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Spatial and temporal variation of size at maturity in an intensive crustacean fishery with limited management

Alec B.M. Moore [a,*], Adam J. Delargy [a,b], Ruth P. Cann [a], Charlotte Heney [a], Lewis Le Vay [a], Harriet Lincoln [a], Ian D. McCarthy [a], Natalie Hold [a]

[a] School of Ocean Sciences, Bangor University, Askew Street, Menai Bridge, Anglesey LL59 5AB, United Kingdom
[b] School for Marine Science and Technology, University of Massachusetts Dartmouth, New Bedford, MA, USA

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ABSTRACT

The edible crab *Cancer pagurus* supports a valuable northeast Atlantic fishery, but concerns have been raised about declining catches and its management relies heavily on minimum landing sizes (MLSs). Furthermore, few data are available on spatial and particularly temporal variation in maturity of this and other crab species. Here we estimated size at maturity for *C. pagurus* in the Irish and Celtic Seas (north and south Wales, UK, respectively, around 200 km apart) caught during 2020–2021 and compared these to the Wales-wide MLS of 140 mm carapace width (CW) and results of a similar study six years earlier. Using a standard scenario where only stage 1 gonads are considered immature, CW_{50} (50 % of individuals are mature) for all Wales (north and south pooled) was 88 and 107 mm (males and females respectively), in line with regional literature. We found significant spatial variation, with significantly smaller gonadal CW_{50} in north Wales compared to south Wales, for both males (83 cf. 94 mm) and females (98 cf. 114 mm). By 119 mm CW, a high proportion (99 % males, 50–95 % females) were gonadally mature (standard scenario), morphologically mature (most sex and area combinations), and the smallest functionally (ovigerous) and behaviourally mature females had been recorded. We only found evidence for a significant decline in size at maturity since the previous study using a more conservative gonadal scenario, where stages 1 and 2 are considered immature. This found declines for both sexes in north Wales (and all Wales pooled) and females in south Wales. Our results suggest the MLS adequately protects immature individuals, but further management measures may be needed to address reported declines.

1. Introduction

The size at which a fished species attains reproductive maturity is a fundamental metric in the sustainable management of fisheries. Size at maturity is required by some size-based approaches to stock health calculation (ICES, 2017), as well as directly informing the minimum landing size (MLS), a practical enforcement tool that aims to reduce mortality of individuals that have not yet reproduced. Maximum size and size at maturity are known to vary geographically within crab species, including in the UK, where regional differences for the edible or brown crab *Cancer pagurus* have been apparent for well over a century (Edwards, 1979; Somerton, 1981; Hines, 1989; Addison and Bennett, 1992).

Evidence strongly suggests that exploitation drives changes in size at maturity of fished species (Jørgensen et al., 2007; Sharpe and Hendry, 2009), and temporal declines in size at maturity of fished crustaceans have been reported. For example, female American lobster *Homarus americanus* size at maturity declined across most of Canada over a period of 10–80 years, by as much as 30 % in some areas (Haarr et al., 2018). These authors suggested this was an evolutionary response to intense exploitation. In the Irish Sea, across approximately 20 years, the size at maturity of female Norway lobster *Nephrops norvegicus* declined by over 12% to a size marginally above the MLS, thus allowing a far greater portion of reproductively immature females to be landed (Sigwart et al., 2020). This highlights the need for routine monitoring of size at maturity as part of sustainable fisheries management.

Cancer pagurus is fished commercially around the coast of the UK, Ireland and much of its range in northwest Europe, where it is principally caught in baited traps ('pots') along with lobster *H. gammarus* (Edwards, 1979; Haig et al., 2016). As *C. pagurus* fisheries are not subject to EU Total Allowable Catch or national quotas, MLSs are used to protect spawning potential and form the main component of management

* Corresponding author.
E-mail address: a.moore@bangor.ac.uk (A.B.M. Moore).

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(Mesquita et al., 2020; ICES, 2021). As such, accurate size at maturity estimates are important. In Wales, *C. pagurus* forms an important component of seasonal small-scale inshore fisheries, with between 450 and 708 tonnes landed annually into Welsh ports for the period 2015–2019 (Marine Management Organisation, 2022). In a number of European countries including the Republic of Ireland landings per unit effort (LPUE) have shown a decline since around 2015 and there is concern over the status of crab stocks (Marine Institute and Bord Iascaigh Mhara, 2022; pers. comms. ICES Working Group on the Biology and Life History of Crabs). This concern is reflected in recent MLS increases, for example from 130 to 140 mm by the Isle of Man and the Republic of Ireland governments, and from 140 to 150 mm in Northern Ireland (Marine Institute and Bord Iascaigh Mhara, 2020, 2022). However, size at maturity is not routinely monitored, and the most recent estimates are those of Haig et al. (2016). The reliance on MLS to protect spawning stock biomass indicates the need for regular monitoring of size at maturity to ensure that the various MLS measures are effective.

Although the first estimates of Wales-specific size at maturity for *C. pagurus* were not published until 2015 (Haig et al., 2015a), size restrictions have been in place in Welsh waters for over 130 years. An MLS equivalent to 108 mm carapace width (CW) was introduced across much of the UK in 1877 which was increased to 115 mm CW in 1951 (Edwards, 1979). Geographic differences in MLS between north and south Wales management jurisdictions existed for around 30 years, with those in the south always being greater. They were first introduced in 1986 and then amended in 1989 (increased to 125 and 130 mm CW in north and south Wales respectively), with further increases in the early 1990s (130 and 140 mm CW for north and south). In early 2016, a Wales-wide MLS of 140 mm CW was introduced (The Specified Crustaceans (Prohibition on Fishing, Landing, Sale and Carriage) (Wales) Order 2015), which retained the existing MLS applicable in south Wales, but increased the MLS in north Wales from 130 mm. Although this change received broad support in prior consultation, responses included a concern that a ban on landing smaller crab (130–140 mm CW) in north Wales, that are an optimal size for retail sale, would represent a significant economic loss (Welsh Government, 2014). This highlights the need for local evidence of spatial variation in crab biology to avoid both over- and under-exploitation of fisheries (Olson et al., 2018).

Maturity in *C. pagurus* can be defined in several ways, all of which have challenges and which can produce different size estimates, as reviewed by Haig et al. (2016) and briefly outlined here. Behavioural maturity (the size at which successful copulation occurs) is typically based on detecting externally visible 'sperm plugs' in the oviducts of mated females. However, this indicator may be of limited value for fisheries management given that small, physiologically immature females can be copulated (Edwards, 1979; Mesquita et al., 2020). Morphological maturity is based on the size at which anatomical features display a departure ('breakpoint') from isometric growth as a secondary sexual characteristic. This is most obvious in the enlarged chelae (claws) of larger male *C. pagurus*, as they are used when competing for mates. In females, the relative width of the abdominal flap has been used to determine morphological maturity, although its value has been questioned (Haig et al., 2016; Mesquita et al., 2020). Physiological maturity (or gonadal maturity used herein) is the presence of developed gamete-producing gonads. Quantifying this (usually as CW at which 50 % of individuals are mature, CW50) is typically based on macroscopic visual examination of gonads and assignment to discrete maturity stages (e.g. 1 immature, 2 developing, 3 mature). Challenges of this approach include potential misclassification error between developing and resting stages, particularly in comparison to the 'gold standard' of microscopic histology, and uncertainty as to whether stage 2 should be considered mature or not (Larssen et al., 2015; Mesquita et al., 2020). Attaining any one of the preceding maturity types does not necessarily mean an individual will produce offspring, which is the maturity metric most useful for management purposes. Functional maturity is therefore the 'ideal' to quantify, but it has been variably defined (e.g. Tallack, 2007; Haig et al., 2016) and is further complicated by the rarity of ovigerous ('berried') females entering pots (Brown and Bennett, 1980). Collectively, the advantages and disadvantages of each maturity type highlight the need to collate several complementary strands of evidence when estimating size at maturity.

In the absence of baseline data for Wales, Haig et al. (2015a) examined gonadal, morphometric and behavioural maturity for *C. pagurus* from north and south Wales. Combined Wales-wide estimates were then published as part of a wider study across NW Europe (Haig et al., 2016). These authors recommended repeat sampling, at least every three years, in keeping with European Commission policy. In the present study, we followed the methodology of Haig et al. (2015a), (2016) and aimed to 1) estimate the current size at maturity of *C. pagurus* of both females and males from north, south and all of Wales (respectively representing locations in the Irish Sea ICES VIIa, Celtic Sea ICES VIIg and pooled) and compare it to regional studies; 2) compare the size at maturity with current MLS of 140 mm CW, to examine the relationship between biological and management aspects of this species; and 3) examine possible changes in size at maturity over time in *C. pagurus* by comparing our results with those of the previous study of Haig et al. (2016).

2. Materials and methods

2.1. Sample collection

In order to provide comparable results, the methodology of Haig et al. (2016) was followed unless otherwise stated, and to avoid repetition the reader is referred to that study for detailed information. All crabs were obtained between late October 2020 and mid-January 2021. Most were from commercial fishers using baited pots during their normal operations, using the same broad locations that Haig et al. (2015a) used for most of their samples for both north Wales (Conwy, Liverpool Bay area, ICES VIIa Irish Sea 35E6) and south Wales (Solva, St. Brides Bay area, ICES VIIg Celtic Sea 32E4)(Fig. 1.). Small individuals were hand collected from the intertidal at low water on spring tides from

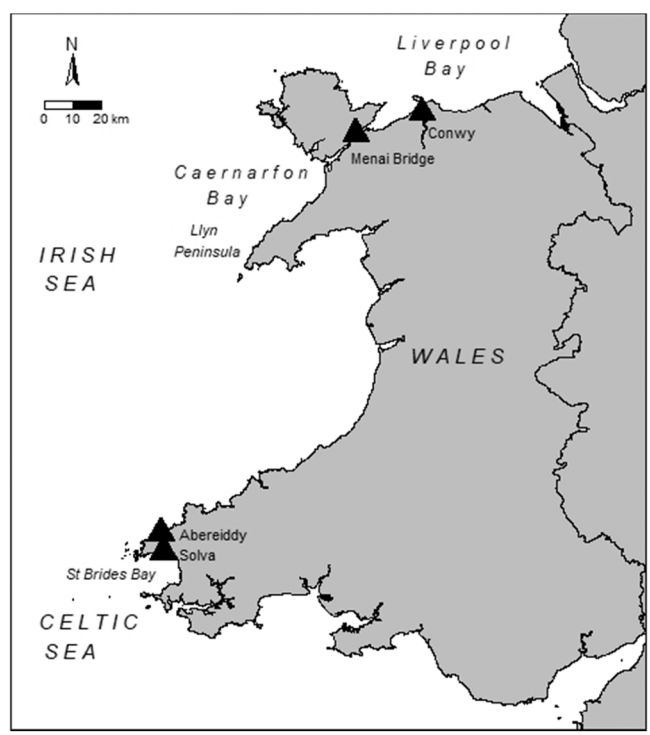

Fig. 1. Map of Wales showing major waterbodies and sampling locations (denoted by black triangles). See text for details.

locations nearby (≤20 km) to the fishing operations (Menai Bridge for north Wales, Abereiddy for south Wales, Fig. 1). Undersized crabs were retained under dispensation from Welsh Government. In addition, morphometric measurements were also collected by scientific observers aboard commercial fishing vessels in 2019 and 2021 from the same locations as crabs for lab analysis, with some additional north Wales samples from the western Llyn peninsula (southern Caernarfon Bay) (Fig. 1).

2.2. Laboratory methods

Crabs were defrosted or killed humanely by spiking if examined fresh, blotted dry, assigned a unique reference number, and weighed (g). Female crabs were visually examined for the presence of sperm plugs (Edwards, 1979). Carapace width was measured (mm), along with abdomen width for females, and the sum of three right cheliped dimensions to arrive at a single "claw" dimension for males (as per Haig et al., 2016; see Fig. 2 in Ungfors, 2007). The crab was then opened by holding it down inverted on its carapace and forcing the abdomen away from the suture line with thumb pressure. Excess ventral carapace shell, membrane, mouthparts, and liquid in the carapace were all removed. Gonads were visually examined in the lab and a maturity stage was agreed and assigned there, based on the scale and photographs provided in Haig et al. (2016). For crab individuals where gonad stage could not be readily assigned (especially discriminating between female stages 2 and 5), four experienced readers examined photographs independently of other readers and carapace width; only those crabs with majority or complete consensus were included in the analysis.

Our experience of conducting visual macroscopic assessment of gonadal maturity in the laboratory highlighted some opportunities to improve methodology. The photograph of male maturity stage 2 provided in Haig et al. (2016) made it difficult to identify diagnostic characters, so a clear example of small but clearly developing male gonads are provided in Supplementary Material to address this. We also suggest that, in addition to the underside of the removed carapace, the dorsal part of the exposed body is inspected for gonadal material. The smallest mature crab we recorded (71 mm CW stage 3 male) had no testes or vas deferens visible on the carapace, but clearly had paired, swollen, sperm-filled vas deferens retained in the body. For females, we found that the description of stages 3 (i.e. ovaries with "slight pink appearance, covering <50 % of cavity") and 4 ("orange, red obvious ovaries, covering >50 % cavity") in Haig et al. (2016), was problematic for classifying some individuals (e.g. bright red but <50 %; pale orange and around 50 %), and Larssen et al. (2015) confirmed that colour of ovaries varied for each stage. We therefore consistently applied the 50 % threshold for lobe coverage: above this we classified all individuals stage 4 (mature), consistent with the 'late mature' stage in the refined scale of Larssen et al. (2015).

For the definition of functional maturity we follow Haig et al. (2016) for males, i.e. those that have attained both gonadal and morphological maturity, and we define berried females as functionally mature.

2.3. Statistical analysis

2.3.1. Gonadal maturity

All statistical analyses were conducted in R (R Core Team, 2021), and we conducted re-analysis of raw gonadal and morphological data available from Haig et al. (2016) alongside our data, to ensure consistency. For size at maturity based on gonad development we explored two scenarios. In keeping with the previous study (Haig et al., 2015a, 2016) and other similar work (e.g. Öndes et al., 2017), a standard scenario ('Scenario 1′) considered stage 1 crabs of both sexes immature, and all other stages mature. To acknowledge uncertainty around whether stage 2 crabs are mature or not (Tully et al., 2006; Ungfors, 2007), 'Scenario 2′ was more conservative and considered stages 1 and 2 of both sexes immature, with stage 3 males and stage 3–5 females considered mature.

After conversion to binary format (immature and mature), the proportion of mature crabs (p_i) were estimated from the carapace width (CW_i) and were assumed to allow a sigmoidal relationship (Eq. 1).

$$p_i = \frac{e^{\beta_0+\beta_1 CW_i}}{1+\quad e^{\beta_0+\beta_1 CW_i}}\# \tag{1}$$

The parameters β_0 and β_1 were estimated by logit transforming Eq. 1

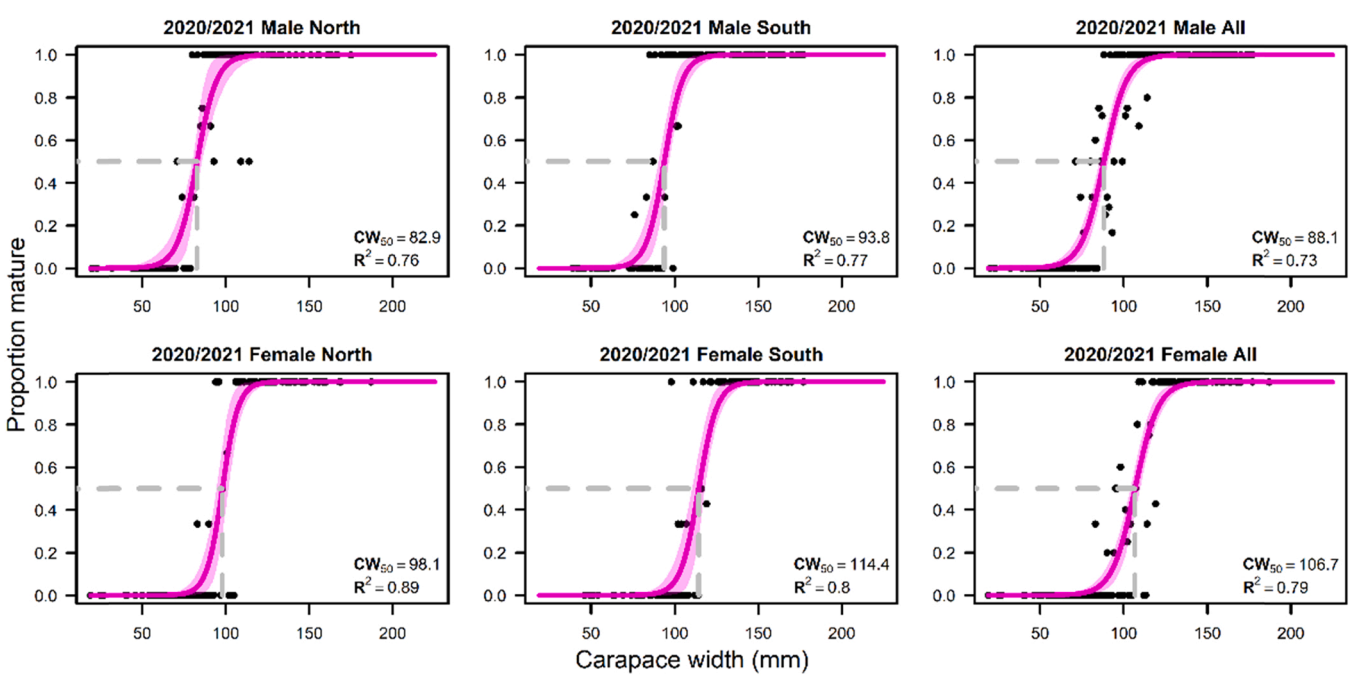

Fig. 2. Maturity ogives for size at 50% gonadal maturity (CW_{50}) from logistic regression for edible crab *Cancer pagurus* in Welsh waters, for 2020–2021 using scenario 1 (stage 1 immature, other stages mature). Curved dashed lines represent 95 % confidence intervals; the point where the straight dashed lines meet is the size at which 50 % of individuals are mature.

to a linear equation and fitting as a binomial generalised linear model (Eq. 2).

$$log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 CW_i \# \quad (2)$$

The carapace width at which 50 %, 95 % and 99 % of the crabs were mature (hereafter CW_{50}, CW_{95} and CW_{99}) were derived from the beta parameters estimated in Eq. 2, where k is the desired percentage (Eq. 3). This model fitting process was applied to subsets of the data corresponding to each combination of study, sex and location.

$$L_k = \frac{\log\left(\frac{\frac{k}{100}}{1-\left(\frac{k}{100}\right)}\right) - \beta_0}{\beta_1} \# \quad (3)$$

Confidence intervals (95 %) around each size-at-maturity curve and the $L_k$estimates were obtained by ordinary bootstrap resampling of the beta parameters using the 'car' package (Fox and Weisberg, 2019).

2.3.2. Morphometric maturity

Two regression approaches, segmented and piecewise, have previously been used to estimate morphometric maturity in *C. pagurus* to identify breakpoints indicating departure from isometric growth for abdomen width (mm, females) and claw dimensions (mm, males) against body size (CW) (Haig et al., 2016; Mesquita et al., 2020). In the present study these were conducted for each combination of study (2014/2015 and 2020/2021), sex and location by fitting the models to each subset of data, as for the gonad maturity analysis. Piecewise regression required iteratively fitting linear models to the relationship between CW and either of the metrics previously mentioned (Y) around potential allometry breakpoints (K) (Eq. 4) (Mesquita et al., 2020).

$$Y_i = \begin{cases} \alpha_0 + \alpha_1 CW_i, & CW_i < K \\ \alpha_2 + \alpha_3 CW_i, & CW_i \geq K \end{cases} \# \quad (4)$$

The α parameters are the intercepts and slopes of the lines either side of the breakpoint. Breakpoints were tested in 1 mm intervals and ranged from 59 to 122 mm, which were the lowest and highest values from any of the confidence intervals for any subset in the segmented regression analysis (discussed in the next paragraph). Each model fitted with each breakpoint was compared to a linear model containing no breakpoint by AIC value, to verify whether the inclusion of a breakpoint was beneficial. Only breakpoints where the breakpoint model had an AIC value more than two AICS values lower than the non-breakpoint model were considered further. For each study, sex and location subset the optimal breakpoint was identified as the breakpoint used in the model(s) with the lowest residual sum of squares (RSS). If multiple models had the lowest RSS, then multiple breakpoints were reported.

The second technique was segmented regression, implemented using the "segmented" R package (Muggeo, 2022). This technique is also iterative but differs from the piecewise regression by assuming the two lines must meet at the breakpoint (Muggeo, 2022; Mesquita et al., 2020). We used a starting value for the breakpoint of 110 mm for all study, sex and location subsets, compared each model to linear models containing no breakpoint and estimated 95% confidence intervals around the optimal model estimated breakpoint from the model estimated standard error.

Piecewise regression may be more appropriate where there is a transition phase of growth because the technique does not constrain the lines to meet at the breakpoint estimate (Mesquita et al., 2020).

3. Results

3.1. Sample composition and behavioural maturity

A total of 605 crabs (311 north Wales, 294 south Wales) spanning a wide size range (females 19–187 mm CW; males 20–177 mm CW) were collected between late October 2020 and mid-January 2021 for visual assessment of gonads and morphometric analysis in the laboratory. Morphometric measurements from a further 1097 individuals (611 females and 486 males) were obtained onboard commercial vessels during fieldwork in 2019 and 2021.

Females with visible sperm plugs were rare, with only nine individuals recorded [3% of all 304 females examined; six in north Wales (3.9 %); three in south Wales (2 %)]. Sizes of females with sperm plugs ranged from 114 to 169 mm CW (117–169 north; 114–129 south). Gonadal maturity stages of these individuals in the north were mostly stage 5 resting (83 %) with one mature (17 %). Those in the south comprised one resting (33 %) and two indeterminate maturity (67 %).

3.2. Gonadal maturity

The smallest gonadally mature crabs recorded were a 71 mm CW stage three male, and an 83 mm stage two female, both from north Wales (Table 1). The minimum size at which mature crabs were recorded was smaller in north Wales for both sexes (stages 2 and 3), and the minimum size of stage 4 females was also smaller in the north. The largest immature (stage 1) crabs were three females of 119 mm CW from south Wales. Conversely, the largest immature male was in north Wales (Table 1).

Estimates of gonadal size at maturity (CW_{50}, CW_{95} and CW_{99}) for scenarios 1 and 2 are presented in Table 2, with maturity ogives for CW_{50} scenario 1 having narrow confidence intervals (Fig. 2). For scenario 1, the CW_{50} for males pooled across Wales was 88 mm, however, males in the north had a significantly lower CW_{50} than south Wales (Fig. 3). The scenario 1 CW_{50} estimate for females was 107 mm and female estimates were significantly greater than the respective male estimates (15–20 mm greater) (Fig. 3). Like males, the CW_{50} of females was significantly smaller in north Wales than the south (Fig. 3). Scenario 2 CW_{50} estimates followed the same patterns, but with consistently higher CW_{50} estimates (Table 2, Fig. 4).

For scenarios 1 and 2, estimates of CW_{50} and CW_{95} and their upper 95% confidence intervals (CIs) were all less than the Wales-wide MLS of 140 mm CW (Table 2). Average estimates of CW_{99} also fell below the MLS, although some upper CIs were marginally above this value (Table 2).

There were no significant differences in CW_{50} across most combinations of sex and location when comparing Haig et al. (2016) (2014/2015) and current studies (2020/2021) when using scenario 1 (Fig. 3). In contrast, for scenario 2 significant declines in CW_{50} over time were detected for both sexes in north Wales and all of Wales, and females in south Wales. There was no significant change detected in male CW_{50} in south Wales (Fig. 4).

3.3. Morphometric maturity

Estimates of morphological maturity breakpoints for both segmented and piecewise regression were similar at around 115 mm (range 113–119) CW for most combinations of sex and area (Table 3, Fig. 5). The exceptions to this were all the segmented derived breakpoints for

Table 1
Minimum size (carapace width (CW), mm) of mature stages (2–4) and maximum size for immature (stage 1) recorded for edible crab *Cancer pagurus* in Welsh waters, October 2020-January 2021. Maximum values are in bold for each stage and sex.

Sex	Location	Smallest mature (mm CW)			Largest immature (mm CW)
		Stage 2	Stage 3	Stage 4	Stage 1
Male	North	74	71	n/a	**109**
	South	**76**	**83**	n/a	102
Female	North	83	108	125	105
	South	**98**	**139**	**129**	**119**

Table 2
Estimates of size (carapace width (CW), mm) at gonadal maturity (CW_{50}, CW_{95}, CW_{99}) from logistic regression for edible crab *Cancer pagurus* in Welsh waters, October 2020-January 2021. CI = 95 % confidence interval range. All values are in mm, with those in bold greater than the existing Wales-wide minimum landing size of 140 mm.

Sex	Area	CW_{50} (CI)	CW_{95} (CI)	CW_{99} (CI)
Scenario 1 (only stage 1 is immature)				
Male	North	83 (80–86)	100 (90–110)	110 (95–124)
	South	94 (90–97)	110 (103–116)	119 (110–128)
	All Wales	88 (85–91)	108 (103–113)	119 (111–127)
Female	North	98 (95–102)	112 (105–117)	120 (110–127)
	South	114 (110–118)	130 (124–135)	139 (129-**147**)
	All Wales	107 (104–110)	127 (122–132)	138 (130-**145**)
Scenario 2 (stage 1 and 2 are immature)				
Male	North	89 (86–93)	113 (102–123)	126 (111-**141**)
	South	100 (97–103)	113 (106–120)	121 (110–131)
	All Wales	95 (92–98)	117 (111–123)	129 (121–138)
Female	North	108 (105–111)	119 (112–124)	125 (115–132)
	South	119 (116–122)	130 (123–135)	137 (127-**144**)
	All Wales	114 (111–116)	128 (124–132)	136 (130-**141**)

females, which showed wide confidence intervals and notably smaller estimated breakpoints. There was also a significant difference in breakpoints between north and south Wales (72 and 100 mm CW respectively) (Table 3, Fig. 5).

No significant differences in breakpoints were detected in the segmented regression analysis, based on overlap of CIs, between the two studies. However, the overlap in CIs was extremely marginal for females in north Wales between the two time periods (Fig. 5). Conversely, there were large increases (ca. 30–40 mm) in breakpoints estimated by piecewise regression between the two time periods for all sex and location combinations (Fig. 5).

3.4. Functional maturity

Only three (1 %) of all examined females were found to be functionally mature (i.e. berried). These were two from the north (116 and 136 mm CW) and one from the south (150 mm CW). For males (all Wales pooled), using the definition of attainment of both morphological and gonadal maturity and the results noted above, functional maturity was attained at around 119 mm CW. This size represents the upper limit of breakpoint estimates (Table 3) and the size at which nearly all (CW_{99}) males are gonadally mature (Table 2).

4. Discussion

This study successfully used a range of methods to estimate size at maturity in a commercially important crab species, and to detect significant spatial, and possible temporal, variation. Although each of these methods are known to have limitations, these are widely accepted as being appropriate for management advice (Mesquita et al., 2020). In addressing the first of our three aims (i.e. estimating size at maturity), we provide detail below on each of the approaches used, before discussion of spatial and temporal variation and relationship to MLS.

4.1. Gonadal maturity

Minimum sizes of mature crabs in our study were slightly larger (71 and 83 mm CW for males and females respectively) than found in Haig et al. (2016) (63 and 68 mm CW respectively). Our scenario 1 CW_{50} estimates for all Wales of 88 mm (males) and 107 mm (females) were similar to those from Haig et al. (2016) for all Wales (87 and 103 mm, respectively), pooled samples from several locations across northern Europe (88 mm and 105 mm, respectively; Haig et al., 2016), and the Isle of Man (89 and 108 mm CW, respectively; Öndes et al., 2017). However, our results are smaller by 12–18 mm (for males) and 19–29 mm (females) than scenario 1 CW_{50} estimates from Sweden (101 and 132 mm, respectively), and the east and west coast of Scotland (101–106 (males), 127–128 mm (females))(Ungfors, 2007; Mesquita et al., 2020). Estimates of CW_{50} under scenario 2 were slightly larger, as would be expected. In addition, we found a novel result of significant small scale spatial differences in size at gonadal maturity with both scenarios, with a smaller CW_{50} in north Wales compared to the south. The previous Welsh study did not find a north-south difference, although different model averages and marginally overlapping CIs suggested some difference for females could exist (Fig. 3). Comparison of males was constrained by very wide confidence intervals for south Wales in

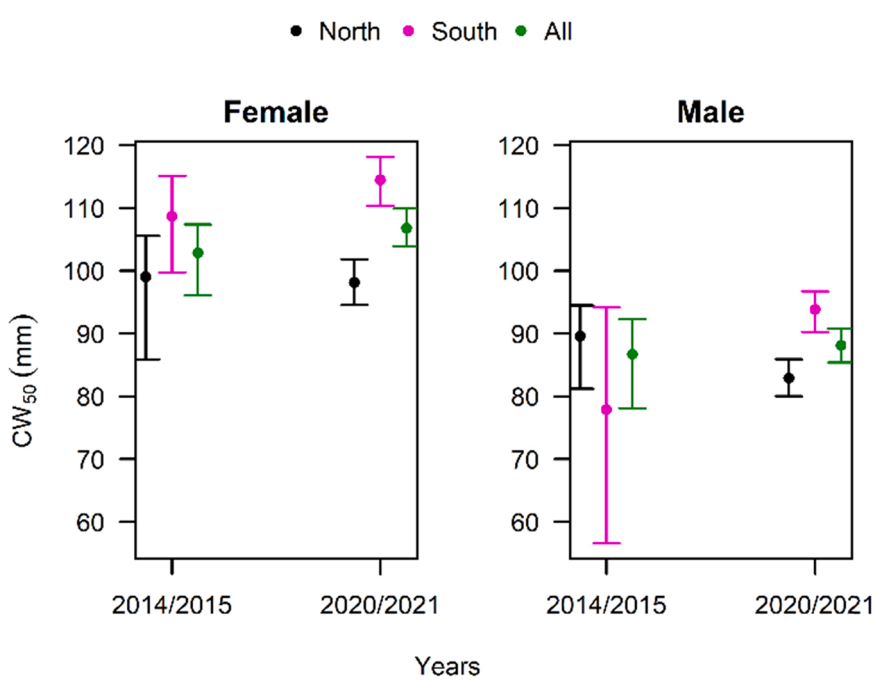

Fig. 3. Estimates of size at 50% gonadal maturity for edible crab *Cancer pagurus* in Welsh waters, for autumn/winter 2014/2015 and 2020/2021 using scenario 1 (stage 1 immature, other stages mature). Dots represent model averages; whiskers represent 95 % confidence intervals.

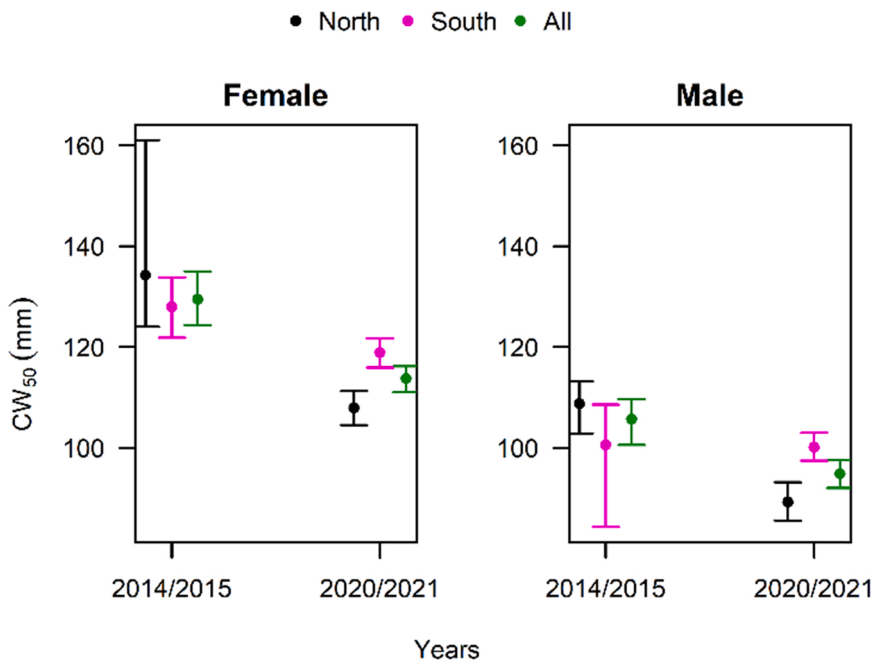

Fig. 4. Estimates of size at 50 % gonadal maturity for edible crab *Cancer pagurus* in Welsh waters, for autumn/winter 2014/2015 and 2020/2021 using scenario 2 (stage 1 and 2 immature, other stages mature). Dots represent model averages; whiskers represent 95 % confidence intervals.

Table 3
Estimates of size (carapace width (CW), mm) at morphological maturity breakpoints estimates for edible crab *Cancer pagurus* in Welsh waters, 2019–2021. CI = 95% confidence interval range. BP = breakpoint. All values are in mm.

Sex	Area	Segmented BP (CI) (mm)	Piecewise BP (mm)
Male	North	116 (111–122)	113
	South	117 (112–122)	119
	All Wales	116 (113–120)	117
Female	North	72 (59–84)	115
	South	100 (92–108)	115
	All Wales	85 (75–94)	115

Haig et al. (2015a).

Spatial differences in size at maturity in crustaceans are well known (Mesquita et al., 2020, and references therein), and they can occur at small spatial scales: Sigwart et al. (2020) reported significant differences in size at 50 % maturity in Irish Sea *Nephrops norvegicus*, from stations as little as approximately 10 km apart. However, the reasons for such differences are less well understood. Several studies on *C. pagurus* maturity have not shown any apparent geographic pattern (Bakke et al., 2018). Spatial differences in reproductive parameters could be genetic, although a recent molecular study around Wales and adjacent waters found support for a single panmictic stock without strong spatial structure (McKeown et al., 2018). Environmental influences are likely to play a role on growth, size, and age, at maturity. For example, water temperature has been identified as a key factor in moult frequency of lobster in European waters, and the reproductive biology of the blue swimmer crab in western Australia (Coleman et al., 2021; Johnston and Yeoh, 2021) For *C. pagurus*, Bakke et al. (2018) hypothesized that females matured at a larger size in the colder water found at higher latitudes but found no evidence for this when tested by sampling along a north-south gradient on the Norwegian coast. However, as a likely result of slower growth in colder water, these authors did find that frequency of moulting decreases northwards. As such, they suggested that crabs would have a higher age at maturity in more northerly areas compared to those in the south and would therefore be more sensitive to overfishing (Bakke et al., 2018).

Seasonal timing of sample collection is an important consideration in size at maturity studies. To target when the greatest proportion of crabs would have mature gonads, Haig et al. (2016) (and, to ensure consistency, our study) sampled in 'late autumn to winter', based on a study from Sweden (Ungfors, 2007) and Brown and Bennett (1980) who sampled year-round, in the western English Channel to find November was the month of peak female maturity. As aspects of life cycle such as presence of sperm plugs and peak moulting are known to occur later in the year in more northerly areas (Haig et al., 2016 Bakke et al., 2018), it is likely that gonadal development follows this pattern. Furthermore, Brown and Bennett (1980) and Ungfors (2007) only reported female gonad development. As mating takes place between a 'soft' (recently moulted) female and a 'hard' (intermoult) male (Edwards, 1979; Bennett, 1995), it is likely that the greatest proportion of gonadally mature males occurs earlier in the year. Autumn sampling may therefore underestimate male size at maturity and separate sampling times for each sex (e.g. summer for males) might be warranted in future studies. Collectively, these issues highlight the need for a robust understanding of seasonal and spatial variation in reproductive parameters at a local level for the proper design of, and interpretation of results from, *C. pagurus* size at maturity studies.

4.2. Morphological maturity

At around 116 mm CW (range 113–119 mm CW), most of the estimates of morphological maturity were similar among males (segmented and piecewise) and females (piecewise). This finding is similar to the 110 mm CW suggested by Edwards (1979) as a general rule for male *C. pagurus* morphological maturity.

In our study, male morphometric maturity was attained around 20–30 mm CW greater than gonadal maturity CW_{50} (scenario 1)(88 mm CW all Wales), with morphological maturity more similar to gonadal CW_{99} estimates of 119 mm CW (all Wales, scenario 1). This is in line with established knowledge of an average pubertal moult increment of around 25 mm (Edwards, 1979; Mesquita et al., 2020). It suggests a significant number of males could be gonadally mature but morphologically immature, and likely less able to successfully compete for

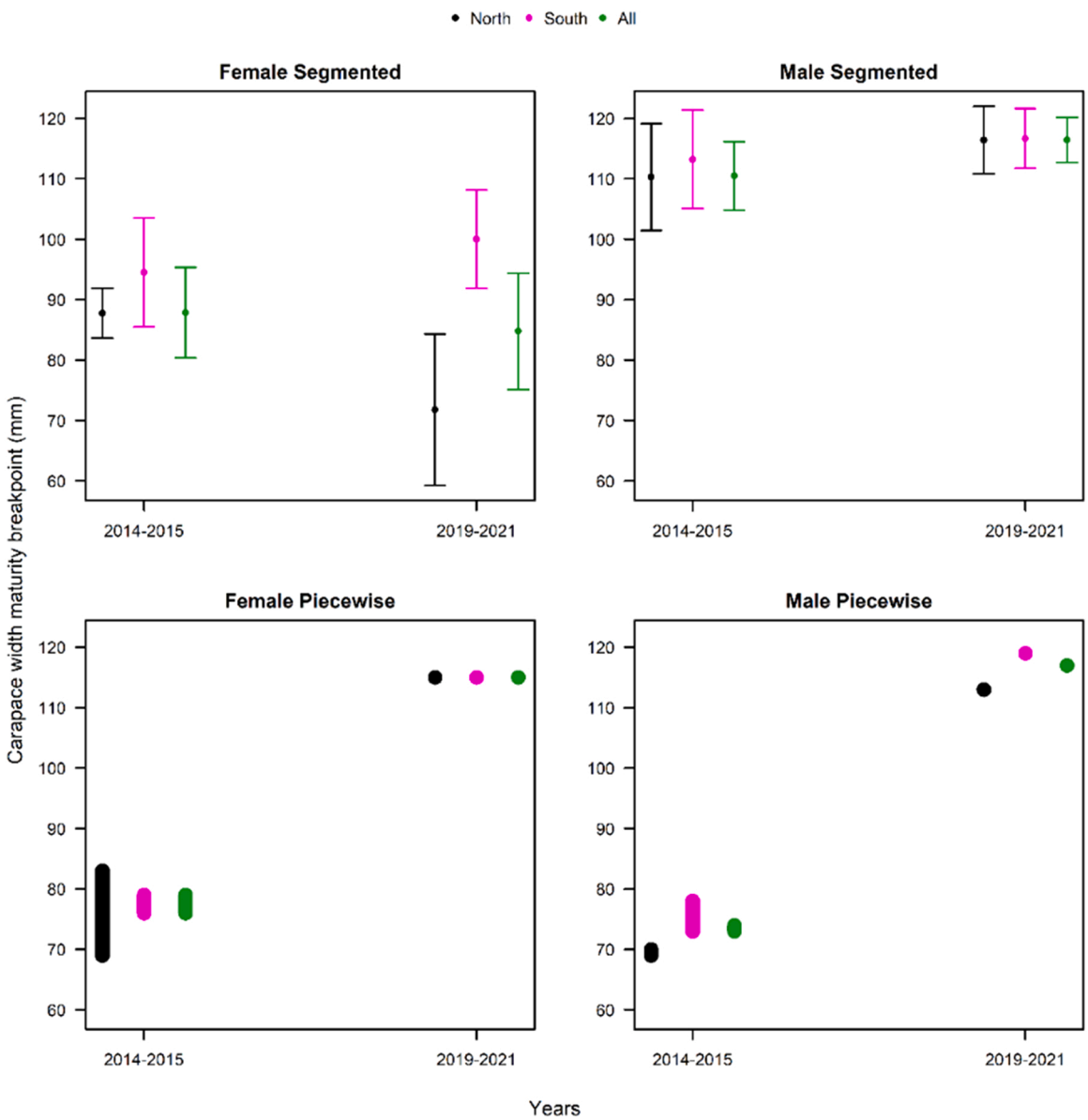

Fig. 5. Estimates of size at morphological maturity breakpoints (departure from isometric growth for claw dimensions (males) and abdomen width (females)) for edible crab *Cancer pagurus* in Welsh waters, for autumn/winter 2014–2015 and 2019–2021. The two plots on the top row are for segmented regression (dots represent model averages, whiskers represent 95 % confidence intervals). Plots on the bottom row are for piecewise regression, with ranges for the 2014/2015 study representing multiple estimates with an equal probability of being correct.

mates (Haig et al., 2016), and that by the time they are morphologically mature, nearly all males are gonadally mature (Edwards, 1979).

For females, the two regression methods in our study predicted very different size at maturity breakpoints (all Wales: 85 mm CW segmented, cf. 115 mm CW piecewise) with segmented having wide confidence margins. Mesquita et al. (2020) found similarly wide confidence margins for segmented, and inferred this was due to a gradual, rather than a sudden change in, growth pattern. This is because the segmented approach assumes the two regression lines either side of the breakpoint must meet, and therefore the technique struggles to estimate a breakpoint when the transition from morphological immaturity to maturity is gradual. In contrast, it is thought that the piecewise approach may be better suited to picking up gradual changes towards allometric growth. Indeed, in this study the confidence intervals around the piecewise regression were narrow and the all Wales estimate of the breakpoint at 115 mm CW aligns well with the gonadal maturity CW_{50} estimated under scenario 2 (114 mm CW).

It has been hypothesised that female abdomen width may not be related to size at maturity, but instead to fecundity (Mesquita et al., 2020). These authors also raised broader concerns about using morphological breakpoint approaches for female *C. pagurus* maturity. Studies sampling in a variety of geographic locations have found no evidence of allometric growth in female *C. pagurus* at many locations, while finding it in others (Haig et al., 2016; Bakke et al., 2018), and the large sample size we collected across a wide size spectrum failed to provide conclusive results for females using segmented regression. As a tool in isolation, especially using segmented regression, care should be taken using morphological approaches. However, combining piecewise regression with gonadal maturity may provide additional evidence to support functional maturity estimates.

4.3. Behavioural maturity

The low incidence of female crabs with sperm plugs (3 %) that were

recorded was the same as the previous Welsh study conducted at a similar time of year (Haig et al., 2015a, 2016). This result was not unexpected, as the prevalence of sperm plugs in newly moulted females is highly seasonal and location-dependent (Edwards, 1979; Haig et al., 2016; Mesquita et al., 2020). Our sampling in late autumn and winter was likely outside the main period of recently moulted (and mated) female crab in summer to early autumn in Welsh waters (various fishers, pers. comm.; unpublished data). The prevalence of visible sperm plugs appears to decline rapidly over a short period of time as visible sperm plugs were present in 42 % of females we examined off north Wales (during other onboard sampling) on one day in early October 2019. This disparity with our late autumn and winter sampling aligns with Tallack (2007), who found peak sperm plug prevalence around the Shetland Islands (Scotland) of around 70 % in October, falling rapidly to around 25 % in November and 0 % by December.

The minimum size at which we recorded sperm plugs (114 mm CW) in the laboratory was also similar to that of 118 mm CW recorded by Haig et al. (2016). Although the presence of sperm plugs has previously been used to generate estimates of size at 50 % maturity (Tallack, 2007), the fact that gonadally immature females are often mated means behavioural maturity determined by the presence of sperm plugs is of limited value for management purposes (Bennett, 1995; Mesquita et al., 2020). However, whilst caution using this method is needed when estimating CW_{50}, it does give an indication of the smallest size at which females are likely to be behaviourally, and possibly functionally, mature. Of interest is that this size is similar to the smallest berried female (116 mm CW), gonadal CW_{50} under scenario 2 (114 mm CW), the breakpoint using piecewise regression in this study (115 mm CW).

4.4. Functional maturity

For males across all Wales, both segmented and piecewise estimates of morphological maturity were similar at 116 mm (CI 113–120) CW and 117 mm CW respectively. This is a similar to the size (119 mm CW) at which 99 % of males (all Wales) attained gonadal maturity (CI 111–127), under scenario 1. Under scenario 2, the morphological breakpoints were similar to the CW_{95} of 117 mm CW (CI 111–123). Thus, a very high proportion of males above the morphological breakpoint size of 116–117 mm CW will be gonadally, and therefore, functionally (using this definition) mature. Importantly, this is around 23–24 mm below the MLS of 140 mm, meaning that most males will have the opportunity to mate before recruiting to the fishery.

The size of the smallest functionally mature (berried) female we recorded was similar to males at 116 mm CW, about the same as the smallest (115.6 mm CW) from Wales in 2015 in an unpublished fecundity study (Haig et al., 2015b), and within 5 mm of the smallest berried crab reported from several locations in the greater North Sea region (Williamson, 1900; Tallack, 2007; Ungfors, 2007; Bakke et al., 2018). Berried crab have long been known to rarely enter pots (Williamson, 1900): the low incidence we recorded is therefore both expected and likely to significantly under-represent the full size range of available berried crabs. Furthermore, it is not known whether minimum sizes of functional (or other types of) maturity in *C. pagurus* reported in the literature reflect broader population-level parameters or simply represent individual variation (and arbitrary sampling in the case of berried females). Our knowledge of the critical berried life history stage is limited and warrants further research. One study (Latrouite and Noël, 1993) found that English Channel *C. pagurus* placed in aquaria became berried at much smaller sizes (≥75 mm CW) than that reported in the wider literature. Furthermore, commercially fished decapod crustaceans that are berried may not necessarily carry fertilised, or fully fertilised, eggs: in a study of 20 berried American lobster *Homarus americanus*, 30% had unfertilised or partly fertilised clutches (Johnson et al., 2011).

Synthesizing our all Wales estimates of female maturity shows that the smallest berried individual (116 mm CW), the smallest female carrying sperm plugs (114 mm CW), gonadal CW_{50} maturity under scenario 2 (114 mm CW) and morphological maturity using piecewise regression (115 mm CW) are almost identical in size (114–116 mm CW). Therefore, although caution is required due to the low catchability of berried females, it appears as though the onset of functional maturity aligns with the CW50 of gonadal maturity and the morphological (piecewise) maturity breakpoint. This is to be expected as functional maturity is often achieved at larger sizes than gonadal maturity (all functionally mature individuals need to be gonadally mature, whereas not all gonadally mature individuals have to be functionally mature).

4.5. Change over time

Overall, we found no clear evidence of a significant decline in size at maturity of *C. pagurus* in Welsh waters between 2014/2015 and 2020/2021 which might be expected to occur if intensive overexploitation was occurring (Jørgensen et al., 2007; Sharpe and Hendry, 2009). Principally, we found no evidence of a decline in size at gonadal maturity, employing the widely used scenario 1. In addition, there was no obvious decline in the size of behaviourally mature and functionally mature (berried) females, and the minimum sizes of gonadally mature individuals. Comparison of morphological maturity breakpoints between the two studies revealed either no change (segmented) or a significant increase in size at maturity (piecewise), although this analysis was likely constrained by few small (< ca. 80 mm CW) individuals being sampled in Haig et al. (2016).

However, using the more conservative gonadal maturity scenario 2 (where stages 1 and 2 are immature), we found significant declines in size at maturity for females (all locations) and males (north and all Wales). This could be an example of declining size at maturity as observed in other heavily fished crustaceans like *Nephrops norvegicus* (Sigwart et al., 2020). Slight declines in female *C. pagurus* gonadal maturity size estimates were also reported from two of three fished areas sampled in Norway between 2003 and 2014 (Bakke et al., 2018), although these authors acknowledged the possibility of random variation and recommended regular monitoring. Likewise, caution is required in interpreting our findings as it is possible that they may simply highlight methodological issues with sampling and visual assignment of gonad categories. Like Haig et al. (2016), we sampled the majority of our crabs in the same period (November and December) to minimise ontogenetic differences in developmental stage, but it is possible that a difference in other factors (e.g. seawater temperature, food availability) between the two studies could result in a relatively advanced gonad development stage in crabs of a given size. For example, this could result in a greater proportion of stage 3 mature females compared to stage 2 developing (but immature) in a less favourable year, thus giving different size at maturity estimates. Scenario 1 may be less sensitive to this, as stage 1 immature individuals might require a pubertal moult (outside of the November/December sampling period) before they could start developing into stage 2. Like Bakke et al., (2018), we recommend ongoing monitoring to determine if our findings represent a real trend.

While longer-term changes in size at maturity have been recorded in other fished decapods in the north Atlantic (Haarr et al., 2017; Sigwart et al., 2020), there is little data available for *C. pagurus*. Bakke et al., (2018) found a slight decrease in gonadal (scenario 1) CW_{50} between 2003 and 2014 in two areas of Norway, but could not rule out random variation, rather than fisheries-driven decline. Based on the results of various regional studies Bakke et al., (2018) also suggested a broad decline in *C. pagurus* gonadal maturity CW_{50} over the previous decade or so, but it is possible these simply represent spatial variation in reproductive parameters or methodological differences.

Major commercial fisheries for *Cancer pagurus* have been operating around Britain since the late 1800s, with almost the entire coast of Wales considered crab fishing ground since this time (Olsen, 1883; Edwards, 1979). It is therefore plausible that changes to biological parameters such as maximum size and size at maturity have occurred, but

longer-term historic data should be considered where possible, rather than just recent data, to avoid 'shifting baseline syndrome' (Pauly, 1995). No data are readily available for the Welsh coast, but some are for females on the North Sea coast of northern England and eastern Scotland. In 1895 "*ordinary size at* [gonadal] *maturity…is above 6 in.* [152 mm][CW]…*between 6½ and 7 in.* [165 mm and 178 mm] *the great majority are mature"* whereas "*a large proportion of the crabs are mature between 5 and 6 in.* [127–152 mm]" (Williamson, 1900). A recent female gonadal maturity CW_{50} of 128 mm from this region (Mesquita et al., 2020) is at the lower end of, or considerably smaller than, these historic estimates. Although there are likely methodological and natural spatial differences between the studies, and in the absence of other shorter-term comparisons, it is plausible that *C. pagurus* size at maturity has declined historically. For fisheries of this and other species to be sustainable into the future over the long term, further research is needed to understand past changes.

4.6. Management implications

The results of this study will be of interest to managers, fishers and stakeholders, where MLSs are a key consideration. We found significantly smaller gonadal maturity in north Wales compared to the south. This broadly corresponds to the historically smaller MLS in north Wales for *C. pagurus* (and also for lobster *H. gammarus*) prior to the 2016 introduction of a Wales-wide MLS (Welsh Government, 2014). However, our results do not necessarily support a north-south difference in MLS as they are based on only two discrete sampling locations. This may simply reflect spatial variation in *C. pagurus* biology rather than a north-south cline (Bakke et al., 2018), and there is evidence of significant spatial variation in biology of other invertebrates and fish around the Welsh coast (Nash et al., 2000; Hold et al., 2021).

Our findings indicate that (for both scenarios) at least 95 % of both sexes of *C. pagurus* will have attained gonadal maturity by the time they reach the current Wales-wide MLS of 140 mm CW, and that nearly all males will be functionally mature by this size. It is however important to acknowledge that the link between these maturity definitions and actually contributing to the population through recruitment is poorly understood. Nevertheless, based on maturity estimates being under the MLS, we consider that mortality in the pot fishery of immature *C. pagurus* which have not yet spawned is unlikely to be a cause of falling CPUE that has been reported for this species in Wales and further afield (various fishers and *C. pagurus* biologists, pers. comm.). However, recruitment overfishing (i.e. the depletion of reproducing adult biomass) could still be occurring, but overfishing may not necessarily be happening to a degree that causes a decline in the size at maturity. In the Republic of Ireland, the MLS of 140 mm has been deemed to significantly protect the stock from recruitment overfishing, although available data there indicates declines in stock abundance and recruitment in recent years(Marine Institute and Bord Iascaigh Mhara, 2022). While we demonstrate that current management measures (in the form of the MLS) allows crabs to spawn at least once, they could be expanded to consider the effect of overfishing on larger individuals. Over 25 years ago, Bennett (1995, p. 97) noted that "*The scope for further optimization of technical controls* [on the UK *C. pagurus* fishery] *like MLSs is limited. Future management of* C. pagurus *stocks is likely to depend upon fishermen and managers grasping the nettle of direct effort regulation*". This call for effort control has been echoed by some Welsh pot fishers (Pantin et al., 2015; pers. comms. with fishers), yet there are currently no *C. pagurus* effort or landings limits in Wales or the wider UK. Other evidence-based concerns that may have population-level impacts on life history stages of *C. pagurus* include a narrow temperature range for successful larval development in the face of warming sea temperatures (Weiss et al., 2009), mortality of berried females in Irish Sea scallop dredge fisheries (Öndes et al., 2016), autumn fisheries for congregating pre-spawning females that could cause recruitment overfishing (Bennett, 1995), and use of *C. pagurus* as a preferred bait in Wales' valuable whelk *Buccinnum undatum* fishery (Pantin et al., 2015).

We collected a large sample across a wide range of crab sizes in two locations and used complementary methods to build a picture of size at maturity, acknowledging the limitations of each approach. We found similar results to previous and regional studies, suggesting our results are accurate. Our findings suggest that the current MLS should protect much of the population to spawn at least once. However, further management measures may be needed to address reported declines. In addition, an increased understanding of the seasonal and inter-annual reproductive cycles of these crabs at a local level in Welsh waters, along with a better understanding of the potential error or bias associated with methodology would improve confidence in these conclusions.

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CRediT authorship contribution statement

Alec B.M. Moore: Methodology, Investigation, Resources, Formal analysis, Project administration, Writing – original draft, Writing – review & editing, Visualisation. **Adam J Delargy:** Formal analysis, Methodology, Software, Visualisation, Writing – original draft. **Ruth P. Cann:** Investigation. **Charlotte Heney:** Investigation, Resources. **Lewis Le Vay:** Writing – review & editing. **Harriet Lincoln:** Investigation, Resources. **Ian D McCarthy:** Writing – review & editing, Project administration, Funding acquisition. **Natalie Hold:** Conceptualization, Methodology, Formal analysis, Writing – review & editing, Project administration, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106450.

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