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Fecundity of *Cancer pagurus* in Welsh waters; a comparison with published literature

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Technical summary

The decapod crab species *Cancer pagurus* is currently the most valuable crab fishery in UK waters. Fecundity is the reproductive rate of crabs measured by the number of eggs she produces; which is important for fisheries managers, as it is used to calculate the reproductive potential of a stock. Together with information on survival between life stages it is possible to estimate the expected number of recruits entering each life stage and then into the fishery. To date no published studies report the fecundity for Welsh *C. pagurus;* although there are a number of published studies on *C. pagurus* from the North Sea. A total of 96 gravid female *C. pagurus* were obtained from the static gear fishery in Welsh waters in 2014. Morphometric measurements were taken and external eggs were staged, measured and counted. Crabs were then dissected and internal ovary structure and condition was noted and hepatopancreas was removed and weighed to determine an index of body condition. The state of the female prior to capture was noted and each crab was assigned a condition index depending on which limbs and how many were missing (and were beginning to heal or regrow, thus were not lost during capture, transport or storage). Fecundity increased with carapace width; however, the strength of relationship varied with region and between this and other published research. Total fecundity varied between 26,590 and 2,836,000 eggs per female from crabs sized between 116 and 198 mm carapace width; this is within the range of other published research for this species. Most females carried eggs at an early stage of development (early gastrula) and as such, they were all approximately 400 µm in size. Morphologically more eggs are carried on the two proximal pleopod pairs, and significant differences of egg numbers between pleopods were observed. Crabs that had lost one claw and other limbs also had much lower fecundity and a variable ratio of eggs between the pleopods; though sample size of damaged females was too small for this trend to be significant. The hepatosomatic index decreased with increasing fecundity indicating that producing more eggs required more energy, regardless of animal size.

This research highlights the complexity in energetic trade-offs between condition, fecundity and energy reserves. Research is currently underway to determine if crab condition effects the level of energy provided to each individual egg; which would in turn determine the survivability of the larvae.

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 (ICES, 2012). 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).

Oviposition

From January to June oviposition (egg laying) occurs; usually four months after copulation (Shields, 1991). However, spawning can be delayed for up to 15 months (Pearson, 1908). English populations of *C. pagurus* are "berried up" (or ovigerous/carrying eggs) between January and March, with a peak in the season between April and June. The appearance of berried females early in November has been reported, but is thought to only account for 1% of the berried population for the season (Shields, 1991).

Estimating numbers of berried hens is difficult as gravid *C. pagurus* migrate from rocky habitats to softer bottom habitats, and display passive behaviours as well as reduced feeding (Howard, 1982). Berried hens will dig a pit and sit in a hollow of soft sediment to enable the abdominal flap to open fully; this allows protection whilst the eggs are brooded (Brown and Bennett, 1980). This behaviour is necessary as it takes around 12-24 hours for the eggs to adhere to the pleopods (Edwards, 1971). The female changes the frequency of egg ventilation due to an increase in oxygen demand as the eggs develop (Naylor et al., 1999).

Berried hens are thought to rarely enter baited traps (Howard, 1982). This is not true for other species of *Cancer,* for example *C. antennarius* and *C. anthonyi* will actively enter pots when berried (Shields, 1991). If berried hens remain in traps or are stressed they will consume their own, or each other's eggs (personal observation and from gut contents observations); other observations have been of females stripping the eggs from their abdomens with their chela, presumably as a stress response. Welsh fishermen have reported either having "never seen a berried hen in many years of fishing" or will "catch hundreds” in a season. This presents some very interesting possibilities for future research investigating migration routes and habitat choices of berried hens.

Brooding and larval release

Once extruded, the eggs are brooded for approximately eight months at which point they are ready to hatch as protozoea larvae. After this short-lived stage the larvae undergo five zoeal stages before metamorphosing into the final moult stage known as the megalopa. Within 24 hours the megalopa can settle out of the water column and onto the seabed (Edwards, 1979). *C. pagurus* broods in winter and the release of larvae coincides with spring plankton blooms, this allows larvae better opportunities to feed and then settle during warmer summer months. The annual reproductive pattern allows for optimum growth during periods of warm water and high food availability (Hines, 1991). The main hatching period of larvae occurs between May and September in Yorkshire and Irish waters (Edwards, 1979).

Fecundity

C. pagurus are iteroparous, meaning they can breed for multiple seasons and have the ability to breed more than once in their lifetime (Wootton, 1990). Fecundity has been defined as the potential reproductive capacity that an individual exhibits by producing viable eggs or sperm. In this study “Fecundity” refers to the potential annual fecundity represented by the total number of mature yolky oocytes in the brood of a female.

Understanding fecundity from a fisheries biology perspective permits better estimates of recruits from a standing brood stock (providing we also understand the natural mortality rates between larval and adult stages). The term “recruitment” refers to a life stage of an animal surviving to the next phase of life. For example larvae released during one brooding season will survive and mature to become juvenile recruits; or four year old animals may survive to grow large enough to “recruit” into the fishery in the following year. Recruitment can be hard to predict as mortality rates vary between life stages and also seasonally or regionally. We will not address mortality rates in this report but we suggest that future research is needed in this area.

Fecundity data was obtained from published studies using a visual data retrieval program (Tummers, 2006) . The available published literature provided six individuals from Scotland (Williamson, 1900), 45 from the Shetlands (in the North Sea; Tallack, 2007), 39 from the Kattegat and Skagerrak in Sweden (Ungfors, 2007) and 10 from Yorkshire in England (Edwards, 1979). On average 35% of variance in potential fecundity can be determined by the size of the female (carapace width). This variance is reflected by the variability in reported egg numbers for *C. pagurus* (345,000-3,880,000 eggs per brood). This variability may be caused by egg loss during brooding.

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 stores, or as a proxy for the health of an animal.

Methods

In the winter of 2013, 38 berried female *Cancer pagurus* were obtained from Welsh waters and a further four female samples were obtained from a previous study in 2012 from the Isle of Man. An additional 53 berried females were obtained from Welsh waters in winter 2014 totalling 95 *C. pagurus* females. Females were kept frozen and samples were thawed at room temperature before dissection. Wet weights and the following morphometrics were recorded: carapace width and length; abdomen width, right propodus (claw) height, length and width.

The egg mass on a female *C. pagurus* is attached to the pleopods, which are arranged in eight biramous pairs (Figures 1 and 2). The total egg mass was dissected away and weighed separately. All weights were measured to the nearest 0.01 g. Subsamples of between 0.2 - 0.5 g were taken by randomly selecting small bunches of eggs from around the entire egg mass. The total egg number from the subsample was counted using a bogorov tray under a dissecting microscope. Six eggs from each subsample were measured and staged using a compound microscope. Staging was determined using descriptions from the available published literature (Norman, 1989 and Edwards 1979; Table 1).

Table 1. Developmental stage and description of Cancer pagurus eggs (Tallack, 2007, after Norman, 1989 and Edwards, 1979).

Stage	Description	Colour
1	Newly spawned, full of yolk and lacking cleavage	Bright orange
2a	Cleavage, few large cells (early blastula)	Bright orange
2b	Many small cells visible (early gastrula)	Bright orange
3	Eyespots first visible	Red-orange
4a	Chromatophores first visible	Brown
4b	Chromatophores and eyespots well developed and heart evident	Dirty grey

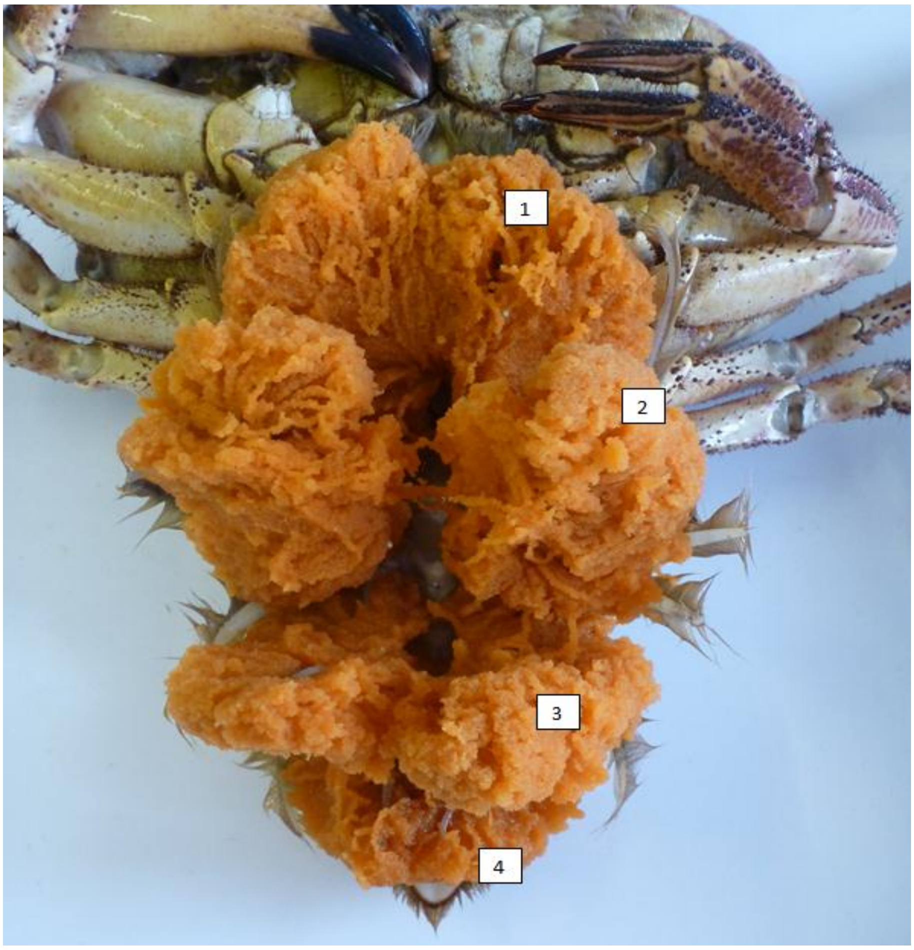

Figure 1. The biramous pleopod pairs on the abdomen of a Cancer pagurus female

Figure 2. Biramous pleopod pair one with egg mass attached, from a female Cancer pagurus

Wet weight estimates for fecundity were made on the 96 female *Cancer pagurus*. Of those, 53 egg masses were dried to constant weight to estimate dry weight fecundity for comparison between methods. Crabs were dissected and the hepatopancreas was removed and weighed to the nearest 0.01 g. To assess the amount of damage experienced by samples, a damage ranking was assigned to determine if an increase in observed damage had any effect on fecundity (Table 2) as physical damage may result in a reduction in levels of growth and/or reproductive behaviour (Clapp and Clark, 1989). It has also been suggested that appendage loss may decrease the individual's ability to copulate and can also reduce fecundity (Dial and Fitzpatrick, 1981). Damage index was compared with hepatopancreatic (or hepatosomatic) index (HSI) and total egg mass wet weights (analysis of co-variance) to determine if limb loss effected either HSI or egg production.

Table 2 Condition index to categorise the level of injury sustained by each Cancer pagurus female prior to capture

Condition	Description
1	No damage
2	Missing 1-2 legs/leg regrowth
3	Missing >2 legs/leg regrowth
4	Missing one claw
5	Missing one claw and some legs
6	Missing both claws
7	Missing both claws and some legs

N.B. Damage index was determined as the limbs missing prior to capture, as evidenced from healing wounds or re-growing limbs. Limbs lost in the capture or freezing process were not considered as missing for the purpose of the index.

The ovaries were observed for the presence of un-spawned eggs. Females with internal eggs present were assessed to see if fecundity was underestimated for these individuals.

Pleopod capacity

In addition to the total fecundity, the pleopod capacity of each female was investigated. To take into account the size of the crab we derived the pleopod index using the following equation: $Pleopod\ index = \frac{\text{Pleopod egg mass wet weight (g)}}{\text{Carapace width (mm)}} * 100$

Pleopod ratio was plotted for each pleopod pair.

Statistical methods

The difference between fecundity estimates from dry and wet weight samples of the same egg mass was compared using a Mann-Whitney U test (as data was found to be normal though variance was unequal as determined by Kolmogorov-Smirnov and Levene's test for equal variance).

Relationships between fecundity and carapace width were explored using linear regressions, ANOVA and where appropriate Tukey HSD post-hoc testing. Test assumptions were assessed using residuals plots for normality, independence, heteroskedasticity and Cook's distance.

A linear model was chosen to determine influences on fecundity (as number of eggs per female) with carapace width, condition, hepatosomatic index as the predictor variables. The assumptions were checked for the preferred model by plotting residuals for heteroskedasticity (standardised residuals against fitted values), normality (Q-Q plot) and outliers (Leverage and Cook's distance plots).

RESULTS

Methodology

Dry and wet weight estimates of fecundity were significantly different (W=709, $p<0.001$). The median value of dry weight estimated for fecundity calculation was higher than the wet weight estimate (380,200 and 192,800 eggs respectively). Mean and standard deviation for dry weight estimates (442,200±311,744) were higher than for wet weight estimates (225,300±153,937); however, dry weight estimates were more variable between individuals.

Fecundity

From the sampled size range of 115.6 to 198 mm carapace width, the fecundity estimates ranged between 26,590 and 2,836,000 eggs per female. Fecundity (eggs per female) data did not display a strong positive relationship with carapace width, though it was significant and did not violate model assumptions (R^2=0.10, p=0.001).

The linear model was applied using the following parameters:

$$\text{LnFecundity} \sim \text{Carapace Width} + \text{Condition} + \text{Hepatosomatic Index}$$

The above model did not violate any assumptions and was significant for all parameters except for condition, which was only just non-significant (R^2 adj = 0.29, $p<0.001$; Table 3). Fecundity was responded in a positive trend with an increase in crab size (CW), though negatively with HIS; and varied with condition.

Table 3. An analysis of variance table on the linear model using fecundity (natural log) as the response and carapace width, condition and hepatosomatic index as predictor variables

Parameter	Degrees of Freedom	Sum of squares	F value	P value = or <
Carapace width	1	11.783	13.20	0.001
Condition	4	8.134	2.28	0.067
HSI	1	17.039	14.21	0.001
Residuals	82	73.196		

Fecundity was not significantly different between each condition, though visual analysis of the data showed the mean value for condition 5 (one claw and some limbs missing) was lower (Figure 3).

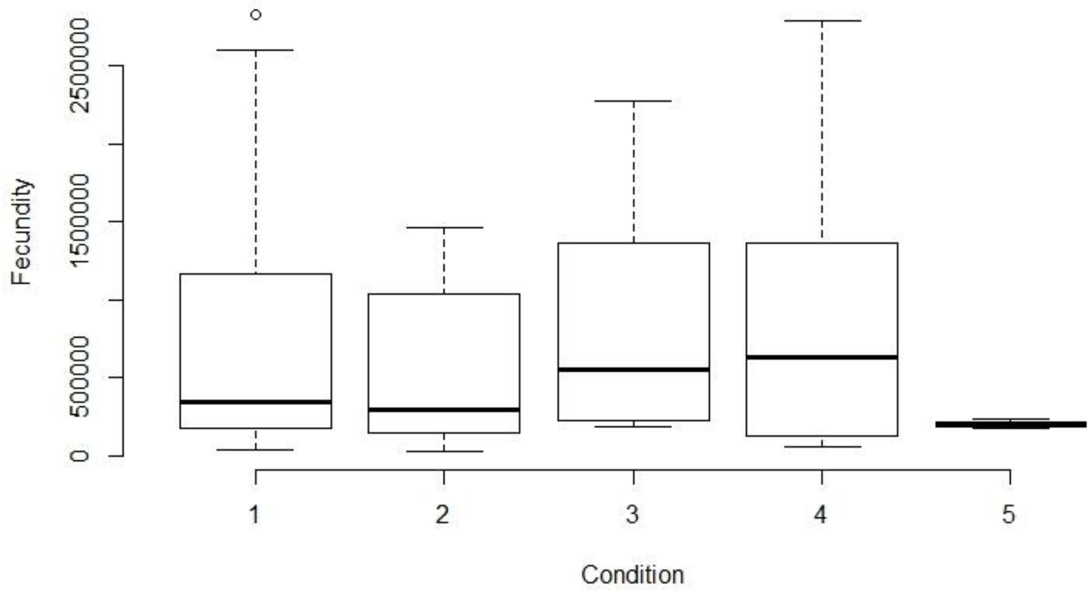

Figure 3. Fecundity index for Cancer pagurus categorised into each condition (1, all limbs present to 5, one claw and some legs missing). Number of crabs in each condition are as follows: Condition 1, n=58; Condition 2, n=15; Condition 3, n = 10; Condition 4 n = 5; Condition 5, n = 3.

Hepatosomatic Index and Fecundity

With an increase in the fecundity there was a significant decrease in the hepatosomatic index (Figure 4). This relationship was significant when modelled without any other parameters and did not violated the assumption of the model. Hepatosomatic index did not vary between crabs assigned to different condition indices (ANOVA).

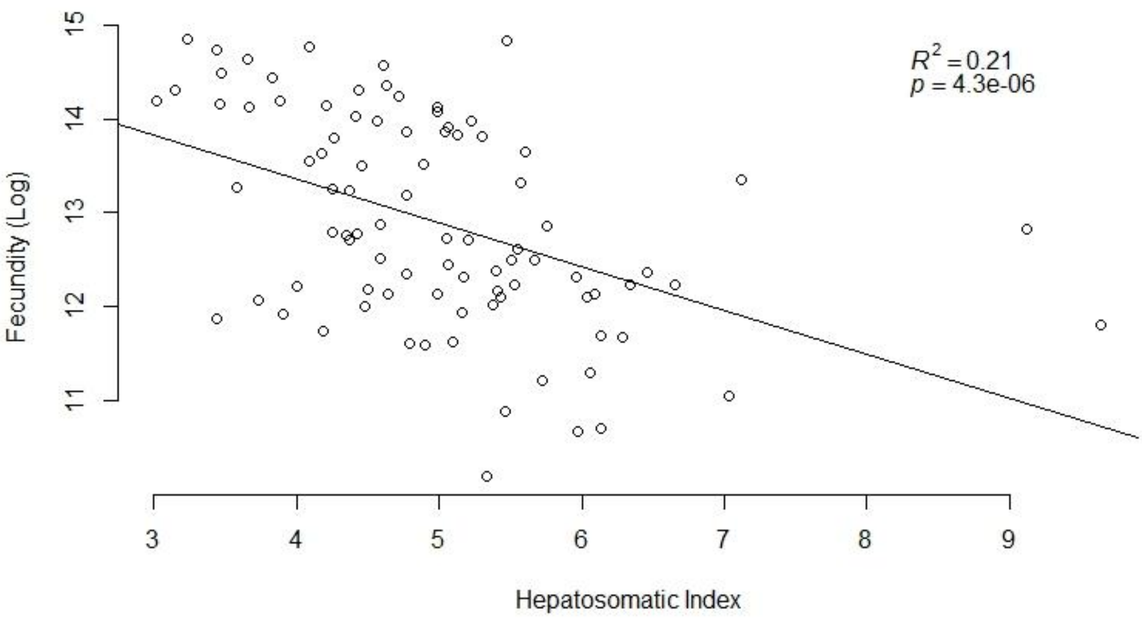

Figure 4. Linear relationship between fecundity and the hepatosomatic index. R^2 and p value situated in the top right corner for the regression analysis.

Pleopod capacity

Pleopod pairs one and two (being the two most proximal pairs; see Figure 1) carried a larger egg mass than pleopod pairs three and four (Figure 5). The pleopod ratio for the pleopod pairs one to four were significantly different from one another for every female (one-way ANOVA, $F_{3,360}=18.71$, $p<0.001$). A Tukey HSD post-hoc test revealed that there were significant differences between all pleopod pairs ($p < 0.05$) with the exception of pleopod pairs one and two, which were not significantly different from each other ($p = 0.99$).

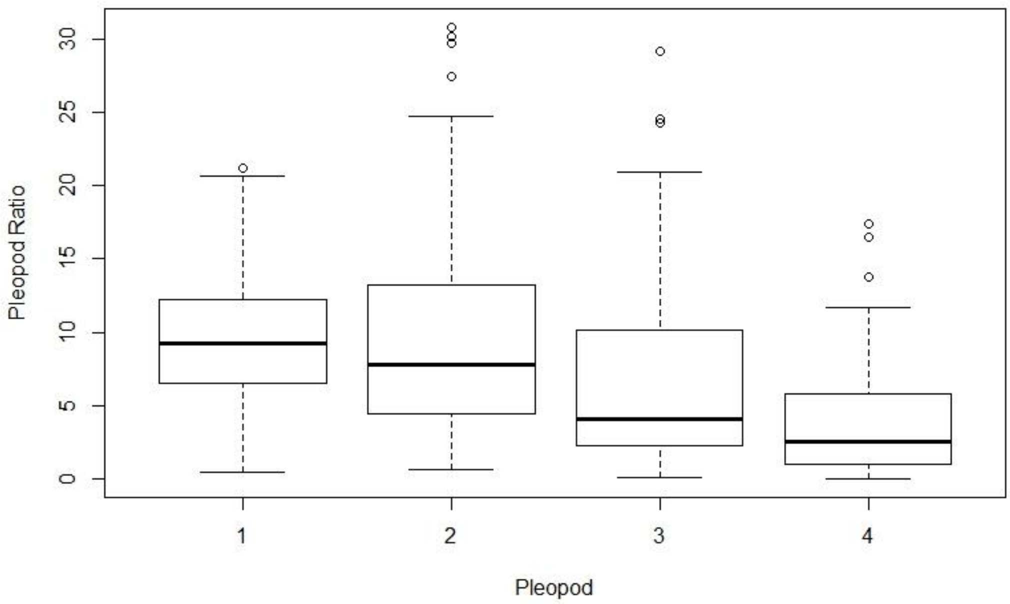

Figure 5. The relative ratio of eggs occurring on the four pleopod pairs for Cancer pagurus (n = 96 crabs). Pleopods 1 and 2 are the most proximal and consistently carry more eggs than the two distal pleopod pairs.

A pleopod capacity was taken as the sum of the egg weight from each pleopod and multiplied by two (as per Tallack, 2007) and were tested for variation between condition index to determine if condition had an impact on the pleopod capacity. Pleopod capacity significantly varied between all condition indices (one-way ANOVA $F_{4.459}$=3.114, p=0.0154) which was also supported by a post-hoc Tukey HSD test (and see Figure 6). The post-hoc test concluded that there were significant differences between condition indices of five and one (p=0.05) and of five and three (p=0.03).

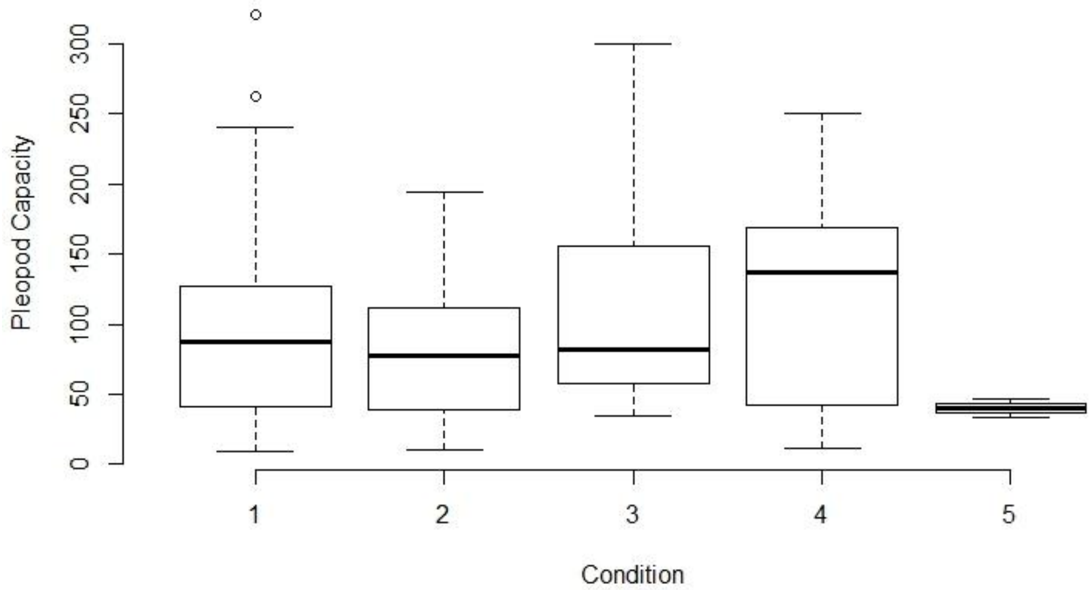

Figure 6. The pleopod capacity, calculated as the sum of the egg weights x2 (Tallack, 2007a) *for Cancer pagurus assigned to five of the seven possible condition indexes (n = 96 crabs).*

Egg size

Egg size ranged from 350–440 µm; with a mean value of 401 µm (Figure 7). Of the 96 sampled females, the dominant egg stages observed across the whole egg mass were: stage 1 (1 crab), 2a (2 crabs), 2b (early gastrula, 89 crabs), 3 (12 crabs). No significant difference was observed between the size of the female and the average egg size, one-way ANOVA, $F_{1,88}$=2.161, p= 0.145. No significant difference was observed between the egg sizes at each stage nor female body size (one-way ANOVA, $F_{1,78}$=3.365, p=0.0704 and $F_{1,5}$=1.841, p=0.233 for stages 2b and 3 respectively).

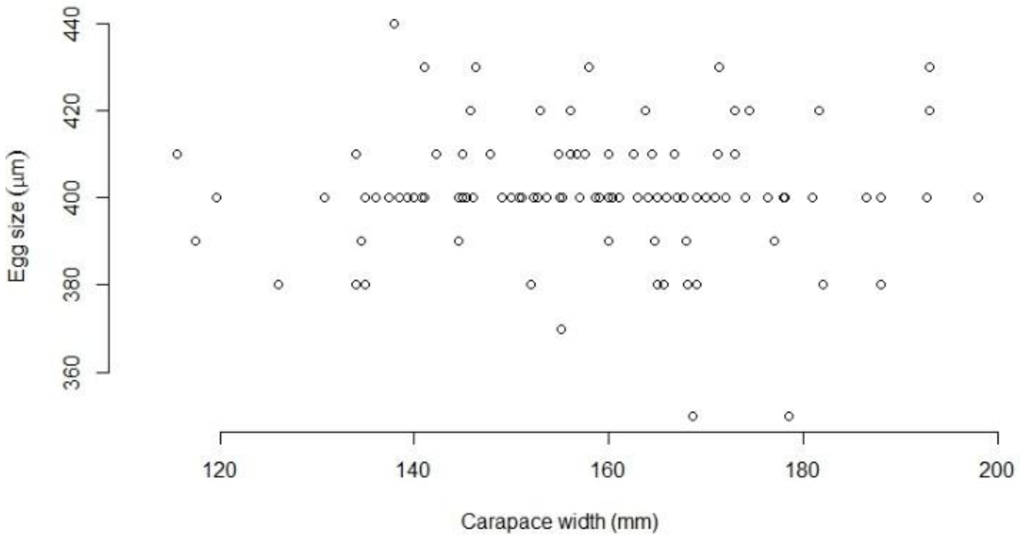

Figure 7. Carapace width and mean egg size of six eggs measured from 95 Cancer pagurus caught in Welsh waters in 2014

Regional comparisons with published data

A comparison of fecundity against the published literature revealed that fecundity estimates in this study were more variable but fit within the current findings for *Cancer pagurus.* Wet weight estimates from the literature fell within our data, though dry weight estimates were mostly below that found in the literature (Figure 8 & 9). Fecundity data could be predicted by carapace width for the data when all data was combined for a linear model (R2 = 0.30, p<0.001). The model was not improved when data source (our study or published literature) or laboratory method (wet or dry weight of eggs used to estimate fecundity) was added.

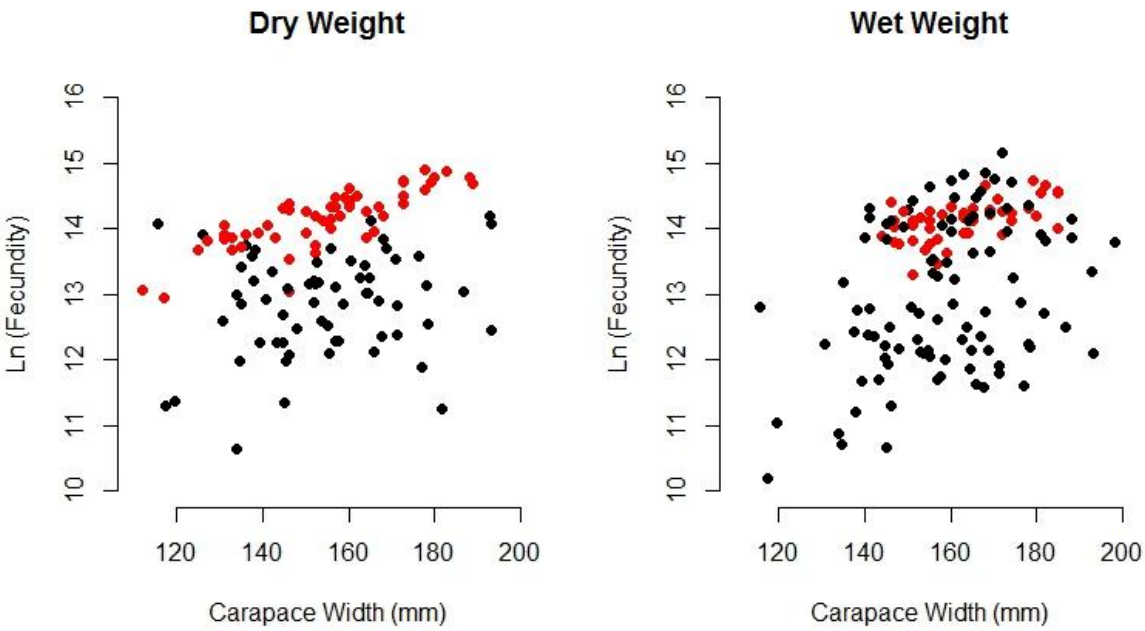

Figure 8. Carapace width as a predictor for fecundity estimates using dry weight (left) and wet weight (right) laboratory methods to obtain fecundity estimates. Black circles are this study, red circles are data from the literature

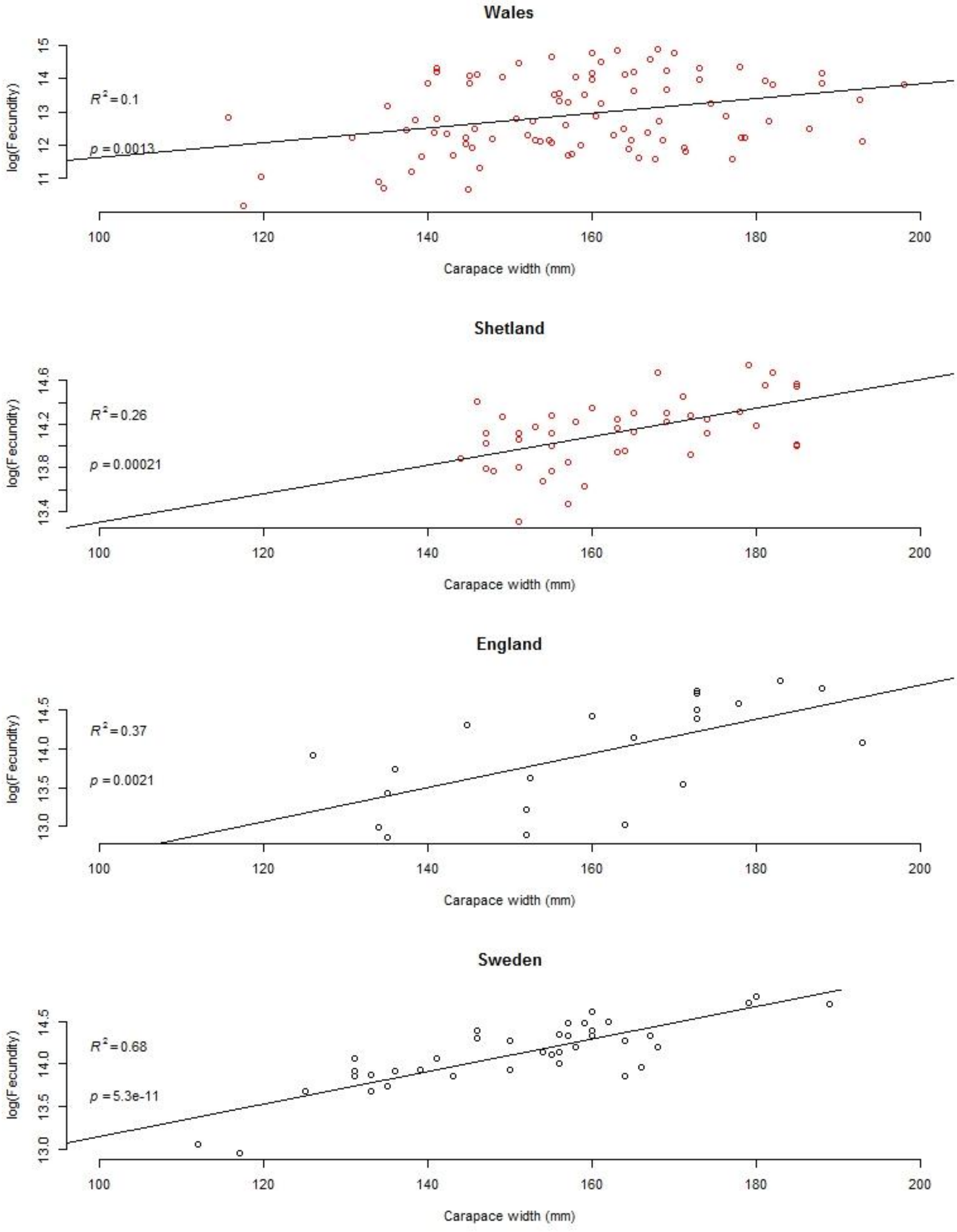

Figure 9. A scatter-plot of carapace width (CW) by estimated fecundity (ln number of eggs) for populations of Cancer pagurus in Wales (this study), Shetland (Tallack, 2007b), *Scotland (Williamson, 1900), England (Edwards, 1967) and Sweden (Ungfors, 2007). Linear trend lines are fitted and the R^2 and significance values are provided in the top left corner of the individual plots. Red circles indicate wet weight fecundity method and black indicates dry weight method.*

Table 4. A summary of the range in findings from our and other published research on fecundity for Cancer pagurus. Linear regression descriptors for comparative studies of Cancer pagurus fecundity-size relationships (see also Figure 9), method used to determine fecundity and fishing method also reported.

Location	n	CW	Fecundity	p value	Reported R^2	Mean egg diameter (μm)	Method	Fishing method
Wales UK (this study)	96	115.6-198	41800-3,880,000	0.014	0.056	401	Wet/Dry	Pot caught
Isle of Man (this study)	4	150-174	1,597,000 - 3,880,000	0.2433^{NS}	0.36	400	Wet	Trawl
Shetland (Tallack, 2007a)	45	129-212	780,000- 2,400,000	<0.001 ***	0.29	-	Wet	Pot caught
Scotland (Williamson, 1900)	6	128-178	460,000 - 3,000,000	0.1708^{NS}	0.26	-	Dry	Trawl
England (Edwards, 1967)	10	145-183	1,632,000 - 2,876,500	0.01589*	0.48	508	Dry	Pot caught
Sweden (Ungfors, 2007)	39	113-190	500,000 - 2,500,000	<0.001***	0.68	383±20*	Dry	Gillnet (29), Pot (10)

DISCUSSION

It is the popular belief that berried *Cancer pagurus* cannot be caught in pots. Some literature states that berried females are unlikely to enter a baited pot due to loss of appetite; a change in behaviour and diurnal migrations (Howard, 1982). All samples from the current study were obtained from traps (crab pots). Anecdotal evidence suggests that in some areas it is very common to catch berried crabs in pots. Females are either extruding their eggs once caught, or they remain attracted to pots for a short time after exuding their eggs. No observations of females part-way through egg extrusion were made. Even the few females observed with very fresh broods (sticky egg masses) did not contain ovaries full of eggs, thus all females had completed their egg laying. It is possible that where berried hen crabs are commonly seen, there exists a migration route of berried females, migrating to a location suitable for brooding their eggs. This is an interesting hypotheses that could be tested using a combination of tagging and trawl or diver surveys. Further, the identification of brooding habitats and seasonal patterns for *C. pagurus* is vital as there is some concern for an increase in gravid crabs caught as scallop bycatch during the crab brooding season in specific locations.

The linear relationship between fecundity and carapace width (CW) is reportedly strongly positive for *Cancer pagurus* (Ungfors, 2007); however, the relationship observed in this study was only weakly positive, and improved when considering other response variables for condition and energy reserves. This study highlights that variability may be influenced by a number of factors, such as the condition of the female prior to laying, and possibly egg loss due to natural causes or catch method. The catch method (static gear / crab pots) has been used in other studies with lower variability (Ungfors 2007), therefore it is not possible to determine how much catch method contributes to the variability. Welsh fishermen have observed berried hens eating and pulling off their own eggs using their chela when they have been caught in pots. Presumably it would be possible to detect if this was happening by the difference in the proportion of eggs distributed across the four pleopods; though no such trend was found in low fecundity females. In other research we have observed male and female *C. pagurus* stomachs full of bright orange eggs, presumably conspecific eggs. The consumption of eggs is probably not unusual as a stress response for this species. It was not possible to determine if egg loss occurred prior to capture. No eggs were observed in the stomachs of the females and observations of the egg masses did not show any signs of obvious recent trauma. Analysis method is also not likely to cause the amount of variation seen (as wet weights produced less variation than dry weight estimates of fecundity).

C. pagurus do not feed during brooding, and so it is presumed that for this species, the stored energy reserves are important for adult survival through to the end of the brooding. The HSI was lower in female *C. pagurus* with greater fecundity suggesting that for *C. pagurus* there is a trade-off between energy stores and fecundity. Fecundity in *C. pagurus* may be determined by energy stores prior to producing eggs; and if conditions to accumulate the necessary energy stores are temporally and spatially variable we would expect to see variation in fecundity responding to body condition more than body size. Research has shown an energetic trade-off between repair and reproductive effort (Dial and Fitzpatrick, 1981). Body condition at mating may have a direct effect on the number of eggs by diverting energy away from egg production into repair. There was a marked decrease in fecundity for females with one claw and some legs missing (condition index 5). This finding was only slightly significant due to the low sample size of damaged females (only 4 of the 96 crabs from Wales displayed a condition 5). This is worthy of further investigation to determine if crab condition effects energy stores, which in turn effects fecundity. This would be of particular interest to countries that allow the landings of claws only, as decreasing the fecundity in a population of *C. pagurus* could have longer term recruitment effects.

Typically the eggs seen were newly laid, no late stage eggs were observed confirming that at advanced gravid stages, crabs are not likely to be caught in potting gears. The reports of egg size in the available literature vary for *C. pagurus* (see Table 4). The size of the eggs within an egg stage was thought not to vary between females (Hines, 1991) and this was observed for female *C. pagurus* in this study. The majority of the egg stages were early gastrula. As eggs develop, the yolk is progressively ingested by the embryo, the eggs then appear darker in colour and eyespot are visible; though this development of the size of the egg should remain the same until the heart is visible (stage 4b) and they are ready to hatch at which point the eggs are noticeably larger. This could explain the larger egg diameter that was observed in English samples (Edwards, 1967).

In comparison with other literature our fecundity estimates were considerably variable. This variability was present regardless of laboratory method used (wet / dry estimates), location, or region in Wales. Many of the fecundity estimates were lower than the published literature which may be the result of either: greater egg loss experienced prior to obtaining the samples (though there was no evidence for this in either the visual inspection or pleopod ratio of eggs); or it is a true artefact of low egg numbers produced by Welsh crabs. Future research is needed to determine the source of variation in fecundity for this species.

Current and future research

Research on maternal provisioning is currently underway on the females sampled in this study. We hope this research will provide a more in-depth understanding of the interplay between energy stores, fecundity and maternal provisioning. This research will be of interest to fisheries management as low quality eggs are known to produce larvae with lower survival rates, decreasing the abundance of recruits resulting from any given brood. For recommended future research: an *in situ* laboratory or mesocosm approach to keeping berried hens would also enable investigation into brood attachment and natural brood loss throughout the egg-carrying season.

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