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# A standardized assessment of geographic variation in size at maturity of European lobster (*Homarus gammarus* L.) in the North East Atlantic

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Assessing size at maturity for European lobster *Homarus gammarus* across the North East Atlantic remains a fundamental knowledge gap for this commercially valuable fishery. This study for the first time collates existing data on physiological maturity of female European lobster *H. gammarus* across the North East Atlantic, including new data from Scotland, Wales, and the Isle of Man. Physiological estimates of size at maturity were undertaken using 1309 lobsters from 11 locations using a standardized methodology. Carapace length (CL) at which 50% of the sampled population had reached physiological maturity (CL<sub>50</sub>) varied between populations, ranging from 82 to 92.5 mm. CL<sub>50</sub> estimates reported here are broadly similar for historic population samples in England, but estimates for Irish samples were lower than previous results. The development of a *H. gammarus* specific staging guide and methodology in this study enables the future comparison of potential fluctuations in female size at maturity.

**Keywords:** European lobster, fisheries, *Homarus gammarus*, maturity, reproduction.

## Introduction

Lobster fisheries are a significant economic component of small scale coastal fisheries worldwide, with European lobster *Homarus gammarus* being no exception. This species contributes to a low volume, high-value fishery. It typically comprises <3% of overall shellfish landings in the United Kingdom but is the fourth most valuable (MMO, 2020) with 2827 tonnes landed in 2020 (FAO, 2020) with similar trends in Ireland (343 tonnes), France (611 tonnes), and Scandinavia (135 tonnes) (FAO, 2020). Despite its high economic and socio-economic importance, fisheries for this species are usually still classed as data deficient, with variable national sampling schemes providing snapshots of stock composition based principally on landed proportions of stocks.

Fisheries targeting *H. gammarus* are classed as open access and occur year round. Catchability however is affected by both intra- and interspecific species interactions (Emmerson *et al.*, 2022). Temperature is seen as the primary driver in influencing interactions with the fishery and perceived catch rates (Lizárraga-Cubedo *et al.*, 2015; Emmerson *et al.*, 2022). *H. gammarus* fisheries are managed broadly without any input controls (e.g. pot limits or seasonal closures) or output controls (e.g. quota). Historically, sex-specific regulations have not occurred in *H. gammarus* fisheries except the Isle of Man where implementation of a berried ban (females lobster with extruded eggs) (Isle of Man Government, 2003) has taken place since 2003. Recent concerns relating to fishing mortality and potential negative effect on yield per re-

cruit has resulted in the implementation of a berried ban across the England, (UK Government, 2017). The primary method of regulation within *H. gammarus* fisheries however still hinges on the implementation of appropriate minimum landings size (MLS) and in some cases, maximum landing size (MaxLS—Ireland and Scotland). Setting size-selective harvesting regimes, with (mls) appropriate to the size-at-maturity, is generally regarded as a basic principle of good management in crustacean fisheries (Bannister, 1999). Such measures are implemented based on assumptions about growth and size at maturity (SaM), with recent, regionally specific data often lacking.

To understand the scale of appropriate management for *H. gammarus*, increased research using genetic analysis has been undertaken in recent years to define stock boundaries. Results from North East Atlantic stocks broadly suggest that across large geographic distances (approximately thousands of kilometres) (Triantafyllidis *et al.*, 2005—mtDNA) and at local levels (approximately hundreds of kilometres) (Watson *et al.*, 2016; Ellis *et al.*, 2017—microsatellite) *H. gammarus* populations remain genetically homogenous, signifying genetic mixing. However, reproductive characteristics, influenced by regional environmental drivers, appear to vary and suggest that management should be applied at a regional scale [*H. gammarus*—Free (1994), Tully *et al.* (2001); *H. americanus*—Little and Watson (2005), Waddy and Aiken (2005)]. Fecundity, for example, shows regional patterns in *H. gammarus* (Ellis *et al.*, 2015), indicating underlying spatial en-

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**Table 1.** Estimates of SaM in female *H. gammarus* published in peer review and grey literature.

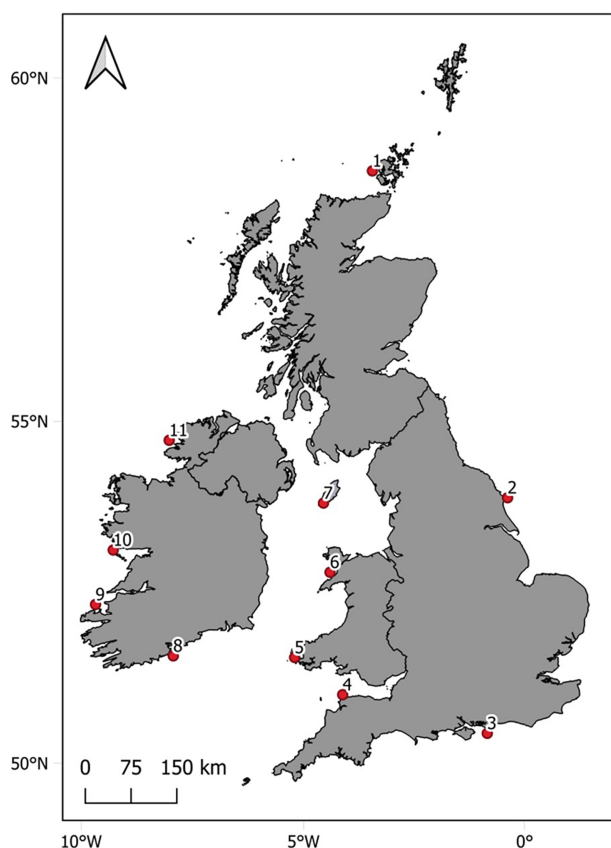
Maturity	Method	CL <sub>50</sub>	CL mature	Country	Year	n	References
Morphological	Abdomen	79 mm	–	Scotland – Firth of Fourth	1999–2000	353	Lizárraga-Cubedo <i>et al.</i> (2003)
Morphological	Abdomen	98 mm	–	Scotland—Hebrides	2000–2001	255	Lizárraga-Cubedo <i>et al.</i> (2003)
Morphological	Abdomen	86 mm	85–104	Wales—Anglesey	1961	–	Simpson (1961)
Morphological	Abdomen	77 mm	77–97	Wales—Pwllheli	1961	217	Simpson (1961)
Morphological	Abdomen	~75 mm	–	Isle of Man	2016	29	Emmerson <i>et al.</i> (2016)
Functional	Ovigerous	–	103–106	France—Le Croisic	2009	10 402	Laurans <i>et al.</i> (2009)
Functional	Ovigerous	90 mm	–	England— Yorkshire	1989–1991	–	Free <i>et al.</i> (1992)
Functional	Ovigerous	82.5 mm	–	England—Selsey	1989–1991	–	Free <i>et al.</i> (1992)
Functional	Ovigerous	100 mm	–	Wales—Dale	1989–1991	–	Free <i>et al.</i> (1992)
Functional	Ovigerous	~92–100 mm	–	England— Yorkshire	2008–2009/ 2012–2013	~6800	Wood (2018)
Functional	Ovigerous	107 mm	–	Ireland—North- west	1998–1999	22 530	Tully <i>et al.</i> (2001)
Functional	Ovigerous	116 mm	–	Ireland—West	1998–1999	22 530	Tully <i>et al.</i> (2001)
Functional	Ovigerous	122 mm	–	Ireland—South- west	1995	22 530	Tully <i>et al.</i> (2001)
Functional	Ovigerous	140 mm	–	Ireland—South- East	1998–1999	22 530	Tully <i>et al.</i> (2001)
Functional	Ovigerous	95 mm	–	Scotland—Firth of Fourth	1999–2000	353	Lizárraga-Cubedo <i>et al.</i> (2003)
Functional	Ovigerous	98 mm	–	Scotland—Hebrides	2000–2001	255	Lizárraga-Cubedo <i>et al.</i> (2003)
Functional	Ovigerous	93 mm	–	Scotland—Orkney	1969	–	Thomas (1969)
Functional	Ovigerous	88 mm	–	Isle of Man	2015	–	Emmerson <i>et al.</i> (2016)
Functional	Ovigerous	99 mm	–	France—Le Conquet	1976–1981	–	Latrouite <i>et al.</i> (1984)
Functional	Ovigerous	98 mm	–	France—Ile d'Yeu	1976–1981	–	Latrouite <i>et al.</i> (1984)
Functional	Ovigerous	79 mm	–	Sweden	1979–1982/1989	9775	Ulmestrand (2003)
Functional	Ovigerous	~80 mm	–	Norway—Kvitsoy	–	–	Agnalt, (unpublished)
Functional	Ovigerous	~62 mm	–	Norway—Tysfjord	1992–2005	–	Agnalt <i>et al.</i> (2009)
Physiological	Gonad	96 mm	–	Ireland—North- West	1998–1999	129	Tully <i>et al.</i> (2001)
Physiological	Gonad	92.5 mm	–	Ireland—West	1998–1999	92	Tully <i>et al.</i> (2001)
Physiological	Gonad	94 mm	–	Ireland—South- West	1995	109	Tully <i>et al.</i> (2001)
Physiological	Gonad	95 mm	–	Ireland—South- East	1998–1999	118	Tully <i>et al.</i> (2001)
Physiological	Gonad	83 mm	–	England— Bridlington	–	101	Free (1994)
Physiological	Gonad	87/97 mm	–	England—Selsey	–	151	Free (1994)
Physiological	Gonad	80 mm	–	Wales—Dale	–	27	Free (1994)

vironmental drivers influencing reproductive biology (Agnalt *et al.*, 2009). Consequently, management based on reproductive characteristics such as size at first maturity presents an effective method for reducing recruitment overfishing in management units. Such management can protect spawning stock biomass but is reliant on obtaining reliable and accurate estimates of regional SaM (Waddy and Aiken, 2005). Increasing importance is therefore placed on understanding the fundamental biological characteristics that underpin effective national and regional sustainable management (Lowerre-Barbier *et al.*, 2011).

In the case of *H. gammarus*, SaM varies geographically (Table 1), as it does in other decapods [*H. americanus*—Watson *et al.* (2013); Waller *et al.* (2021); Ellertson *et al.* (2022); *Panulirus homarus homarus*—Kulmiye *et al.* (2006); *Cancer pagurus*—Haig *et al.* (2016); *Palaemon serratus*—Emmerson *et al.* (2017); *Maja* spp.—Corgos and Freire (2006); *Nephropidae* spp.—Ayza *et al.* (2011)]. Thus far, CL<sub>50</sub> for *H. gammarus* is reported as varying from 79 to 140 mm carapace length (CL) with a variety of techniques and terminology having been applied across studies, highlighting

the need for established replicable methodologies and consistent terminology (Waddy and Aiken, 2005; Laurans *et al.*, 2009).

Estimations of maturity in *H. gammarus* have been based on three different approaches: (i) morphological, (ii) gonadal (physiological), and (iii) functional. Morphological estimates are based on demonstrating allometric growth associated with the development of secondary sexual characteristics in *H. americanus* (Conan *et al.*, 2001). In female *H. americanus*, increases in the second abdominal segment width are observed, associated with the accommodation and attachment of fertilized ova. The reliability and effectiveness of characterizing allometric growth patterns as a tool for estimating maturity has been challenged in the past, owing to observed gradual changes in growth throughout a lobster's life-history stages (Conan *et al.*, 2001; Comeau and Savoie, 2002) or limited success in detecting allometric growth (Tully *et al.*, 2001). Similar observations have been made in other decapods (Haig *et al.*, 2016). However, a number of examples of allometric growth patterns associated with maturity have been reported in *H. gammarus* (Free, 1994; Lizárraga-Cubedo *et al.*, 2003; Ryan,



**Figure 1.** Sampling locations for *H. gammarus* physiological SaM research. Samples collected from (1) Orkney, Scotland; (2) Bridlington, England; (3) Selsey, England; (4) Ilfracombe, England; (5) South Wales, Wales; (6) North Wales, Wales; (7) Isle of Man; (8) South East, Ireland; (9) South West, Ireland; (10) West, Ireland; and (11) North West, Ireland.

2012) and other decapod species (Emmerson *et al.*, 2017). Furthermore, Émond *et al.* (2010) showed that a number of allometric growth changes do occur at various life-history stages, the onset of maturity being one. However, historical comparisons of morphological maturity estimates remain difficult due to differences in approaches to statistical analysis (Simpson, 1961; Lizárraga-Cubedo *et al.*, 2003; Mallet, 2003).

Gonadal or physiological maturity studies have assessed maturity based on gonad staging, with gonads characterized in terms of size, weight, and colour to infer maturity. Variable interpretations of gonad development stages have led to discrepancies and ambiguity between studies. Waddy and Aiken (2005) highlighted the misinterpretation and use of different staging criteria in *H. americanus*. These issues make it difficult to compare studies and therefore difficult to provide reliable management advice on a regional basis. Existing studies for *H. gammarus* described physiological maturity at either national or regional levels; Ireland (Tully *et al.*, 2001); England (Free, 1994; Cefas, 2004); and Wales (Free, 1994). In these studies, however, (1) they employed different staging methodologies in which maturity was assigned and (2) the foundation of criteria utilized was originally developed for *H. americanus* (Aiken and Waddy 1980) questioning its suitability/applicability. The significant differences in baseline biology known between *Homarus* spp. (Coleman *et al.*, 2019), indicates the need to develop *H. gammarus* specific SaM criteria. Free (1994) previously developed SaM criteria to estimate

maturity across three populations in England and Wales but this criteria has never been broadly applied or used in subsequent SaM estimates (Tully *et al.*, 2001).

Functional maturity estimates have been based on the visible indicators of maturity. In the case of *H. gammarus*, this has been the ovigerous state in females (Latrouite *et al.*, 1984; Tully *et al.*, 2001; Laurans *et al.*, 2009; Wood, 2018). Undoubtedly, functional maturity is the most readily and easily applied method of estimating SaM in *H. gammarus* (Table 1). Standard fishery sampling programmes in government agencies usually collect these types of data. However, this method is sensitive to a number of possible confounding variables that need to be considered in designing sampling regimes and in the interpretation of data: egg production is not annual in *Homarus* spp.; spawning frequency is size related; there is an egg bearing season, which may vary geographically; and catchability of ovigerous females may be different to females that are immature or not berried (Tully *et al.*, 2001; Agnalt, 2008; Laurans *et al.*, 2009).

The aim of this study is to characterize geographic variability in SaM using a standardized protocol. The specific objectives of the study are to (i) compile existing physiological maturity data for *H. gammarus* from published and grey literature sources, (ii) apply a unified gonad staging criteria and consistent method of analysis across all samples for physiological data, (iii) use the outcomes from (ii) to estimate SaM of *H. gammarus* in North East Atlantic populations, and (iv) produce a standardized maturity staging guide from newly collected samples. By applying this approach, for the first time, we will be able to provide comparable estimates and assessment of SaM for *H. gammarus* for a significant portion of the area where it is commercially exploited.

## Material and methods

### Data extraction from literature

To evaluate geographic differences in physiological SaM, data were collated from all available historic data sources (Free, 1994; Tully *et al.*, 2001; Cefas, 2004), assessing maturity across 11 locations spread across the British Isles and Ireland (Figure 1).

### Physiological maturity samples and laboratory method

New live female lobsters were collected from Wales (North  $n = 61$ ; South  $n = 77$ ) and the Isle of Man ( $n = 84$ ) in 2019, with lobsters obtained from the Orkney ( $n = 116$ ) commercial fishery through sea observer trips and fisher self-collection in 2017 ( $n = 58$ ), 2018 ( $n = 21$ ), and 2019 ( $n = 37$ ) from a pre-determined size range (50–115 mm CL). Additional samples ( $n = 121$ ) collected in Galway, Ireland in 2008 were made available, which were not previously used in the estimates by Tully *et al.*, (2001). Sample collection coincided with the post-moult/pre-spawning period in each location (August/September). Derogations for the retention of sublegal lobsters were obtained from the relevant government institution at each location.

Prior to destructive sampling, live lobsters were chilled until dead with the exception of samples from the Isle of Man, where samples were frozen prior to destructive sampling. The following morphometric measurements were taken to the nearest millimetre using vernier callipers: (1) CL and (2)





**Figure 2.** Location of ovary observation window and of ovary development stages used to assess physiological maturity in female European lobsters *H. gammarus*.

abdomen width (measured at the widest point of the second abdominal segment) as per Conan *et al.* (2001). Lobsters were dissected using small dissection scissors, cutting from the posterior margin of the carapace extending up to  $\frac{3}{4}$  of the CL and extending ~1 inch and then back, thus providing a gonadal observation window. The carapace and connective tissue were carefully removed exposing ovaries and hepatopancreas beneath (Figure 2).

### Physiological maturity criteria

New and historical data were assessed and classified as mature against six primary [adapted from Tully *et al.* (2001)] and one secondary criteria. Due to the nature of the historical data, sites varied in the number of criteria from which maturity could be assessed, a minimum of two criteria were required for a site to be included in SaM estimates. Each lobster was assessed using the maximum number of criteria possible and had to meet all available primary criteria to be classed as physiologically mature or if this was not the case, it had to show evidence of previous spawning as described below. The primary criteria were as follows.

- (1) Ovary colour. Ovaries were photographed and visually staged using the description of female stages from Waddy and Aiken (2005) (Table 2); typically  $\geq$  stage 4 was classed as mature due to dark green colour associated with secondary vitellogenesis (Figure 2).

- (2) Ovary factor  $> 150$ . Ovary factor ( $O_f$ ) was calculated by carefully removing the ovary and weighing it to the nearest milligram with an ovary factor calculated per sample using the following equation:

$$O_f = \frac{\text{ovary weight (mg)}}{CL(cm)^3} \times 10.$$

- (3) Abdomen width/carapace ratio greater than the smallest observed berried female derived from regional commercial sampling.
- (4) Egg diameter  $> 1.0$  mm were classed as mature (Tully *et al.*, 2001), with egg diameter calculated by removing and observing five ova and measured under  $\times 3$  magnification on an Olympus dissecting microscope.
- (5) Cement gland stage  $> 1$ . Cement gland development is known to coincide with egg extrusion, with development indicating preparation of spawning.
- (6) Moults stage C4 (inter-moults).

Or

- (1) Evidence relating to previous oocyte maturity, indicated by presence of yellow ova in the ovary following vitellin reabsorption (Comeau and Savoie, 2002) or previous spawning events, indicated by yellow colouration at the distal end of the oviduct (Waddy and Aiken, 2005) were used to identify mature individuals. In these cases, previous spawners would have low  $O_f$ , cement gland stage  $< 1$ , and could therefore be

**Table 2.** Physiological criteria for categories of ovary development in American lobster *H. americanus* (Waddy and Aiken, 2005).

Immature ovary	Developing ovary	Mature ovary	Spent/resorbing ovary
Stage 1: Ovary white Oocytes < 0.5 mm Ovary factor < 100	Stage 2: Ovary yellow, orange, beige Or pale green Oocytes < 0.8 mm Ovary factor < 100  Stage 3: Ovary light to medium green Oocytes < 1.0 mm Ovary factor < 200  Stage 4a (autumn): Ovary medium to dark green Oocytes 0.1–1.6 mm Ovary factor < 200	Stage 4b (spring): Ovary medium to dark green Oocytes 0.8–1.6 mm Ovary factor 200–325  Stage 5: Ovary dark green Oocytes 1.0–1.6 mm Ovary factor > 325  Stage 6: Ovary dark green Oocytes 1.4–1.6 mm Ovary factor > 400  Stage 6a: Postovulation (oocytes free in ovary)	Stage 7: Ovary large; flaccid, white or yellow; may have residual green oocytes

Stage 4b and greater is classified as being mature (Waddy and Aiken, 2005).

assigned as immature due to bi-annual spawning events of *Homarus* spp. If previous spawning was evident, the individual was classified as mature irrespective of the other criteria.

### Statistical analysis

All statistical analyses were run in the statistical package R (R Core Team, 2020). Physiological maturity data were converted to binary form (immature = 0, mature = 1), with lobsters binned in 5 mm size increments. SaM ogives for each location were estimated using a logistic regression model (Roa *et al.*, 1999) reformulated by Walker (2005) to produce

$$P_i = \left\{ 1 + e^{-\ln(19) \frac{CL_i - CL_{50}}{CL_{95} - CL_{50}}} \right\}^{-1},$$

where  $P(i)$  is the proportion of the population that is mature at a given CL.  $CL_{50}$  is CL at which 50% of individuals are mature. Curve parameters were estimated using a generalized linear model (GLM) with a logit link function and a binomial error structure. Confidence intervals were determined by bootstrapping the GLM (10000 runs). The base code used was originally constructed by Harry (2013). Similar analysis was also used to estimate Carapace width<sub>50</sub> in *Cancer pagurus* (Haig *et al.*, 2016). This analysis provides estimates of female  $CL_{50}$  per location or the size at which 50% of females are predicted to be mature.

## Results

### Size distribution and assignment of ovary stages

Lobsters ranged in size from 58 to 143 mm CL, with the number of individuals per ovary stage varying among locations (Figure 3). Every effort was made to collect an equal number of individuals per size class from the new survey locations (Orkney; Wales; and Isle of Man). This was however not possible, either due to lack of interaction of size classes with the fishery (<75 mm CL) or derogation limits imposed by regional licencing bodies. These limitations resulted in some regions obtaining fewer sublegal/immature individuals. Clear differences in the distribution of ovary stages across size classes were observed among locations (Figure 3). A high number

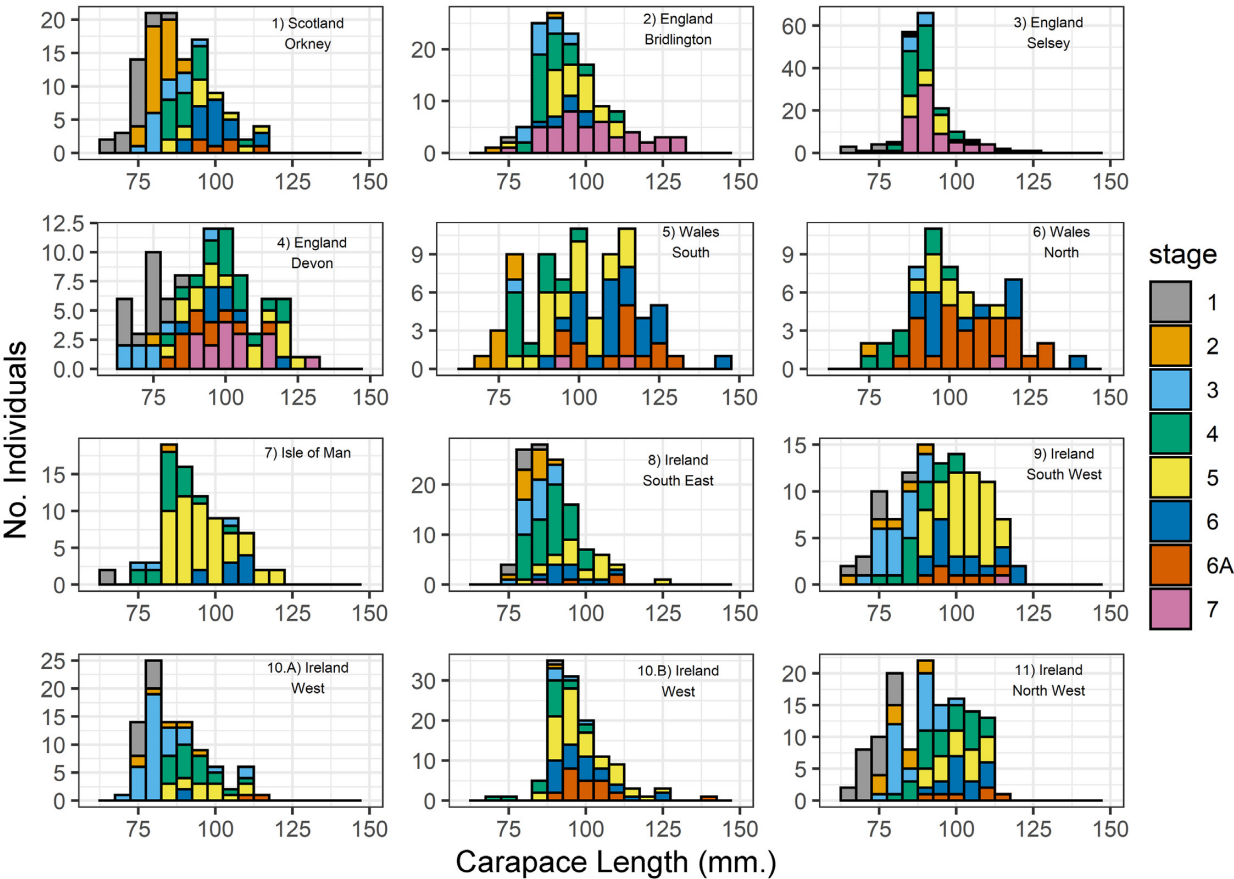
of individuals classified as spent (stage 7) were observed in English samples compared to other regions.

### Estimates of $CL_{50}$

Female lobster physiological maturity was assessed at 11 locations. The smallest observed physiological mature individual was 73.5 mm CL at Bridlington, England (Table 4). Due to the use of data from various historical studies, not all individuals could be assessed against the full criteria available (Table 3).  $CL_{50}$  ranged from 78.4 to 94.1 mm CL (Figure 4), with the rate of maturity seen to vary between locations. CIs were wider where smaller lobsters were not available (Figure 4—Isle of Man) and instances where a greater variation of ovary maturation stages in size classes was present (Figure 3) indicating a more gradual process of maturation across a number of size classes, such as those exhibited by North Wales (Table 4:  $a = -15.63$ ,  $b = 0.18$ ). In comparison, a more distinct maturation process was exhibited in Scotland Orkney, with a steeper ogive (Table 4:  $a = -40.59$ ,  $b = 0.43$ ) and coinciding with less variation of ovary stages across size classes (Figure 3). No estimation of SaM could be provided for new samples collected for 2008 West Ireland samples. The lack of convergence is attributed to the skewed sample distribution and the associated lack of immature individuals (Figure 3).

### *Homarus gammarus* staging guide

Using compiled dissection data across all study locations, *H. gammarus* physiological criteria/definitions were defined (Table 5), with those previously described by Aiken and Waddy (1982) used as a guide. Broadly comparable rates of ovary development (ovary factor) and oocyte size were evident between *H. americanus* and *H. gammarus* from ovary development stage 1 to 4. The cut off of 150  $O_f$  remains a valid criterion in the determination of maturity in conjunction with the other classifiers, specifically ovary stage. In the case of *H. gammarus*, the use of an  $O_f$  of 200 as per *H. americanus* would result in the potential misclassification of individuals as immature (Figure 5). Further divergence in ovary development was observed in stages  $\geq 4$  with *H. gammarus*



**Figure 3.** Length frequency histograms for all female *H. gammarus* used to estimate SaM per study location, with the number of individuals assigned to each ovary development stage per 5 mm size class displayed. Location 10B relates to new data collected in 2008. Attention is drawn to the different y-axis for each plot.

**Table 3.** Available maturity criteria used to assess each population based on dissections or from previous studies.

Study	Location	Ovary colour	Ovary factor	Cement gland	Abdomen width/carapace ratio	Previous spawning	Oocyte diameter
Coleman <i>et al.</i> (this study)	Orkney, Scotland	X	X	X	X	X	X
Free (1994)	Bridlington, England		X	X			
Free (1994)	Selsey, England		X	X			
Cefas (2004)	Devon, England	X	X	X	X	X	X
Coleman <i>et al.</i> (this study)	North and South, Wales	X	X		X		X
Coleman <i>et al.</i> (this study)	Isle of Man	X	X		X	X	
Tully <i>et al.</i> (2001); Tully (unpublished)	South East, South West, West, North West; Ireland	X	X	X	X	X	X

seen to develop both larger oocytes and larger ovary factors than that of *H. americanus* (Table 5).

**Discussion**

The development of a standardized maturity criteria, staging guide and methods of data analysis provides the first opportunity to compare SaM estimates for *H. gammarus* both temporally and spatially, whilst providing a baseline for future studies. The use of multiple criteria for assessing physiological maturity reduces potential biases in interpretation by

individual assessors. The maturity criteria employed here were based on those used by Tully *et al.* (2001) and McIntyre *et al.* (2017). Strict classification of mature individuals was based on all criteria for which the animal could be assessed in a given population being met, or based on evidence of previous vitellogenesis and/or spawning. This approach increases the reliability of estimates provided (Waddy and Aiken, 2005). Estimates presented here are broadly similar to historical estimates of SaM in the literature, with key differences observed for Irish samples (Table 4). These differences in Irish samples can be attributed to the inclusion of the criteria of

**Table 4.** Summary statistics and SaM ( $CL_{50}$ ), lower confidence intervals (LCI) and upper confidence intervals (UCI) for each population of *H. gammarus* around the North East Atlantic.  $CL_{50}$  estimates in parenthesis are historical estimates [Ireland—Tully *et al.* (2001)].

Region	Year	<i>n</i>	CL range (mm)	Smallest mature CL	$CL_{50}$ (mm)	LCI (mm)	UCI (mm)	Previous spawning %	a	b	$R^2$
(1) Orkney, Scotland	2017–2019	116	58–115	85	92.5	90.8	94.1	18	−40.59	0.43	0.79
(2) Bridlington, England	1991	130	68–130	73.5	85.7	80.6	89	–	−15.96	0.18	0.38
(3) Selsey, England	1991	181	64–126	76	84.2	81.1	86.5	–	−16.62	0.19	0.29
(4) Ilfracombe, England	2004	91	61–130	79.7	88.8	85.3	92.4	23	−17.94	0.2	0.71
(5) South Wales	2019	77	68–143	82	90.2	86.2	94.1	–	−18.41	0.2	0.67
(6) North Wales	2019	61	75–140	76	86.2	75.2	91.6	–	−15.63	0.18	0.45
(7) Isle of Man	2019	84	63–120	82	82	76.6	85.2	10	−16.80	0.20	0.44
(8) South East, Ireland	1996	118	74–127	86	87 (96)	85	88.7	–	−24.46	0.28	0.49
(9) South West, Ireland	1998	109	60–120	78.5	87.1 (94)	83.6	90.2	61	−16.85	0.19	0.62
(10) West, Ireland	1998	92	70–115	86	88.6 (92.5)	86.8	90.3	35	−36.68	0.41	0.77
	2008	121	72–141	88	–	–	–	20	–	–	–
(11) North West, Ireland	1998	129	66–114	86	91.9 (96)	90.2	93.8	35	−32.37	0.35	0.80

previous spawning, thus increasing the proportion of individuals classed as mature at smaller CL if they did not meet all other classifying criteria. The majority (61%) of samples from Southwest Ireland showed evidence of previous spawning, with these individuals ranging between 75 and 120 mm CL, translating to a smaller estimate of  $CL_{50}$ . Our attempt to include previously unpublished data from 2008 to provide a comparison of estimates of  $CL_{50}$  for the West of Ireland was not possible due to the limited size frequency distribution of 2008 samples. These were skewed to legal sized individuals (Ireland MLS 87 mm CL) and lacked immature/sublegal sizes (Figure 3 - 10.B). The important use of previous spawning as an overarching criterion in assigning maturity is critical to classifying individuals that have spawned that year (Watson *et al.*, 2013); individuals possessing low  $O_f$  increases the chance of misclassification as immature if such a criterion is not accounted for (Waddy and Aiken, 2005).

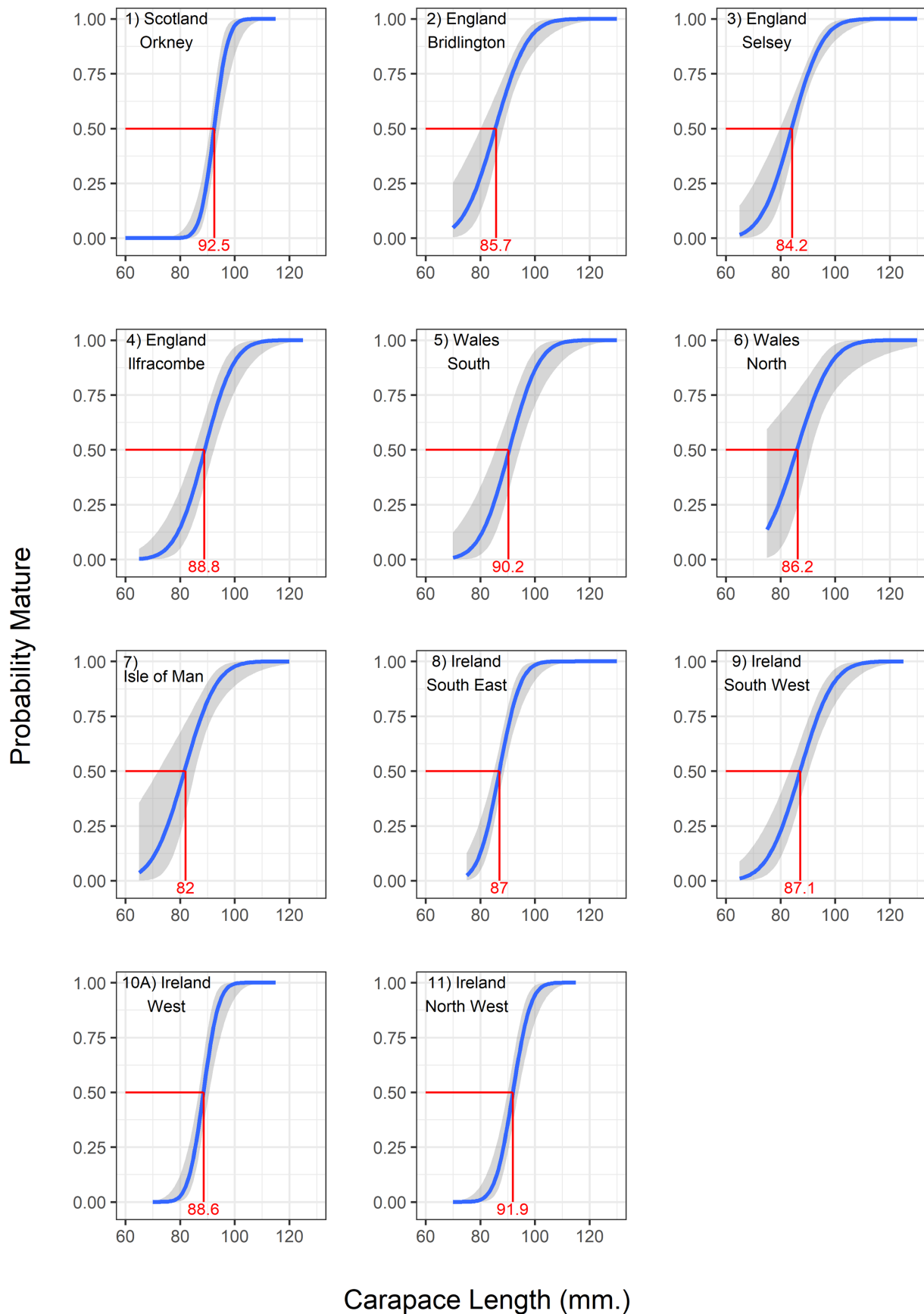
The lack of standardised methodologies/criteria and studies on historical trends of  $CL_{50}$  based on physiological estimates for *H. gammarus* presents a challenge. Specifically in understanding long term effects of fishing pressure or the future impact of climate change on key life-history traits. Declining  $CL_{50}$  has been observed in male snow crab *Chionoecetes opilio* populations in Newfoundland and Labrador, Atlantic Canada over the last 25 years, with declines attributed to increases in fishing pressure (Mullowney and Baker, 2020). Declines in  $CL_{50}$  in *H. americanus* over similar time frames are attributed to climate change (Le Bris *et al.*, 2017; Waller *et al.*, 2021) or a combination of both fishing mortality and climate change (Haarr *et al.*, 2017). Evidence is also emerging of ecosystem responses to climatic shifts in the North Sea. Recent declines in stock biomass of Atlantic cod *Gadus morhua* are attributed to a combination of fishing pressure and climate change (ICES, 2019). Due to the predominantly open access nature of lobster fisheries across North West Europe, it could be theorized that declines of  $CL_{50}$  could have occurred over similar time frames owing to exploitation pressure. The

majority of stocks across Scotland and England are seen to be exploited at levels substantially above candidate  $F_{MSY}$  target reference points and in some cases above candidate limit reference points (Mesquita *et al.*, 2017; Cefas, 2020), leaving stocks vulnerable to fisheries-induced evolution and reduced resilience to climate change.

The use of cement gland staging is regarded historically as a reliable and accurate method for estimating SaM in both *H. americanus*—Aiken and Waddy (1982); Campbell and Robinson (1983); Comeau and Savoie (2002); Watson *et al.* (2013), and a lesser extent *H. gammarus*—Tully *et al.* (2001). By comparison, this study found the assignment of maturity based on cement gland stages difficult, with *H. gammarus* cement gland development observed to be less well defined than that outlined by Aiken and Waddy (1982) even in individuals identified as being in intermoult. Pleopods showed significantly less cement gland development than those recorded on stage 4 pleopods observed on *H. americanus* (Coleman, pers. obs.). The resulting difficulty and consensus on cement glands resulted in removal of this criterion from Welsh and Isle of Man  $CL_{50}$  estimates and its subsequent exclusion from the staging guide. It is important however to acknowledge that sample preservation could have affected pleopod reading, with samples in the Isle of Man frozen prior to reading. Waddy and Aiken (2005) have highlighted that the choice of cement gland stage, timing of sampling of cement glands can all influence SaM estimates. The difficulty in consensual agreement experienced in *H. gammarus* mirrors that of recent *H. americanus* cement gland staging, resulting in ovarian staging designated as the preferred method to assess maturity by the Atlantic States Marine Fisheries Commissions Technical committee (Atlantic States Marine Fisheries Commission, 2020).

In conclusion, this study highlights the necessity of having robust maturity criteria to ensure that reliable estimates of maturity are presented, whilst also providing the basis for future comparison through the creation of a standardized physiological criteria.

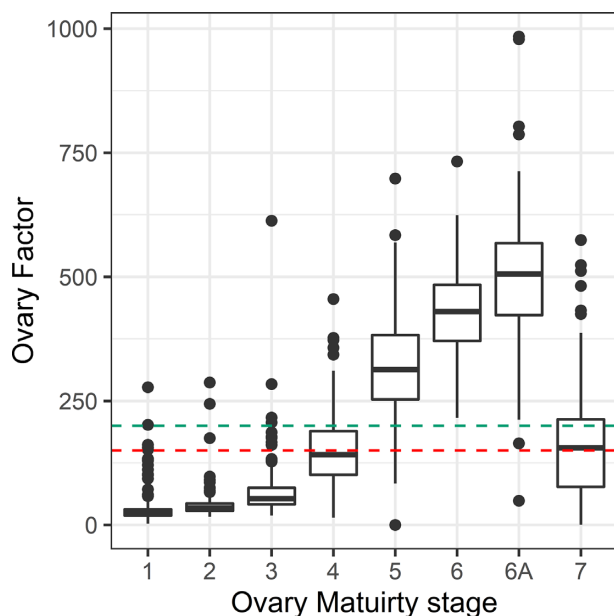




**Figure 4.** Maturity ogives for female *H. gammarus* from 11 populations distributed around the British Isles and Ireland estimated from physiological gonad staging. The horizontal line is the probability of 50% physiological maturity, the red number denotes the estimated size at maturity (SaM). Shaded area are the 95% CIs.

**Table 5.** Comparison of physiological criteria used to categorise ovary development in *H. americanus* (Aiken and Waddy, 1980; Aiken and Waddy, 1982; Waddy and Aiken, 2005) and *H. gammarus* (Coleman *et al.* (this study)).

Stage	<i>Homarus americanus</i> (Aiken and Waddy, 1980)		<i>Homarus gammarus</i> (Coleman <i>et al.</i> (this study))	
	Ovary colour	Oocyte diameter and Ovf	Ovary colour/appearance	Oocyte diameter and Ovf
Stage 1	Ovary White	Oocytes < 0.5 mm Ovf < 100	String like white ovaries. No visible oocyte formation in the follicles.	Oocytes < 0.5 mm Ovf < 50
Stage 2	Ovary yellow, beige, pale green	Oocytes < 0.8 mm Ovf < 100	Ovary thin, strap like. Yellow/lime green. Many empty/white follicles	Oocytes < 0.5 mm Ovf 100
Stage 3	Ovary light to medium green	Oocytes < 1.0 mm Ovf < 200	Ovary thin, strap like. Light to medium green. Larger oocytes beginning to develop but still empty follicles present.	Oocytes < 1 mm Ovf < 100
Stage 4a (Autumn)	Medium to dark green	Oocytes 0.1–1.6 mm Ovf < 200	Ovary thin, strap like filling <50% of dorsal cavity. Dark green. Most follicles show green oocytes. Evidence of previous vitellogenesis may be evident through presence of yellow oocytes/flecks in ovary, and/or previous spawning via distal yellowing of oviduct.	Oocytes 0.5–1.6 mm Ovf < 200
Stage 4b (spring)	Medium to dark green	Oocytes 0.8–1.6 mm Ovf 200–325	NA Study carried out in autumn to coincide with period preceding spawning.	
Stage 5	Dark green	Oocytes 1–1.6 mm Ovf > 325	Plump dark green ovaries—no longer strap like. Fills > 50% of dorsal cavity. Evidence of previous vitellogenesis may be evident through presence of yellow oocytes/flecks in ovary, and/or previous spawning via distal yellowing of oviduct.	Oocytes > 1.2–2.3 mm Ovf 200–550
Stage 6	Dark green	Oocytes 1.4–1.6 mm Ovf > 400	Plump, bulging, dark green ovaries filling dorsal cavity. More granular in appearance than stage 5. Evidence of previous vitellogenesis may be evident through presence of yellow oocytes/flecks in ovary, and/or previous spawning via distal yellowing of oviduct.	Oocytes 1.5–2.6 mm Ovf > 250
Stage 6a	Dark green	Post ovulation—oocytes free in ovary	Bulging, dark green, ovaries taking up whole dorsal cavity. Oocytes free in the ovary. Evidence of previous vitellogenesis may be evident through presence of yellow oocytes/flecks in ovary, and/or previous spawning via distal yellowing of oviduct.	Oocytes 1.5–2.6 mm Ovf > 300
7 (Spent)	White or yellow May have some green residual oocytes.	Large flaccid ovary.	Large flaccid white/cream ovaries. Not strap like as in stage 2/3. Some yellow ova may remain and in some animals may see residual green oocytes especially at the dorsal tips.	Flaccid ovary



**Figure 5.** Boxplot of ovary factor for each ovary maturity stage for all sample locations used to estimate female *H. gammarus* SaM. Dashed red line denotes an ovary factor threshold of 150; and dashed blue line denotes an ovary factor of 200 used in American lobster *H. americanus*.

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## Conflict of Interest

Authors declare no conflict of interests associated with this work.

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## Author Contributions

MC conceived the idea and designed the methodology. MC, OT, NH, and MG provided data. MC analysed the data. MC led the writing of the manuscript, all authors contributed significantly. All authors gave final approval for publication.

## Data Availability

The data underlying this study were provided by OT, NH by permission. Data will be shared on reasonable request to the

corresponding author with permission of co-authors where required.

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