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Size at maturity of the edible crab (*Cancer pagurus*) in Welsh waters

PRIFYSGOL BANGOR UNIVERSITY

Jodie Haig, Julia Pantin, Harriet Salomonsen & Michel J. Kaiser

School of Ocean Sciences, College of Natural Sciences, Bangor University

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Technical summary

Introduction

Cancer pagurus is a marine crab species common in UK waters; it is also known as the brown or edible crab in English and as cranc coch in Welsh. *C. pagurus* is a temperate water species with a broad distribution that extends from the NW coast of Norway to south Morocco. *C. pagurus* juveniles are found in high abundance in the intertidal zone and as adults up to a depth of 100m (Harrison and Crespi, 1999). *C. pagurus* frequently occur on rocky grounds, under boulders and on coarse sediments, though females prefer soft sandy substrates, suggesting a gender-specific habitat preference (Harrison & Crespi, 1999).

C. pagurus is the most valuable crab fishery in UK waters. In 2011, around 12,000 tonnes were landed in England and Wales, and a further 554 tonnes in the Isle of Man (MMO, 2014). The highest catches of *C. pagurus* occur between June and November; this is also when a high proportion of non-berried females are caught. *C. pagurus* is not a quota species anywhere in its distribution. In the UK, current management measures include a national restriction on the number of shellfish licenses available, and a ban on the landing of berried hens (gravid females) and "soft" (recently moulted) individuals (CEFAS, 2012). In Welsh waters the crab fishery is considered data poor, and successful future management will require a better understanding of the reproductive biology, size at maturity and fecundity of *C. pagurus*.

Life history

From December to February female crabs moult and are soft enough to allow for copulation (Pearson, 1908). Males will locate a female before she moults and will pair up with her for between three and 21 days. During this time males will "mate guard" the female by carrying her around under their abdomen. Only larger males will succeed in retrieving a female that is being mate guarded. When the female is ready to moult the guarding male may assist her out of her old cast using his chelipeds (pincers). After moulting, the male carefully turns the female over onto her back and uses his chelipeds to expose her genital openings by opening her abdominal flap (Edwards, 1966). During copulation, the male sex organs are introduced into the vulvae of the female and fertilisation occurs. As the male releases the sperm, a fluid is produced from the cells that line the female's spermatheca; the fluid then hardens on contact with seawater and forms the "sperm plug" (Pearson, 1908). The sperm plug prevents the loss of sperm and also prevents further copulations and seawater from entering the reproductive tract (Edwards, 1966; Williamson, 1904). To further ensure that females do not mate with another male, mate guarding may persist for up to two days, after which point, males will leave the females and seek another mate (Edwards, 1966).

Health index

The hepatopancreas, also known colloquially as "tomalley" in the food industry, is the mid-gut gland that fulfils the role of both the liver and pancreas. The hepatopancreas has three different functions in decapod crustaceans; it is considered as the main storage organ for metabolic reserves, secretes digestive enzymes including protease, amylase and lipase, and is the main site for assimilation (Warner, 1977). The hepatopancreas can be used as an index for the amount of energy stored, or as a proxy for the health of an animal.

Cancer pagurus is known to host the external rhizocephalans parasite, *Sacculina sp.* (Stentiford, 2008); though the prevalence in Welsh waters is not known. Black spot is a bacterial infection that causes necrotic shell lesions. Ayres and Edwards (1982) coined the term "black spot" owing to the black lesions on the exoskeleton. Black spot is reported to render the meat bitter and the unsightly nature of the lesions makes the crab less marketable (Stentiford, 2008). In South Wales, in 1998, 50% of crabs had at least one lesion (Vogan et al., 1999). Here we investigate if any of the known diseases affect the health index of *C. pagurus*.

Maturity

In fisheries research the size (carapace width) at which 50% of the sampled animals are mature is often reported; in this report we will refer to this as the CW_{50}. Research on size at maturity has estimated that *Cancer pagurus* matures at between 100 and 133 mm carapace width (Table 1). The most recent published research to date on the CW_{50} of *C. pagurus* was Tallack's study (2007a), conducted in Scotland in 2001. Selective mortality through fishing has been shown to induce evolutionary change in the biological parameters of commercially prosecuted populations (Kuparinen and Merilä, 2007; Swain et al., 2007). For this reason, it is important to monitor length frequency, growth and size at maturity through time for populations under size selective fishing pressure.

The methods used to determine maturity in *C. pagurus* can be broken down into three types: Behavioural, Functional, and Morphometric. Behavioural maturity is when copulation occurs, resulting in the presence of a sperm plug in the female, though this will not result in a brood unless the ovaries are fully developed. In *C. pagurus* immature females have been observed with sperm plugs and estimates of size at maturity based on these observations result in much smaller CW_{50} estimates than those for functional estimates (Tallack, 2007a; Ungfors, 2008). Functional maturity is the complete development and production of offspring after a successful pairing. The most obvious (functional) method of determining maturity is the presence of eggs on the female, and in the absence of an opportunity to collect and dissect many different sized crabs, is perhaps the most reliable method. Morphometric measurements of maturity are less reliable and can only accurately determine maturity if allometric growth patterns of external features relate to internal maturation processes. Allometric growth is when one part of the anatomy grows faster than another. In crabs the allometric growth of chelae, abdomen widths and first pleopods are known to be secondary sexual characteristics in crabs (Hartnoll, 1974). The sexual dimorphism of chelae and abdomen widths has been observed in more than 25 different brachyuran crabs as chelae size becomes increasingly important for combat, display and courtship for mature males and abdomen width to accommodate eggs in mature females (Hartnoll, 1974). The rate of allometric change (positive allometry) may be abrupt, for example after a single pubertal moult; or it may be gradual, occurring over multiple moults (Warner, 1977).

Table 1. Size at maturity of Cancer pagurus in the published literature. 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}	CW mature	Method	Country	Year	n	Sex	Reference
Behavioural	**106.6**		Sperm in spermathaeca	Sweden	2002	399	F	(Ungfors, 2007)
Behavioural	**118.5**		Sperm plug present	Sweden	2002	399	F	(Ungfors, 2007)
Behavioural		**105-211**	Sperm plug present	England			F	(Brown and Bennett, 1980)
Behavioural	**122.9**		Sperm plug present	Scotland	1999-2001	812	F	(Tallack, 2007b)
Functional	**131.8**		Gonad development	Sweden	2002	399	F	(Ungfors, 2007)
Functional	**120**		Gonad development	Ireland	1998		F	(Tully et al., 2006)
Functional	100.9		Gonad development	Sweden	2002	271	M	(Ungfors, 2007)
Functional		>110	Gonad development	England	1961-1966		M	(Edwards, 1979)
Functional	104.3		Gonad development	Scotland	1999-2001	73	M	(Tallack, 2007b)
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 and Bennett, 1980)
Functional		**140-184**	Ovigerous	Scotland	1985		F	(Hines, 1991)
Functional		**118**	Ovigerous	Scotland	1999-2001	1396	F	(Tallack, 2007b)
Functional		**127-216**	Ovigerous	England	1961-1966		F	(Edwards, 1979)
Functional	**143.7**	**100**	Ovigerous	Scotland	1999-2001	1025	F	(Tallack, 2007b)
Morphometric	**103.7**		Abdomen	Sweden	2002	399	F	(Ungfors, 2007)
Morphometric		110	Chelae	England	1961-1966		M	(Edwards, 1979)
Morphometric	**115.9**		Abdomen	Scotland	1999-2001	412	F	(Tallack, 2007b)
Morphometric	101.6-109.5		Chelae	Scotland	1999-2001	402	M	(Tallack, 2007b)
Morphometric	**147.3**		Pleopod	Scotland	1999-2001	131	F	(Tallack, 2007b)
Morphometric	119.5		Chelae width	Sweden	2002	271	M	(Ungfors, 2007)
Morphometric	122.3		Chelae height	Sweden	2002	271	M	(Ungfors, 2007)
Morphometric	122.5		Chelae depth	Sweden	2002	271	M	(Ungfors, 2007)

Methods

In the winter of 2014/2015, 435 crabs were collected from Welsh waters to determine size at maturity. Crab catches relied on industry collaboration and therefore all samples were caught by active fishers in Wales, using standard static gear (a mix of soft and hard eyed crab pots, typically with a 45 mm mesh). Samples were collected from Conwy in north Wales to Solva in south Wales (Pembrokeshire) in order to determine any regional trends in maturity.

Laboratory methods

Each crab was photographed, then whole wet weight, carapace width, abdomen width and chela measurements were taken (right chelae height, length and width; Figure 1). When the right chelae was missing, the left one was measured as the chelae are not dimorphic (Ungfors, 2007). A claw morphometric estimate was given by adding all three chelae measurements together, as individually they have been shown to display a departure from isometric growth in other *C. pagurus* maturity studies (Tallack, 2007a; Ungfors, 2007). Crabs were assigned a condition based on the number of limbs lost (and in a state of healing or regrowth, Table 2). Also noted was the bacterial infection "black spot"; which was only assigned to crabs if the lesion penetrated through the carapace (Figure 2). Surface marks that were not obviously lesions were not recorded as black spot. Moult stage was assigned as per Table 3.

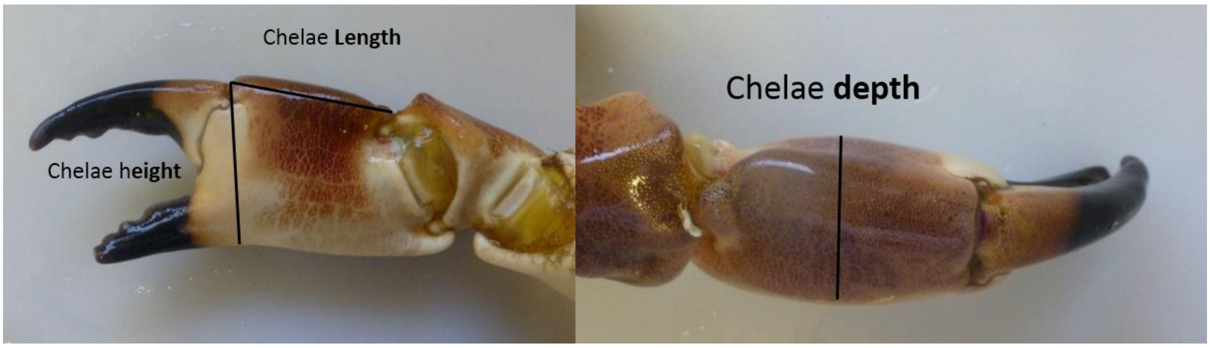

Figure 1. A photograph of the claw (chelae) morphometric measurements taken for Cancer pagurus

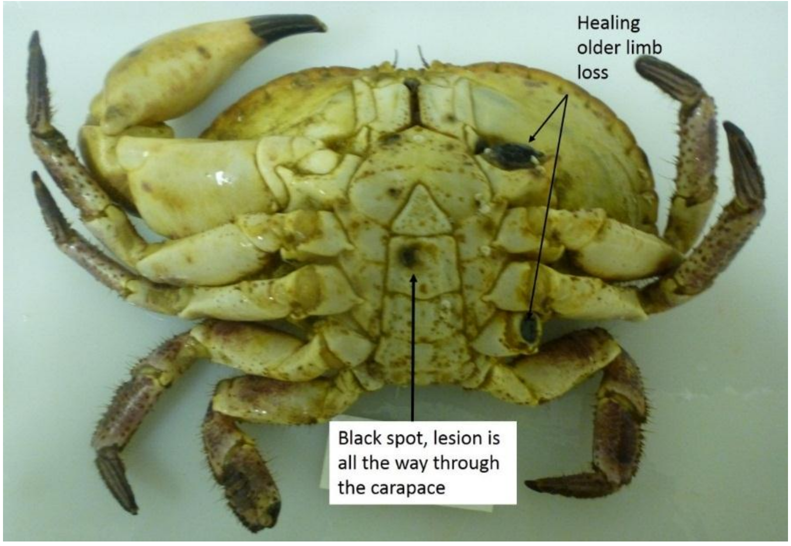

Figure 2. This male Cancer pagurus has a small amount of black spot on the abdomen, black spot was only diagnosed if the lesion penetrated the carapace layer. This crab was also missing one claw and one leg (thus would be categorised as condition 5). It is clear that these wounds were received prior to capture as healing has begun.

Table 2. Condition index assigned to all Cancer pagurus. The index did not include legs which were broken due to rough handling or transport. Recent and post-mortem limb loss is pink with no evidence of a protective skin layer forming (which is sometimes black)

Index	Description
1	All legs present. No black spot. No damage.
2	One or two legs missing
3	More than two legs missing (number of missing limbs noted)
4	One or both claws missing
5	One or both claws missing and some legs missing

Table 3. One of four moult stages were assigned to each Cancer pagurus using an accepted classification system from the published literature (Edwards, 1979; Ungfors, 2007)*.*

	Moult Stage	**Description**
1	Early post moult	Soft, white, clean, very sharp toes, you can usually slightly depress the clean white carapace spaces either side of the abdomen
2	Recent moult	Clean, not fully hardened yet, sharp toes
3	Inter-moult	Some biofouling, worn toes
4	Degraded	Usually lots of biofouling including tube worms and larger barnacles, limbs missing, holes, usually a bit smelly (underside hairs usually thick with biofilm).

NB crabs may be stage 3 with no bio-foul, or stage 2 with broken toes. The moult stages were confirmed during dissection by noting the thickness of the carapace.

The crab was dissected by using kitchen shears to cut around the outside margin the dorsal carapace, then carefully lifting the central body mass to reveal the hepatopancreas and gonads (Figures 3 & 4). The hepatopancreas was carefully removed and weighed for a hepatosomatic index. The gonad was then photographed and stages three and four from females and only three from males were removed to obtain gonad wet weight for a gonadosomatic index. Crabs in poor condition, which may have died some time prior to freezing typically contained liquefied internal organs, these individuals did not have the hepatopancreas weighed; and in extreme cases gonads were not weighed.

Crabs were dissected and the hepatopancreas was removed and weighed. The gonad was then photographed and assigned to categories (Table 4; Figures 5 & 6).

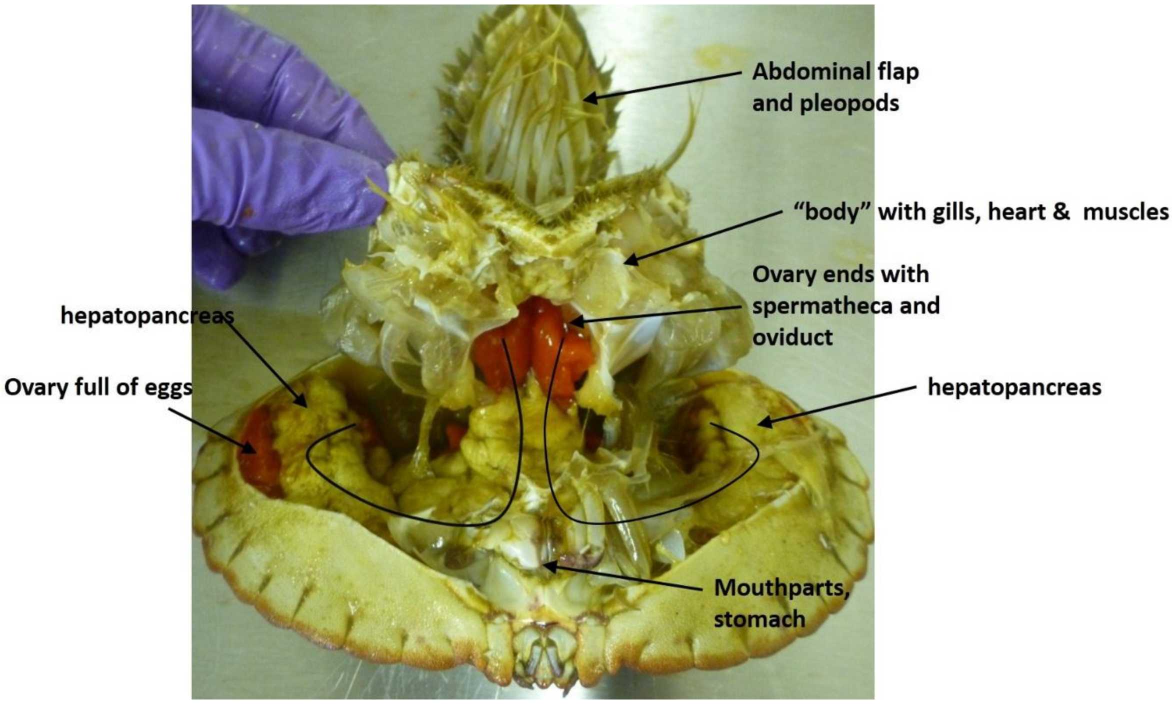

Figure 3. The internal structure of Cancer pagurus showing hepatopancreas and a mature ovary full of bright orange eggs. The black lines overlay the shape of the ovary as it curves around and into the central body mass

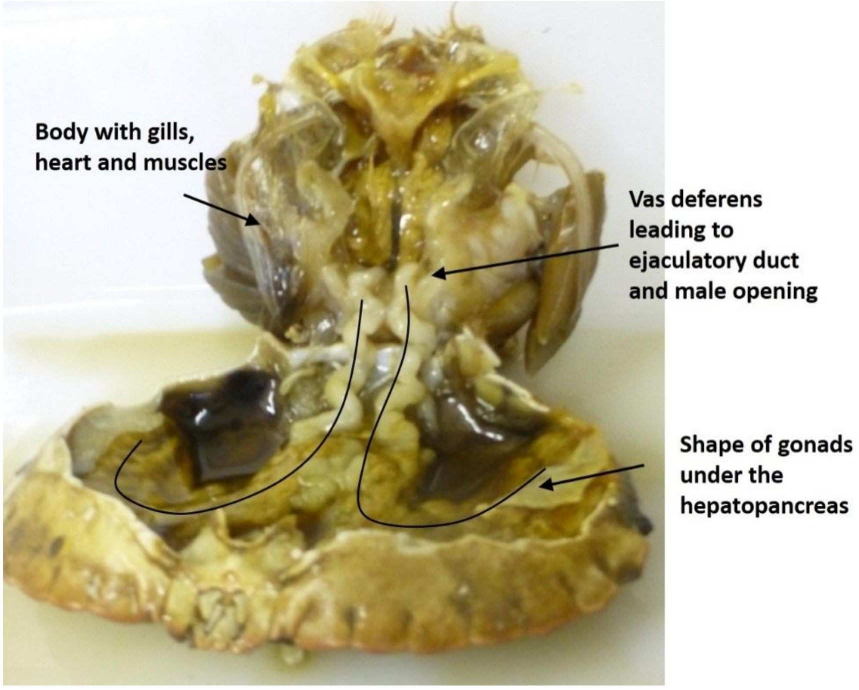

Figure 4. The internal structure of male Cancer pagurus showing hepatopancreas and underneath is the white vas deferens full of sperm. The black lines overlay the shape of the vas deferens as it curves around and into the central body mass.

Table 4. Female and male visual gonad stages for Cancer pagurus obtained from the literature (See Table 1).

Female Stage	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. Remnant eggs**
Male Stage	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 & white**	

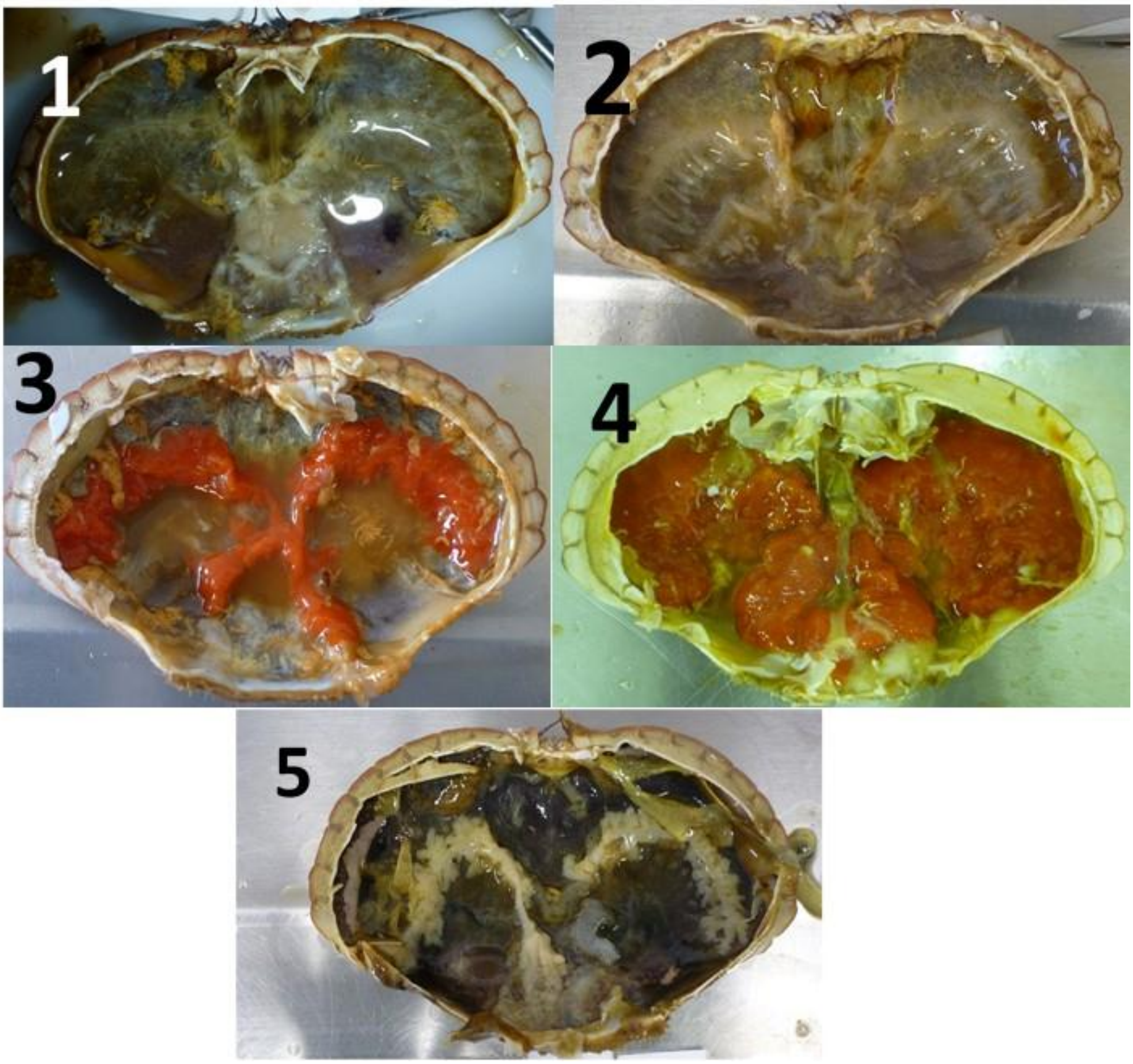

Figure 5. Photographs of female Cancer pagurus gonad stages. 1, immature; 2, developing; 3, early stage mature; 4, mature; 5, spent or resting.

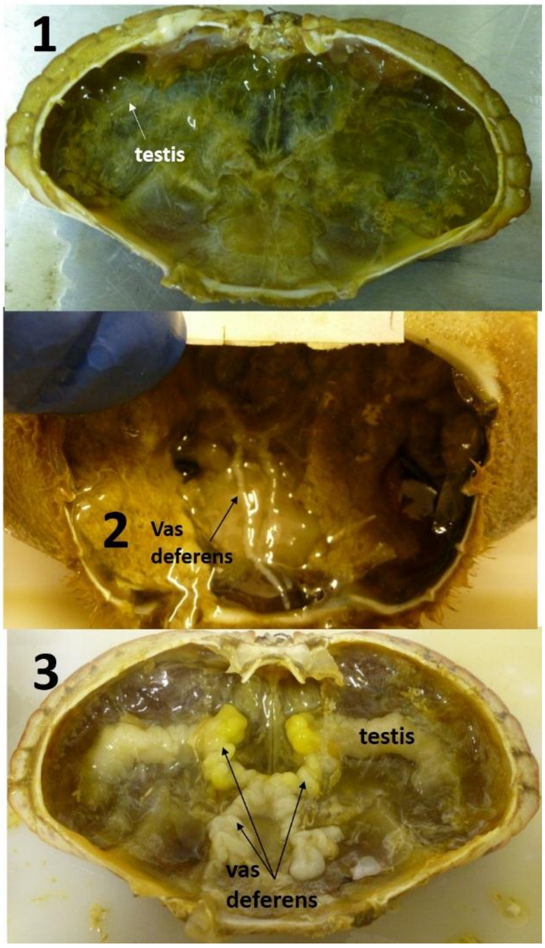

Figure 6. Photographs of male Cancer pagurus gonad stages. 1, immature; 2, developing; 3, mature. Spent males were classed as mature, they were visually similar to stage three, though less sperm were present in the vas deferens.

Other observations

During initial inspection, prior to dissection, the presence of sperm plugs, parasites and black spot was recorded.

Statistical methods

All statistical analyses were run in R (R Core Team 2014). Relationships were modelled using a linear regression, and analysis of variance. Where appropriate a Tukey honestly significant difference test was applied to determine interactions between response and predictor variables.

Model and test assumptions were tested for normality, heteroskedasticity and outliers. Kolmogorov-Smirnov or a Q-Q plot was used to test for normality, a Levene's test or residual plots for equal variance and leverage and Cook's distance plots were used to check for outliers in modelled data.

To produce maturity ogives, the maturity stage data was converted to binary form (immature = 0 and mature = 1). Mature stage one was considered immature and all other stages were mature. Population estimates for size at maturity were estimated using a logistic regression model (Roa et al., 1999) reformulated by Walker (2005) to produce:

$$P(l) = P_{MAX}(l + e^{-\ln(19)\left(\frac{l-\beta 1}{\beta 2-\beta 1}\right)})^{-1}$$

Where *P(l)* is the proportion of the population mature at carapace width; β1 and β2 are curve parameters corresponding to CW_{50} and CW_{95} respectively, and P_{MAX} is the asymptote. Parameters were estimated using a generalised linear model with a logit link function and a binomial error structure. Confidence intervals were added by bootstrapping the generalised linear model (runs at 10,000). The significance of the fitted models were tested by comparing the deviance explained relative to the null model using chi-squared tests. The base R code was constructed by Alastair V Harry and is available online (Harry, 2013)

To determine if males or females show morphological changes with the onset of maturity, an iterative search procedure was used with the following linear model in a piecewise regression:

$$CW \sim CLAW*I(x<c) + x*I(x>c),$$

"I(x < c)" and "I(x > c)" are considered binary variables, where "I(x > c)" equals 1 if *x* is less than the breakpoint (departure from isometric growth) and 0 if it is greater. There are therefore two sets of parameters being modelled within the regression depending on whether the data is greater or less than the breakpoint. The breakpoint, c, is the lowest residual mean standard error value was obtained for each iteration (Crawley, 2007; Lemoine, 2012). A larger dataset of morphological measurements was available for these analyses. Data from on-board observing, processor sampling, size at maturity, and fecundity research was pooled. We were also able to collaborate with other Bangor University staff running a separate project on *Cancer pagurus* (NERC project, UK (NE/J007544/1) "Climate change and the costs of survival in two species of marine crabs with contrasting abilities to compensate for environmental change" (www.saloa.org; Dr Coleen Suckling and Dr Nia Whitely). In this collaboration we measured and weighed all available juvenile *C. pagurus*.

RESULTS

Cancer pagurus samples were collected between November 2014 and March 2015. A total 435 crabs were assessed for size at maturity, 219 crabs were from North Wales and 216 were from South Wales (Table 5). The smallest crab in the study was 30 mm carapace width (CW) and the largest was 220 mm CW. Of the 435 crabs assessed, 84% were found mature (Figure 7). For female *C. pagurus* 80% were found mature (84% in northern samples and 74% in southern samples). For male *C. pagurus* 88% were found mature (83% in northern samples and 93% in southern samples). The smallest observed mature female was 68.3 mm CW in North Wales and 75.2 mm CW in south Wales; for males the smallest was 68.8 mm CW in North Wales and 63.0 mm CW in south Wales.

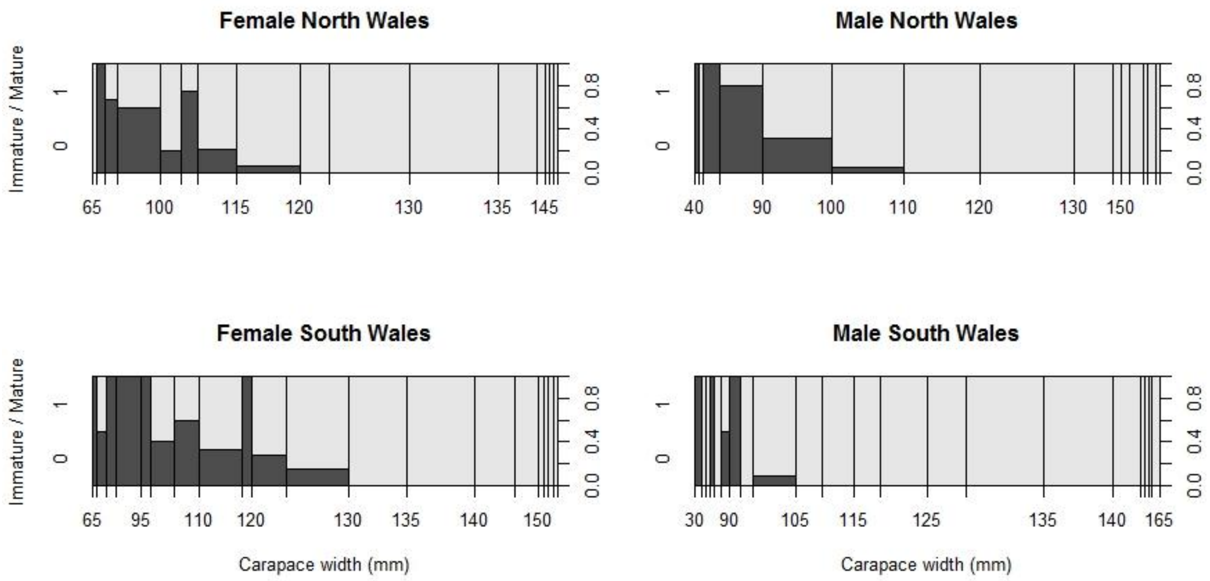

Figure 7. Proportion of mature Cancer pagurus at each sampled carapace width from north and south Wales caught between November 2014 and March 2015. The width of the bin represents the number of samples within it, the dark grey portion is the immature crabs (maturity stage 1); the light grey is the proportion of mature crabs (maturity stages 2-5).

The size (carapace width) at which 50% of crabs were mature (CW_{50}), was predicted by the generalised linear models (with binomial distribution). Males were found to mature at a smaller size than females for both north and south Wales. Confidence intervals around the male CW_{50} for south Wales was wider, probably due to fewer small males being sampled from the south.

Table 5. Table of summary statistics, CW_{50} and CW_{95} results with the 95% confidence intervals calculated using a maximum likelihood bootstrap method (r=10000). *n*, number of crabs caught for each sex, in each location for the size at maturity study between November 2014 and March 2015; CW, carapace width; LCI, lower 95% confidence interval; UCI, upper 95% confidence interval.

Location	*n*	Sex	Min CW	Median CW	Mean CW	Max CW	LCI	**CW_{50}**	UCI	LCI	CW_{95}	UCI
North Wales	110	F	68.3	124.8	120.8	179.4	86.64	**99.3**	105.9	114.27	123	130.47
South Wales	96	F	68	128	124.5	182	100.03	**109**	115.45	126.1	136	145.88
All females	206	F	68	125.8	122.5	182	96.35	**103**	108.05	123.29	130	136.65
North Wales	109	M	46.9	115.6	114.7	220	82.19	**89.9**	94.96	100.2	108	114.84
South Wales	120	M	30	125	120.6	164.8	56.25	**78**	94.65	93.77	109	115.14
All males	129	M	30	120	117.8	220	78.45	**87**	92.8	103.41	109	114.32

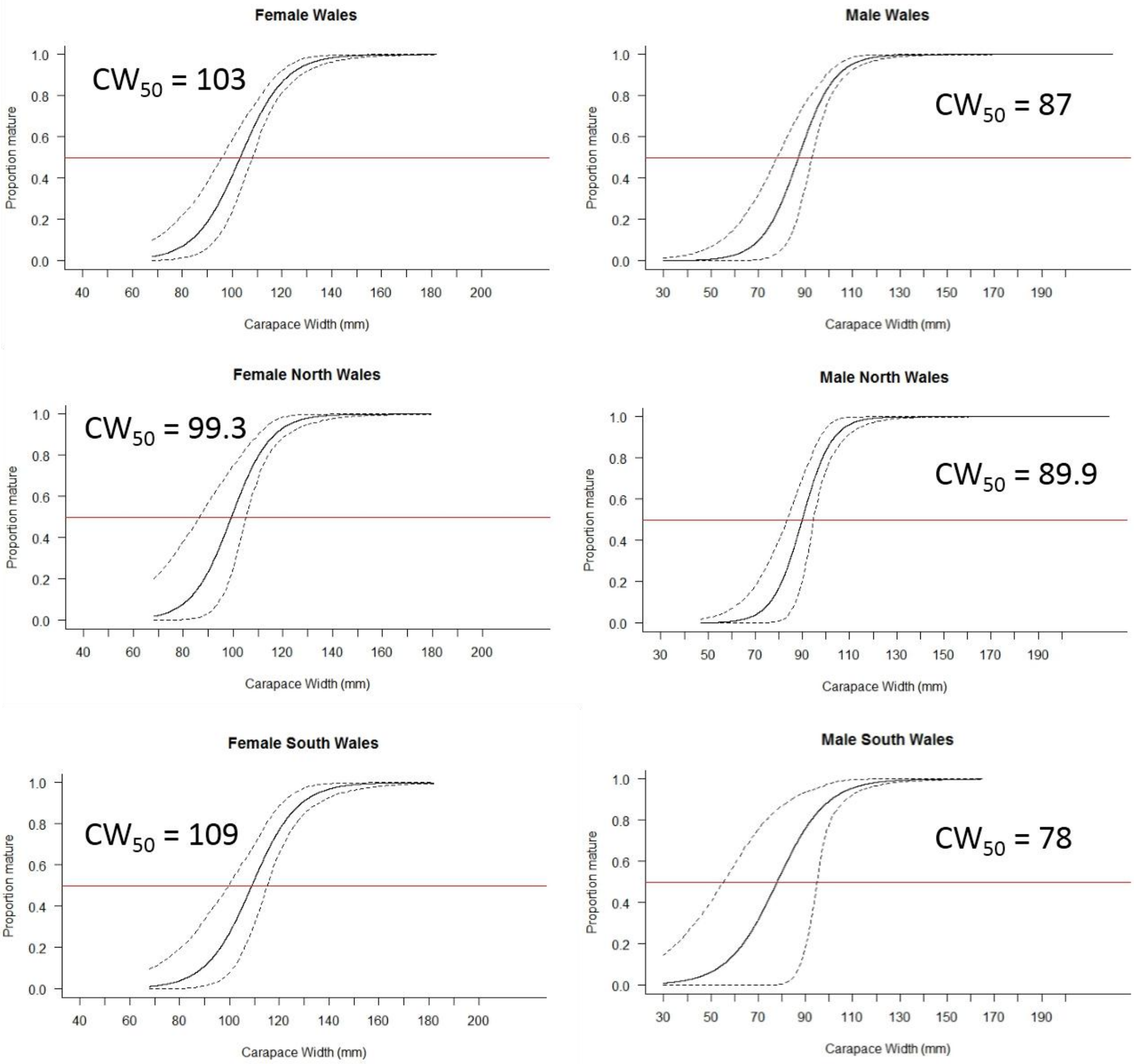

Figure 8. Maturity ogives for male and female Cancer pagurus caught in Welsh waters between November 2014 and March 2015. The red horizontal line is the proportion of 50% mature. The CW_{50} is the size at which 50% of the crabs sampled were mature. Dotted lines are the 95% confidence intervals obtained by bootstrapping the modelled data (r=10,000).

Observation of behavioural maturity

Only seven of the 206 females observed had sperm plugs present. The smallest female observed with sperm plug was 118 mm CW.

Trade-off between body condition and reproduction

Hepatosomatic index was significantly different between maturity stages for females ($F_{4,195}$= 11.41, p< 0.001) and males ($F_{2,211}$ = 10.61, p<0.001). Crabs in the "mature" stages (four for females and three for males) had significantly lower HSI than all other stages (TukeyHSD, all p<0.01). Boxplots showed a decreasing trend in HSI with progressive maturation (Figure 8).

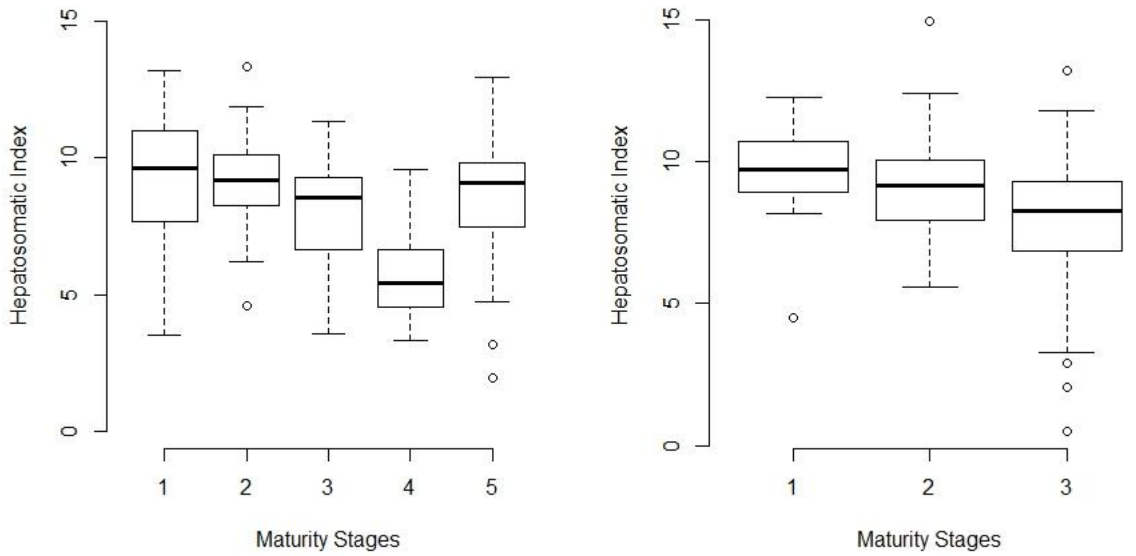

Figure 9. HSI and Maturity stage for females (left) and males (right) for Cancer pagurus caught in Welsh waters between November 2014 and March 2015.

Parasite presence / effects

Of all the crabs caught, only one was infected by the rhizocephalans parasite, *Sacculina sp.* The infected crab was a male, size 31.9 mm CW, 5.2 g, condition four, moult stage one. It was not possible to obtain a GSI or HSI for this individual for comparisons.

An analysis of covariance was used to determine if there was an interaction between HSI, blackspot and maturity stage. Crabs with blackspot showed significantly lower HSI values ($F_{1,410}$ = 10.25; p = 0.001) and HSI varied with maturity stage ($F_{1,410}$ = 23.41, p<0.001) though no interaction was found between the two.

Physical damage and reproduction

The skewed gonadosomatic index (GSI) data was log transformed for all analyses. GSI was significantly different between condition indices, sex and maturity stage (linear model; $R^2 = 0.35$, $p < 0.001$) though the model violated the assumption of normality. The model performed better when maturity stage was removed ($R^2 = 0.37$, $p<0.001$) and GSI was significantly different between sexes ($F_{1,175} = 53.85$, $p<0.001$), conditions ($F_{4,175} = 6.92$, $p< 0.001$) and with a significant interaction between condition and sex ($F_{4,175}=8.66$, $p<0.001$; and see Figure 10). The hepatosomatic index was not found to vary between condition indices regardless of sex or maturity stage.

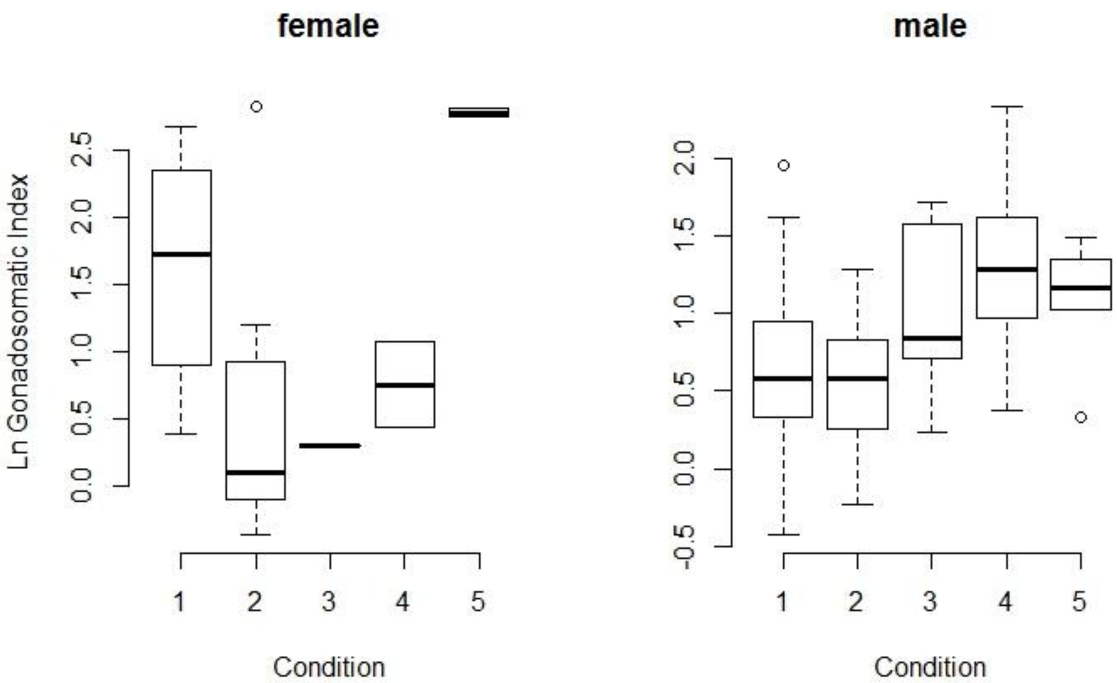

Figure 10. Gonadosomatic index (GSI) for each category of the condition index assigned to Cancer pagurus females and males caught in Welsh waters between November 2014 and March 2015.

Morphology and Maturity

A departure from allometric growth was detected by an inflection point in the morphometric data for both males and females. Female abdomen width became significantly larger at a carapace width of 95 mm (Figure 11), and male claw dimensions began to increase after a carapace width of 132 mm (Figure 12).

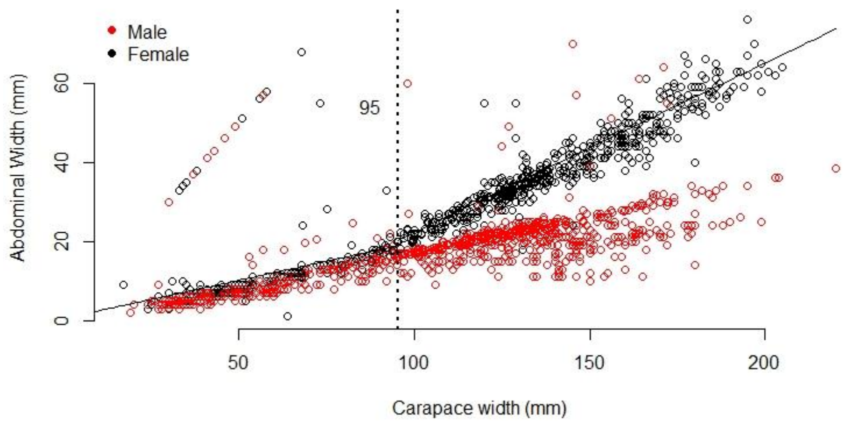

Figure 11. Abdomen width plotted against carapace width for male and female Cancer pagurus caught in Welsh waters between 2013 and 2015. The black dots (females) show a departure from the isometric trend at CW 95 mm (as indicated by the dotted vertical line).

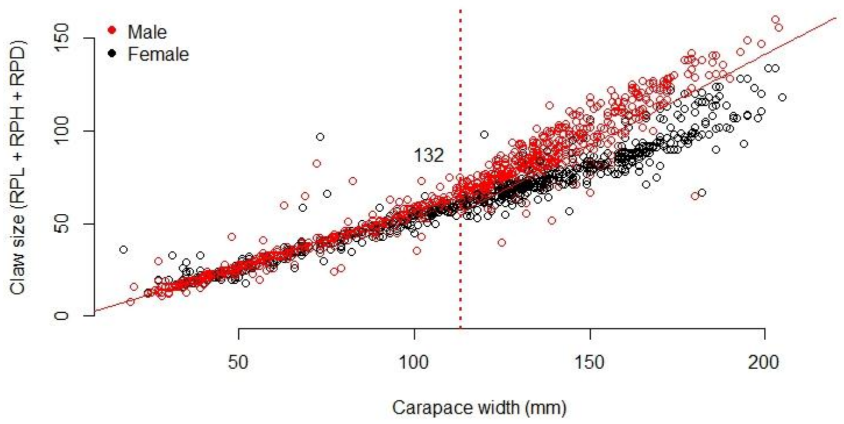

Figure 12. Claw (chelae) measurements against carapace width for male and female Cancer pagurus caught in Welsh waters between 2013 and 2015. The red dots (males) show a departure from the isometric trend at CW 132 mm (as indicated by the dotted vertical line).

DISCUSSION

A decreasing size at maturity?

The majority of the sampled crabs were found to be mature (84%). Given the available literature on the size at maturity for *C. pagurus* it was hypothesised that crabs below 100 mm CW would be mostly immature. However, 38% of animals below 100 mm CW were found in visually mature stages. Males matured at smaller sizes than females and this has been observed in other research (See Table 1). The CW_{50} observed for Welsh crab populations in this study was much smaller than Scottish (Tallack, 2007a), Swedish (Ungfors, 2007), or Irish crab populations (Tully et al., 2006). There is some cause for concern if size at maturity is decreasing in a population, and although there are no previous studies on size at maturity for Welsh populations to compare with, we can compare with geographically proximal studies. *C. pagurus* populations in the UK have a high degree of gene flow (pers comm. Hayley Watson, Aberystwyth University, 2015) and can be considered a single genetic stock; though they are exposed to spatially variable environmental conditions and fishing mortality rates; thus comparisons between regions must be used with caution.

A decrease in size at maturity occurs when the cost of growth outweighs the cost of reproducing (or the benefit of maturing early is greater than the benefits of a larger body size; Roff, 1992). This can occur in populations experiencing size selective mortality, for example, if the large individuals are selectively fished (Roff, 1992). Maturing early may occur if population abundance decreases to a level where finding a mate becomes more difficult, or if the environment can no longer provide adequate resources for growth. Results from the recent stock status assessments in the UK revealed that current fishing mortality rates are above target and limit reference points for the population and beyond that which would provide maximum yield-per-recruit (ICES, 2012). Without historical data it is not possible to conclude that fishing mortality is driving down the size at maturity for Welsh populations of *C. pagurus*. This study provides important data for future comparisons of the reproductive state of Welsh populations.

Reproductive strategy

The hepatosomatic index (HSI) is typically used as a measure of health (as it is a measure of stored fats in the crab). Patterns in the HSI can indicate reproductive strategy as a pattern of energy flow during periods of gamete (egg and sperm) production. In physiological trade-off theory many animals fall under "Income vs Capital" breeders, where one species will use energy for reproduction as it is produced (income breeders) and others will store energy prior to a reproductive effort (capital breeders; Stearns, 1992). For *C. pagurus,* HSI decreased with maturity stage indicating that as reproduction progresses, energy is used and not replaced (suggesting a capitalist strategy). This strategy continues through with female crabs as the HSI decreased as fecundity increased, regardless of crab size (Haig et al., 2015).

Comparing size at maturity using different methodologies

The estimates of size at maturity varied with method, the smallest female observed with sperm plugs (**behavioural** method) was 118 mm CW, whilst **morphometric** methods indicated maturity at 95 and 132 mm CW for females and males respectively. By dissecting crabs to visualise **functional** maturity, the smallest mature *C. pagurus* was 68.3 mm CW for females and 63 mm CW for males. Morphometric indications of maturity are used in fisheries research when the destructive sampling of crabs is not possible. The onset of morphometric changes in *C. pagurus* does not align with functional maturity for either sex. Claw dimensions do not show allometric patterns until they are on average 45 mm CW larger than the CW_{50} estimates. Females on the other hand are displaying a significant change in abdomen size at a smaller body sizes than CW_{50}. The onset of positive allometry varies with sex in many other brachyuran crabs (25 species) as well; with males typically showing the strongest positive allometry after puberty and females prior to puberty (Hartnoll, 1974). The use of morphometric estimates of maturity in isolation will underestimate the number of mature male crabs, and depending on the length frequency of the population will slightly overestimate the number of mature females (the CW_{50} was only 8 mm larger than morphometric inflection point). Without historical data it is not possible to determine if the difference between morphometric and functional maturity estimates has increased, decreased or remained the same. As fishing pressure is known to alter growth patterns over ecological and evolutionary timescales (Kuparinen and Merilä, 2007); we may expect to see the relationship between morphometric and functional maturity alter with time and also with fishing pressure.

Conclusion

This study shows that *C. pagurus* stocks in Wales are maturing at a smaller size than the minimum landing size (between 135-145 mm CW), thus ensuring that both males and females have the opportunity to reproduce at least once prior to capture. That the size of maturity is smaller than adjacent populations is reason enough to investigate further, and more frequently Fisheries researchers have identified that size at maturity studies should be undertaken at least every three years (according to the minimum requirements of the Data Collection Framework, set out by the European Commission). This study provides a baseline for Welsh crab populations going forward with recommendations for temporal replicate studies to be undertaken.

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