



Estimating catchability and density of the European lobster *Homarus gammarus* from continuous, short-term mark–recapture data

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ABSTRACT: Despite the commercial and ecological importance of the European lobster *Homarus gammarus*, estimates of the population dynamics within socio-economically important fishing areas remain understudied. We implemented a mark–recapture approach to estimate population density, rates of loss and catchability of *H. gammarus* off the coast of northeast England, an important area for lobster fishers, and one of high exploitation. The short-term study used continuous trapping data from a commercial parlour trap array, fished over 6 wk. Over 9 haul occasions, 562 lobsters were marked using persistent external T-bar tags with unique ID numbers; 13.7% of these lobsters were subsequently recaptured. Catch data were used to determine the relationship between trap soak time and the effective fishing effort over time. Capture histories and effort data were analysed using a modified Cormack-Jolly-Seber (CJS) model, adapted for the short-term and continuous nature of the study. Model estimates of male lobster density varied depending on capture occasion between 732 (95% CI = 423, 1267) and 2730 (95% CI = 1585, 4701) lobsters per km². Similarly, female density was estimated at between 2410 (95% CI = 476, 12176) and 8060 (95% CI = 1592, 40810) lobsters per km². Low rates of loss of individuals from the area and large differences in catchability between sexes led to a female-skewed density estimate. If these findings are corroborated, the effects of sex-specific catchability and the potential for biased sex composition in populations and catches should be addressed in stock assessments and when interpreting sex ratio data in commercial catches.

KEY WORDS: Fisheries management · Tagging · Density · Catchability · Population parameters

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1. INTRODUCTION

Mark-recapture (MR) approaches to estimating population size and density were first implemented over a century ago (Petersen 1896, Lincoln 1930) and are now regularly applied in cases where direct census or sampling methods are problematic (Jolly 1965,

Seber 1965). The basic principle of the Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) model applied to MR data involves estimating the probabilities of capture (ρ) and survival (φ) via the repeated recapture of uniquely marked individuals, thereby allowing interpretation of catch numbers in terms of population size within the study area at the

time of sampling (Cormack 1964, Jolly 1965, Seber 1965, Dunnington et al. 2005). This approach is well-suited to fisheries because direct observation is often difficult, particularly for mobile and cryptic animals, and fishing by its nature samples only portions of the available population. Furthermore, the approach offers the user greater understanding than catch data alone by quantifying the losses and gains of individuals that drive population change, an insight into population-level effects that cannot be provided by fishery-dependent data (Seber 1982, Lebreton et al. 1992, Burnham & Anderson 2002). Stock assessments typically use changes in catch-per-unit-of-effort (CPUE) as a proxy for changes in abundance. However, owing to the complex behavioural interactions of clawed lobsters around baited traps typically used in their capture (e.g. Watson & Jury 2013), there is little understanding of how their CPUE relates to the true abundance on the seabed. Despite the potential for MR to provide fishery-independent estimates of abundance that explicitly account for capture probabilities, this technique has not been previously applied to European lobsters in UK coastal waters, and to date there are no published estimates of European lobster densities in these waters. European lobsters form one of the most economically valuable portions of UK inshore landings (Marine Management Organisation 2020), yet current knowledge gaps continue to limit efforts for evidence-based management.

Most standard CJS MR studies are conducted over long time periods, where sampling is defined as a discrete event, with population processes occurring between sampling occasion t and sampling occasion $(t + 1)$. However, sampling over short time periods via baited traps does not conform to this sampling design, as the capture process is continuous (i.e. captures can happen any time between setting and hauling a trap) and operates alongside population processes such as immigration and death. Bell et al. (2003) developed a MR approach to estimate densities of brown crabs *Cancer pagurus* from short-term trapping studies, later extended to the American lobster *Homarus americanus* (Dunnington et al. 2005). This approach uses continuous logistic parameters that operate alongside the sampling process, rather than discrete probability parameters occurring between them. This allows for estimates of instantaneous rate parameters that are used to scale catch data and subsequently estimate local abundance over the study period.

Here, we implemented an adapted short-term CJS MR method that takes account of the natural decay in catchability that occurs in traps over the duration of sampling occasions (Addison & Bell 1997, Fogarty &

Addison 1997, Bell et al. 2001). The aim of this study was to estimate the abundance of the local lobster population within a region of high exploitation. Estimates of catchability and rate of loss were coupled with fishery-independent catch data, and estimates of effective fishing effort were used to estimate lobster abundance and density. Potential sources of error or uncertainty are discussed to help provide a credible and suitable method for future population assessments.

2. MATERIALS AND METHODS

The study was conducted between 5 September and 10 October 2012, at a site 3.2 km east of Blyth, Northumberland (Fig. 1). Depth varied from 17 to 32 m. The seabed was a mixture of substrates but was dominated by rock and cobble forming 2 distinct patches. The site is regularly fished by commercial trap-fishers, with high catches of lobster taken from the area annually (Turner et al. 2013); in 2019, approximately 303 t were landed at Northumberland ports (Marine Management Organisation 2020). Although commercial fishing continued within the area

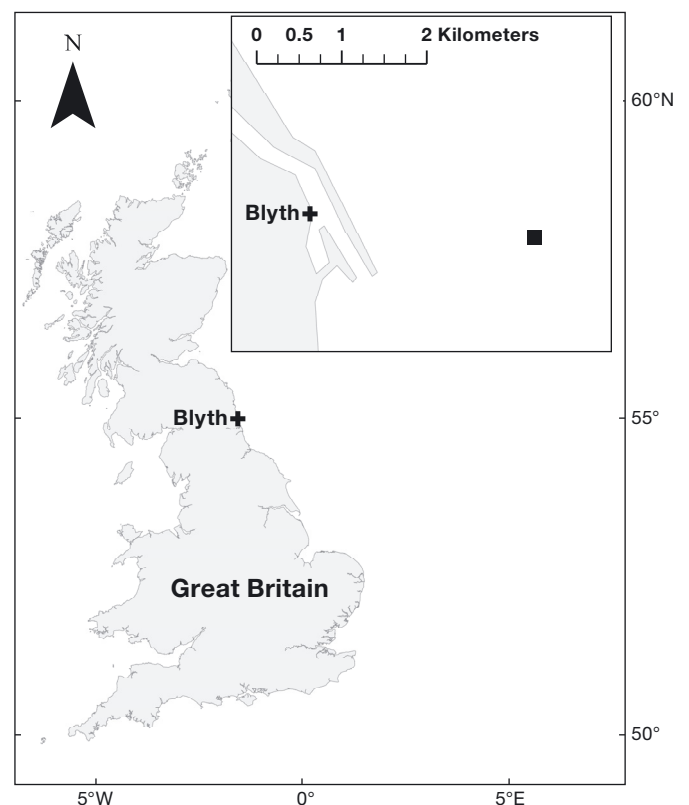


Fig. 1. Location of the study site Blyth, England. Black box in the inset: mid-point of the trapping study site

during the study period, there was none within the vicinity of the array; therefore, external fishing effort interactions were assumed to be negligible. A total of 64 steel-framed parlour traps (10 mm) were used; these measured (length \times width \times height) $0.68 \times 0.46 \times 0.38$ m, with a single-side 130 mm fixed diameter entrance. To prevent the escape of sub-legal lobsters, no escape gaps were fitted. Each trap was baited with a single frozen flatfish (20–30 cm total length), replaced upon each haul occasion.

The array consisted of 8 identical strings of 8 traps, set north to south perpendicular to the tidal flow, with approximately 40 m between traps and 100 m between strings to prevent interaction between traps (Smith & Tremblay 2003). Strings were spatially referenced with GPS and water depths for each occasion. Strings remained within ~ 15 m of their initial locations. Traps were soaked for 5 d prior to the first haul occasion to generate a sample of animals for initial marking. Subsequently, hauling occurred at approximately 4 d intervals over a 5 wk period; however, due to weather restrictions, soak times varied between 2 and 7 d (Table S1 in the Supplement at www.int-res.com/articles/suppl/m715p079_supp.pdf).

Upon hauling, individual trap catches were stored in separate containers. Biometric data were recorded for every lobster caught, including carapace length (rear of eye socket to base of carapace), sex, presence of eggs, general condition and capture location (string and trap number). Individuals were marked with a persistent T-bar tag with a unique 4-digit ID (TBA1, 50×2 mm; Hallprint), inserted into the abdominal musculature between the carapace and the first abdominal segment, offset from the centre to avoid the abdominal artery and vital organs. When applied correctly, T-bar tags remain post-ecdysis and are sufficiently durable to enable identification after several years without affecting survival or appearing to impact behaviour (Smith et al. 2001, Moland et al. 2011a). Recaptured animals had their unique ID and capture location recorded. All lobsters were released in the vicinity of the trap in which they were caught at the same time as traps were reset. If lobsters were seriously damaged, they were removed from the study.

2.1. Model framework

A general CJS model (Cormack 1964, Jolly 1965, Seber 1965) framework was used, whereby the probability of observing individual capture histories (CHs) is defined by a series of parameters that describe the capture and movement process. Sampling occurred

over 9 occasions, during which previously marked individuals were recaptured and unmarked individuals were marked and released. Consequently, for each recaptured marked individual, a CH was generated, in which one of 3 observed states was recorded for each day after first release: 0, not observed or no traps hauled that day; 1, captured and released; -1 , captured and removed from the study due to damage that would impact survival or catchability.

The probability of a particular CH occurring is the product of a series of probabilities of the possible fate of the individual over each day following first marking (Lebreton et al. 1992). Given the individual's availability within the 'capture area', i.e. the area over which traps exert an influence and the area around traps from which a lobster could potentially enter the area of influence (Bell et al. 2003), 3 possible fates could be defined: (1) the lobster does not enter a trap but remains in the capture area; (2) the lobster enters a trap and is observed; or (3) the lobster does not enter a trap and dies or permanently emigrates from the capture area. The probability of one of these fates occurring can be described by 3 parameters describing fishing and population processes between release occasions: probability of capture (p), probability of survival (φ) and fishing effort (f). Given the short timescale of the study, it was assumed that movement processes would dominate over survival processes; therefore, φ is hereafter referred to as site fidelity (i.e. the probability of not permanently emigrating) (Lebreton et al. 1992).

The MR model required the following assumptions to be met (Lebreton et al. 1992): (1) marked individuals mix freely with unmarked individuals; (2) marks remain present and are always detected or the rate of mark loss is known; (3) capture and marking does not alter survival, site fidelity or the probability of capture relative to unmarked individuals; (4) individuals that leave the study area do not return, i.e. emigration from the study site is permanent; (5) interspecific interactions within and around the trap do not affect capture probability; and (6) the effort exerted and probability of capture is equal across all traps.

For short-term trap fishing, where traps are hauled and immediately reset, the capture process is complex and considered continuous (i.e. capture could occur at any point between one haul and the next). Effectively, the model treated a sampling occasion — the hauling and setting of traps — as a single point in time. Therefore, calculations within the model were on a continuous scale, with capture and population processes described as instantaneous rates operating simultaneously (cf. Dunnington et al. 2005). This

allowed for easier incorporation of the unequal sampling intervals (Bell et al. 2003, Dunnington et al. 2005). Logistic transforms of the initial parameters p and φ were used to generate continuous terms for catchability (q) and mortality (μ), respectively, that were bounded by 0 and 1 (Lebreton et al. 1992).

CHs recorded in a reduced m -array (Burnham et al. 1987) allowed for expected values (E) of each recapture-cell (m_{ij} ; Table S2) to be calculated. For example, the expected value for CH of 101 (i.e. marked and released, not observed and then observed again) for occasions $i, j-1$ and j respectively, may be calculated as:

$$E[m_{ij}] = R_i \times P(\text{available})_{j-1}^i \times P(\text{capture})_j^{j-1} \quad (1)$$

where m_{ij} is the number of lobsters released on occasion i and recaptured for the first time on occasion j ; R_i is the total number of marked lobsters released on occasion i ; and the final 2 terms are probabilities (P) of the fates leading up to being recaptured on occasion j . $P(\text{available})_{j-1}^i$ is the probability of remaining available for capture within the capture area (i.e. not dying or emigrating) from release occasion i , up to and including occasion $j-1$, without being captured. $P(\text{available})_{j-1}^i$ can be expressed in terms of the parameters q and μ as:

$$P(\text{available})_{j-1}^i = \exp(-\sum_{j-1}^i (f_{j-1} q_{j-1} + t_{j-1} \mu_{j-1})) \quad (2)$$

where f_{j-1} is the effective fishing effort between occasion i and occasion $j-1$, and q_{j-1} is the catchability on occasion $j-1$. As f effectively scales q by the time over which traps are set, soak time is not included in this expression ($f_{j-1} q_{j-1}$). The second expression, ($t_{j-1} \mu_{j-1}$), includes t_{j-1} , the soak time (t) in days between occasions i and $j-1$, and μ_{j-1} is the rate of loss on occasion $j-1$.

$P(\text{capture})_j^{j-1}$ (Eq. 1) is the probability of being caught, given the individual's availability in the capture area, between occasion $j-1$ and j . This can be expressed in terms of continuous parameters as:

$$P(\text{capture})_j^{j-1} = (1 - \exp(-(f_j q_j + t_j \mu_j))) \quad f_j q_j / f_j q_j + t_j \mu_j \quad (3)$$

Eq. (3) assumes that f , q and μ occur simultaneously and compete with each other. The last term, $f q / f q + t \mu$, expresses the proportion of losses due to fishing, and the first term expresses the total number of losses. This expression is derived from the Baranov catch equation, in which the term $f q$ is equivalent to fishing mortality and $t \mu$ is equivalent to natural mortality during the time between occasions (Baranov 1918).

Given that the fate of each individual is independent but the parameters between individuals within the same release cohort are the same, MR data are considered frequencies from a multinomial distribu-

tion (Lebreton et al. 1992); this gives the probability of any particular combination of a number of fates for each release cohort. The kernel of the log-likelihood for the model of a parameter vector θ , $\ln L(\theta)$, can be calculated as:

$$\ln L(\theta) = \sum_{i=1}^i (\sum_{j=i+1}^j m_{ij} \ln P[m_{ij}] + (R_i - \sum_{j=i+1}^j m_{ij}) \ln P[R_i - \sum_{j=i+1}^j m_{ij}]) \quad (4)$$

where the probability of the recapture cell m_{ij} (Table S2), $P[m_{ij}]$, can be summarised using expectations from Eq. (1):

$$P[m_{ij}] = E[m_{ij}] / R_i \quad (5)$$

The probability of the not recaptured cell for row i , $P[R_i - \sum_{j=i+1}^j m_{ij}]$, the number of individuals released in cohort i that are never seen again, can be calculated as:

$$P[R_i - \sum_{j=i+1}^j m_{ij}] = 1 - \sum_{j=i+1}^j m_{ij} P[m_{ij}] \quad (6)$$

Estimated parameters from the model were scaled by f , creating meaningful constraints between soak times of different lengths (see Section 2.3). To find the values of q and μ that maximise the log-likelihood value, a quasi-Newton algorithm was used (Press et al. 1989). For the purposes of interpretation, parameters q and μ were back-transformed to give the probability of capture per effective effort exerted by traps on occasion j (p_j , not the same as $P(\text{capture})$), and the probability of site fidelity on each day of the interval leading up to occasion j (φ_j):

$$p_j = 1 - \exp(-q_j) \quad (7)$$

$$\varphi_j = \exp(-\mu_j) \quad (8)$$

The variance-covariance matrices for the logistically transformed parameters were calculated numerically, and approximate standard errors (SE) for derived parameters were obtained using the delta method (Press et al. 1989, Burnham & Anderson 2002, Dunnington et al. 2005). The goodness-of-fit (GoF) tests, generated in programme MARK, use the second part derivative method to generate derivatives numerically (Cooch & White 2011). Matrices obtained in this way were suitable for the population size estimate.

Once estimates of parameters μ , q and f were obtained, the population size (N) could be estimated through the following calculation, allowing for appropriate scaling of catch data per occasion, j :

$$N_j = C_j / (P(\text{capture})_j) \quad (9)$$

where N_j is the population of lobsters over the entire soak time from which the observed catch at occasion

j , C_j , is drawn. The variance–covariance matrix was then used to obtain SE and confidence intervals (CIs) for the population size estimates for each sex over each capture occasion following initial capture. The population estimate is presented in terms of abundance within the capture area.

Sex was included as a grouping variable, g , to allow for differences in catchability or site fidelity to be modelled and population estimates between sexes compared. Due to the short time period of the study, each estimate was essentially a separate estimate of the same population, making it possible to derive a mean population estimate for each group. As SE could not be aggregated into the mean, the standard deviation of all estimates was used to gain SE and 95% CIs of the range of values.

To estimate density, the size of the capture area from which the catch was drawn is required. The capture area, the trapping area of a single trap (defined as the area within which the capture probability during trap deployment was greater than 0; Bell et al. 2001) was assumed to be a circle with radius equal to the radii of the home range. The home range radii of free-ranging *H. gammarus* have been estimated to be between 10 and 250 m (Moland et al. 2011a, Skerritt et al. 2015). In reality, the capture area is influenced by many factors, such as lobster behaviour or physiological status, habitat type, current speed, water temperature and other dynamic environmental processes (e.g. Dunnington et al. 2005, Geraldi et al. 2009, Lees et al. 2018, Skerritt et al. 2020). The trapping area of a single trap in this study was, therefore, set at a nominal radius of 100 m. A minimum convex polygon was drawn around the experimental strings on this basis, covering an area of ca. 0.42 km² (Fig. S1).

2.2. Model fitting

In total, 25 possible models were defined for the MR data. The simplest model estimated constant parameters across groups (i.e. sexes) and time (i.e. sampling intervals) (μ, q). In the most complex model ($\mu_{g \cdot t} q_{g \cdot t}$), parameters q and μ varied independently over time (t) and between groups (g). Also included in the analysis were additive models (Lebreton et al. 1992), where parameters differed between g but vary in parallel over t , e.g. ($\mu_{g+t} q_{g+t}$). To select the most parsimonious model, the minimum value of the Akaike information criterion (AIC) in its bias-adjusted form (AIC_c) was used (Burnham & Anderson 2002). Models within 2 units of the most parsimonious model

were also supported and were considered as alternative models (Burnham & Anderson 2002). Model averaging was not deemed necessary, as population size estimates were insensitive to model choice within the likely set of candidate models.

GoF tests were conducted in program MARK (program RELEASE ‘TEST 2’ and ‘TEST 3’). Data were entered in the form of aggregated CHs. Two assumptions are tested by RELEASE: (1) every marked animal in the population immediately after time i has the same probability of surviving to time $i + 1$ and (2) every marked animal present in the population at time i has the same probability of recapture. Due to low numbers of captures and recaptures, parametric bootstrapping (1000 iterations, MARK) was used to further assess model uncertainty by comparing the observed model deviance to a distribution of deviances generated from simulated CHs. Bootstrapping was also used to estimate the over-dispersion parameter, where a value close to 1 suggests data were not over-dispersed and indicates that the model was correctly specified.

2.3. Effort modelling

Given unequal soak times between haul occasions and parameter probabilities defined as instantaneous rates changing between occasions, it was essential to adjust the value of f applied on each day of the soak time. Catch is assumed to have an asymptotic relationship with soak time (Eq. 10), due to trap saturation and a decline in bait attractiveness (e.g. Addison & Bell 1997).

$$C_t = C_\infty (1 - e^{-bt}) \quad (10)$$

where C_∞ is the asymptotic catch, C_t is the catch for a soak time of t , and b is the rate at which the increase in catch declines over time.

If f exerted by a string of traps j was set equal to 1 over the first day of the soak time, f on any subsequent day could be calculated as:

$$f_{ij} = f_{i-1,j} e^{-b} \quad (11)$$

No independent estimates of b exist for *H. gammarus*. However, declines in catch per unit time observed in the catch data as soak times increased can be used to infer the value of b . The following approach was used to determine a value for b :

$$\ln(1 - C_{tj}/C_\infty) = -bt \quad (12)$$

where C_{tj} is the catch of string j over time t ; this was the real catch of individual strings for each

occasion. Previous studies have found that this approach is equivalent to more rigorous approaches (Bell et al. 2003) and we consider this approach to be more appropriate for the estimation of the local population size.

3. RESULTS

In total, 562 lobsters were marked and released and 77 (13.7%) were recaptured. Of those marked, 273 were male and 289 were female (M:F = 1:1.06); however, of those recaptured, 57 were male and 20 were female (M:F = 2.85:1). The independence of traps within the array was investigated using *t*-tests. Traps around the perimeter (outside traps) may experience higher catch rates because the area of bait influence overlaps less with neighbouring traps. Therefore, traps were grouped based on their position within the array to investigate if catch rates differed between traps or strings within the array and those on the perimeter. Catch rates per trap were found to differ significantly between inside and outside strings ($t = 1.96$, $df = 574$, $p < 0.001$); however, the catch rate per trap was not significantly different between inside traps and outside traps ($t = 1.96$, $df = 574$, $p = 0.44$). This apparent interaction between inside and outside strings was unlikely to impact our model estimates, as the aim of the study was to estimate population size within the trapping area; therefore, the trap array (64 traps) was considered the sampling unit, not individual traps.

3.1. Mark–recapture data and model selection

Recapture rates were 21 and 7% for males and females respectively. AICc values for the 25 nested models (Table 1) indicate the most parsimonious model was μ, q_g ($AIC_c = 728.95$). According to this model, rate of loss (μ) remained constant throughout the study period and between groups (mean \pm SE: $0.0002 \pm 0.005 \text{ d}^{-1}$), suggesting almost complete site fidelity (i.e. no population turnover) for all lobsters over the entire study period. Catchability (q) also remained constant throughout the study period but varied significantly between the groups (0.017 ± 0.002 and $0.006 \pm 0.001 \text{ d}^{-1}$; male and female, respectively), indicating males were 2.77 times more susceptible to capture than females. Catchability estimates for the second-ranked model were similar (0.017 ± 0.003 and $0.005 \pm 0.001 \text{ d}^{-1}$, male and female, respectively).

3.2. Goodness-of-fit

There was no significant difference in the recapture probabilities throughout the sampling period of Group 1 (male) and Group 2 (female) when data were pooled (TEST_{2,15}: $p = 0.493$). However, there was a lack of data for some occasions for Group 2 (female) due to a low number of recaptures. There was also no evidence that φ differed between marked individuals during any of the capture occasions (TEST_{3,16}: $p = 0.495$). When the observed model deviance of 139.97, attained by parametric bootstrapping (1000 iterations), was compared to simulated deviances, the probability of a deviance as large, or greater than, the observed value was $p = 0.13$. Data were also not over-dispersed (general model dispersion = 1.164). The general model (μ, q_g, q_t) and those nested within, including the most parsimonious model (μ, q_g), sufficiently fitted the data and were an adequate basis for inference about population size at the study site.

Table 1. Model selection statistics for the 25 candidate models sorted by Akaike's information criteria adjusted for small sample size (AICc). lnL: log likelihood of the model; NP: number of separately identifiable parameters

Model	-2lnL	NP	AICc	$\Delta AICc$
μ, q_g	722.93	3	728.95	0.00
$\mu_g q_g$	722.87	4	730.91	1.97
μ, q_{g+t}	718.44	10	738.73	9.78
$\mu_g q_t$	734.26	3	740.28	11.33
$\mu_g q_{g+t}$	718.44	11	740.79	11.84
$\mu_t q_g$	721.15	10	741.44	12.49
$\mu_{g+t} q_g$	720.03	11	742.38	13.43
μ, q_t	742.59	2	746.60	17.65
μ, q_{g^*t}	713.61	17	748.48	19.54
$\mu_g q_{g^*t}$	713.61	18	750.59	21.65
$\mu_{g+t} q_t$	730.63	10	750.92	21.97
$\mu_g q_t$	731.12	10	751.40	22.46
$\mu_t q_{g+t}$	718.04	17	752.91	23.97
$\mu_{g+t} q_{g+t}$	716.85	18	753.83	24.88
μ, q_t	737.76	9	755.99	27.05
$\mu_{g^*t} q_g$	719.07	18	756.05	27.11
$\mu_t q_t$	740.63	9	758.86	29.91
$\mu_{g+t} q_t$	726.10	17	760.97	32.03
$\mu_t q_{g^*t}$	713.21	24	763.01	34.06
$\mu_{g+t} q_{g^*t}$	712.21	25	764.17	35.22
$\mu_{g+t} q_t$	729.91	17	764.78	35.84
$\mu_{g^*t} q_{g+t}$	715.31	25	767.27	38.32
$\mu_t q_t$	737.24	15	767.92	38.97
$\mu_{g^*t} q_{g^*t}$	712.08	30	774.94	45.99
$\mu_{g^*t} q_t$	725.75	24	775.55	46.60

3.3. Effective effort estimation

There was insufficient information to quantify C_{∞} ; however, as effort adjustment is relatively insensitive to the choice of C_{∞} (Bell et al. 2003), a value of 72 was used. This was derived from the highest observed catch of lobsters in a single trap plus one, multiplied by the number of traps in a string $[(8 + 1) \times 8 = 72]$. Using real catch data and this value for C_{∞} , b was estimated to be 0.146 (Eq. 12). This value of b was used to estimate the effective effort f for each soak time (Eq. 3). The first day of soak was constrained to $f = 1$, as all traps were assumed to have equal f upon first setting, with differences in catchability being accounted for within the MR model.

3.4. Population size and density estimation

Estimates of abundance for males within the trapping area based on the top-ranked model $\mu \cdot q_g$ ranged between 307 (95% CI = 178, 532) and 1147, (95% CI = 666, 1974); for females, this was between 1012 (95% CI = 200, 5113) and 3385 (95% CI = 669, 17140) (Fig. 2A). The second-ranked model $\mu_g q_g$ produced almost identical abundance estimates to the top-ranked model. Estimates for males ranged between 300 (95% CI = 90, 1001) and 920 (95% CI = 257, 3292), and female abundance estimates ranged between 1013 (95% CI = 431, 2382) and 3391 (95% CI = 1591, 7567) (Fig. 2A). Although abundance estimates for the second-ranked model were very similar between the 2 models, estimates of female abundance were more precise in the second-ranked model $\mu_g q_g$ (Fig. 2A). Using a minimum convex polygon with an area of 0.42 km² for the capture area, the density of male lobsters was estimated between 732 (95% CI = 423, 1267) and 2730 (95% CI = 1585, 4701) lobsters km⁻². Female density was estimated between 2410 (95% CI = 477, 12176) and 8060 (95% CI = 1592, 40810) lobsters km⁻².

4. DISCUSSION

Our estimates are the first density estimates for *Homarus gammarus* in the UK and highlight potential sex-specific catchability. The estimates from this study lie within a feasible range as indicated by other studies of related species; for example, Rowe (2002) estimated densities of 10000–20000 *H. americanus* km⁻² and Dunnington et al. (2005) estimated 65000 *H. americanus* km⁻². Bowlby et al. (2008) estimated

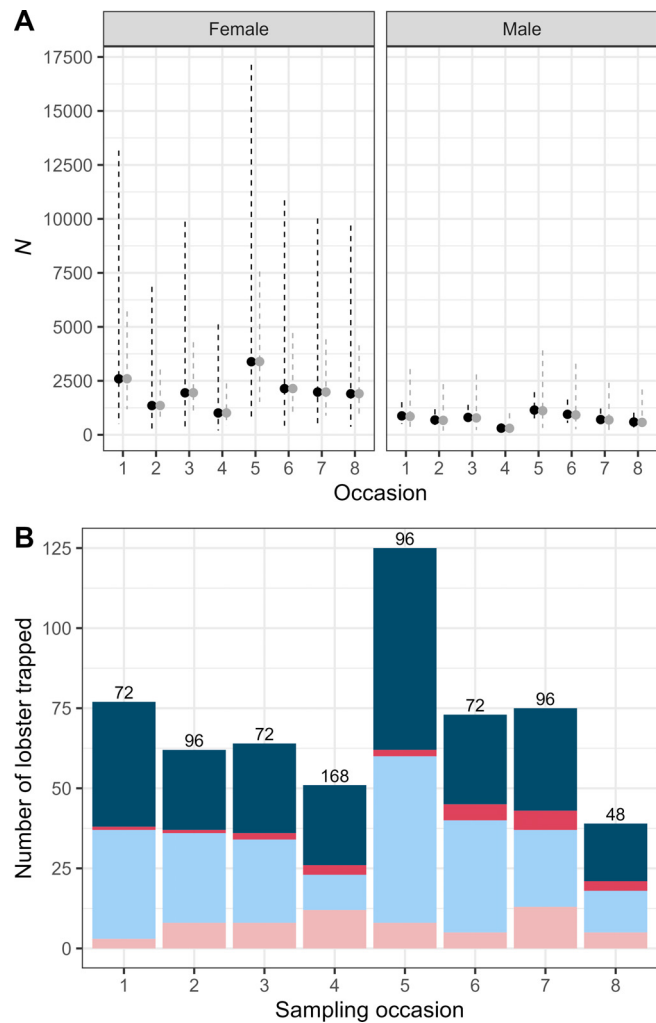


Fig. 2. Comparison of capture–mark–recapture (A) abundance estimates for females and males with 95% CIs (black: top-ranked model $\mu \cdot q_g$; grey: second-ranked model $\mu_g q_g$) and (B) total catch of lobster per occasion (dark colours: females; light colours: males; blue: new captures; red: recaptures). Numbers above bars: soak times in hours

450–500 *H. americanus* km⁻² using otter trawl surveys; however, in this case, the otter trawl possibly resulted in the incomplete sampling of complex habitats favoured by lobsters and underestimated lobster densities (Wahle & Steneck 1991). The only other published estimate for *H. gammarus* abundance, 155 ± 76 *H. gammarus* per km of shoreline, is from within an atypical population in an unfished Norwegian fjord and used the Petersen estimator (Petersen 1896, Seber 1982, Agnalt et al. 2009). However, the catch rate over the study period (0.11–0.49 lobsters trap⁻¹ d⁻¹) is comparable to a previous *H. gammarus* study in Yorkshire, England (range: 0.26–0.71; Lovewell et al. 1988). In recent decades, high densities of *H. ameri-*

canus have occurred due to the positive effect of ocean warming on lobster recruitment in the northern Gulf of Maine (Oppenheim et al. 2019, Boudreau et al. 2015, Goode et al. 2019). Concurrent over-exploitation of groundfish stocks and a subsequent reduction in predation pressure on *H. americanus* resulted in further increases in recruitment success, and thus increased abundance and exploitation of new habitats (Boudreau & Worm 2010). In turn, increased fishing effort and historically high landings followed (Boudreau et al. 2015). Population growth at a local scale has also been further accelerated by the considerable trophic contribution from lobster trap bait (Grabowski et al. 2010).

The proportion of the mean estimated population observed in the catch during this study (36, 14 and 20% for male, female and total population, respectively), compares favourably with Dunnington et al. (2005; *H. americanus*), who observed approximately 18% of the estimated population. Although traps only sample a proportion of the population, they are relatively inexpensive and easy to deploy and can be used in almost all habitats. Direct visual counts via diver surveys may be possible but, in general, effective visual counts are restricted to conditions with good visibility due to the cryptic nature of the lobsters, low current conditions and shallower depths. Previous work comparing MR model estimates of abundance to those derived from diver-based visual counts has found them to be similar (Dunnington et al. 2005).

An MR analysis assumes that the tagged proportion of the population is representative of the wider population in MR studies; however, the trappable proportion of the population will change in relation to physiological and environmental conditions. Unfortunately, at present, size-, sex-, site- and season-specific movement rates for *H. gammarus* are not well understood (but see Moland et al. 2011a, Skerrett et al. 2015, Lees et al. 2018, 2020), and these knowledge gaps limit our understanding of the how lobsters may respond to bait plumes. In addition, the area of bait influence will vary spatially and temporally due to the hydrodynamics of bait plumes, and bait decay (Beier & Noss 1998, Castro et al. 2001). Current population estimates do not include uncertainty surrounding the size of the capture area. However, *H. gammarus* are generally regarded as resident in an area (Moland et al. 2011a,b), and site fidelity was estimated to be almost 100%. Therefore, it is unlikely that the catch is drawn from a larger area than the 100 m radius assumed in this study.

Low catch rates are often found during MR studies and can impact the precision of model estimates,

leading to uncertainty surrounding subsequent management decisions (e.g. Dudgeon et al. 2015). Low catch rates are also common in European lobster fisheries and were notable during this study. Increasing the sample size and number of fishing occasions at each site could have improved the precision of model estimates. Similarly, an increase in the number of traps could increase subsequent recaptures; however, adding more traps can make setting and hauling more logistically challenging. In addition to the uncertainty due to low recapture rates, unquantified tag loss can also be a problem during MR studies, resulting in an overestimation of abundance estimates and an underestimation of survival. The impact of tag loss during this study was assumed to be negligible, and field observations indicate losses to be less than 1% over a period of 2–12 mo (Skerrett 2014). Tag-induced mortality was not observed during tagging, and no tag mortality occurred during *ex situ* tank studies in which a cohort of similarly tagged lobsters were kept under observation for 3 mo (Skerrett 2014). Therefore, tag-induced mortality was not considered to impact results.

While it is not possible to draw general conclusions about the lobster population from a short-term, single-site trapping study, some potential differences in abundance and catchability characteristics between sexes were identified by the model. The significantly female-biased sex ratio within the estimated total population (M:F = 1:2.7) is largely due to the estimated differences in catchability in the model. Despite an almost equal sex ratio in the observed and marked catch, only 7% of females (compared to 21% of males) were recaptured. This would imply that the pool of female lobsters from which the catch was drawn is larger than that of male lobsters. Despite UK lobster sex ratios previously reported to be skewed in favour of females (Thomas 1955), this is rarely reflected in trap catch data (Northumberland Inshore Fisheries and Conservation Authority unpubl. data). The increased proportion of females unavailable for capture could be attributed to a temporal change in female behaviour. The study took place towards the end of the breeding season and, typically, ovigerous females only begin to appear from September onwards (Pawson 1995, Debuse et al. 1999, 2003). Ovigerous females—females in the process of finding or being guarded by a mate or those becoming more defensive and less active during reproduction and moulting—are less likely to enter a baited trap, particularly in areas of higher lobster densities (Steneck 2006). Male lobsters may also have greater mobility than females, allowing for increased

foraging and interaction with baited traps (Moland et al. 2011a, Skerritt et al. 2015). The mean spring home range estimate (95% utilisation distribution) calculated for acoustically tagged lobsters within the same locale (Skerritt et al. 2015) was 2 times larger for males than females; however, this difference was not significant. Given the nature of passive acoustic telemetry data gathered using a positional array, it is possible that larger male home ranges were underestimated due to males leaving the array during longer distance movements, and thus underestimating the difference between male and female home ranges. These potential behavioural differences between male and female home ranges are of a similar magnitude to current density estimates and may have contributed to this apparent decrease in female catchability. Further studies during the non-breeding season are required to fully understand the possible impact of seasonality and behavioural changes on catchability.

The temporal variability in population size is likely due to the short-term nature of the study and the highly variable catch rate between sampling occasions rather than an observed change in the local population, suggesting that the current model did not capture all variability in the capture process. Although both top models supported constant catchability, it is possible that the short-term nature of the project and the relatively small sample size resulted in a lack of statistical power for more complicated models. Unequal soak times were accounted for in the model (mean soak time: 90 h, range: 48–168 h; Fig. 2, Table S1); however, the assumption of asymptotic trap saturation may not have adequately addressed the variability in catch. Traps left for long periods have fewer new lobsters entering and increased escapements, which leads to uncharacteristic trap catches (Jury et al. 2001). Over long soak times, observed catch is not the number of lobsters that have entered the trap over the soak, but the number of lobsters present and observed at the time of hauling. For example, low numbers of lobsters were caught on sampling occasion 4 despite the large cumulative effective effort over the extended soak (168 h). Similarly, during recapture occasion 5 there was a large catch of new lobsters (2 times higher than the other 96 h soaks) relative to the number of recaptures, which inflated the population estimates for this occasion. Ideally, complete sampling would be coupled with equal soak times between all occasions, eliminating the need to estimate effective effort. However, equal soak times are scarcely achievable due to the nature of working at sea. Validating model estimates using diver surveys to esti-

mate abundance would have provided an opportunity to assess model performance but, as previously mentioned, diver surveys are not always appropriate and come with their own challenges.

Population estimates for the top 2 models were also found to be very similar and were rather insensitive to model choice. Instead, they are largely scaled by catch. Understanding micro-scale population changes and triggers for these changes in catch would aid the modelling of population processes. For example, the lobster and crab catch rates during the study were inversely proportional, and these intraspecific interactions likely impact the catch rate of smaller, subordinate lobsters (Addison 1995, Skerritt et al. 2020). While it was assumed that these interactions had no impact on population estimates, they likely added to the variation in the catch rate and are not represented in the model. The capture process is influenced by numerous factors, many of which are unobservable and difficult to predict (Fogarty & Addison 1997, Ziegler et al. 2003). Adequately explaining this variability is an ongoing challenge for shellfish research.

5. CONCLUSIONS

This study provides the first density estimates of *Homarus gammarus* and estimates of sex composition using an adapted CJS model framework to analyse catch and recapture data, and it raises important questions about European lobster stocks. The observed dichotomy between catchability of the sexes highlights our lack of understanding surrounding the capture process. Management measures are based on the observed landings, and therefore important aspects of population dynamics due to differences in catchability may not be observed. A management focus on trends in observed landings and recruitment as indicators of population health is, perhaps, one reason why this short-term MR method has not been implemented more widely for commercial species. However, for many benthic species, including *Homarus* spp., understanding how local conditions drive changes in abundance is of critical importance, where even a short-term 'snapshot' study could be informative. Despite the well-studied limitations of trap sampling, estimates from a previous study using this method compared favourably with diver surveys. As this study further demonstrates, when the correct sampling design is used, MR studies that incorporate several hauling occasions within a small area have the potential to provide discrete estimates of popula-

tion size, catchability coefficients and rate of loss, which are all important parameters for assessing fish stocks. However, short-term does not mean without the known logistical or analytical challenges associated with MR methodology; estimates from this study were still sensitive to low recapture probabilities that occurred due to natural variability in the capture process. Additional MR studies are required to assess the sensitivity of this approach to the length of the study period and the size of the study area. Currently, our lack of knowledge surrounding how lobster behaviour interacts with the capture process hinders our ability to further elaborate on what may be driving possible differences in catchability between the sexes over the study period.

Despite the uncertainty surrounding population size estimates, our approach provides a credible method for estimating recapture and site fidelity rates over small areas and has the potential to inform fisheries management at a regional scale. This approach could be used to quantify abundance throughout management jurisdictions and understand population dynamics in relation to changes in fishing pressure, the implementation of protective measures within the fishery (e.g. legal size limits or the creation of marine protected areas) or changes in habitat availability such as existing or proposed subsea structures (e.g. offshore wind turbines). Integrated approaches that combine multiple methodologies such as MR studies with behavioural data from movement studies and habitat-level mapping will provide the most insight into lobster population dynamics.

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