# Size-at-maturity of Brown Crab (*Cancer pagurus*) in Scottish waters based on gonadal and morphometric traits

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## Abstract

Minimum landing sizes (MLS) are commonly used to manage crustaceans and are generally set above the size at first maturity to ensure that some protection is afforded to exploited stocks. Despite the economic importance of the brown crab fishery in Scotland, the species is considered data-poor and only limited information is available on size-at-maturity. This study provides, for the first time, estimates of the size-at-maturity of brown crab on the east and west coasts of Scotland using gonadal and morphometric criteria. Gonadal maturity was determined from female ovary and male testes, which were classified macroscopically into development stages and their relationship with body size modelled using a logistic regression. Body morphometric maturity was studied by analysing morphometric changes in growth in the male chelae and female abdomens using generalized additive models and regression models to estimate the size at which changes in allometric relationships occur. Estimates of size-at-maturity using gonad development were 101-106 mm carapace width (CW) for males and 127-128 mm for females. Size-at-maturity based on the morphometric characters were 120-148 mm CW for males and 131-142 mm for females. Results show that brown crab maturity is likely to occur at lower sizes than the current MLS in Scotland, implying that crabs may be able to reproduce at least once before being harvested. Regional variations in local populations should be considered when setting a MLS and this study suggests that the current MLS of 150 mm is appropriate for both areas considered.

**Keywords:** *Cancer pagurus*, brown crab, size-at-maturity, minimum landing size, data-limited fisheries, Scotland

## 1. Introduction

The brown crab (*Cancer pagurus*) is a benthic decapod crustacean present in the eastern Atlantic from north Norway to West Africa and living in a wide range of sediments (Hayward and Ryland, 1990). Brown crabs are commercially harvested in Scotland by inshore and offshore fishing fleets using traps and the fishery supports many local communities. The Scottish fishery expanded to offshore areas in the 1990’s with landings showing a generally increasing trend since then, accounting for over 20% of total European landings with a first sale value of £26.8 million in 2018 (Mesquita *et al.*, 2017; STECF, 2017; Scottish Sea Fisheries Statistics, 2018). Vessels fishing for brown crabs in Scotland are required to hold a licence with a shellfish entitlement and there are EU measures in place to restrict fishing effort in ICES Subarea VI (EC, 2004), but the fishery is not subject to any EU total allowable catch (TAC) regulations or national quotas for landings.

The setting of a minimum landing size (MLS) is a widely used strategy to manage crustacean fisheries (Brown and Bennett, 1980; Tully *et al.*, 2001; Hearn, 2004; Woll *et al.*, 2006). The goal of the MLS as a management measure is to allow individuals to reproduce at least once before being harvested (Ungfors, 2007). There are various brown crab MLS enforced around Europe and within the UK for different brown crab fisheries. The main regulatory mechanism in Scotland is an MLS of 150 mm carapace width (CW) around the Scottish coast except in the Shetland Islands where the MLS is 140 mm (The Specified Crustaceans Order, 2017). Determining an appropriate MLS is reliant on size-at-maturity information and MLS is typically set above the size-at-maturity $L_{50\%}$, defined as the CW at which 50% of the individuals are estimated to be mature (Somerton, 1981; Quinn and Deriso, 1999). It should be noted however that if the MLS is set at any size below that at which 100% of the crabs are mature, some immature crabs may be landed legally.

Maturity in decapod crustaceans can be defined based on several different types of criteria: behavioural, gonadal, morphometric and functional. An individual is defined as behaviourally mature when they are able to copulate, evidenced by the presence of sperm plugs (seminal secretions delivered during mating) in the oviducts of female crabs (Hartnoll, 1969; Edwards, 1979). Identification of gonadal or physiological maturity (the two are arguably equivalent) is based on the presence of spermatophores in males and developed ovaries in females and occurs when the reproductive organs are capable of producing gametes (Edwards, 1979; Corgos and Freire, 2006). Body morphometric maturity occurs when changes in the growth pattern of certain body parts take place at the start of sexual activity. In female crabs, an increase in growth rate of the abdomen and pleopods has been described at the onset of maturity, reflecting the role these body parts play in covering and protecting the eggs (Hartnoll, 1974). In male crabs, the chelipeds (which are used for combat, display and courtship) start to grow more rapidly than those of females of the same body size and this change has been associated with the start of reproduction (Bliss and Abele, 1982). Functional maturity refers to when a combination of behavioural, gonadal and body morphometric maturity enables the successful production of offspring (Tallack, 2007). Hartnoll (1969) proposed that (functional) maturity is achieved when crabs reach an intermoult stage called "puberty moult" at which both gonadal and external morphological changes start to occur. Female crabs have been reported to copulate prior to the moult of puberty, indicating that behavioural maturity does not necessarily indicate that animals are functionally mature since gonadal/morphometric development may still not be sufficiently advanced (Wilhelm, 1995).

In the case of characteristics which unambiguously indicate maturity (i.e. maturity can be treated as a 0,1 variable), a binomial GLM (logistic regression) (McCullagh and Nelder, 1989) can be fitted to estimate the size at which 50% of animals are mature. For morphometric measurements, it is expected that the onset of maturity will be indicated by a change in growth rate and several possible statistical approaches could be used. Both piecewise (Pardo *et al.*, 2009) and segmented (Williner *et al.*, 2014) regression approaches have previously been applied in crabs, while Generalized Additive Models (GAMs) (Wood, 2006) offer a more flexible approach to describing changes in growth rate.

Despite the economic importance of the brown crab fishery in Scotland, this species is considered data-limited in terms of understanding basic population parameters such as age, size-at-maturity and fecundity (Haig *et al.*, 2016; ICES, 2016). Given that growth and maturity may vary depending on environmental factors and population density, it is important that estimates of size-at-maturity are updated regularly over time and are stock-specific. For widely distributed species such as brown crab, these regional variations in biology should be taken into account when setting MLS (Bennett, 1995; Öndes *et al.*, 2017). A number of studies have been carried out on brown crab maturity around the British Isles and more widely across Europe, predominantly based on gonadal maturity, morphometric characters or presence of sperm plugs. Studies on this species in Scotland have been limited to Shetland and Orkney (Tallack, 2007; Haig *et al.*, 2016). There have also been studies in Bay of Biscay (Le Foll, 1984), Norway (Haig *et al.*, 2016; Bakke *et al.*, 2018), Ireland (Tully *et al.*, 2006), Skagerrak and Kattegat (Ungfors, 2007), Wales (Haig *et al.*, 2016), Isle of Man (Haig *et al.*, 2016; Öndes *et al.*, 2017), east coast of England and English Channel (Smith, 2010; Haig *et al.*, 2016).

This study provides, for the first time, estimates of the size-at-maturity of brown crab on the east and west coasts of Scotland. The maturity of both sexes was considered by evaluating the development of gonads and analysing morphometric changes in growth in the male chelae and female abdomens. Behavioural maturity was also considered by investigating the presence of sperm plugs in female crabs in the eastern and western populations. The maturity estimates obtained are compared with those estimated elsewhere, thus increasing the knowledge of the species biology. The findings of this study are relevant to inform management of the Scottish brown crab fishery and the suitability of the current MLS.

## 2. Material and methods

### 2.1. Sample collection

Brown crabs used in this study were collected from three fishing vessels working in the east and west coasts of Scotland during seven sampling events, from March to June 2015 (Table 1). The three vessels used baited creels without escape panels to capture brown crabs as part of their typical fishing operations. Samples were obtained from ICES rectangle 42E7 on the east and 45E2, 45E3 and 46E3 on the west coast (Figure 1). In order to detect the point at which maturity is achieved, it was necessary to sample a wide range of sizes to ensure inclusion of both immature and mature individuals. A derogation was issued to the vessels participating in the study allowing the landing of both crabs below the MLS and of ovigerous females. Following each collection trip, crabs were either sampled fresh or frozen for further examination. Since few immature males were obtained from the east coast during the first two sampling trips, a third trip was conducted in this area aiming to increase the number of small-sized males available for sampling (Table 1).

## 2.2. Laboratory methods

Frozen crabs were left for a minimum of two hours at room temperature before processing. Each individual was scored for shell condition (hard, soft or broken) and for any evident signs of diseases. Studies have shown that crabs with severe levels of shell disease such as “black spot” condition, often display alterations to several organs (Stentiford, 2008) which could interfere with growth and maturation. All crabs were examined to determine the sex and all length measurements were made to the nearest 0.1 mm below using digital Vernier callipers.

The size of a brown crab is described by the CW, measured as the maximum width of the carapace perpendicular to the antero-posterior midline of the carapace. To analyse maturity from body morphometry of males, measurements of the left cheliped were taken for cheliped depth (ChD), height (ChH) and length (ChL). Cheliped measurements were made as described by previous studies (Tallack, 2007; Ungfors, 2007). If the left cheliped was missing or regenerating, measurements were taken from the right cheliped instead. Females were inspected to determine the presence of any egg shells or sperm plugs in the spermatheca. The morphometric indicators of maturity used in this study for females were the abdominal width (AW) and pleopod capacity as estimated from the pleopod weight (PW). The AW was measured on the fifth abdominal segment at the broadest part (Ungfors, 2007). To obtain PW, female pleopods were cut at the base, removed from the abdomen and weighed to the nearest 0.001 g.

To determine gonadal maturity, crabs were dissected with the female ovary and male testes and vas deferens classified macroscopically into development stages. Gonad stages were classified as reported in a recent study (Haig *et al.*, 2015) based on visual descriptions for female (Edwards, 1979; Ungfors, 2007) and male (Ungfors, 2007) maturity stages (Table 2).

## 2.3. Data analysis

### *2.3.1. Generalized linear models (GLMs)*

Male crabs were classified as mature at developmental stages 2 and 3. For female crabs two scenarios were considered, given uncertainty about whether stage 2 corresponds to mature animals (Tully *et al.*, 2006): scenario 1 included a classification of mature females as those at stages 2-5 and scenario 2 considered mature females as those at stages 3-5. The gonadal maturity data were converted into binary format (0: immature; 1: mature) and modelled using a logistic regression by applying a GLM with a “logit” link function, the response variable being maturity, and using CW as an explanatory variable, separately for each combination of area and sex. Since the response variable was [0,1], a binomial model was used, with a logit link function. The expected value of the proportion of mature individuals $E(p_i)$, is given by

$$E(p_i) = \frac{e^{\beta_0+\beta_1 \mathrm{CW}_i}}{1 + e^{\beta_0+\beta_1 \mathrm{CW}_i}},$$

where $\mathrm{CW}_i$ is the carapace width of length category (midpoint) $i$ and $\beta_0$ and $\beta_1$ are parameters of the model. $E(p_i)$ is a sigmoid curve bounded between 0 and 1 (Wood, 2006) and the expected number of mature individuals, $\mu_{\mathrm{i}}$ is

$$\mu_i = E(p_i)N_i\ ,$$

with $N_i$ being the total number of individuals at length category $i$. Applying the “logit” link function $g(\mu_i)$ implies the linear relationship:

$$g(\mu_i) = \log\left(\frac{\mu_i}{N_i - \mu_i}\right) = \beta_0 + \beta_1 \mathrm{CW}_i\ .$$

Parameters $\beta_0$ and $\beta_1$ were estimated by maximum likelihood. The length at which 50% of individuals are mature ($\mathrm{L}_{50\%}$) is achieved when $g(\mu_i) = 0$ resulting in $\mathrm{L}_{50\%} = -\beta_0/\beta_1$.

### *2.3.2. Generalized additive models (GAMs)*

To study morphometric maturity, GAMs were applied to visualize and describe the relationships between CW (explanatory variable) and the various response variables, i.e. each of the claw measurements ChD, ChH and ChL for males, and CW versus abdominal width and pleopod weight, AW and PW respectively, for females. The GAMs were fitted separately for each area using an identity link function assuming a Gaussian error distribution. The smoothness parameter on each of the measurements was estimated with generalized cross validation (GCV) (Wood, 2006). For each GAM fitted, an additional linear model was also fitted without smoothing and an F test used to compare the models and statistically test whether the smooth term resulted in a significant improvement in model fit.

### *2.3.3. Segmented and piecewise regression*

To calculate the CW at which changes in allometric relationships occur (body morphometric maturity), piecewise regression and segmented regression were also applied, using the same metrics as in the GAMs (males: ChD, ChH and ChL; females: AW and PW). The piecewise regression was implemented by fitting linear models using an iterative regression method previously used on brown crab (Somerton, 1980; Haig *et al.*, 2016) as follows:

$$Y_i = \begin{cases} \alpha_0 + \alpha_1 \mathrm{CW}_{i,} & \mathrm{CW}_i < K \\ \alpha_2 + \alpha_3 \mathrm{CW}_i, & \mathrm{CW}_i \geq K \end{cases},$$

where $Y_i$ is any of the morphometric measures mentioned above, $K$ is the allometry breakpoint, and parameters $\alpha_0$ and $\alpha_1$ are the intercept and slope to the left of $K$ (CW < $K$) and $\alpha_2$ and $\alpha_3$ are the intercept and slope to the right of $K$ (CW ≥ $K$). The breakpoint $K$ is determined using an iterative approach, partitioning the data and refitting the model at different values of $K$ until the breakpoint resulting in the minimum residual sum of squares is found (Somerton, 1980). A t-test was then performed to determine whether the slope term $\alpha_3$ is statistically different from $\alpha_1$, i.e. whether term $\alpha_3$CW can be excluded from the model and the $Y_i$ could be described using a single slope ($\alpha_1$). A slope value equal to 1 represents isometric growth while slope values below or above 1 represent negative or positive allometric growth respectively.

A second regression method, segmented regression (Muggeo, 2003), was also fitted to the same morphometric datasets to identify breakpoints and respective confidence intervals (CIs). The segmented regression differs from the piecewise regression in the sense that it requires the fitted lines to join at the estimated breakpoint. The segmented fitting process is iterative and based on the minimization of a parameter which measures the “gap” (at each possible breakpoint) between two fitted straight lines (Muggeo, 2008). The algorithm converges when the standard error of the breakpoint is minimized.

All statistical analysis was performed in R environment (R Core Team, 2016). GAM models were fitted with R package mgcv v. 1.8-23 (Wood, 2011). The segmented regression models were fitted using the R package segmented v. 0.5-1.4 (Muggeo, 2008).

## 3. Results

A total of 1008 brown crabs was collected for this study, 486 from the east and 522 from the west of Scotland (Table 1), with females making up 43% of the total number sampled. Less than 2% of the animals had carapace damage (7 individuals) or showed mild signs of blackspot disease (11 individuals) and all crabs were used in the maturity analysis. Male crabs ranged between 73 and 211 mm CW and females were 83-204 mm CW. The length frequency distributions of crabs captured are shown in Figure 2 for each area and sex. Most of the crabs collected had CW in the range 130-150 mm, with a noticeable drop in numbers below 120 mm (except for the east coast males). No ovigerous females were caught in the sampling trips and further inspection of the pleopods revealed no egg shells present in any of the females sampled.

### 3.1. Behavioural maturity

No evidence of sperm plugs was found in the east coast female crabs (Table 3) which were collected in March. On the west coast, where collection took place from April to June, over 84% of females carried sperm plugs, including individuals in most length classes (83 to 204 mm CW). The proportion of females showing evidence of having mated was above 70% in most length classes (Figure 2, top right graph). In the west coast females, no relationship was found between the proportion of plugged females and CW.

### 3.2. Gonadal maturity

The smallest crabs with mature gonads, by sex, were a 86 mm CW male and a 110 mm CW female, both caught on the east coast (Table 3). The gonadal size-at-maturity $L_{50\%}$ as estimated using GLMs was 101 mm (N=290, 95% CI [98-103]) for males on the east coast and 106 mm (N=283, 95% CI [102-110]) on the west coast (Figure 3). For females, $L_{50\%}$ was estimated at 128 mm (N=196, 95% CI [125-131]) in the east and 127 mm (N=239, 95% CI [124-130]) in the west, when gonadal stage 2-5 was assumed to correspond to mature animals (scenario 1). Under scenario 2, where only animals in stages 3-5 were classified as mature, $L_{50\%}$ was 146 mm (95% CI [143-150]) in the east and 145 mm 95% CI [143-147] in the west (Figure 4). In both areas females were estimated to mature at a larger size than males. Confidence intervals (95%) were generally narrow around the estimated $L_{50\%}$ although slightly wider when lower numbers of crabs around $L_{50\%}$ were available (e.g. west coast males) (Table 3). All these maturity ogives except those for females under scenario 2 imply that most crabs would be mature at the current MLS of 150 mm (Figure 3 and Figure 4).

### 3.3. Body morphometric maturity

GAMs were used to visualise the data before implementing regression methods to estimate potential breakpoints corresponding to body morphometric maturity. As part of the GAMs model validation, visual inspection of the residuals indicated no obvious departures from normality and plots of the residuals against the explanatory morphometric variables showed no patterns. A summary of the GAM results is shown in Table 4. GAM models with a non-linear (d.f.>1) smooth term were found to provide a better fit than a linear model without smoothing for all morphometric measurements against CW (F test, $p \leq 0.001$), except for AW in the west coast females (p=0.142) (Table 4). This implies that a non-linear fit is more appropriate for these data as confirmed by the degrees of freedom estimated for the GAMs (d.f.>1) (Table 4). Breakpoints corresponding to body morphometric maturity were identified by applying regression methods (piecewise and segmented) to the relationships described above between CW and measurements of claws, abdomen and pleopods. A summary of the results of piecewise regression and segmented regression is presented in Table 5. The outputs of the morphometric analysis using each of the regression methods are compared to the GAMs in Figure 5 and Figure 6 (piecewise regression) and Figure 7 and Figure 8 (segmented regression). For male brown crab, breakpoints based on chelae measurements varied between 120 and 148 mm CW. Breakpoints estimated for males using the same regression method on three male chelae measurements were slightly larger in the west (compared to those estimated for the east) but fairly consistent within each area. The two regression methods gave very similar results for the west coast males with the piecewise breakpoints estimated to be within the CI for the segmented breakpoints (Table 5). On the east coast, the estimated breakpoints occurred at larger CW for the piecewise regression than for the segmented regression (Figure 5 and Figure 7). Brown crab female breakpoints ranged between 131 and 173 mm CW based on AW and PW (Table 5). Estimated breakpoints based on AW had large CIs in the east and west coast for both the segmented and piecewise regression (Figure 6 and Figure 8). Breakpoints estimated for PW were slightly larger in the east coast for both regression methods and had narrower CIs (segmented regression). For all morphometric measurements except AW, growth of the relevant body part speeded up after the estimated breakpoint, for both males and females with the slope for larger animals being steeper (more positive) than the slope for smaller animals.

## 4. Discussion

The size range of sampled individuals (73-211 mm CW) appeared to be sufficient to cover the range of sizes-at-maturity estimated by different methods in this study. Difficulties associated with capturing smaller crabs are likely to be related to the selectivity of the traps used in the fishery, in which animals below 60 mm CW are rarely found (Brown, 1975; Addison and Lovewell, 1991). In the present study, both $L_{50\%}$ and morphometric breakpoints were estimated to be within the size interval within which the majority of crabs were caught.

No females carrying eggs were collected during the study. Egg capsules adhering to the pleopods could also potentially indicate individuals that had recently carried eggs but, again, no evidence of this was found. It is unlikely that functional maturity occurs outside the size range sampled (Edwards, 1979) and the absence of ovigerous females in the sample may be explained by their low catchability (they are rarely caught by commercial vessels) as their behaviour means they are unlikely to enter traps (Howard, 1982; Bennett, 1995; Ungfors, 2007). Therefore, it is not possible to draw any conclusions about size at functional maturity from the data obtained in this study.

### 4.1. Behavioural maturity

Since the formation of sperm plugs follows copulation and they are not found in unmated females, sperm plugs are indicators of mating activity and hence of behavioural maturity in cancrid crabs (Hartnoll, 1969; Brown and Bennett, 1980; Oh and Hankin, 2004). Copulation in brown crabs occurs immediately after the females moult (when the shell is soft) and studies around Britain, Ireland and Norway detected a moulting peak from early summer to late autumn (Edwards, 1979; Brown and Bennett, 1980; Tallack, 2007; Ungfors, 2007). Around the coast of Britain, spawning and incubation continues throughout winter, where eggs remain attached to the pleopods for a period of seven to eight months after which hatching takes place during spring to summer (Edwards, 1979). Sperm plugs were found in most females sampled on the west coast but none were present in the east coast crabs. East coast sampling of crabs took place earlier (females in March, males from March to April) than in the west coast (April-June) although even the earliest sampled crabs on the west showed clear signs of sperm plugs being present in most individuals. The differences in the prevalence of sperm plugs may be attributed to temporal differences in mating cycles between east and west coast populations if the optimal environmental conditions favourable for moulting are different in the two areas. This could be tested by conducting experiments in which crabs were collected in several sampling events throughout the year rather than in a single season.

As most west coast females showed evidence of sperm plugs, even amongst the smaller size classes from ~80 mm CW, it can be concluded that the size at first behavioural maturity (presence of sperm plugs) is lower than the first size-at-maturity estimated, for example, from the gonadal analysis. Brown and Bennet (1980) noted the presence of sperm plugs of recently moulted females as small as 105 mm CW in the English Channel while Edwards (1979) reports that copulation confirmed by sperm plugs occurred in 50% of crabs in sizes 108-115 mm CW in a study conducted in Yorkshire and southwest Ireland. However, observations on egg-carrying animals, in the areas mentioned above, suggested that females do not carry eggs until they reached 127 mm CW and over. While the presence of sperm plugs shows that copulation has occurred it does not necessarily result in the production of eggs and offspring (Wilhelm, 1995). Female crabs are generally considered functionally mature when they are capable of producing and carrying eggs and males when they can mate successfully (Hartnoll, 1969). This implies that crabs must also achieve gonadal and morphometric maturity before they can be treated as fully mature (Hartnoll, 1969; Ungfors, 2007).

### 4.2. Gonadal maturity

The estimated $L_{50\%}$ for females was similar on the east and west coasts. However, the classification of gonad maturity stage “2” as mature (scenario 1) or immature (scenario 2) unsurprisingly has a noticeable effect on the estimated $L_{50\%}$, with estimates under the latter scenario being higher by ~18 mm. The difference between the two estimates highlights the importance of selecting an appropriate maturity criterion. The classification of crabs showing underdeveloped gonads (stage 2) as mature or immature is difficult. Tully et al. (2006) point out that there are uncertainties about whether such crabs had spawned in previous years (in which case they would be resting mature) or not (uncertain maturity but possibly immature) and to correctly identify maturity status requires histological preparation of the gonads. It should be noted that during the sampling stage of the study we were able to distinguish mature females in stage 5 (resting/recovery) from immature females (stage 1) based on differences in the appearance of the gonads (Table 2). A recent study suggested a high correlation between the microscopic development of brown crab gonads and the macroscopic stages proposed by Edwards (1979) and commonly used in most size-at-maturity studies (Larssen *et al.*, 2016). Larssen et al. (2016) showed that all macroscopic “stage 2” crabs analysed were mature from a microscopic perspective and proposed that some of the “stage 1” animals could be separated between strictly immature and developing mature. This supports our size-at-maturity results under scenario 1, in which females on both the east and west coast were mature (from a gonadal perspective) at 127-128 mm CW, suggesting that values obtained under scenario 2 may be too high. This approach has also been followed by other recent studies on brown crab gonadal maturity, which also considered development “stage 2” females to be mature (Haig *et al.*, 2016; Öndes *et al.*, 2017).

Males were found to have mature gonads at smaller sizes (101-106 mm CW) than females. This observation is consistent with other studies elsewhere, suggesting maturity based on gonad staging occurs at a similar size in different areas in Europe (Ungfors, 2007). The $L_{50\%}$ found in this study is comparable with those found for both sexes in Shetland (Tallack, 2007) and the eastern Channel (Smith, 2010), and those found for females in Bay of Biscay (Le Foll, 1984), Ireland (Edwards, 1979; Tully *et al.*, 2006) and Sweden (Ungfors, 2007). Other studies in England (North Sea and Western channel), Isle of Man, Norway, Orkney and Wales (Smith, 2010; Haig *et al.*, 2016; Öndes *et al.*, 2017; Bakke *et al.*, 2018) suggest smaller maturation sizes for both males (85-92 mm CW) and females (97-112 mm CW), while supporting the difference between the sexes (Table 6).

Differences in the size of maturity between populations of the same species have been identified for many crustacean species such as tanner crab (Somerton, 1981), blue swimmer crab (De Lestang *et al.*, 2003), snow crab (Orensanz *et al.*, 2007), western rock lobster (Melville-Smith and De Lestang, 2006), European lobster (Lizárraga-Cubedo *et al.*, 2003) and Norway lobster (Tuck *et al.*, 2000; Queirós *et al.*, 2013). Environmental factors (such as temperature and salinity), population density, mortality, predation rates and individual size may contribute to this variation (Hines, 1982; Tuck *et al.*, 2000; Ungfors, 2007).

The classification of gonads into development stages has been widely used to assess sexual maturity in crustaceans. Some studies have highlighted that histological techniques perform better than ovary colour schema in assessing physiological maturity due to variations prevalent in the aspect of gonads related with differences in diet (Quinitio *et al.*, 2007; Crowley *et al.*, 2018). However, it has also been noted by Quinitio *et al.* (2007) that colour and size of the ovaries, as determined by macroscopic analysis, are frequently closely related to cellular development. The only specific study addressing this issue for brown crab supports that gonad developmental staging is a sound measure of maturity with microscopic results showing a good correlation between macroscopic gonad development (Larssen *et al.*, 2016).

### 4.3. Body morphometric maturity

Determining maturity from reproductive indicators can be costly and time-consuming due to the internal examinations required. If morphometric indicators could be used in determining the onset of body morphometric maturity, they would be more practical and less expensive for use in the field. GAM models suggested that there is a growth change in several morphometric measurements in relation to CW, with evidence of the growth of the relevant body parts speeding up relative to body size. However, the fitted smooth curves do not allow us to identify points of inflection potentially associated with body morphometric maturity. Techniques such as segmented or piecewise regression, allow for the identification of breakpoints by partitioning the data and fitting separate line segments to the two sub-sets of data – however, it should be noted that if growth rate gradually and continually increases, the breakpoint identified may be an artefact. The breakpoints calculated with both the piecewise and segmented regression were generally similar for the two methods except for the east coast males (higher estimates obtained using the piecewise regression). At sexual maturity of crustaceans some body parts are known to grow discontinuously in relation to CW with the relative growth rate after maturity increasing or decreasing (Somerton, 1980). Here, positive allometries were detected at the breakpoints for males (ChD, ChH and ChL) and females (PW), with both piecewise and segmented regression and a negative allometry (AW) for west females (both methods) and east females (piecewise). Positive allometries in male chelae and female abdomens were also found for brown crab elsewhere (Tallack, 2007; Ungfors, 2007; Haig *et al.*, 2016; Öndes *et al.*, 2017). The main difference between the regression methods applied here is that in the segmented regression, the two lines are required to join at the breakpoint while in the piecewise this is not the case. If there is a transition phase between juvenile and adult growth, the piecewise regression is likely a better choice of model to identify breaks in the data because it allows for more flexibility by not constraining the lines to meet at the CW breakpoint estimate. The small discrepancies between the two regression models, for example those found for the east coast males, seem to imply that identifying the point at which the relationship changes may be difficult in some cases.

Overall, male size-at-maturity estimates based on morphometric criteria (120-144 mm CW) were larger than those calculated using gonad stage information, for samples from both the east and west. The male morphometric measurements, ChD, ChH and ChL, resulted in similar breakpoint estimates.

For females, body morphometric maturity estimates with PW (131-142 mm CW) were relatively close to those estimated with the gonadal methods for both the east and west of Scotland (Figure 9). The breakpoints calculated for the AW measurement had large CIs (segmented regression) which, again, supports a gradual shift in growth pattern rather than a sudden change. For AW in both areas, the minimum residual sum of squares between data and model (corresponding to the breakpoint) occurs at high CW, where sampling data were relatively sparse. In the case of west coast females, the relationship between CW and AW would be better represented by a straight line as confirmed by the smoothing term of the GAM model not being significant. A similar result was found by Haig et al. (2016) and it is hypothesised that AW may be more related to female fecundity than size-at-maturity for brown crab.

Attainment of morphological maturity appears to be gradual (as shown by the GAM models) and the larger values estimated for breakpoints in the morphometric data in relation to the gonadal $L_{50\%}$ suggest that morphological maturity in brown crabs may only be detected after gonadal maturity, possibly requiring an additional moult for the changes to became noticeable. Other morphometric studies of brown crab have suggested that post-pubertal positive allometry is not detectable until at least 20 mm of post-maturity growth occurs (Ungfors, 2007; Haig *et al.*, 2016). Despite some uncertainty over the variation of the estimated breakpoints, morphometric indicators can be used in addition or as an alternative to gonadal indicators as they are cheaper, less invasive and do not require sacrifice of the specimen (Somerton, 1980).

### 4.4. MLS implications

Minimum landing sizes are used to manage brown crab fisheries in Scotland and elsewhere. They are generally derived from maturity studies and should be set above the size at first maturity to ensure that some protection is afforded to the spawning stock whatever the level of fishing effort (Addison and Bennett, 1992). The size-at-maturity found in this study varied according to the criteria used (e.g. gonadal, morphometric). The gonadal size-at-maturity was similar in the two sites sampled in the east and west coasts of Scotland. These results are indicative of gonadal size maturation ranges which are in line with those previously reported in Scotland for the Shetland Islands (Tallack, 2007) but considerably higher than those recently found elsewhere in the UK, including in Orkney, Scotland (Haig *et al.*, 2016). Geographic differences in size-at-maturity may, for example, be attributed to the existence of different populations or environmental control occurring in different areas (Orensanz *et al.*, 2007). In addition, it cannot be excluded that parameters related to the life history, such as the size-at-maturity, may vary over time, although no specific studies for brown crab are available.

Males were shown to have mature gonads at smaller sizes [98-110 mm] than females [124-150 mm]. However, the CI range of breakpoints estimated for changes in growth (considering the two morphometric methods) seems to encompass similar body size ranges for both sexes (112-152 mm for males and 126-146 mm for females, excluding the estimates with AW). Males and females of decapod crustacean species are known to have different growth rates, reflecting the fact that females use more energy for reproduction than males after puberty. It has been suggested, for other species of the genus *Cancer* (Rock crab) and other crabs (for example, Dungeness crabs), that males should be larger than females if they are to successfully embrace and guard a female (Terretta, 1973; Christy, 1987; Dunn and Shanks, 2012), although smaller males can be successful if no larger individuals are around. The more rapid growth in male chelipeds may be an advantage when competing with other males for mating (Hartnoll, 1969; Edwards, 1979). It is possible that male gonadal maturity is achieved at smaller sizes than females, implying that small males, despite being capable of breeding, may become more successful later, when they reach larger sizes.

Estimates using morphometric methods were found to be more variable (between areas for both sexes, and between regression methods for males) than those using gonadal information. Few brown crab studies have used morphometric information but our results agree with previous authors that morphometric indicators indicate a larger size at maturity than do gonadal indicators (Ungfors, 2007; Haig *et al.*, 2016; Öndes *et al.*, 2017). When defined, body morphometric indicators of maturity may be good candidates to set conservative MLS as it seems likely that functional maturity is achieved prior to its detection by morphometric methods. In Europe, MLS for brown crab varies widely between areas, ranging from 110 to 160 mm CW, although most areas use 130-140 mm CW (ICES, 2016). Haig et al. (2016) suggested that given crabs mating behaviour, it may be appropriate to manage both males and females at the same MLS. Recently, the MLS in Scotland was increased from 140 to 150 mm CW in most areas as part of a local management plan to improve the sustainability of local stocks and protection of juveniles (The Specified Crustaceans Order, 2017). Considering gonadal maturity, virtually all male crabs are likely to be mature before they reach 150 mm. However, in females, the answer depends on whether maturity stage 2 can be considered as mature – this appears to be likely as shown by Larssen *et al*. (2016). In the case of morphometric maturity, although $L_{50\%}$ appears to be below MLS, we have no way to identify the size at which 100% of crabs are mature. Consequently, while it seems fairly certain that the current MLS is above $L_{50\%}$, it is also true that as many as 50% of female crabs (although likely fewer) could be immature at that size. The difference between the estimated $L_{50\%}$ and the current MLS implies that crabs are likely to be able to reproduce at least once before being captured, assuming an average moulting increment of 25mm (Edwards, 1979).

Regional differences are likely to occur in the size-at-maturity of brown crab, and more studies from other regions in Scotland are desirable to appropriately inform the management of the fishery.

When providing a size-at-maturity estimate, it is vital that the methods and criteria used are clearly defined and a conservative MLS should be chosen to ensure animals are functionally mature (Tallack, 2007). It has been suggested that catches obtained by traps typically contain disproportionately greater numbers of large crabs, whereas those obtained using active fishing methods, such as trawling, will better represent size composition of the population (Smith *et al.*, 2004). In addition, some studies suggest that mature female crabs are more likely to enter traps than immature animals (Jivoff and Hines, 1998; Potter and De Lestang, 2000). If this is the case, maturity studies based on trap fishing may underestimate the $L_{50\%}$ of females. To account for these uncertainties a precautionary MLS should therefore be based on the higher estimates of size-at-maturity to ensure individuals are mature before removal and a buffer may be considered to allow for potential discrepancies in estimates from different methods.

In conclusion, results of the present study suggest that the current MLS is consistent with the goal of allowing crabs to reproduce at least once before they are captured. However, the study also highlights some issues in interpretation of both morphometric and gonadal data: points of inflection in body growth are both statistically poorly defined and of questionable biological meaning, while the interpretation of gonad size is hindered by the likelihood of seasonal gonad regression in mature animals. Indeed the study also confirms that evidence of copulation can be seen in physiologically immature animals, so that the concept of behavioural maturity is not very useful for setting MLS. Year-round sampling (to account for seasonality of reproduction) and studies on possible sampling biases (e.g. avoidance of traps by ovigerous females) are evidently needed, coupled with histological examination of gonads to confirm the reliability and interpretation of results obtained and potentially identify the best methodology (e.g. an optimal sampling period). Finally, histological studies on gonads of captured crabs are needed to test the hypothesis that the MLS genuinely permits animals to reproduce prior to capture.

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## Table Legends

Table 1. Sampling details including brown crab numbers collected for the maturity study.

Table 2. Female and male gonadal maturity stages in brown crabs as reported by Haig et al. (2015), based on visual descriptions (Edwards, 1979; Ungfors, 2007).

Table 3. Size-at-maturity ($L_{50\%}$) and summary statistics obtained from gonadal maturity data from brown crabs using a logistic regression in the east and west coast of Scotland.

Table 4. Summary of GAM models fitted between CW and a set of morphometric measurements in brown crabs sampled from the east and west coast of Scotland.

Table 5. Summary of the regression analysis (piecewise and segmented) performed for relationships between CW and a set of morphometric measurements in brown crabs sampled from the east and west coast of Scotland.

Table 6. Estimates of size-at-maturity ($L_{50\%}$) based on gonad examination for brown crab in the literature.

## Figure Legends

Figure 1. Map of the sampling areas on the east and west coast of Scotland. Black circles within the ICES rectangles indicate the locations where brown crabs were captured.

Figure 2. Length distribution of sampled brown crabs by sex and area. Grey shading indicates females containing sperm plugs.

Figure 3. Proportion of mature males by size in the east (left) and west (right) of Scotland. Points are sampled data and curves estimated from GLMs. $L_{50\%}$ indicates the size at which 50% of the crabs were mature using the gonadal criteria. The dashed lines are 95% confidence intervals.

Figure 4. Proportion of mature females by size in the east (left) and west (right) of Scotland. Points are sampled data and curves estimated from GLMs. $L_{50\%}$ indicates the size at which 50% of the crabs were mature using the gonadal criteria. The dashed lines are 95% confidence intervals. Scenario 1 (top): females in stages 2-5 classified as mature. Scenario 2 (bottom): females in stages 3-5 classified as mature.

Figure 5. Relationship between carapace width (CW) and different morphometric measurements (cheliped depth (ChD), height (ChH) and length (ChL)) for male brown crab with fitted GAMs (black line, grey bands are 95% CIs) and piecewise regression (red line). The vertical dashed line is the breakpoint estimated by the piecewise regression.

Figure 6. Relationship between carapace width (CW) and different morphometric measurements (abdominal width (AW) and pleopod weight (PW)) for female brown crab with fitted GAMs (black line, grey bands are 95% CIs) and piecewise regression (red line). The vertical dashed line is the breakpoint estimated by the piecewise regression.

Figure 7. Relationship between carapace width (CW) and different morphometric measurements (cheliped depth (ChD), height (ChH) and length (ChL)) for male brown crab with fitted GAMs (black line, grey bands are 95% CIs) and segmented regression (blue line). The vertical dashed line is the breakpoint estimated by the segmented regression (95% CI is shown as a horizontal line around the breakpoint).

Figure 8. Relationship between carapace width (CW) and different morphometric measurements (abdominal width (AW) and pleopod weight (PW)) for female brown crab with fitted GAMs (black line, grey bands are 95% CIs) and segmented regression (blue line). The vertical dashed line is the breakpoint estimated by the segmented regression (95% CI is shown as a horizontal line around the breakpoint).

Figure 9. Summary of brown crab sizes at maturity ($L_{50\%}$) by sex and area estimated in this study. Gonadal maturity methods represented by black circles and squares; other symbols correspond to morphometric methods, black: segmented regression, grey: piecewise regression. The vertical dashed lines are the current MLS in Scotland (140 mm CW in Shetland, 150 mm CW elsewhere).

## Tables

Table 1

| Date | Fishing area | Harbour landed | Rectangle | Vessel ID | Number collected |
|---|---|---|---|---|---|
| 18/03/2015 | East coast | Gourdon | 42E7 | 1 | 176 |
| 19/03/2015 | East coast | Gourdon | 42E7 | 1 | 236 |
| 24/04/2015 | East coast | Gourdon | 42E7 | 1 | 74* |
| 20/04/2017 | West coast | Fraserburgh | 45E2/46E3 | 2 | 140 |
| 11/05/2017 | West coast | Ullapool | 45E2 | 2 | 203 |
| 25/05/2015 | West coast | Stornoway | 45E3 | 3 | 80 |
| 04/06/2015 | West coast | Stornoway | 45E3 | 3 | 99 |
| | | | | **Total Number =** | **1008** |

*Males only

Table 2

| **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 and white |

Table 3

| **Area** | **Sex** | **N** | **CW range (mm)** | **Maturity range (mm)** | **% plugs** | **L$_{50\%}$ (mm)** | **CI (mm)** |
|---|---|---|---|---|---|---|---|
| East - scenario 1 | F | 196 | 97-191 | 110-191 | 0 | 128.1 | 125-131 |
| East - scenario 2 | F | 196 | 97-191 | 125-191 | 0 | 145.7 | 143-150 |
| West - scenario 1 | F | 239 | 83-204 | 114-204 | 84.1 | 127.2 | 124-130 |
| West - scenario 2 | F | 239 | 83-204 | 124-204 | 84.1 | 144.9 | 143-147 |
| East | M | 290 | 73-196 | 86-196 | - | 100.6 | 98-103 |
| West | M | 283 | 74-211 | 94-211 | - | 106.5 | 102-110 |

Scenario 1: mature females in stages 2-5; scenario 2: mature females in stages 3-5; Sex: F-females; M-males; N: number of crabs sampled; CW range: size range of animals collected in each area; Maturity range: size range of mature animals; % plugs: percentage of females containing sperm plugs; L$_{50\%}$: size at which 50% of crabs were mature; CI: 95% confidence interval on L$_{50\%}$.

Table 4

| **Area** | **Measurement** | **Sex** | **N** | **GAM** | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Adjusted $R^2$ | Deviance explained (%) | GCV score | d.f. | p |
| East | AW | F | 196 | 0.93 | 93.2 | 3.73 | 2.0 | <0.001 |
| West | AW | F | 239 | 0.93 | 93.2 | 3.94 | 5.1 | 0.142 |
| East | PW | F | 196 | 0.88 | 88.0 | 0.57 | 4.0 | <0.001 |
| West | PW | F | 238 | 0.85 | 85.7 | 0.80 | 4.5 | <0.001 |
| East | ChD | M | 276 | 0.94 | 94.1 | 2.19 | 4.1 | <0.001 |
| West | ChD | M | 280 | 0.87 | 87.6 | 3.69 | 3.6 | 0.001 |
| East | ChH | M | 276 | 0.94 | 93.6 | 6.03 | 4.1 | <0.001 |
| West | ChH | M | 280 | 0.90 | 90.2 | 7.11 | 4.0 | <0.001 |
| East | ChL | M | 276 | 0.95 | 95.1 | 3.57 | 4.1 | <0.001 |
| West | ChL | M | 280 | 0.90 | 89.8 | 5.64 | 4.0 | <0.001 |

d.f: total degrees of freedom estimated for each model; p-value (p) provides a result on significant differences between GAM models with a smooth term on the response variable and a linear model (F test).

Table 5

| **Area** | **Measurement** | **Sex** | **N** | **Piecewise regression** | | | **Segmented regression** | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Slopes | BP (mm) | p | Slopes (L,R) | BP (mm) | CI |
| East | AW | F | 196 | 0.390,0.204 | 168.5 | 0.017 | 0.384,0.409 | 142.2 | 103-181 |
| West | AW | F | 239 | 0.393,0.263 | 161.4 | 0.005 | 0.402,0.248 | 173.1 | 156-190 |
| East | PW | F | 196 | 0.077,0.161 | 139.9 | <0.001 | 0.075,0.16 | 141.6 | 137-146 |
| West | PW | F | 238 | 0.06,0.149 | 135.4 | <0.001 | 0.062,0.156 | 130.6 | 126-135 |
| East | ChD | M | 276 | 0.207,0.278 | 136.5 | <0.001 | 0.187,0.279 | 119.6 | 112-127 |
| West | ChD | M | 280 | 0.2,0.27 | 127.5 | <0.001 | 0.195,0.271 | 133.5 | 123-144 |
| East | ChH | M | 276 | 0.328,0.426 | 137.1 | <0.001 | 0.296,0.442 | 119.7 | 112-127 |
| West | ChH | M | 280 | 0.321,0.462 | 145.6 | <0.001 | 0.322,0.469 | 143.7 | 137-151 |
| East | ChL | M | 276 | 0.294,0.374 | 136.5 | <0.001 | 0.270,0.385 | 119.6 | 112-127 |
| West | ChL | M | 280 | 0.282,0.399 | 147.9 | <0.001 | 0.284,0.407 | 144.4 | 137-152 |

Slopes: the slope of the regression lines for smaller (left) and larger (right) animals; BP: estimated breakpoint; p-value (p) provides a t-test result on slope differences (piecewise regression); CI: 95% confidence interval on the breakpoint (segmented regression).

Table 6

| Area | Sex | $L_{50\%}$ (mm) | Reference |
|---|---|---|---|
| France – Bay of Biscay | F | 117 | (Le Foll, 1984) |
| England – Eastern channel | M | 105 | (Smith, 2010) |
| England – Eastern channel | F | 126 | (Smith, 2010) |
| England – Western channel | M | 90 | (Smith, 2010) |
| England – Western channel | F | 112 | (Smith, 2010) |
| England – North Sea | M | 89 | (Smith, 2010) |
| England – North Sea | F | 109 | (Smith, 2010) |
| England – North Sea | F | 104 | (Haig *et al.*, 2016) |
| Ireland northwest | F | 120 | (Tully *et al.*, 2006) |
| Ireland southwest | F | 127-139 | (Edwards, 1979) |
| Isle of Man | M | 85 | (Haig *et al.*, 2016) |
| Isle of Man | F | 107 | (Haig *et al.*, 2016) |
| Isle of Man | M | 89 | (Öndes *et al.*, 2017) |
| Isle of Man | F | 108 | (Öndes *et al.*, 2017) |
| Norway | F | 109 | (Haig *et al.*, 2016) |
| Norway | F | 112 | (Bakke *et al.*, 2018) |
| Scotland – Orkney | M | 92 | (Haig *et al.*, 2016) |
| Scotland – Orkney | F | 97 | (Haig *et al.*, 2016) |
| Scotland – Shetland | M | 104 | (Tallack, 2007) |
| Scotland – Shetland | F | 133 | (Tallack, 2007) |
| Sweden – Skagerrak and Kattegat | F | 132 | (Ungfors, 2007) |
| Wales | M | 87 | (Haig *et al.*, 2016) |
| Wales | F | 103 | (Haig *et al.*, 2016) |

## Figures

Figure 1

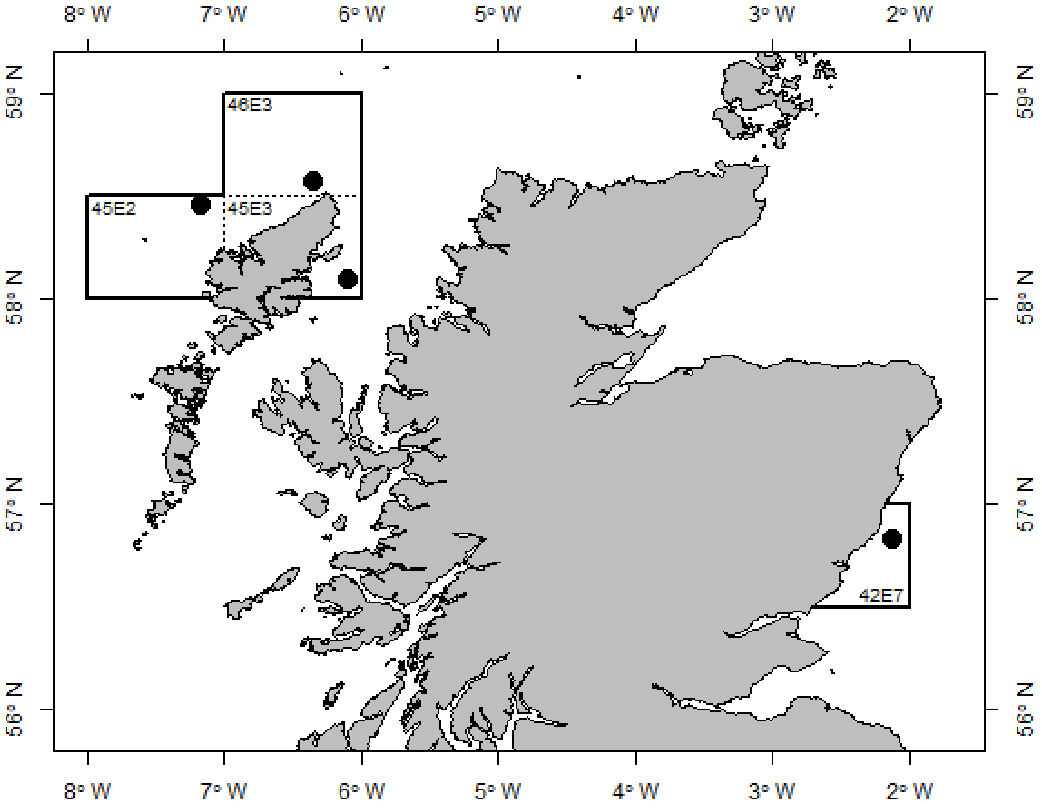


Figure 2

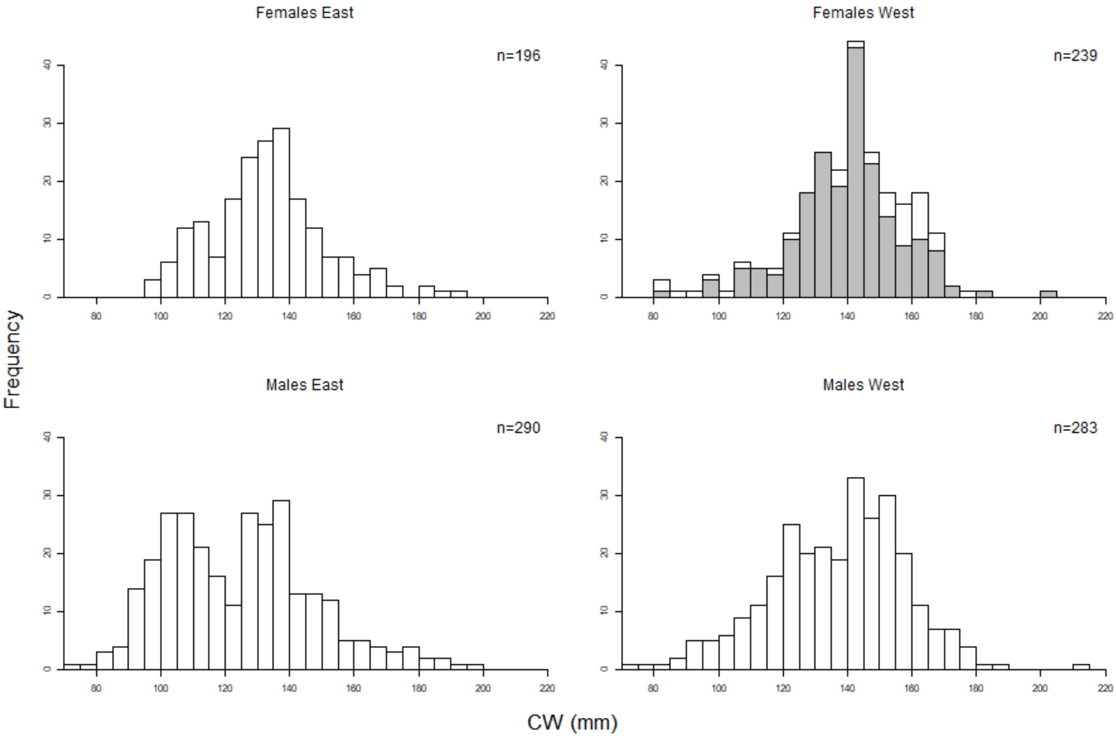

Females East
n=196
Females West
n=239
Males East
n=290
Males West
n=283
Frequency
CW (mm)
0
10
20
30
40
80
100
120
140
160
180
200
220

Figure 3

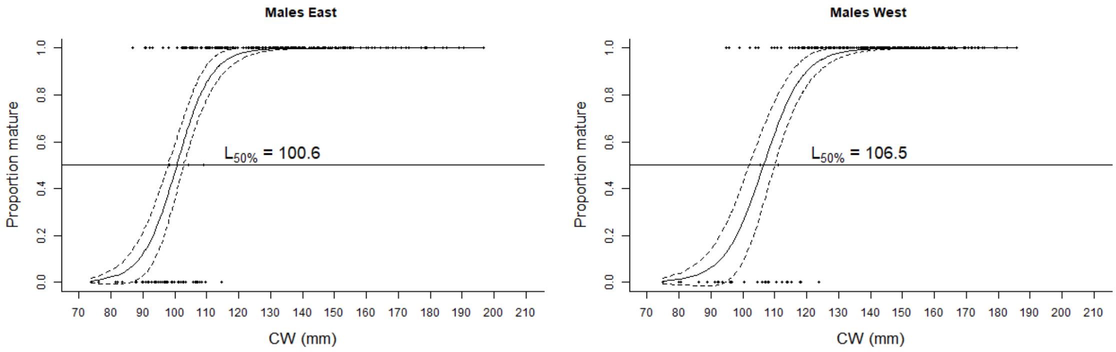

Males East
Proportion mature
1.0
0.8
0.6
0.4
0.2
0.0
$L_{50\%}$ = 100.6
70 80 90 100 110 120 130 140 150 160 170 180 190 200 210
CW (mm)
Males West
Proportion mature
1.0
0.8
0.6
0.4
0.2
0.0
$L_{50\%}$ = 106.5
70 80 90 100 110 120 130 140 150 160 170 180 190 200 210
CW (mm)

Figure 4

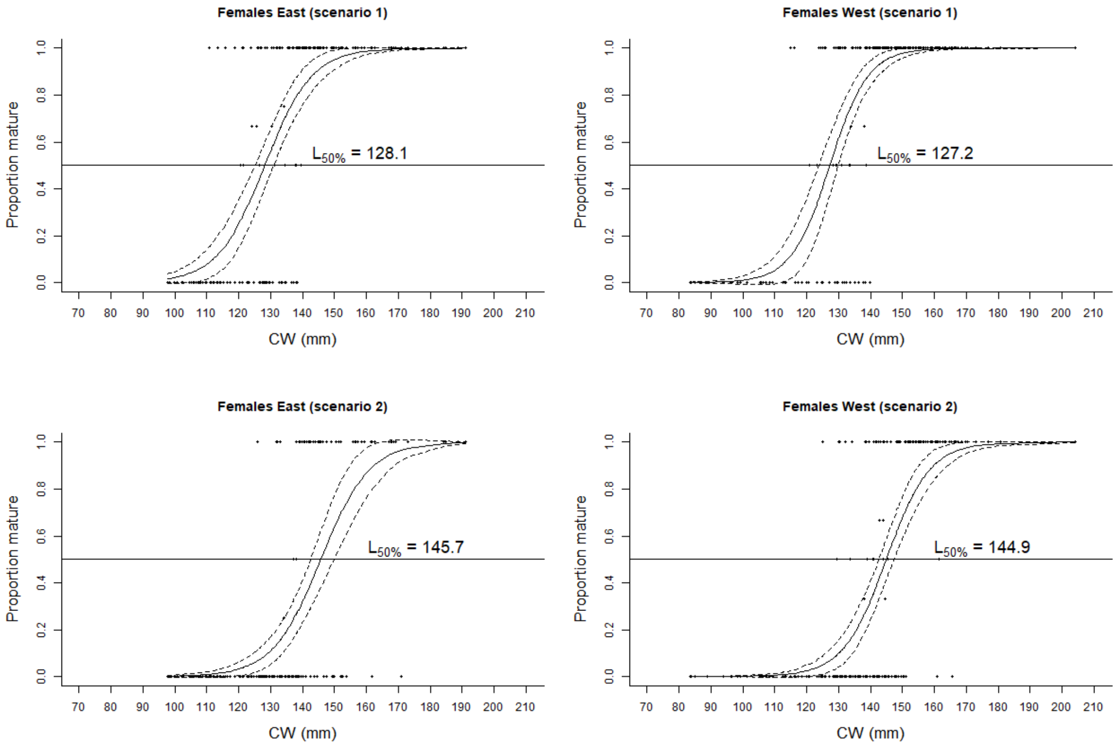

Females East (scenario 1)
Females West (scenario 1)
Females East (scenario 2)
Females West (scenario 2)
Proportion mature
CW (mm)
0.0
0.2
0.4
0.6
0.8
1.0
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
$L_{50\%}$ = 128.1
$L_{50\%}$ = 127.2
$L_{50\%}$ = 145.7
$L_{50\%}$ = 144.9

Figure 5

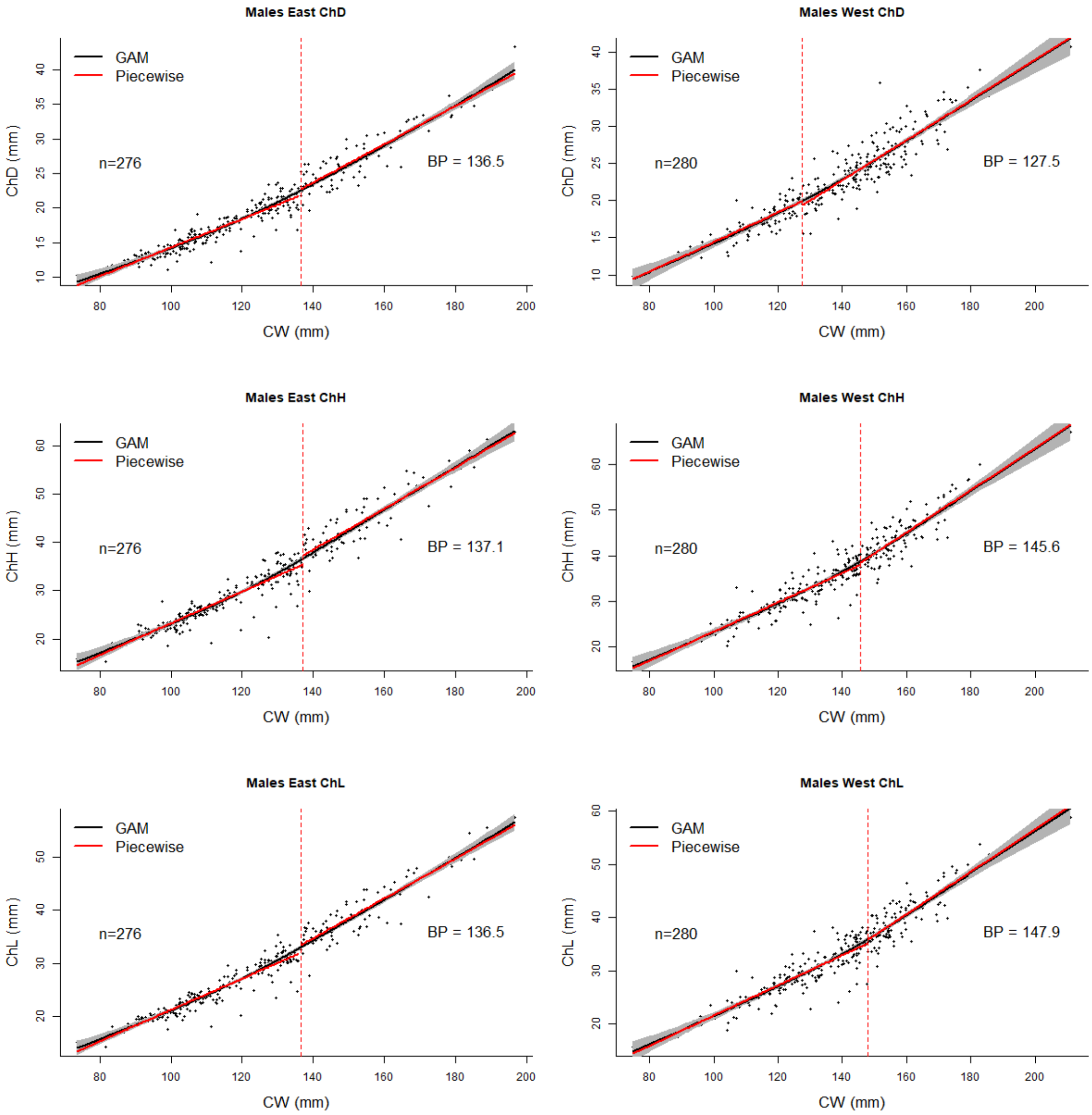

Males East ChD
GAM
Piecewise
n=276
BP = 136.5
ChD (mm)
CW (mm)
Males West ChD
GAM
Piecewise
n=280
BP = 127.5
ChD (mm)
CW (mm)
Males East ChH
GAM
Piecewise
n=276
BP = 137.1
ChH (mm)
CW (mm)
Males West ChH
GAM
Piecewise
n=280
BP = 145.6
ChH (mm)
CW (mm)
Males East ChL
GAM
Piecewise
n=276
BP = 136.5
ChL (mm)
CW (mm)
Males West ChL
GAM
Piecewise
n=280
BP = 147.9
ChL (mm)
CW (mm)
80
100
120
140
160
180
200

Figure 6

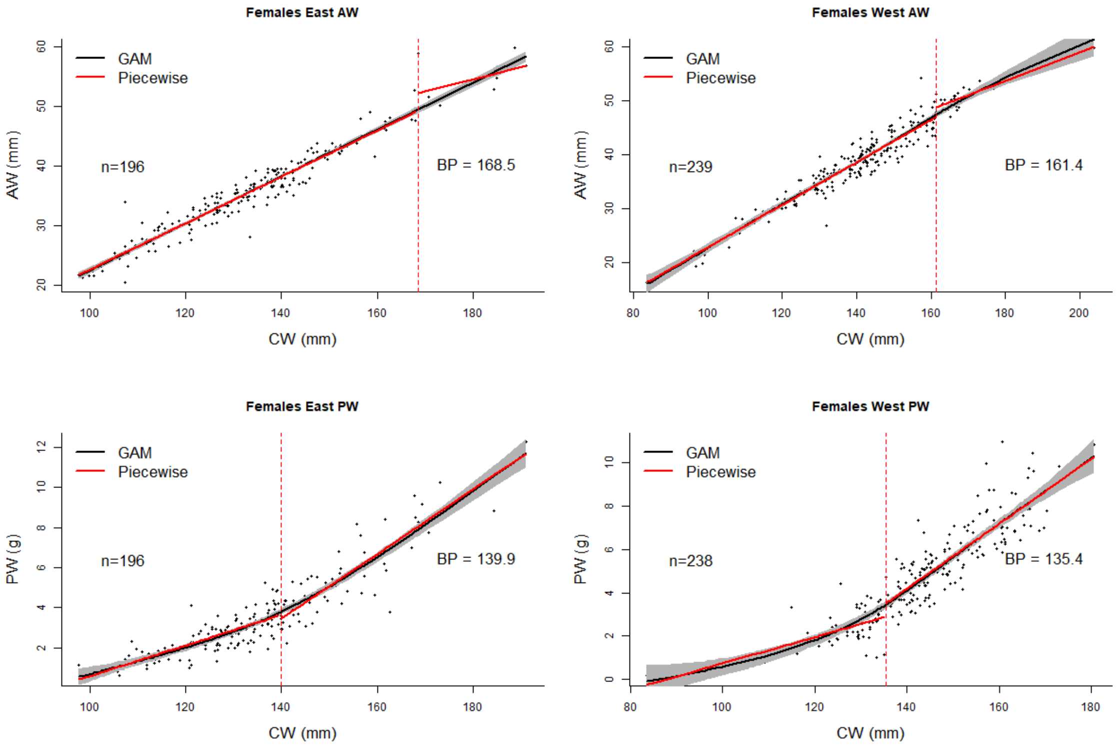

Females East AW
GAM
Piecewise
n=196
BP = 168.5
AW (mm)
CW (mm)
20
30
40
50
60
100
120
140
160
180
Females West AW
GAM
Piecewise
n=239
BP = 161.4
AW (mm)
CW (mm)
20
30
40
50
60
80
100
120
140
160
180
200
Females East PW
GAM
Piecewise
n=196
BP = 139.9
PW (g)
CW (mm)
2
4
6
8
10
12
100
120
140
160
180
Females West PW
GAM
Piecewise
n=238
BP = 135.4
PW (g)
CW (mm)
0
2
4
6
8
10
80
100
120
140
160
180

Figure 7

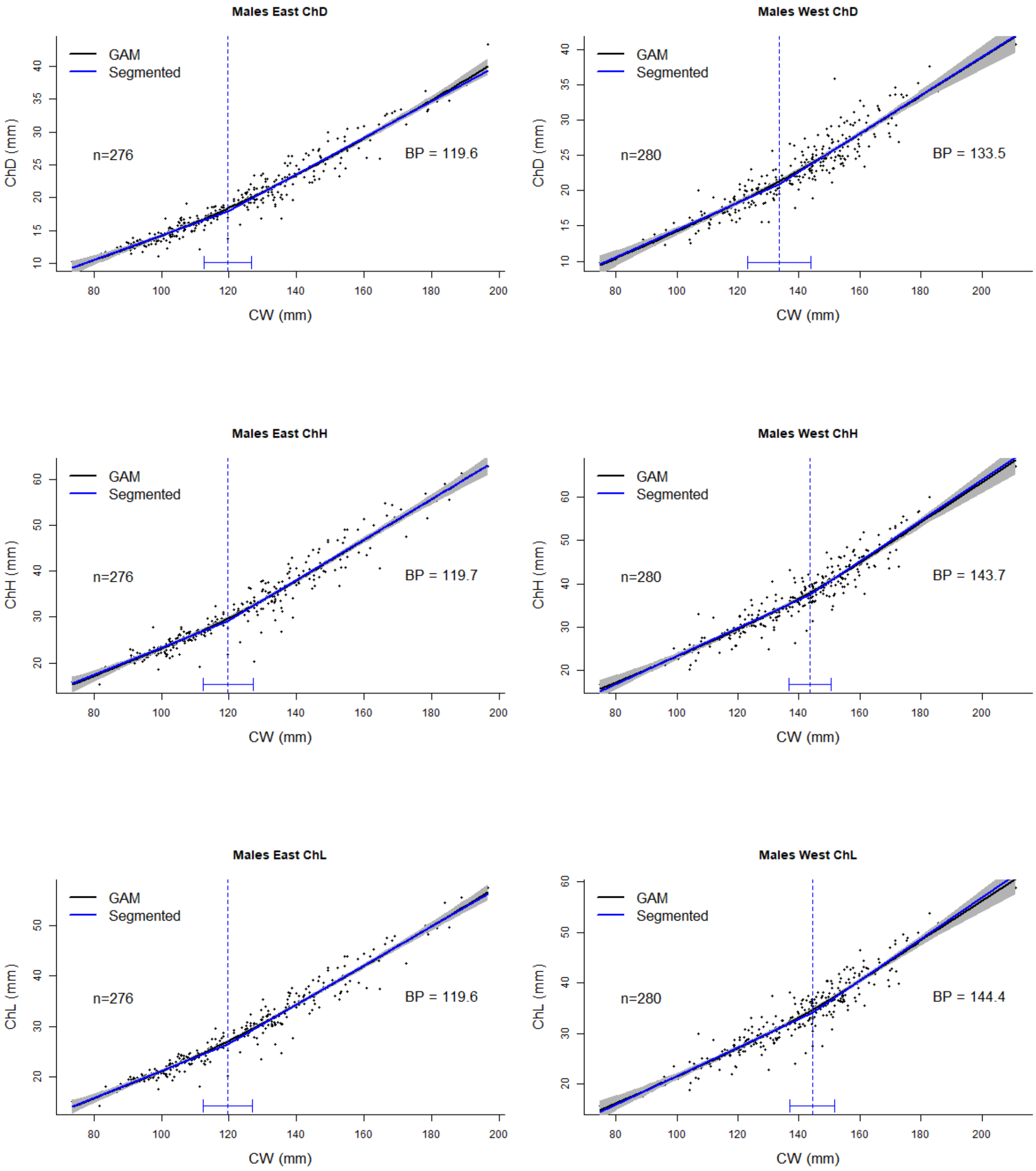

Males East ChD
GAM
Segmented
n=276
BP = 119.6
ChD (mm)
CW (mm)
Males West ChD
GAM
Segmented
n=280
BP = 133.5
ChD (mm)
CW (mm)
Males East ChH
GAM
Segmented
n=276
BP = 119.7
ChH (mm)
CW (mm)
Males West ChH
GAM
Segmented
n=280
BP = 143.7
ChH (mm)
CW (mm)
Males East ChL
GAM
Segmented
n=276
BP = 119.6
ChL (mm)
CW (mm)
Males West ChL
GAM
Segmented
n=280
BP = 144.4
ChL (mm)
CW (mm)

Figure 8

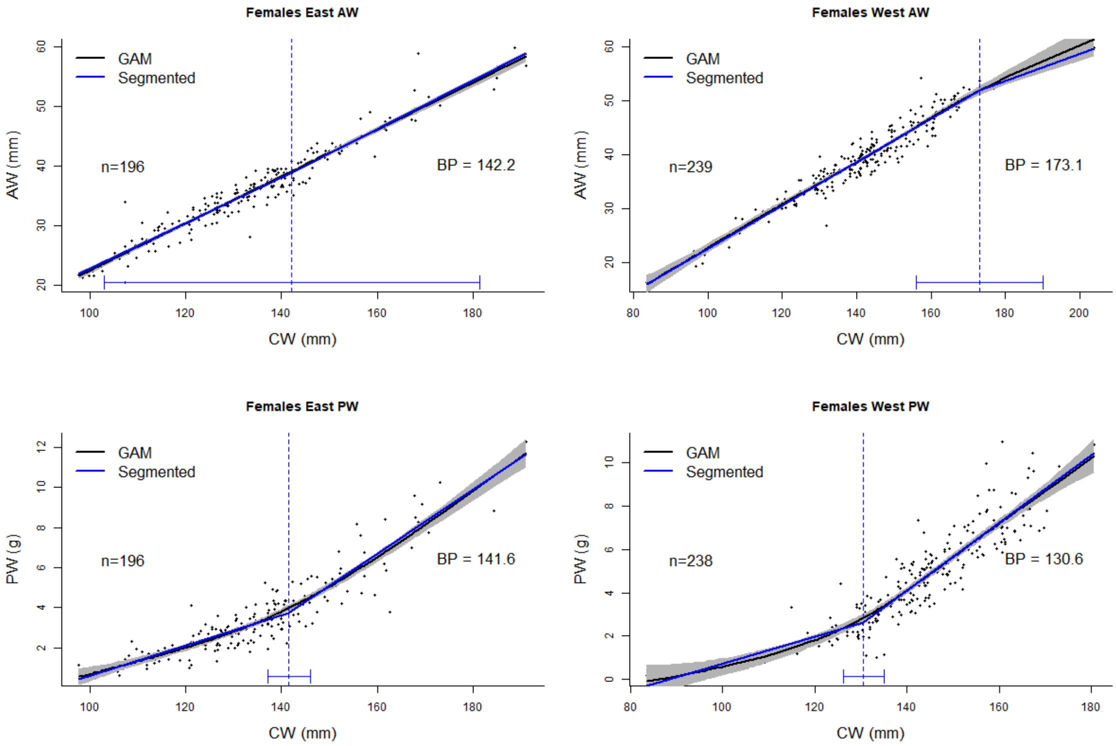
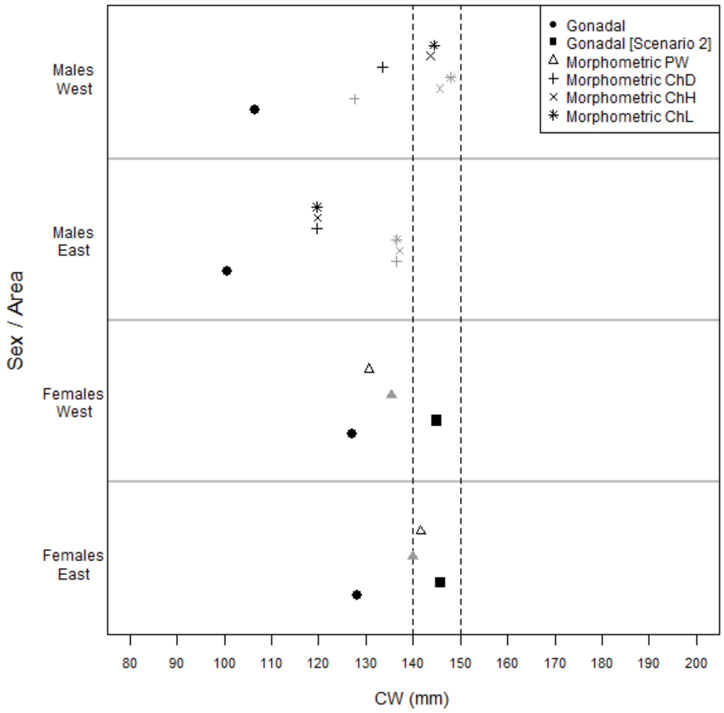

Females East AW
GAM
Segmented
n=196
BP = 142.2
AW (mm)
20
30
40
50
60
100
120
140
160
180
CW (mm)
Females West AW
GAM
Segmented
n=239
BP = 173.1
AW (mm)
20
30
40
50
60
80
100
120
140
160
180
200
CW (mm)
Females East PW
GAM
Segmented
n=196
BP = 141.6
PW (g)
2
4
6
8
10
12
100
120
140
160
180
CW (mm)
Females West PW
GAM
Segmented
n=238
BP = 130.6
PW (g)
0
2
4
6
8
10
80
100
120
140
160
180
CW (mm)

Figure 9


Gonadal
Gonadal [Scenario 2]
Morphometric PW
Morphometric ChD
Morphometric ChH
Morphometric ChL
Males West
Males East
Females West
Females East
Sex / Area
80
90
100
110
120
130
140
150
160
170
180
190
200
CW (mm)