel placed in a tank (9 × 1 × 0.7 m) with circulating water (11–13°C, salinity 33). Three creels per tank were used (in separate compartments), and bait (fish) was hung on the outside of the creel. Over 10 d, all possible combinations were tested twice, in random order and with eight creels per night. The proportion of escapes per size class and escape gap was calculated.

The future Swedish edible crab landing potential if a MLS is implemented from the SOM results of this study was estimated. Five alternative values of MLS were simulated for females (the four calculated CW50s plus one precautionary), and five alternative values of MLS for males (the three CW50s plus two precautionary). The percentage of the landing potential compared with recent capture (%, numbers of crabs) without implementation of a MLS but an escape gap of 75 mm was calculated for females and males, respectively, on the assumption of MLS being knife-edged, and from data on the sex-specific size frequency in commercial catches. The data on crab size composition in commercial catches were gathered at different sites along the Swedish coast between 1999 and 2003: (i) females in the Skagerrak (Strömstad, n = 4112; Fjällbacka, n = 1842; Lysekil, n = 363) and the Kattegat (offshore Groves Bank, n = 2259; inshore Varberg, n = 465) and (ii) males in the Skagerrak (Strömstad, n = 1743; Fjällbacka, n = 1642; Lysekil, n = 705) and the Kattegat (offshore Groves Bank, n = 710) (Figure 1).

Results
The proportion of females with a developed ovary (developing or mature) was 41% during summer and 64% during autumn (\( \chi^2 = 47.1, p \ll 0.001, n = 920 \)) (Figure 3). The ovaries of 30–50% of females of intermediate size (124–149 mm CW) were in a resting stage in summer, compared with <25% in autumn. In autumn, most females of intermediate size were in an undeveloped stage, but irrespective of season, larger females (≥150 mm CW) were generally classified as mature. Most crabs in CW classes ≤124 mm were immature and undeveloped. During autumn, the proportion of females with developing or mature ovaries was

![Figure 3. Ovary stages during (a) the summer months June–August (n = 521), and (b) the gonad development period September–December (n = 399) of crabs in 5 mm CW intervals (endpoint of interval shown). The data are based on inter- and post-moulting crabs.](https://academic.oup.com/icesjms/article-abstract/64/2/318/2182562 by guest on 19 February 2019)
higher for inter-moult (80%) than for post-moult females (51%) ($\chi^2 = 35.1, p \ll 0.001, n = 399$).

The proportion of mature females based on the reproductive characters, ovary development, spermathecae, and sperm plug presence increased with CW (Figure 4). CW$_{50}$ is 132, 107, and 118 mm, respectively (logistic regression, Table 1). The general patterns of gonad development for inter-moult and post-moult males were similar (Figure 5a, b), but post-moult males were more often classified as immature or developing (52%) than inter-moult males (26%) ($\chi^2 = 44.4, p \ll 0.001, n = 631$). The proportion of mature males based on gonad development per 5 mm CW size class increased with CW (Figure 5c). CW$_{50}$ was 117 mm if a developing gonad was considered immature, and 101 mm if it was considered mature (Figure 5c, Table 1).

A two-phase regression model fitted the allometric data better than a one-phase model for both sexes: the SSR for linear regression of the two-phase model was lower than for a one-phase regression of juveniles and adult data combined (Table 2). The total SSR on allometric data of female AW showed a minimum at 95–104 mm CW and a second minimum at 125–139 mm CW (Figure 6a). Minimum total SSR was at 125–129 mm CW for male length propodus (RPL), and at 119–124 mm CW for male height propodus (RPH) (Figure 7, inset).

The CW$_{50}$ based on morphometric data was 104 mm for females (Figure 6b, Table 1) and 122, 122, and 120 mm for male RPL, RPH, and RPW, respectively (Figure 7, Table 1). Dividing data into juvenile and adult groups based on an iterative process fitted the linear regression better than the pooled data set (AW $F = 529.9, p \ll 0.05$; RPL $F = 306, p \ll 0.05$; RPH $F = 515.8, p \ll 0.05$; RPW $F = 464.8, p \ll 0.05$). The growth coefficient of adult female AW decreased, whereas the juvenile and the male chela (RPL, RPH, and RPW) showed greater positive allometry during adult growth (Table 1, coefficient B). The 95% confidence interval did not overlap between juvenile and adult phases for either variable (Table 3).

Fecundity, measured as the number of fertilized eggs, increased with female CW (linear regression $r^2 = 0.68$, and log-log linear regression $r^2 = 0.71, p < 0.000, n = 39$; Figure 8a) in the size

![Figure 4](https://academic.oup.com/icesjms/article-abstract/64/2/318/2182562/16422818252) by guest on 16 February 2019

Table 1. Regression ($\log Y = \log A + B \log CW$) summary of the iterative assignment of morphometric data, where Y is abdomen width (AW); RPL, RPH, or RPW (log A1 and B1 = juvenile phase; log A2 and B2 = adult phase) of edible crab.

<table>
<thead>
<tr>
<th>Sex and morphometry</th>
<th>Log A1 constant</th>
<th>B1 coefficient</th>
<th>Log A2 constant</th>
<th>B2 coefficient</th>
<th>Log A constant</th>
<th>B coefficient</th>
<th>CW$_{50}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abdomen</td>
<td>−1.8864</td>
<td>1.5986</td>
<td>−1.4619</td>
<td>1.4152</td>
<td>−24.2413</td>
<td>0.2337</td>
<td>103.7</td>
</tr>
<tr>
<td>Spermatheca</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−19.034</td>
<td>0.1785</td>
<td>106.6</td>
</tr>
<tr>
<td>Sperm plug</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−3.0957</td>
<td>0.0261</td>
<td>118.5</td>
</tr>
<tr>
<td>Ovary</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−17.002</td>
<td>0.1289</td>
<td>131.8</td>
</tr>
</tbody>
</table>

| **Males**           |                 |                |                 |                |                |               |           |
| RPL                 | −1.280           | 1.276           | −1.9649         | 1.6033         | −8.0619        | 0.0666        | 122.5     |
| RPH                 | −1.306           | 1.304           | −1.577          | 1.454          | −7.7268        | 0.0632        | 122.3     |
| RPW                 | −1.245           | 1.185           | −1.588          | 1.357          | −7.1330        | 0.0597        | 119.5     |
| Scenario (i)        | −                 | −               | −                | −              | −7.6669        | 0.0655        | 117.0     |
| Scenario (ii)       | −                 | −               | −                | −              | −14.809        | 0.1468        | 100.9     |

The adult proportion of morphometric and reproductive data is fitted by non-linear least squares to the logistic equation: Proportion mature = $1/(1 + A e^{(B/CW)_{50}})$, and the coefficients $A$ and $B$ are given. CW$_{50}$ is calculated from these coefficients ($-\log A/B$). Two scenarios of maturity stage of male gonad are considered: (i) developing gonad treated as immature and (ii) developing gonad treated as mature. The iterative process fitted data in the CW range 100–149 mm for females and 94–149 mm for males to the juvenile or the adult phase. The method is based on that of Somerton (1980).
range 113–190 mm CW. At that size range, fecundity was between 0.5 and 2.5 million eggs. Relative fecundity, calculated as the relationship between number of eggs and body weight, was independent of CW (linear regression, \( p = 0.39 \)) and fitted poorly to other models (\( r^2 = 0.02 - 0.07, \ p > 0.07 \)) (Figure 8b). The relationship between dry weight of the egg mass and body weight ranged between 5 and 28% (average 13%, s.d. ±5%). Egg diameter (\( \mu \text{m} \)) was independent of the number of eggs per batch (linear regression, \( p = 0.197, r^2 = 0.044, n = 39 \)) (Figure 8c) or female CW (linear regression, \( p = 0.278, r^2 = 0.032, n = 39 \)). The mean oocyte diameter averaged over subsamples and crabs was 383 \( \mu \text{m} \) (s.d. ±20). The ovaries of all ovigerous females were macroscopically classified as resting; a greyish loose appearance of small ovaries in primary vitellogenesis. Only one ovigerous female showed signs on the carapace of recent molting, i.e. it was relatively soft and whitish; the rest had a hard carapace with fouling organisms. The smallest ovigerous female (113 mm) had no sperm in the spermathecae, as did all other ovigerous females.

Escapements from creels with different gap sizes are shown in Table 4. The proportion of escapement of different size classes indicate that a 90 mm gap is required to allow escapement of the larger crabs in the experiment (135 – 144 mm CW).

**Discussion**

**Size at onset of sexual maturity**

SOM of female edible crab in the Skagerrak and the Kattegat is in accord with the results of maturity studies on the species in other European areas. Sperm plugs are observed in the gonadopore from 100 mm CW (this study) and larger in several areas (105 – 211 mm CW in the English Channel, Brown and Bennett, 1980; > 107 mm Yorkshire data, Edwards, 1979), and CW50 based on sperm plug presence is close to our 118 mm (116 mm CW East Coast England, Edwards, 1979; 115 – 119 mm CW Shetland, Tallack, 2002a). A CW50 derived from observations of sperm in the spermathecae has not been calculated before. However, our results indicate that mating takes place at smaller crab sizes than expected from sperm plug indices: the CW50 based on sperm plugs is also likely overestimated, as shown in Figure 4c. The ovary develops at a similar body size in different areas of Europe. The CW50 of 132 mm in Swedish waters (this study) are comparable with the 130 – 134 mm CW at the Shetland Islands (Tallack, 2002a), the 127 – 139 mm off southwest Ireland (Edwards, 1979), and the 132 – 138 mm around Ireland (ICES, 2004). However, Le Foll (1986) reported a CW50 in the Bay of Biscay based on ovary

**Table 2. Comparison of a one- and a two-phase relationship between AW and CW of females, and of RPL, RPH, and RPW of males.**

<table>
<thead>
<tr>
<th>Sex, size, and morphometry</th>
<th>SSR1</th>
<th>SSR2</th>
<th>F</th>
<th>p</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>LJ &lt; 104 mm</td>
<td>0.186</td>
<td>0.177</td>
<td>9.076</td>
<td>&lt;0.05</td>
<td>2 and 361</td>
</tr>
<tr>
<td>LJ &lt; 109 mm</td>
<td>0.199</td>
<td>0.187</td>
<td>11.904</td>
<td>&lt;0.05</td>
<td>2 and 375</td>
</tr>
<tr>
<td>LJ &lt; 124 mm</td>
<td>0.317</td>
<td>0.305</td>
<td>10.052</td>
<td>&lt;0.05</td>
<td>2 and 515</td>
</tr>
<tr>
<td>Males LJ &lt; 110 mm</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RPL</td>
<td>0.079</td>
<td>0.075</td>
<td>3.22</td>
<td>&lt;0.05</td>
<td>2 and 125</td>
</tr>
<tr>
<td>RPH</td>
<td>0.070</td>
<td>0.065</td>
<td>4.65</td>
<td>&lt;0.05</td>
<td>2 and 125</td>
</tr>
<tr>
<td>RPW</td>
<td>0.095</td>
<td>0.092</td>
<td>1.97</td>
<td>ns</td>
<td>2 and 125</td>
</tr>
</tbody>
</table>

SSR1 is the sum of squared residuals when combining juveniles and adults to one phase, and SSR2 the same when splitting into two phases. Data of intermediate sizes (LJ – LAM) are not included in the one-phase regression. The data fit a two-phase linear regression better \( (F \text{-statistic}) \) than a one-phase regression (except for the data on RPW). The method is based on that of Gaertner and Laloe (1986).

The CW50 determined from the different biological characters may be used as background for implementation of an MLS in the Skagerrak and the Kattegat. The effect of different potential MLS (CW50) on the Swedish catch potential is shown in Figure 9. The simulated impact on the capture potential of females subjected to implementation of a 104, 107, 118, 132, or 140 mm CW as MLS led to a decrease in the number captured with increasing MLS in the Skagerrak and the Kattegat. The decrease was more severe in the Skagerrak (Koster, Fjällbacka, and Lysekil) than in the Kattegat (Varberg inshore, Groves Bank offshore). A MLS of 140 mm in the Skagerrak resulted in an estimated local specific capture potential of 33–57% of the present catch, but in the Kattegat the result was a 80–87% decline. In Figure 9b, the simulated impact of 101, 122, 130, or 140 mm MLS on male capture potential is shown. A MLS of 140 mm CW in the Skagerrak reduced the capture potential to 32–51%, and in the Kattegat to 80% of the present catch by number.
development to be as low as \( \sim 111 \text{ mm} \) (i.e. 73 mm CL). This may be an effect of living in southern parts of the species distribution, where the water is warmer, and temperature does impact the size at sexual maturity in other crab species (Fisher, 1999; de Lestang et al., 2003; Defeo and Cardoso, 2004). In this study, the CW\(_{50}\) assessed from ovary development during autumn included both post- and inter-moult females: excluding post-moult crabs might move the logistic curve to the left (significant differences in gonad development between post- and inter-moult females in autumn), resulting in a lower CW\(_{50}\), possibly explaining the geographical differences in ovary maturation. No CW\(_{50}\) has been reported for large female crabs in the English Channel (Brown and Bennett, 1980), which borders the Bay of Biscay, but 85% of females \( > 115 \text{ mm} \) (all size categories lumped together) had developed gonads in autumn (Brown and Bennett, 1980).

A report from an ICES study group on crab biology and life history point to 130 mm CW as the SOM of maturity of female \( C. \) pagurus in the North Sea (ICES, 2003). However, the size distribution of ovigerous females (H. Hallbåck, unpublished data, \( q_{25} = 142, q_{50} = 152, q_{75} = 162 \text{ mm}, \text{ min} = 109 \text{ mm} \)) in the Skagerrak and the Kattegat indicates that most females do not spawn until yet another moult. The size range of ovigerous females in the Skagerrak and the Kattegat is of the same magnitude as elsewhere in Europe: in the English Channel, ovigerous females range from 133 to 205 mm (mean 166 mm) (Brown and Bennett, 1980). The smallest observed ovigerous female from the English east coast was 129 mm CW, but out of 200 females examined, most that were ovigerous were \( > 152 \text{ mm} \) (Edwards, 1979). Pearson (1908) measured the smallest ovigerous female in northern parts of the North Sea at 115 mm.

Table 3. 95% confidence intervals of coefficient \( B \) in the linear regression \( \log Y = \log A + B \log CW \), where \( Y \) refers to measures of abdomen, right propodus length, right propodus height, and right propodus width, and CW is the carapace width.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Juvenile ( B )</th>
<th>Adult ( B )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abdomen</td>
<td>1.565–1.633</td>
<td>1.390–1.439</td>
</tr>
<tr>
<td>RPL</td>
<td>1.236–1.316</td>
<td>1.560–1.647</td>
</tr>
<tr>
<td>RPH</td>
<td>1.270–1.337</td>
<td>1.419–1.490</td>
</tr>
<tr>
<td>RPW</td>
<td>1.147–1.223</td>
<td>1.315–1.399</td>
</tr>
</tbody>
</table>

The confidence interval does not overlap between juveniles and adults of either variable.
of 16 ovigerous females of 122–159 mm at a site off northwest Norway (Woll, 2003) gave an indication of the size of ovigerous females in Norwegian waters. Statistical analyses (minimum of SSR) and graphical observations (Figure 6) of female allometric data indicate three cohorts: one with relatively steep allometric growth of the abdomen <105 mm CW, one with relatively less growth of crabs 105–133 mm CW, and one for larger crabs with faster growth. Interestingly, Tallack (2002b) found a change in relative AW in females >100 mm, consistent with the present findings of first minima at 95–104 mm and a CW50 of 104 mm. Tallack (2002b) also noted that female pleopod capacity had an inflection point at 138 mm CW. This phenomenon is also observed in snow crab (Chionoecetes opilio; Alunno-Bruscia and Sainte-Marie, 1998), those authors suggesting a downscaling in the allometry of intermediate-sized crabs brought about by later structural limits on abdomen size. The size at which sexual maturity of females is attained covers a wide range. It seems that cul- 

from other areas. Edwards (1979) observed male crab gonads from Yorkshire and southwest Ireland, and based on the presence of a ripe vas deferens, suggested that most males >110 mm were mature. Similar studies around the Shetland Islands suggest maturity (CW50) at 110–114 mm CW (Tallack, 2002a). The CW50 in the Bay of Biscay is at about 102 mm (67 mm CL), on the basis of histological analysis of gonad development (Le Foll, 1986). In the current work, classification of the gonads of inter-

and post-moult males suggests that shell condition does have an impact on gonad development (Figure 5). This finding is contrary to that of other authors, who suggest that gonad maturation is not affected by moulting (e.g. Edwards, 1979; Pinho et al., 2001), but a change during the year in male Cancer magister sperm content has been shown by Swiney and Shirley (2001). Enlargement of the male chela at 110 mm CW (the onset of maturity) is reported by Edwards (1979), some 9–12 mm less than the CW50 of Swedish male crabs assessed on the basis of morphometry. However, the intersection point discriminating Shetland juvenile male crabs from adults is calculated to be 102–105 mm CW (Tallack, 2002b), a value conspicuously lower. Differences in methodology (inter-

Table 4. Summary of the edible crab escapement experiment of creels equipped with traps with gaps of different diameters (75–90 mm).

<table>
<thead>
<tr>
<th>CW (mm)</th>
<th>75 mm</th>
<th>80 mm</th>
<th>85 mm</th>
<th>90 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total (%)</td>
<td>F</td>
<td>M</td>
<td>Total (%)</td>
</tr>
<tr>
<td>115–119</td>
<td>0</td>
<td>0</td>
<td>93.8</td>
<td>7</td>
</tr>
<tr>
<td>120–124</td>
<td>0</td>
<td>0</td>
<td>37.5</td>
<td>3</td>
</tr>
<tr>
<td>125–129</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>130–134</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>135–139</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>140–144</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Four females (F) and four males (M) of each range of CW class were located within a creel, and each combination was run overnight on two occasions. The total proportion of escapes (%) are given per gap and CW class (n = 16), as is the sex-specific number of escapes.
be excluded. Application of morphometric and reproductive data that considers the developing male gonad to be immature results in a CW50 at the higher end of these findings (117–122 mm CW). However, interpreting developing gonads as mature yield a value of CW50 at the lower end, close to a CW50 based on histological analyses in the Bay of Biscay. Campbell and Eagles (1983) considered male gonads that were slightly developed to be immature, because of their low numbers and the small developing spermatophores. In summary, the onset of sexual maturity for males is at size ranges between 100 and 120 mm CW, if based on the findings herein and in earlier literature.

Fecundity of the edible crab (0.5–2.6 million eggs, Figure 8a) is in accord with findings in the UK (0.8–2.9 Million eggs; 145–183 mm CW, Edwards, 1979) that show that fecundity increases with female size. Larger females not only have larger gonads, but their pleopod capacity, sperm content in spermathecae, and AW increases with size (Tallack, 2002b). Any variation in the fecundity between crabs caused by differences in the mouling stage (Hankin et al., 1989) or egg development (O’Clair and Freese, 1988; Shields, 1991) is probably small in this study because all females (except one) were of similar inter-moult stage, there was no visible eye-pigment formation of the eggs, and the eggs were of similar colour. In addition, the eggs were of similar size, despite differences in absolute numbers per batch. However, fecundity standardized for body weight is similar for the females in the size range seen here (Figure 8b) and the egg mass to body weight ration was of similar magnitude to that of other species of the genus Cancer (11–19 %, Hines, 1991). The eggs of cancrid crabs are of similar size, and because of the large body size of the animals, the fecundity of cancrid crabs is among the highest reported (Hines, 1982), especially that of larger females.

**Management recommendations and their effects on catch potential**

Hartnoll (1969) suggested that female crabs are mature when they are capable of extruding eggs, and males when they can mate/copulate successfully. This means that the crabs must be both physiologically and functionally mature before they can be treated as fully mature. To reduce the risk of recruitment-overfishing, landing restrictions on females could be introduced if based on observations on the size-specific proportion of ovigerous crabs in the population. However, few egg-carrying female edible crabs are captured by the fishing gear (Edwards, 1979; Howard, 1982), and female crabs in cold, temperate waters may not spawn annually (Swiney et al., 2003), all of which results in sampling problems and biases. Other characters can be used as indicators for female maturity analysis to overcome sampling problems and biases. Physiological and functional maturity are not synchronized for females, but span wide ranges, and for this reason caution in instituting management action is needed. Further, fecundity is magnitudes higher for large females than for first-spawners, and ovigerous females are likely to have a higher CW50 than assessed through physiological maturity analysis. For male crabs, physiological and functional maturity are more synchronized, and take place at smaller size. However, small physiologically and functionally mature male Chionoecetes opilio and Cancer gracilis rarely take part in reproduction because of competition with larger males (Alumno-Bruscia and Sainte-Marie, 1998; Orensanz et al., 1995). Also, the size of copulating males exceeds that of post-moult females (Hankin et al., 1997), indicating copulation size limits for smaller males. However, Edwards (1966) found that a 110 mm male Cancer pagurus copulated with a 151 mm post-moult female and that the sperm contribution of small male edible crabs was less than expected from gonad and morphometric studies alone.

Maturity characteristics tend to be sampled by traps that may have underestimated the real CW50, because the proportion mature may well be higher in active than in passive fishing gear (Smith et al., 2004). Precautionary management based on a possibly underestimated CW50 along with the diverse maturation process of the exploited edible crab stock in Swedish waters, results in a suggested MLS for females and males of 140 mm CW, particularly if the crab industry develops and fishing effort burgeons. A legislated MLS of 140 mm CW would ensure that almost all of Swedish landings of male edible crabs are physiologically and functionally mature, that 75% of female crabs are physiologically mature, and that approximately 25% of female crabs are
functionally mature. In other words, spawning is relatively intense and fecundity fairly high, so even the larger female crabs may have accessibility to suitable mating partners. I assume that the MLS in force in the English Channel (>140 mm CW) exceeds the size at which 50% are mature (Bennett, 1995). The MLS in neighbouring Norwegian water is just 110 mm CW south of 60°N, and for that reason alone there seems to be reason for Norwegian authorities to reconsider it or to find other ways of improving management of their edible crab resource. The MLS of male Cancer magister is 155–165 mm, a value that allows most male crabs to mate at least once before capture, and capture of female crabs is prohibited (Siddeek et al., 2004). As an alternative for the Skagerrak and the Kattegat, or in combination with a MLS, there could be a legislated change in the size of the present mandatory escape gap to avoid capturing undersized crabs. The diameter of the circular gap would need to be increased from its present 75 mm to 90–92 mm. Such a gap size can be estimated from a length–CW regression (Brown, 1982), assuming that length is a discriminating character. Additionally, the manipulative experiment with different escape gaps conducted here showed that a 90 mm gap is needed for crabs 135–139 mm CW to escape (Table 4). The catchability of ovigerous females in creel fisheries (for crab and lobster) is so low that restriction on landing probably does not need to be considered. However, the bycatch of ovigerous female crabs in, for example, gillnet fishing for lumpfish or flatfish, which causes high levels of crab mortality, does need to be assessed. Seasonal closure of the crab fishery during peaks in moulding may be necessary to decrease handling mortality of crab pre-recruits and recruits, particularly if fishing effort burgeons.

The catch potential will be affected along the Skagerrak coast but to a lesser extent in the Kattegat (Figure 9). Stock assessment of crustacean fisheries (Smith and Addison, 2003) estimates both short- and long-term yield benefits from instituting an appropriate MLS, and it also yield other advantages that make the management action acceptable to stakeholders (the professional fishers). Length cohort analyses of edible crab on the east coast of England have shown long-term gains in yield per recruit and biomass per recruit attributable to increases in the MLS (Addison and Bennett, 1992). In addition, increasing fishing effort to overcome short-term losses did not counterbalance the long-term gain to the population. Considering stock–recruitment relationships and the higher economic value of larger crabs may even result in greater gains than are immediately obvious, but density-dependent effects may limit those benefits. Assessments of the effects of an increase in the minimum size at first capture of Dungeness crab Cancer magister in the USA and Canada indicate increases in future harvest rate (Siddeek et al., 2004), i.e. increases in yield. Similar modelling of yield per recruit for the crab length cohorts present in the Skagerrak and the Kattegat may indicate both short- and long-term beneficial effects of increasing the MLS to 140 mm.

Acknowledgements

I thank all the fishers of the professional crab fishing boats involved in sampling, Hans Hallbäck (IMR), who provided data on the size composition of ovigerous females for comparison with other maturity characters, and two anonymous referees whose comments helped improve the manuscript. The study could not have been performed without support from the SUCOZOMA programme and the development project Swedish West Coast Crab.

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doi:10.1093/icesjms/fsl039