RESEARCH

Movement patterns of a commercially important, free-ranging marine invertebrate in the vicinity of a bait source

Kirsty J. Lees[1*], Aileen C. Mill[1], Daniel J. Skerritt[2], Peter A. Robertson[1] and Clare Fitzsimmons[1]

Abstract

Background: Catch per unit effort is a cost-effective index of abundance and fishing effort, and an integral part of many fisheries stock assessments. Trap fisheries data are often generated using non-standardised methodology and the information to improve the accuracy of estimates is not always available due to current ecological knowledge gaps. Despite its economic importance, the European lobster *Homarus gammarus* has been relatively understudied compared to the closely related *H. americanus*. Previous studies investigating behaviour of *Homarus* spp. in relation to bait sources have been undertaken in aquariums or mesocosms rather than on free-ranging lobsters in the field. This study uses fine-scale acoustic telemetry data, and a null model approach to investigate free-ranging *H. gammarus* behaviour and movement in relation to baited commercial traps.

Results: The distribution of lobsters $n = 11$ was largely similar in the presence and absence of traps. The time spent within 20 m of a trap ranged from 3 min to 16 h 55 min ($n = 27$), and the distance at which lobsters began approaching a trap varied considerably (5.40 m to 125 m, $n = 22$); the mean distances were larger than calculated by previous studies. A fifth of trap approaches resulted in movement against the current indicating a potential olfactory response to a bait plume. A pre-existing non-random association with a trap location may increase the time spent near the trap and reduce the minimum distance between the lobster and the trap.

Conclusions: This is the first study to assess the movement patterns of free-ranging *H. gammarus* in relation to a bait source. The larger approach distances in this study were likely due to the unrestricted ranging behaviour of the tagged lobsters. Aquarium and mesocosm studies provide greater experimental control, but may restrict movement and underestimate the area of bait influence. The use of null models to infer movement patterns of free-ranging lobsters has many advantages over aquarium-based studies. These include better highlighting of individual variability in behaviour, and the potential to elucidate the effects of bait plumes on catchability. Wider application of this approach can be used to improve estimates of catch and stock assessments.

Keywords: European lobster, *H. gammarus*, Fisheries, Acoustic telemetry, Pot-fishing, Bait attraction, CPUE, Stock assessment, Catchability, Movement

Background

Catch per unit effort (CPUE) is widely used within fisheries management as a measure of both catch and effort, information that is necessary for fitting many fisheries stock assessment models [1]. CPUE is usually based on data collected by fishers and provides a convenient, low-cost proxy for relative abundance. However, inherent biases exist within these data and the true relationship between abundance and catch is often unknown [2, 3]. As such, the assumption of linearity between catch and abundance is often violated [4] and the appropriateness of CPUE as a proxy for abundance relies on accounting for changes in catch over time that are not the result of changes in abundance [1, 4]. Methods to standardise

*Correspondence: k.lees1@ncl.ac.uk
[1] School of Natural and Environmental Sciences, Newcastle University, Claremont Road, Newcastle upon Tyne NE1 7RU, UK
Full list of author information is available at the end of the article

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CPUE have been available for many years [5]; generalised linear models, and mixed effects models are now commonly used [4]. However, knowledge gaps still exist regarding the ecology, behaviour, and movement patterns of many commercially important species, and the likelihood of capture is commonly assumed to be equal across all demographics. Consequently, information that could improve the accuracy of CPUE and therefore stock assessments of these species is not always available. Improved abundance estimates in baited trap fisheries will rely on better understanding of the capture process, including attraction to a bait source, so that the probability of attraction and the proportion of the population targeted can be more accurately quantified [6].

Homarus gammarus is an economically important species within the United Kingdom (UK) and throughout its range, for example UK landings by UK vessels were worth £39.5 m in 2016 [7]. Despite its commercial value much of what is known about its ecology is derived from the closely related *H. americanus*. *H. gammarus* are typically fished using strings of multiple two chambered traps, known as parlour traps, these consist of a baited area entered through a tunnel, and a subsequent area that makes escape from the trap unlikely. *H. gammarus* often form a mixed fishery, commonly with *Cancer pagurus*, and as a result any number of intra and inter-specifics can be attracted to the baited static traps. Subsequent behavioural interactions affect the probability of attraction, and the probability of entering the approached trap [3, 8, 9]. The proximity of preferred habitats [10], and the selectivity and immersion time of a trap [2, 11, 12], will likely determine the number of lobsters attracted and subsequently trapped [13, 14]. However, lobster movements and therefore trap encounters are affected by a number of time-varying environmental conditions, such as seasonal changes in water temperature [6, 15–19] and periodic variation in current speed [20–22]. The motivation of individuals to respond to potential food sources can also be affected by internal physiological states relating to moult and the associated predation risk [23], reproduction, and hunger regulation [10, 24]. It is the interplay between these factors that vary at both the individual and population level, and across multiple spatial scales, that make calculating the effective trapping area particularly difficult [6, 25].

Lobsters primarily identify and navigate towards potential sources of food using their highly developed olfactory system [26, 27]. Despite being well studied [20, 28, 29], it remains unclear over what distance a bait plume remains detectable, as chemical signals are mixed and degraded by environmental processes [20, 28]. A number of studies have been undertaken in aquariums [10, 20, 30] where the direction and speed of current, and the degree of mixing can be carefully controlled. Alternatively, studies have been conducted in mesocosms [31–33] that can exclude potential sources of 'background' stimuli, that may confound an observable olfactory response, and can control the density of animals within the study area. While these enclosed environments provide greater experimental control, they can lack realism and restrict movement. The distance over which a bait plume might be detected is determined by both the speed and direction of the current [34] and can vary considerably depending on the target animal [33, 35, 36]. Attempts to identify responses to bait sources have focussed on the orientation of individuals in relation to the prevailing current and have often resulted in uncertainty due to heterogenous conditions [33, 35].

Changes in behaviour in response to a trap have been identified by a notable change in direction [33], or by a change in speed [35] (*C. pagurus*). *H. americanus* has been previously shown to slow down when approaching an odour source; however, these experiments were undertaken within an aquarium and the scale of movements are not directly comparable [20]. No change in speed has been identified in the field [33]. One particular drawback of free-ranging studies is that it is more challenging to definitively relate movement towards a trap to the traps presence, due to the logistical difficulties in validating the behaviour of marine animals. However, by comparing a measure of trap approach generated from the observed data, to one generated under random movement, it is possible to infer whether an approach was non-random, and in part reduce uncertainty regarding the relationship between the movement, and the presence of the trap. The null model approach [37] has been widely used within ecology. Null distributions, generated by resampling or randomisation, provide data without biological mechanism or process. Observed values can then be compared to expected values derived from the null distribution; care is required when specifying the degree of randomness of null distributions so as to avoid Type I [38], or Type II [39] errors.

The aim of this study was to investigate the behaviour of free-ranging *H. gammarus* in the vicinity of baited commercial parlour traps, and the distance of attraction to baited commercial parlour traps. The null hypothesis was that there would be no change in lobster behaviour in the presence and absence of traps, and no relationship between current speed and the distance of attraction to a trap [33]. A further null hypothesis, that patterns in lobster movements in relation to baited traps were random, and that changes in measurable behaviour, such as turn angle and step length, were independent of the traps presence, was tested using a null model approach.

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Methods

Data collection

A VEMCO Positioning System (VPS), (AMIRIX Systems Inc., Halifax, Canada) was deployed approximately 2 km off Blyth, Northumberland (55.1270° N, 1.5103° W) on the 7th of April 2016, (Fig. 1) covering approximately 1.5 km^2. The depth of the study site ranged from approximately 19–29 m. A string of 20 commercial parlour traps was set within the study area on the 30th of March 2016 and hauled after approximately 24 h. Traps were reset and hauled again after 7 days. Fourteen lobsters were caught (carapace length 71–92 mm, 8 females and 6 males) and fitted with a VEMCO Ltd. V13 acoustic transmitter (weight in water 6 g, 1% of body weight). Transmitters were attached above the crusher claw using a harness [40] and were set to transmit every 200–400 s (frequency 69 kHz). Tagging of lobsters took less than 10 min and all tagged individuals were released immediately within the study site.
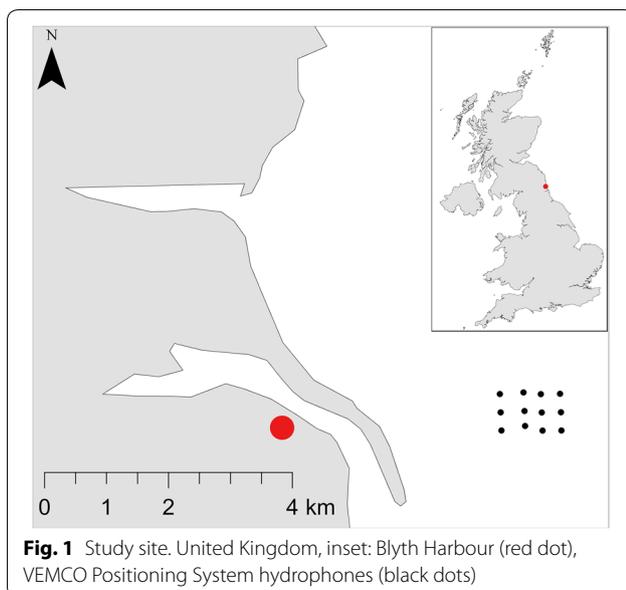
Experimental traps

Twelve separately moored commercial parlour traps were placed across the range of substrates available within the study site. Substrate was characterised using an Olex AS (www.olex.no) echosounder that provided a measure of relative substrate hardness on a linear scale of 1–100, where 100 would represent 0 energy loss and therefore higher values were associated with more reflective substrates. These data were subsequently classified as, 'Soft', such as mud < 60, 'Mixed', such as mud and rock > 60 and < 80, and 'Hard', such as continuous rock > 80. It is not possible to infer habitat type using this method as

substrate roughness is not measured [41]; however, these data are a broad indicator of substrate type and have been previously validated using drop-down cameras in the vicinity of the study site [42]. Trap locations within each substrate were chosen randomly, although an effort was made to avoid areas close to hydrophone moorings and ground lines to avoid entanglement and displacement of hydrophones. All traps were baited with approximately 300 g of whiting *Merlangius merlangus* and plaice *Pleuronectes platessa* in equal proportions; traps were placed at least 50 m apart [43] to minimise adverse interactions and competition from overlapping trapping areas [25]. Traps were also tagged prior to deployment, so that trap locations within the study site were known. Traps were deployed with the entrance closed to avoid retrapping tagged lobsters and the possible effects of trap saturation on lobster behaviour [3, 44, 45]. Traps were deployed on the 3rd of May 2016 and were subsequently rebaited and moved to new locations on the 12th and the 24th of May 2016. Only ten traps were redeployed during the 3rd deployment as two became detached from their marker buoy sometime during the 2nd deployment. A current meter (Nortek Aquadopp 3000 m) was deployed in the centre of the array between the 12th and 27th of May to collect current speed and direction every 10 min.

Data pre-processing

Prior to analysis, detections with high positional error were identified using linear regression between two measures of horizontal positioning error (HPE and HPEm) [42, 46]. The model was weighted by the number of HPEm observations per whole value of HPE. This was to account for the exponential decline in the number of observations as the value of the HPE increased. Observations with a HPE of less than or equal to 24 were removed, limiting the maximum error to approximately 23 m. There was evidence of commercial fishing within the study site. To reduce the possible confounding effects of non-study fishing gear only lobsters that were detected within 20 m of a study trap location during the first 72 h of its deployment were considered to have approached a trap and were included in the analyses. These criteria show consideration of the positional error associated with the data and reduce the likelihood that approaches not initiated by a bait plume were included. Lobster positions recorded between the 7th of April and first trap deployment on the 3rd of May were considered 'pre-trap' data. 'Post-trap' data were defined as positions recorded in the 72 h immediately following deployment of each trap. Data were projected in Universal Transverse Mercator (UTM) Zone 30 using ArcMap 10.2 (Esri) and movement metrics were calculated using Geospatial Modelling Environment [47]. Lobster speed was estimated as the

Fig. 1 Study site. United Kingdom, inset: Blyth Harbour (red dot), VEMCO Positioning System hydrophones (black dots)

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distance between positions at time t and $t + 1$ divided by the associated detection interval.

Data analysis

Analyses were conducted using R 3.4.1 [48]. To investigate the direction of lobster movement in relation to the prevailing current direction, the time stamps of the lobster data were rounded to the nearest 10-min period and then matched to the corresponding current data. If the difference between the lobsters bearing and the current direction was between 150° and 210°, the lobster was assumed to be moving 'against' the current (i.e., in the opposite direction). A turn towards the trap was defined as a turn greater than 30° [33] that resulted in the lobster being detected within 20 m of the trap; the distance from the trap that this turn occurred was defined as the distance of attraction. If a turn towards the trap also resulted in movement against the current, it was considered a potential response to a bait plume. If a lobster reapproached within 5 m of the trap, it was not considered a separate approach. Trajectories were visually assessed using the *trajdyn* function of the R library AdehabitatLT [49] to verify that the lobsters position relative to the trap and associated bait plume. Linear mixed models were used to investigate the relationship between distance of attraction and current speed, time since deployment and the sex of the lobster were also included as additional fixed effects, and lobster ID was included as a subject-level random effect. Distance to attraction followed a log-normal distribution and was transformed prior to analysis. Linear mixed models were built using the R library nlme [50]; nested models were estimated using maximum likelihood and compared using likelihood ratio tests.

There are three null models, based on each post-trap trajectory, were built using AdehabitatLT [49]. Null models either randomised the turn angle, the step length, or both the turn angle and the step length. Null models had the same number of positions and the same fixed start point as the observed post-trap trajectory. The first alternate hypothesis was that the minimum distance between lobsters, and a baited trap was less than would be expected by chance. The minimum distance between the lobster and the approached trap was calculated for each null trajectory and permutation tests were used to investigate non-random movement towards a trap. Models were run 999 times, if the result of the permutation test was $p \leq 0.05$, the model was run again for 99999 times and an updated p value derived. The second alternative hypothesis was that the number of observed lobster detections within 20 m would be greater than expected by chance; this was tested in an identical way to the first.

Results

Twelve of the fourteen tagged lobsters were successfully recorded within the study site during the pre-trap period and eleven were detected during the post-trap period. Six of the remaining eleven lobsters were detected within 20 m of a baited trap. The number of detections for these six lobsters ranged from $n = 383$ (lobster 28187) to $n = 1638$ (lobster 28179) in the pre-trap period and from $n = 81$ (lobster 28192) to $n = 235$ (lobster 28179) in the post-trap period. Lobster 56815 was detected within 20 m of two traps, one during the 2nd deployment and one during the 3rd deployment. The mean error ± 1 s.e. associated with post-trap data ranged from 7.36 m ± 0.20 (lobster 28192, $n = 81$) to 8.84 m ± 0.25 (lobster 28187, $n = 103$). Five lobsters did not move within 20 m of a trap during any of the deployment periods and twenty-nine of the thirty-four traps were not visited, and are not considered further.

Behaviour and movement in the presence and absence of traps

All the traps that were approached were located on 'mixed' or 'hard' substrate (range 69.30–91.50), reflecting lobster movements during the pre-trap period (Fig. 2). Of the twenty-seven visits within 20 m of the approached traps, sixteen were initiated between 2000 h and 0600 h (Table 1). There were seven periods where lobsters were detected within 20 m of the traps for 5 h or more, five of these occurred after 0600 h (Table 1). Duration ranged from 3 min to 16 h 55 min (lobster 28192 and lobster 28187, respectively). The minimum distance to the trap during these periods ranged from 1.03 m to 17.93 m (lobster 56816 and lobster 28187, respectively); two occurred within 12 h of the trap deployment (2.82 m, lobster 28179 and 1.03 m, lobster 56816), a further one occurred within 24 h (9.47 m 56815, 3rd deployment), and another occurred within 48 h (9.68 m, 28192) (Table 1).

There was no clear overall pattern in turn angle (Fig. 3a) or speed (Fig. 3b) between pre- and post-trap periods as there was considerable individual variation (Fig. 4). Three lobsters exhibited a lower median turn angle and higher median speed during the post-trap period (lobsters 28179, 56815, and 28192, Fig. 3a, b), and two only exhibited a change in turn angle or speed (lobsters 28189 and 56816, Fig. 3a, b). Lobster 28187 exhibited higher median turn angles, and lower median speeds during the post-trap period (Fig. 3 a, b). There was evidence of overlapping space use during the post-trap period (lobster 28187, Fig. 4a and lobster 28189, Fig. 4b). Only two lobsters used space during the post-trap period that they had not used during the pre-trap period (28192, Fig. 4d and 56815, Fig. 4f).

Table 1 Continuous time periods within 20 m of the approached trap

Tag ID	Start Time Date	End Time Date	Duration (h) (*n* detections)	Minimum distance (m)
28179	10:19 12-05	20:39 12-05	10.33 (45)	2.82[a]
28179	00:54 13-05	01:04 13-05	0.17 (3)	9.14[a]
28179	01:08 14-05	01:25 14-05	0.28 (4)	5.31[a]
28179	22:11 14-05	22:21 14-05	0.17 (2)	16.81[a]
28179	22:49 14-05	22:53 14-05	0.07 (2)	17.93[a]
28187	22:56 12-05	02:16 13-05	3.33 (5)	5.31
28187	03:28 13-05	20:24 13-05	16.93 (2)	6.37
28187	22:37 13-05	09:45 14-05	11.13 (6)	4.55
28187	16:50 14-05	00:21 15-05	7.52 (18)	2.28[a]
28187	02:56 15-05	03:00 15-05	0.07 (2)	17.66
28187	03:40 15-05	09:24 15-05	5.73 (11)	2.65[a]
28189	12:41 14-05	13:27 14-05	0.77 (5)	8.68[a]
28192	21:52 25-05	21:55 25-05	0.05 (2)	9.68[a]
56815	23:36 14-05	00:11 15-05	0.58 (3)	15.62[a]
56815	07:46 25-05	07:52 25-05	0.10 (2)	9.47[a]
56816	20:07 03-05	21:19 03-05	1.20 (8)	11.32
56816	21:40 03-05	22:01 03-05	0.35 (5)	11.73
56816	22:18 03-05	02:28 04-05	4.17 (21)	1.03[a]
56816	02:50 04-05	03:07 04-05	0.28 (3)	11.22[a]
56816	03:51 04-05	04:49 04-05	0.97 (5)	17.25
56816	05:27 04-05	05:55 04-05	0.47 (4)	17.25
56816	08:18 04-05	08:33 04-05	0.25 (4)	13.77
56816	09:04 04-05	10:04 04-05	1.00 (9)	13.74
56816	10:16 04-05	18:01 04-05	7.75 (6)	10.85
56816	19:02 04-05	22:22 04-05	3.33 (14)	12.16
56816	03:51 05-05	05:11 05-05	1.33 (2)	13.06
56816	06:16 05-05	12:06 05-05	5.83 (9)	11.22

Duration calculated as the time difference between the first and last detection within 20 m

[a] Periods that have resulted from an approach specified in Table 2

Movement in response to a bait source

Lobster movements towards traps in relation to the current direction were investigated for five of the six lobsters (Table 2); the approach by lobster 56816 occurred during the 1st deployment and could not be assessed as the current meter was only deployed from the 2nd deployment onward. The current direction within the study site was north–south in orientation and current speed ranged from 0.001 to 0.415 ms^{-1}.

Eighteen of the twenty-two turns towards the trap, regardless of turn angle, occurred between 2000 h and 0600 h, ten approaches occurred within the first 24 h of deployment. Four turns resulted in movement against the current, only lobster 28179 made more than one turn against the current (Table 2). Four lobsters made multiple turns towards their approached trap (Table 2). The time lobsters spent within 20 m of the trap after an approach varied considerably (3 min lobster 28192–10 h 20 min lobster 28179, Table 1 and Table 2). Lobster 29192 was

only detected once within 20 m of the trap on its first approach (Table 2), and therefore time spent within 20 m could not be estimated for inclusion in Table 1.

The mean distance of attraction for all turns greater than 30°, regardless of current direction, was 31.37 m $\pm$ 6.94 s.e., $n = 22$, and the mean distance of attraction for approaches that occurred within the first 24 h was 27.94 m $\pm$ 10.83 s.e., $n = 10$. The mean distance of attraction for turns towards the trap greater than 30° that resulted in movement against the current was 58.94 m $\pm$ 22.63 s.e., $n = 4$. Trap approach speeds varied between individuals. Twelve of the twenty-two trap approaches (Table 2) resulted in a decrease in speed immediately before arriving at the trap. The initial linear mixed model contained only the subject-level random effect and accounted for 46.53% of the variation within the distance of attraction. The model including current speed as a covariate was significantly better when compared to the random effect only model

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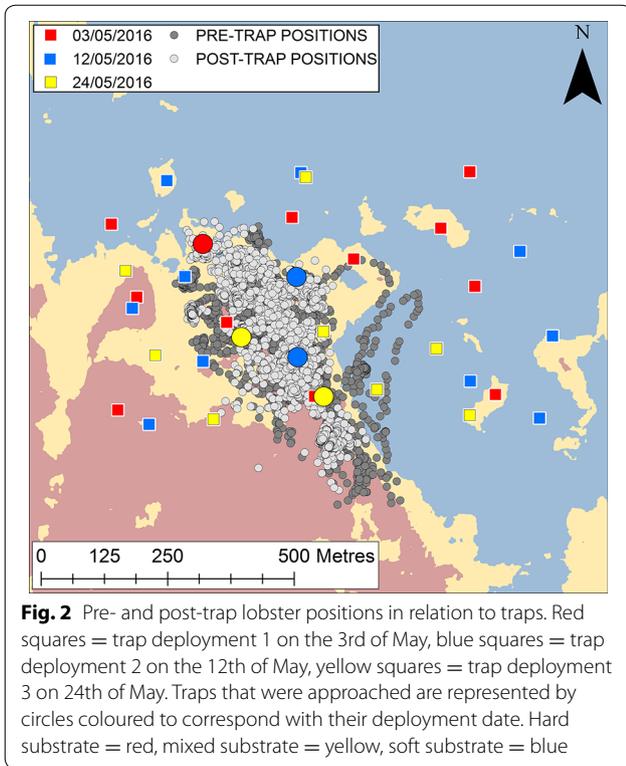
Fig. 2 Pre- and post-trap lobster positions in relation to traps. Red squares = trap deployment 1 on the 3rd of May, blue squares = trap deployment 2 on the 12th of May, yellow squares = trap deployment 3 on 24th of May. Traps that were approached are represented by circles coloured to correspond with their deployment date. Hard substrate = red, mixed substrate = yellow, soft substrate = blue

($\chi^2 = 3.89, df = 1, p = 0.049$); however, current speed was not a significant covariate in this model ($p = 0.070$). The inclusion of additional fixed effects, time since trap deployment ($\chi^2 = 0.16, df = 1, p = 0.688$), and sex of lobster ($\chi^2 = 1.02, df = 1, p = 0.314$), did not significantly improve the model fit when compared to the model containing both current speed and the

subject-level random effect. There was insufficient data to investigate the relationship using only turns that resulted in movement against the current.

Null models

Only lobster 56815 (3rd deployment) was closer to the approached trap than would be expected under random movement for all three null models, turn angle only ($X = 9.47, E = 70.47, p = 0.027$), turn and step length ($X = 9.47, E = 74.57, p = 0.038$) and step length only ($X = 9.47, E = 76.95, p = 0.035$). Three lobsters had a significantly greater number of positions less than, or equal to 20m from the approached trap than would be expected under random movement using null models generated from the post-trap trajectories (Table 3). The observed values were significantly greater than the expected values generated by all three null models for lobster 28179, turn angle ($X = 56, E = 27.75, p = 0.025$), turn angle and step length ($X = 56, E = 7.59, p < 0.001$), and step length ($X = 56, E = 11.11, p < 0.001$). The observed number of positions was only significantly greater than expected for lobster 56815 (3rd deployment) when compared to the null model that randomised the turn angle ($X = 2, E = 0.307, p = 0.033$). The observed number of positions for lobster 56816 was greater than expected when compared to the null model that randomised the turn angle ($X = 92, E = 25.94, p = 0.015$), and the turn angle and step length ($X = 92, E = 28.18, p = 0.008$). Two of the three lobsters (28179 and 56816) had a significantly greater number of positions, less than, or equal to, 20 m from the location of the trap when compared to null models based on the pre-trap trajectories ($p < 0.001$) (Table 4). The number of positions of lobster 56815
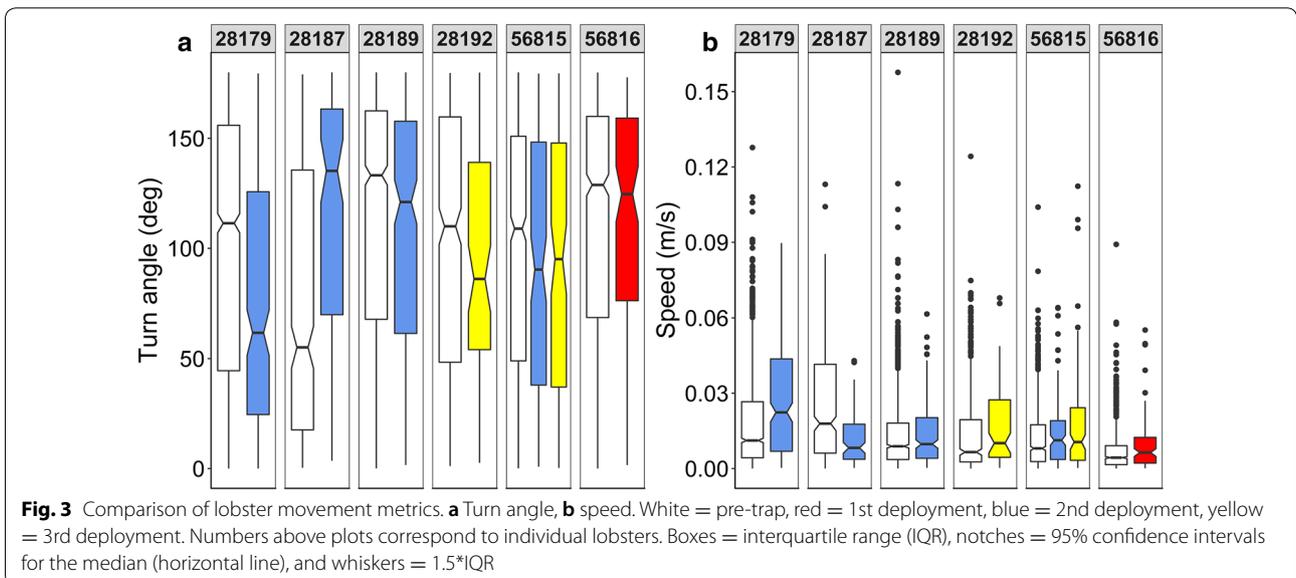
Fig. 3 Comparison of lobster movement metrics. **a** Turn angle, **b** speed. White = pre-trap, red = 1st deployment, blue = 2nd deployment, yellow = 3rd deployment. Numbers above plots correspond to individual lobsters. Boxes = interquartile range (IQR), notches = 95% confidence intervals for the median (horizontal line), and whiskers = 1.5*IQR

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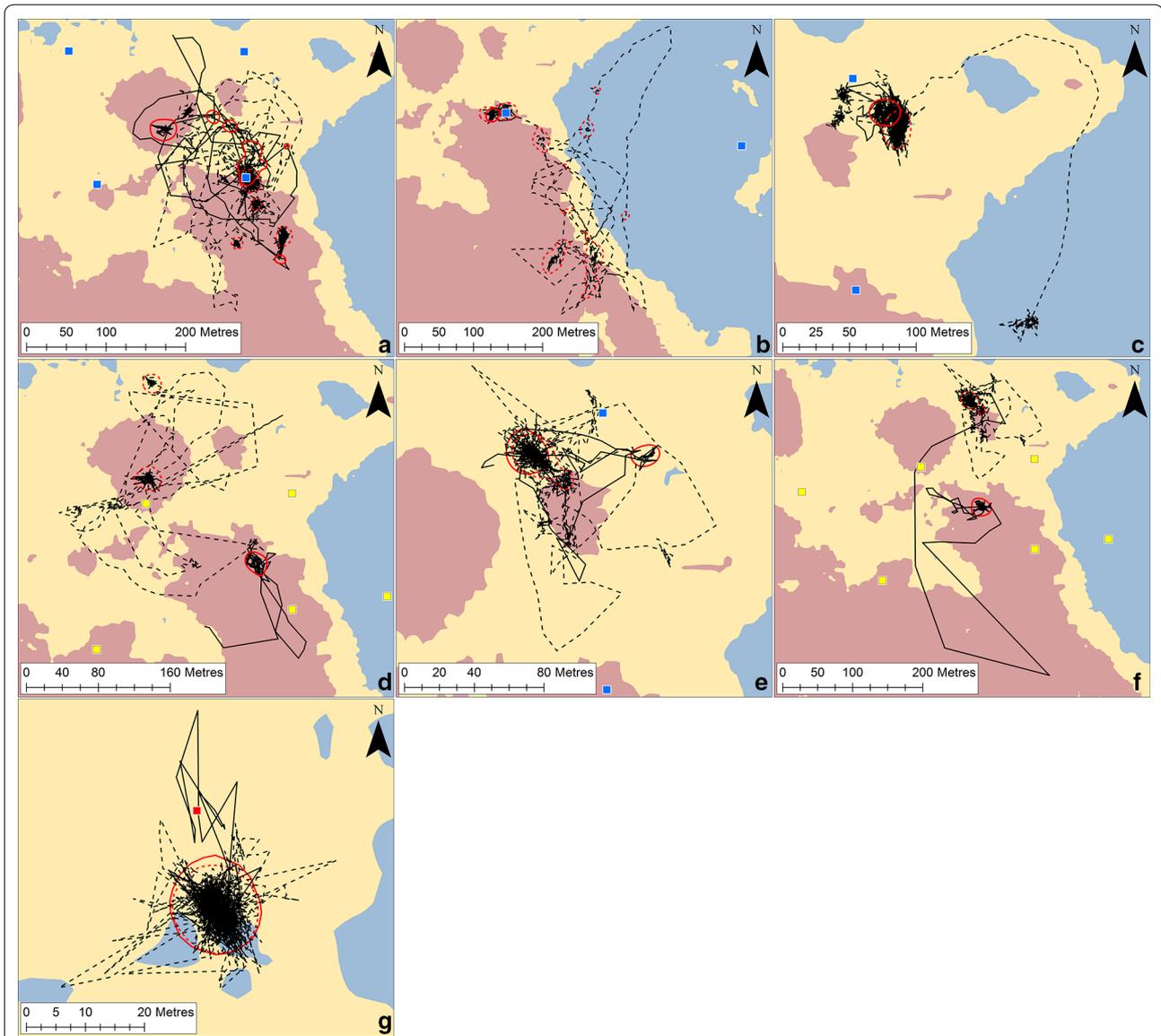
Fig. 4 Movement in the absence and presence of traps. **a** Lobster 28179, **b** lobster 28187, **c** lobster 28189, **d** lobster 28192, **e** lobster 56815 deployment 2, **f** lobster 56815 deployment 3, **g** lobster 56816. Pre-trap trajectories = black dashed line, post-trap trajectories = solid line, pre-trap 50% utilisation distribution = red dashed line, and post-trap 50% utilisation distribution = red solid line. Utilisation distributions were calculated using AdehabitatHR [49], $h = 5.5$, grid = 300, and extent = 0.1. For further discussion on the importance of these parameters see [59]. Coloured squares represent traps deployed at the time of approach

within or equal to 20 m was not significantly greater than would be expected under random movement when compared to null models generated from the pre-trap trajectory ($X = 0, E = 5.68, p = 1.000$).

Discussion

This is the first study investigating free-ranging *H. gammarus* movements in response to baited traps. Although the number of tagged lobsters was small, six of the twelve successfully tagged lobsters appeared to respond to the baited traps, a similar proportion to a previous study [33]. However, five lobsters did not move within 20 m of a trap during any of the three deployments. It was not possible to infer the reason for this, but it does underline the role of individual variation in influencing a response to a bait source [10, 24], and the possibility that not all individuals within a population are equally available to the fishery. The equal sampling of individuals by a fishery is an assumption of assessment models, and a key source of uncertainty [51–53].

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Table 2 Trap approaches resulting from turns greater than 30°

Tag ID	DA (m)	Time	Soak time (deployment)	Relative angle (°)	Current speed (ms⁻¹)	Min. dist. (m)	Speed change
28179	16.35	14:41	4 h (2)	88.31	0.05	8.49	↗
28179	14.17	15:07	5 h (2)	120.35	0.05	9.33	↗
28179	15.35	15:20	5 h (2)	66.07	0.09	2.82	↘
28179	58.37	00:41	15 h (2)	263.19	0.11	9.14	↘
28179	125.55	00:09	38 h (2)	187.69	0.07	5.31	↘
28179	48.87	22:00	59 h (2)	198.33	0.14	16.81	↗
28179	34.27	22:34	60 h (2)	89.41	0.09	17.93	↗
28187	27.99	02:28	16 h (2)	254.09	0.05	6.37	↗
28187	10.27	22:37	36 h (2)	84.79	0.08	7.76	↘
28187	9.03	23:45	37 h (2)	89.53	0.03	5.09	↗
28187	14.68	01:04	38 h (2)	214.33	0.07	4.55	↘
28187	13.40	20:07	58 h (2)	31.49	0.09	2.28	↗
28187	7.57	03:40	65 h (2)	279.87	0.11	2.65	↗
28189	28.64	08:13	45 h (2)	154.85	0.13	8.68	↘
28192	32.68	20:22	34 h (3)	174.13	0.05	12.60	↘
28192	39.25	21:34	35 h (3)	56.30	0.15	9.68	↘
56815	46.48	23:13	60 h (2)	52.63	0.12	15.62	↘
56815	114.64	03:40	17 h (3)	34.53	0.21	9.47	↗
56816	5.40	22:37	10 h (1)	–	–	1.03	↘
56816	6.70	23:20	10 h (1)	–	–	3.14	↗
56816	5.66	00:41	11 h (1)	–	–	3.06	↘
56816	14.74	02:50	14 h (1)	–	–	11.22	↗

DA = distance of attraction, Time = time the approach began, Soak time = complete hours since trap deployment, and Minimum distance = minimum distance between the lobster and the trap. Speed change indicates if the speed of the lobster increased ↗ or decreased ↘ as it arrived at the trap

Table 3 Results from null models (99999 permutations) generated from post-trap trajectories comparing the observed and expected number of positions ≤ 20m from the location of the approached trap

Tag ID	Trap no. (deployment)	Null model	Observed	Expected	Variance	Sim. *p* value
28179	2 (2)	Turn	56	27.75	154.33	0.025
28179	2 (2)	Turn and step	56	7.59	33.83	< 0.001
28179	2 (2)	Step	56	11.11	49.97	< 0.001
56815	3 (3)	Turn	2	0.31	5.88	0.033
56816	7 (1)	Turn	92	25.94	568.36	0.015
56816	7 (1)	Turn and step	92	28.18	521.83	0.008

Table 4 Results from null models (99999 permutations) generated from pre-trap trajectories comparing the observed and the expected number of positions ≤ 20m from the location of the approached trap

Tag ID	Trap no. (deployment no.)	Null model	Observed	Expected	Variance	Sim. *p* value
28179	2 (2)	Turn	574	31.39	773.06	< 0.001
28179	2 (2)	Turn and step	574	2.28	529.00	< 0.001
28179	2 (2)	Step	574	30.52	718.59	< 0.001
56815	3 (3)	Turn	0	5.68	274.41	1.000
56816	7 (1)	Turn	690	83.93	5588.50	< 0.001
56816	7 (1)	Turn and step	690	71.37	4343.33	< 0.001

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Behaviour and movement in the presence and absence of traps

There was no clear overall change in movement or behaviour when the pre-trap period was compared to the post-trap period, although there were differences between individuals. There was evidence of more directional movements characterised by lower median turn angle and higher median speed in the post-trap period for four lobsters, and one lobster exhibited more restricted and tortuous movements reflected in a higher median turn angle and lower median speed. The remaining lobster showed no difference in movement patterns between the pre-trap and post-trap period. Attributing behavioural change to the presence of a trap is difficult as changes in behaviour associated with the presence of a trap are unlikely to be maintained for the duration of a deployment. However, the scale of the movements undertaken in the post-trap period by lobsters 28189 and 56815 (2nd deployment) was distinctly different from the pre-trap period.

Daytime trap approaches have previously constituted 33% of all trap approaches [33]. It is therefore plausible that the lobsters remained at the location because of a trap, particularly as three of the four prolonged periods (greater than 5 h) occurred within 24 h of trap deployment. The time spent within 20 m of a trap in this study ranged from 3 min to almost 17 h, similar to previous studies (10 min and 12 h [33, 35]). However, direct comparisons are difficult due to the differing definitions of an approach [33, 35].

Movement in response to a bait source

Eighteen of the twenty-two approaches in this study occurred between 2000 h and 0600 h reflecting the low daytime activity levels of *H gammarus* [16, 18, 54]. *H. americanus* [33] and *C. pagurus* [35], are more likely to approach traps at night, but there is no recorded relationship between the time of day and the probability of *H. americanus* entering a trap [32].

There were four turns greater than 30° that also coincided with movement against the current. Approaches that did not result in movement against the current may be return journeys to previously known areas [23, 36]. The second approach by lobster 28192 did not result in movement against the current, and it is possible that it navigated back to the trap location known from its previous visit. Other turns that did not result in movement against the current should not be immediately discounted. Lobsters can be lured from their shelters by the presence of traps [10] and it is feasible that a lobster in close proximity to the trap soon after deployment, such as lobster 28179, could have been influenced by a diffuse odour, or the presence of other lobsters. Likewise

the turn towards the trap by lobster 56815 during the 3rd deployment was not against the current, but subsequent detections did result in movement against the current. These less obvious changes in direction made it difficult to decide when a lobster first became 'aware' of a trap and truly began its approach. It is unclear from this small study if identifying a strong directional change is the best arbiter of behavioural change. An increase in speed [35] may provide an alternative indicator. Just over half of the trap approaches in this study resulted in an decrease in speed at the trap. A decrease in speed has been previously reported for aquarium *H. americanus* [20]. However, in a mesocosm study, no change in speed on approach was reported [33]. In a free-ranging study, a lobster could change speed due to terrain or behavioural interactions and more experimental work is necessary before speed can confidently be related to trap approach.

Previous studies [32, 33] have discounted approaches by lobsters that have appeared to 'walk past' traps. Lobsters can fail to approach, or leave the vicinity of a trap, in response to the presence of a more dominant animal and exhibit caution when approaching [10, 55, crabs], [56, *Nephrops*]. As the behaviour of lobsters in this study could not be observed, all approaches were considered. A trap mounted camera [32, 33] could not be used to validate approaches in this study; lobster locations were not known prior to trap deployment, and a location for such a system could not have been prioritised. To minimise uncertainty, data were restricted to the 72 h after deployment and greater confidence should be associated with approaches that occurred within the first 24 h [2].

There was a marginal relationship between distance of attraction and current speed. The number of approaches was small, and it is unlikely that the single current meter was able to adequately capture the fine-scale changes in the current that would be experienced by the lobsters' olfactory system. The directional current could explain the large mean distance of attractions, almost three to five times larger than previously observed for *H. americanus* [33]. The directional current meant that an assumption of a circular plume [33] would have been unrealistic. As the shape of the bait plume was not known, the distance of attraction could not be converted into an estimate of area of bait influence. However, it should not be assumed that a larger distance of attraction would result in a larger area of bait influence, the 'effective trapping area' may actually be smaller under strong current conditions due to dilution [34]. Although this would likely be compounded by reduced movement of lobsters under increased current speeds [22]. It is difficult to draw direct comparisons between experimental studies and free-ranging lobsters. It is likely that mesocosms and aquariums restrict movement and indirectly inflate the number of approaches

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[10], or restrict the maximum distance of attraction [33]. The selection of more sedentary lobsters may also have created a bias that resulted in a reduced distance of attraction [33]. Approaches by free-ranging crabs and lobsters that have originated down current of traps have been initiated at distances of 42 m [35*C. pagurus*] and 120 m [36*Panulirus cygnus*]. Due to the close initial proximity of lobsters 28179 and 56816 to traps, it was sometimes difficult to differentiate general movement from a genuine approach in a small number of cases; this could have potentially biased the results towards longer approach distances.

Null models
Null models were used to investigate two aspects of trap proximity. Firstly, that the minimum distance to the trap during the observed trajectory was less than would be expected under random movement, and secondly, that the number of detections within 20 m of the trap was greater during the observed trajectory than would be expected under random movement. Three lobsters had a greater number of post-trap positions within 20 m of the approached trap than would be expected under random movement; however, two of those three also had a greater number of pre-trap positions within 20 m of the intended trap location than would be expected under random movement. This suggests that both lobster 28179 and lobster 56816 had a previously established association with the trap location, such as a pre-existing shelter or known foraging area. The minimum distances between lobsters and the approached traps were also not significantly different from random for four of the five lobsters. A pre-existing non-random association with a trap location will likely increase the time spent near the trap, and reduce the minimum distance from the trap. However, it is unclear if this proximity translates into increased probability of capture. Lobsters that exhibit wider ranging movement, such as lobster 56815, may encounter more traps than a comparatively sedentary lobster. If however the sedentary lobster is within a heavily fished area, it may have a higher probability of capture. Movement has been positively correlated with catchability for *H. americanus* due to the increased energy expenditure associated with seasonal dispersal [14]. However, movements by *H. gammarus* are generally smaller in scale, and although possible, there is no definitive evidence that resident or dispersal movement states occur [18, 40, 57]. So while increased mobility might result in greater trap exposure [58], it is not clear whether the energetic demands of more localised short-term movements would be sufficient to create a similar relationship between movement and catch. If movement patterns were to differ between life-histories, a relationship between movement and catch could have considerable management implications.

Null trajectories were not constrained to a specific range of substrates, and simulated lobsters were able to move freely depending on the randomisation of the turn angle and, or step length. This reflected lobster movement during the pre-trap period of this study, and lobster movement from an adjacent study area of similar substrate composition [42]. However, it is possible that lobster movements were constrained by other factors that were not accounted for in the models such as, the direction of the current [22] or the distance from a known defensible shelter [23].

Conclusions
The aim of this study was to investigate the behaviour of free-ranging *H. gammarus* movements in response to spatially explicit bait sources, and it is the first to do so. There were no consistent movement patterns between the pre- and post-trap period, although individual movement patterns did vary. The sample size of this study was small, and further estimates of the distance of attraction for free-ranging lobsters are required to describe and understand the full range of behaviours. Acoustic telemetry studies, both observational and experimental, can provide important behavioural information on inshore fisheries species that could improve the estimates of CPUE. However, future experimental approaches are likely to still involve trade-offs between capturing the realism of the system, and controlling for confounding effects. A particular drawback to future free-range studies will be the small number of approaches and the large number of traps that do not elicit a response. Large sample sizes and longer deployment periods, at increased expense, will be required to overcome this. If the distance at which a target species is under the influence of a bait plume is underestimated, it could lead to an inaccurate estimate of both the area of bait influence, and the effective trapping area. Despite the uncertainty associated with free-range studies, the ability of lobsters to move freely underlines the variability of ranging behaviours, and the likelihood that attraction, and therefore catchability is not equal between individuals.

Author details
[1] School of Natural and Environmental Sciences, Newcastle University, Claremont Road, Newcastle upon Tyne NE1 7RU, UK. [2] MRAG Ltd., 18 Queen Street, Mayfair, London W1J 5PN, UK.

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