

# Spatially structured interactions between lobsters and lobster fishers in a coastal habitat: fine-scale behaviour and survival estimated from acoustic telemetry

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**Abstract:** Fishing can have profound impacts on the ecology and evolution of marine populations. Understanding population-level changes ultimately depends on knowledge about individual survival and how it varies in time and space. We used acoustic tags and a network of receivers to monitor individual behaviour and fate of European lobster (*Homarus gammarus*) exposed to commercial and recreational trap fisheries on the Norwegian Skagerrak coast. In August 2011, 50 male lobsters above minimum legal size were tagged and monitored before and during the lobster fishing season. We also quantified the spatial and temporal variation in fishing activity. There was no significant effect of home-range size on the probability of surviving the fishery. However, there was substantial fine-scale spatial variation in fishing activity, and lobsters with short-term home ranges positioned away from trap-dense areas had a significantly higher survival probability. Also, the overall survival probability of 16.7% suggests that fishing depletes the catchable lobster population at a high rate. The current harvesting regime may drive selection in favour of movement behaviours avoiding habitats typically targeted by fishers.

**Résumé :** La pêche peut avoir des lourds impacts sur l'écologie et l'évolution des populations marines. La compréhension des changements à l'échelle de la population dépend des connaissances sur la survie des individus et les variations de cette dernière dans le temps et l'espace. Nous avons utilisé des marqueurs acoustiques et un réseau de récepteurs pour surveiller le comportement individuel et le destin de homards européens (*Homarus gammarus*) exposés à la pêche commerciale et récréative au piège le long de la côte norvégienne du Skagerrak. En août 2011, 50 homards mâles de taille supérieure au minimum légal ont été marqués et suivis avant et durant la saison de pêche au homard. Nous avons également quantifié les variations spatiales et temporelles des activités de pêche. Aucun effet significatif de la taille du domaine vital sur la probabilité de survie à la pêche n'a été noté. D'importantes variations spatiales fines des activités de pêche ont toutefois été observées, et les homards dont les domaines vitaux à court terme se situaient à distance des zones de forte densité de pièges présentaient une probabilité de survie significativement plus grande que celle des autres homards. En outre, la probabilité de survie globale de 16,7 % semble indiquer que la pêche est à l'origine d'un déclin rapide de la population exploitable de homards. Le régime d'exploitation actuel pourrait se traduire par la sélection préférentielle de comportements de déplacement permettant d'éviter les habitats typiquement ciblés par les pêcheurs. [Traduit par la Rédaction]

## Introduction

Coastal fisheries have existed for millennia and can have major impacts on harvested populations and ecosystems (Jackson et al. 2001; Limburg et al. 2008; Olsen and Moland 2010). From a demographic perspective, the removal of old age groups by fishing, a process known as longevity overfishing (Berkeley et al. 2004; Beamish et al. 2006), may lead to reduced population productivity (Venturelli et al. 2009; Shelton et al. 2012). From an ecological perspective, processes such as growth and mating systems may be influenced when fishing reduces population density (Lorenzen and Enberg 2002; Hutchings and Rowe 2008). From an evolutionary perspective, selective harvesting may lead to contemporary genetic changes in fitness-related traits (Olsen et al. 2004; Swain et al. 2007; Biro and Post 2008). A full understanding of these processes depends on knowledge about individual performance, including behaviour, and how this scales to spatial and temporal variation in fisher behaviour and the resulting harvest pressure (Uusi-Heikkilä et al. 2008; Alós et al. 2012; Olsen et al. 2012).

Aquatic animals are not uniformly distributed. Rather, niche requirements result in association with specific habitats and resources (Mittelbach 1981; Rosenzweig 1981) and other less often considered factors such as site familiarity (Piper 2011). Although there is considerable literature on how fish and crustaceans are spatially distributed on large and intermediate scales (e.g., Harding et al. 2005; Ciannelli et al. 2012), knowledge about fine-scale individual behaviours, habitat associations, home range sizes, and how these interact with the behaviour of fishers is lacking for most harvested species (but see Gherini et al. 2009).

Compared with terrestrial systems, it can be difficult to obtain direct observations on the behaviour and fate of aquatic animals in their natural habitats. However, acoustic telemetry allows individuals to be monitored continuously over time in the wild (Heupel and Simpfendorfer 2002; Knip et al. 2012). Here, we use acoustic telemetry to investigate the spatial ecology of European lobster (*Homarus gammarus*), a prized catch in commercial and recreational coastal fisheries (Kleiven et al. 2012). We also quantify fisher behaviour as the fine-scale spatial and temporal distribution of

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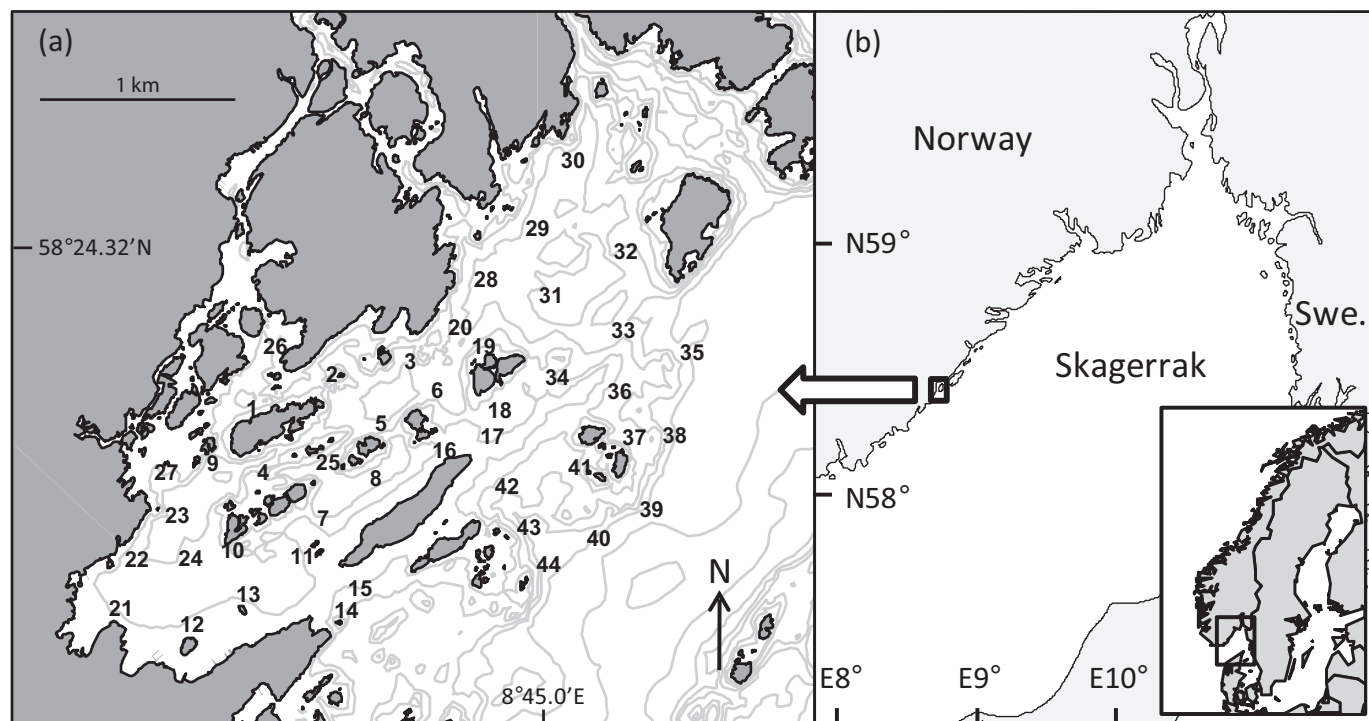
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**Fig. 1.** Study area: the Sømskilen basin and nearby islands (a) on the Norwegian Skagerrak coast (b). Insert in panel (b): the Scandinavian Peninsula (Norway and Sweden (Swe.)), Denmark, and the location of the Skagerrak Sea. Isobaths shown are the 5, 10, 20, 30, 50, 100, and 150 m depth contours. Numbers denote GPS positions of Vemco VR2W acoustic receivers deployed to receive signals sent by acoustic transmitters.



effort within the study area. We hypothesize that the fate of individual lobsters during the fishing season will depend on their spatial ecology as well as fishing pressure within their respective home ranges.

### Materials and methods

This study was conducted within a coastal archipelago on the Norwegian Skagerrak coast (58°24'N, 8°45'E; Fig. 1). Maximum depth is 50 m and the habitat is diverse, including exposed and submerged islands, boulder fields, and flats consisting of soft sediment, eel grass beds, and kelp forest (Olsen and Moland 2010). A partly submerged glacial moraine cuts through the area, forming a rock reef consisting of variable-sized cobble. The habitat found in the area is representative of that found along the majority of the Norwegian Skagerrak coast, of which large swathes may be considered good lobster habitat (Moland et al. 2011a, 2011b). Owing to its close vicinity to human population centres and its multitude of sheltered locations, the coastline is popular for both commercial and recreational lobster fishers.

The European lobster is a large, long-lived decapod crustacean of ecological and commercial importance, distributed from the north of Norway to Morocco in North Africa (Triantafyllidis et al. 2005). The species is considered a nocturnal animal, where light hours are generally spent solitary inside shelters on rocky bottoms (Smith et al. 1998, 1999; Mehrtens et al. 2005; Moland et al. 2011a). European lobsters rarely move more than a few kilometres for periods up to years (Dannevig 1936; Smith et al. 2001; Agnalt et al. 2007; Moland et al. 2011b). Longevity potentially span several decades (Sheehy et al. 1999). In Norway, fishery catch per unit effort has decreased by 65% from the 1950s to 2000s (Pettersen et al. 2009). As of 2008, lobsters in Norway are legally caught in traps fitted with two circular escape vents measuring 60 mm in diameter during a 2-month season (1 October to 30 November). Minimum legal size is 25 cm total length (TL, measured from the

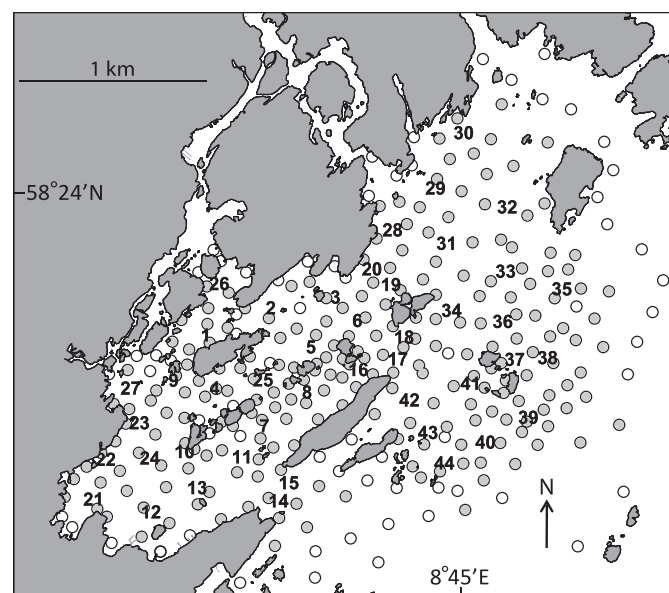
tip of the rostrum to the end of the middle uropod, ≈90 mm carapace length, CL), and there is a trade and landings ban on egg-bearing females. Effort (total number of gear deployed) is limited to 10 and 100 traps for recreational and commercial participants, respectively. A network of marine protected areas in Skagerrak (established in 2006) has demonstrated the usefulness of this management tool in rebuilding local lobster populations (Moland et al. 2013a).

To monitor lobster behaviour and fate in their natural habitats, 44 acoustic receivers (VR2W, Vemco Divison, Amirix Systems Inc., Halifax, Canada) were moored throughout the study area (geographic coverage ≈ 3 km<sup>2</sup>) and attached at 3 m depth using subsurface trawl floats (Fig. 1). We evaluated the detection range of the receivers using a V13-tag with a fixed 5 s interval between signals, transmitting with the same signal strength as tags used in the lobster study. The range test tag was lowered to the sea floor at global positioning system (GPS) positions ( $n = 616$ ) 150–200 m apart throughout the study area. At each position, the range test tag was given a bottom time of 1 min. Range testing resulted in 66 of 616 positions (10.7%) not being detected by any of the receivers. Most of these undetected positions were outside the receiver network or in shallow water near shore (Fig. 2).

Trapping and tagging of lobsters was carried out throughout the study area during 1–31 August 2011. Individuals were caught in standard “parlour” lobster traps baited with frozen Atlantic mackerel (*Scomber scombrus*). Soak time varied from 1 to 4 days. Only males ( $n = 50$ ) were selected to ensure that tagged individuals recovered by fishers would be kept (and subsequently reported) and also to reduce sources of variation in statistical analyses. GPS capture location, carapace length (CL), and total length (TL) were registered for all individuals (Table 1).

Individuals used in this study were equipped with acoustic transmitters (Vemco V13P-L, diameter 13 mm, length 36 mm, mass in seawater <6 g). Tags were programmed to transmit signals

**Fig. 2.** Acoustic range testing in the  $\approx 3 \text{ km}^2$  study area used for monitoring movement and fates of European lobster (see also Fig. 1), showing positions where a range test tag was deployed and detected (shaded circles) or not detected (open circles) by one or more of the acoustic receivers (Nos. 1–44).



(69 kHz) at 110–250 s random intervals (mean 180 s), coded with an ID number to distinguish among individuals. Also, the transmitters were equipped with a pressure sensitive transducer to obtain information about lobster depth use. Transmitters were attached to lobsters by means of a harness made of a cable tie and soft plastic tubing in which both the transmitter and a T-bar tag was inserted (TBA1, 45 mm  $\times$  2 mm, Hallprint Pty. Ltd., Holden Hill, South Australia) This was attached between the most robust denticles on the middle segment (carpus) of the crusher claw limb (Moland et al. 2011b). There are no indications that these devices impair lobster behaviour (Cowan et al. 2007; Moland et al. 2011b). To maximize the return rate of tags from fishers, the T-bar tag informed fishers that a reward would be paid if returned to the Institute of Marine Research. By doing this, it was possible to confirm whether individuals were fished or not as a supplement to the collected acoustic data. Transmitters would be lost when lobsters moulted. Some individuals carried a T-bar tag from an ongoing study ( $n = 16$ ), meaning that these individuals could be recognized even if the telemetry tag was lost. After tagging, lobsters were released at their GPS capture location. The total handling time was 5–15 min, dependent on the number of lobsters caught in each trap. Data stored within receivers were downloaded during 2–7 December 2011, after the end of the 2011 lobster fishing season.

Lobster locations were estimated as 30 min centres of activity, using the algorithm developed by [Simpfendorfer et al. \(2002\)](#). Within an array of receivers with partly overlapping detection ranges, the algorithm estimates a mean position of an animal as the mean position of the receivers weighted by the number of detections at each receiver ([Simpfendorfer et al. 2002](#)). This approach was applied because individual detections will not represent the exact position of a lobster, but simply indicate that it was within listening range of the receiver. From these aggregated data, we then calculated short-term home ranges as the smallest area containing 95% of the utilization distribution (UD95) of an individual (i.e., the area within which an individual can be expected to be found 95% of the time; [Rogers and White 2001](#)). The core area of the home range was estimated as the smallest area containing 50% of the utilization distribution (UD50). For the pur-

**Table 1.** Summary statistics of 50 male European lobster (*Homarus gammarus*) equipped with acoustic transmitters between 4 and 31 August 2011.

	<i>n</i>	Range	Mean	SD
TL (cm)	50	25.0–31.5	27.2	1.7
CL (mm)	50	87–116	97.2	7.3
HR (m <sup>2</sup> )	37*	43 129–641 731	170 660	125 519
SF	37*	0.18–1.00	0.90	0.18
ETE	37*	0.003–0.082	0.029	0.021

**Note:** Minimum legal size in Norway is 25 cm TL. TL, total length; CL, carapace length; HR, September home range (UD95); SF, degree of individual site fidelity; ETE, experienced trap exposure.

\*37 individuals qualified for inclusion in the data analyses (see Materials and methods).

pose of unbiased comparison between individuals, kernel shape (the smoothing parameter) was standardized (i.e., we found a common smoothing parameter ( $h_0 = 50$ ) that produced a biologically meaningful kernel shape to the plots of all individuals), avoiding oversmoothing and kernel shapes that included substantial sections of dry land. The alternative would involve selection of kernel bandwidth based on the unique spatial configuration of position fixes in each individual, resulting in a unique smoothing parameter in each case (e.g., least-squares cross-validation; [Worton 1989](#); [Gitzen et al. 2006](#)).

Separate short-term home ranges were estimated for September and October–November, enabling comparisons between home range as recorded before and during the fishing season. Home ranges were estimated using the R software version 2.12.1 ([R Development Core Team 2012](#)) using the “adehabitat” package ([Calenge 2006](#)).

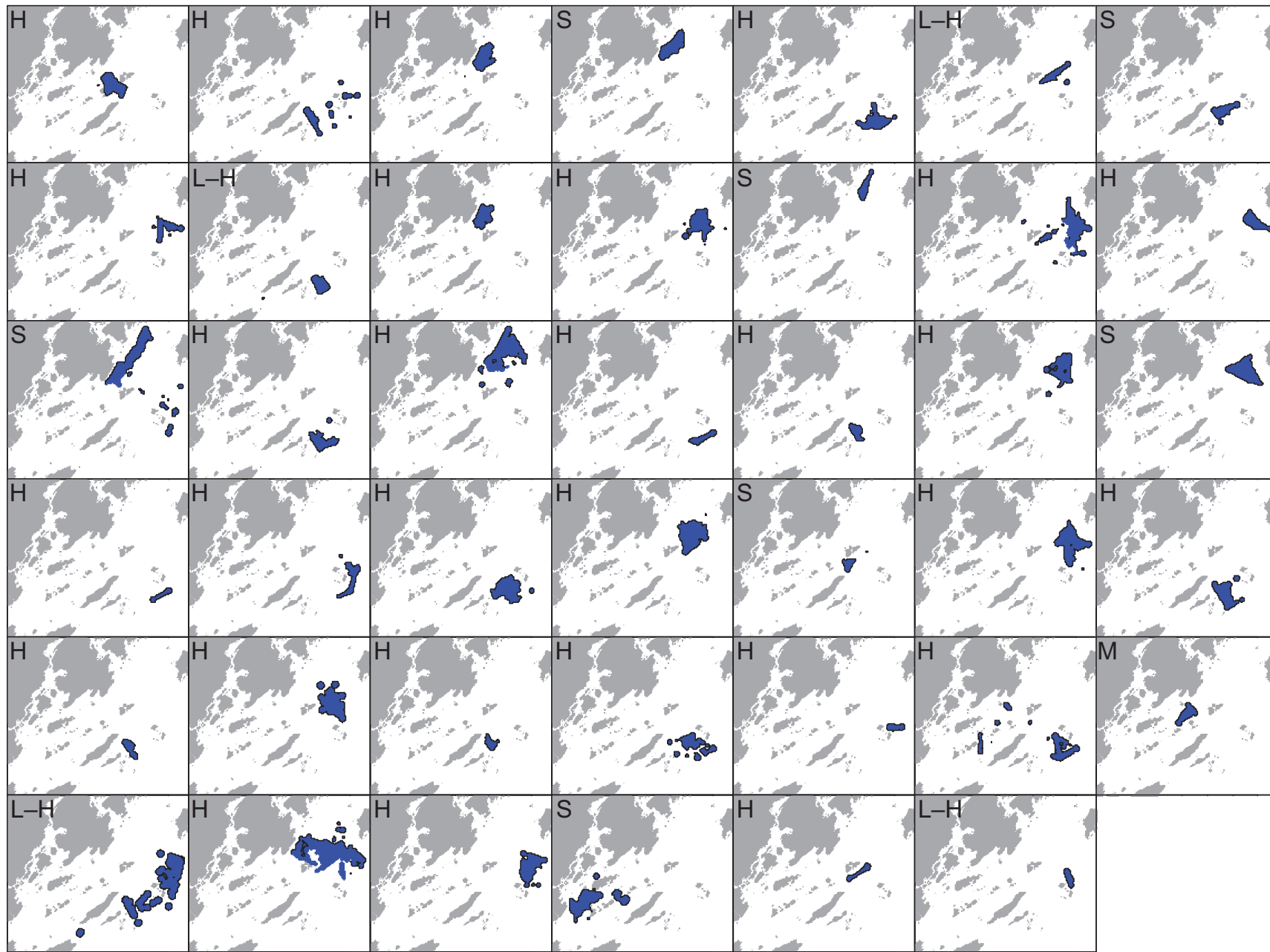
To determine whether lobsters remained within their “before” home range throughout the fishing season, locations estimated for the fishing season for a specific individual were compared with its September home range. A degree of site fidelity was estimated as the number of locations recorded during the fishing season that fell within the individual's September home range, divided by the total number of locations recorded during the fishing season. Based on horizontal and vertical movement data and information from fishers, the following mutually exclusive fates were determined for all lobsters at the end of the fishing season: (i) harvested, (ii) moulted, (iii) dispersed out of study area, and (iv) survived within study area. A lobster was classified as harvested when the signal disappeared from within the study area and confirmed by a fisher returning a tag. A lobster was classified as moulted when the data showed permanent cessation of movement at constant depth for at least 7 days, lasting to the end of the study. A lobster was classified as dispersed when the signal disappeared from one of the outermost receivers. Lastly, a lobster was classified as surviving when horizontal and vertical movement continued throughout the fishing season. Three individuals showed the typical signs of being locked in a trap (i.e., fixed depth and position) prior to signal disappearance, but without subsequent tag-return from fishers. These three individuals were classified as harvested.

Starting on day 2 of the lobster fishing season (2 October 2011), GPS positions of all observed lobster trap surface buoys in the study area, set by recreational and commercial fishers, were recorded with a handheld GPS (Garmin 78xc). Trap counting continued throughout the fishing season three times per week in October and two times per week in November. For analyses of the trap data, we interpolated numbers between field dates. The last day of trap counting was 28 November 2011.

For each lobster the experienced trap exposure was estimated as the accumulated number of traps within their respective fishing season home range, divided by the total number of traps registered throughout the study area during the same time pe-



**Fig. 3.** Short-term home ranges (UD95) of individual European lobster ( $n = 41$ ) for which we obtained continuous movement data during September 2011, estimated from acoustic monitoring (see also Fig. 1). Letters refer to the fate of each individual during October–November 2011: S = survived, H = harvested within study area, L-H = left study area and was subsequently harvested, and M = moulted (late September).



riod. For lobsters that were harvested, only traps counted up to the last day of survival for that individual were included in the estimate. For lobsters that survived the fishery, all traps were included. This allowed us to compare trap exposure among lobsters that were fished at different dates and also take into account the fact that traps were far more numerous in the beginning of the fishing season (see Results).

We implemented two types of survival analyses. First, for lobsters that remained within the study area and yielded sufficient behavioural data, we used logistic regression (Janzen and Stern 1998) to test for effects of individual spatial ecology and trap exposure on the probability of surviving the fishery ( $S$ ):

$$\text{logit}(S) = \beta_0 + \beta_1\text{HR} + \beta_2\text{SF} + \beta_3\text{ETE}$$

where HR represents the individual home-range size (UD95) in September, SF is the degree of site fidelity, and ETE is the experienced trap exposure. We used Akaike's information criterion (AIC) to select the model structure that best balanced bias and variance (Burnham and Anderson 1998). The analyses were performed using the "glm" function in the R package "aod". Second, we estimated survival for all lobsters with known fates, regardless of whether they had remained within or traversed beyond the study area, based on the nonparametric Kaplan–Meier procedure (Cox and Oakes 1984), using the "survfit" function in the R package "survive".

## Results

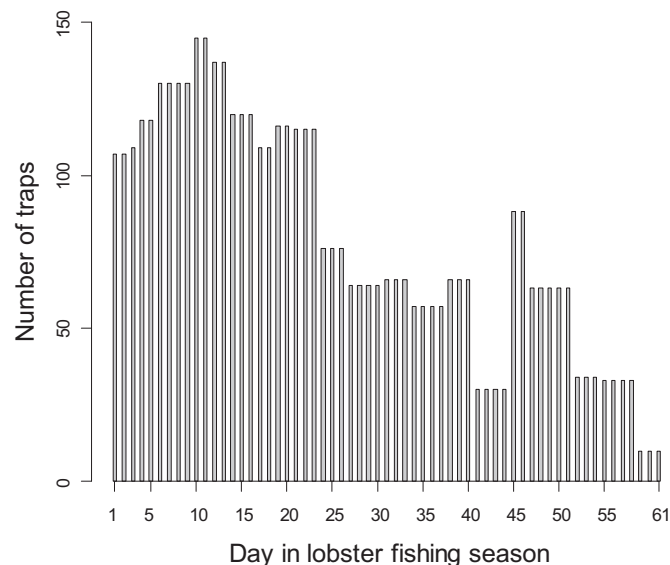
Eight individuals were censored from the survival analyses because of moulting ( $n = 7$ ) or tag malfunction ( $n = 1$ ) prior to the onset of the fishing season. Thus, 42 individuals entered the fishing season with status as alive and carrying a transmitter. Out of these, one individual was reported harvested 16 km northeast of its release position, making calculations of a home range inaccurate for this individual. Four additional individuals traversed outside the detection range of the receivers, preventing accurate home-range estimates for those. For these reasons, 13 lobsters in total were excluded from home-range analysis (Table 1). Most lobsters displayed a high degree of site fidelity. On average, 90.3% ( $\pm 0.3\%$  SE) of locations calculated for October–November fell within each individual's respective September home range. However, four individuals displayed a degree of site fidelity lower than 70% (Table 1). Home-range sizes ranged from 43 129 to 641 731 m<sup>2</sup> in September (mean 170 660  $\pm$  20 635 m<sup>2</sup> SE; Table 1; see also Fig. 3) and from 12 024 to 397 348 m<sup>2</sup> (123 004  $\pm$  12 974 m<sup>2</sup> SE) during the fishing season.

A total of 4781 lobster trap sets were registered throughout the fishing season with a mean of 78 traps per day. Overall fishing activity peaked early in the season (Fig. 4). There was also a marked fine-scale spatial variation in fishing activity, where the highest density of traps was found around islands in the outer part of the study area, towards the open ocean (Fig. 5).

Seven lobsters were confirmed to be active (i.e., survived) after the fishing season had ended (Fig. 5), while 35 lobsters were classified as harvested (32 of which were confirmed by tag return). A total of 16 tagged lobsters were reported harvested during the first week of the fishery. Based on the Kaplan–Meier analysis, the survival probability for the fishing season (October–November) was 16.7% ( $\pm 5.75\%$  SE; Fig. 6).

There was a weak positive correlation between home-range size and trap exposure. However, this correlation was not significant ( $P > 0.05$ ; Table 2). The most supported logistic regression model describing lobster survival included effects of individual trap exposure and home-range size. However, the AIC score of this model was only marginally lower than a simpler model containing only the effect of trap exposure ( $\Delta\text{AIC} \approx 0.17$ ; Table 3), and the effect of home-range size was not significant ( $P = 0.15$ ). According to

**Fig. 4.** Number of lobster traps counted in the study area by the authors during the 2011 fishing season (1 October – 30 November; see also Fig. 5). Note that frequencies are interpolated between trap counting days ( $n = 21$ ).



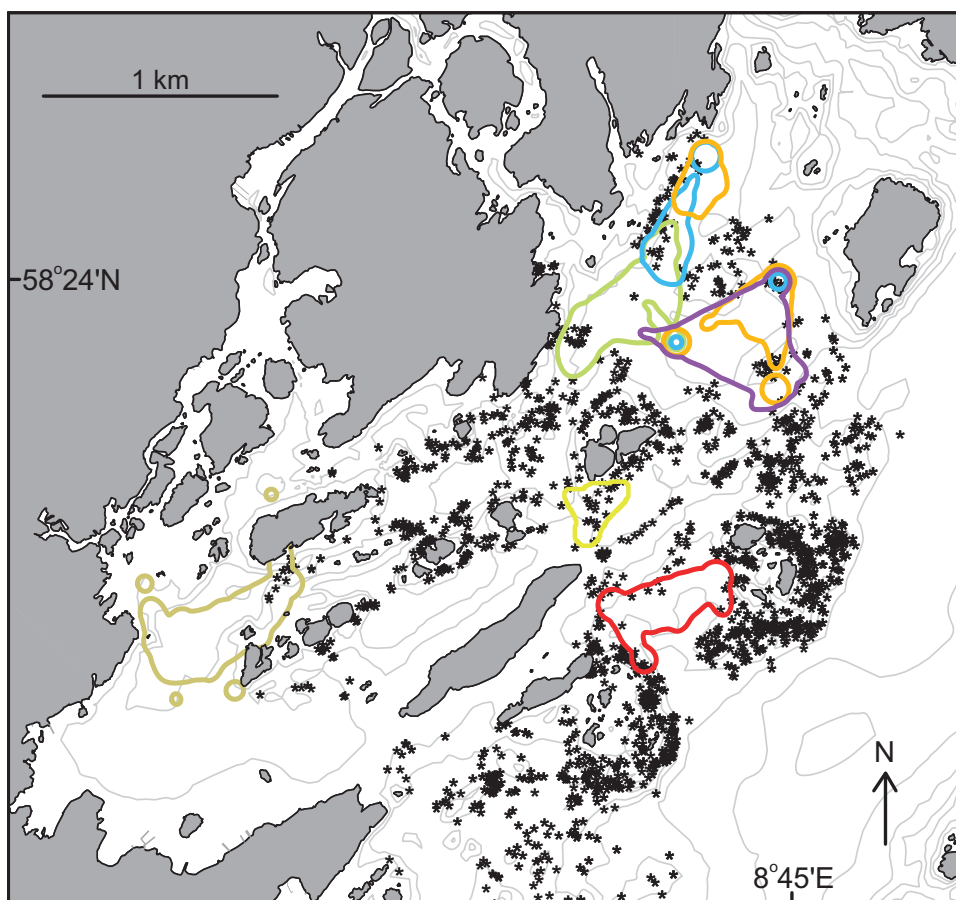
Burnham and Anderson (1998), models that are less than two AIC units apart cannot be easily distinguished. Therefore we draw inference from the simpler model, containing only an effect of trap exposure on survival probability. According to this model, lobsters with more traps within their home ranges (higher experienced trap exposure) had a lower probability of surviving the fishery compared with those with a lower trap exposure ( $\beta_3 = -84.9$ , SE = 42.6,  $p = 0.046$ ). The trap exposure effect was considerable. The lowest observed trap exposure (0.003) would correspond to a predicted survival probability of 0.5, while the highest trap exposure (0.082) would correspond to a predicted survival probability of 0.001. Other candidate models including an effect of site fidelity, or without the effect of trap exposure, had less support and were not considered for inference (Table 3).

## Discussion

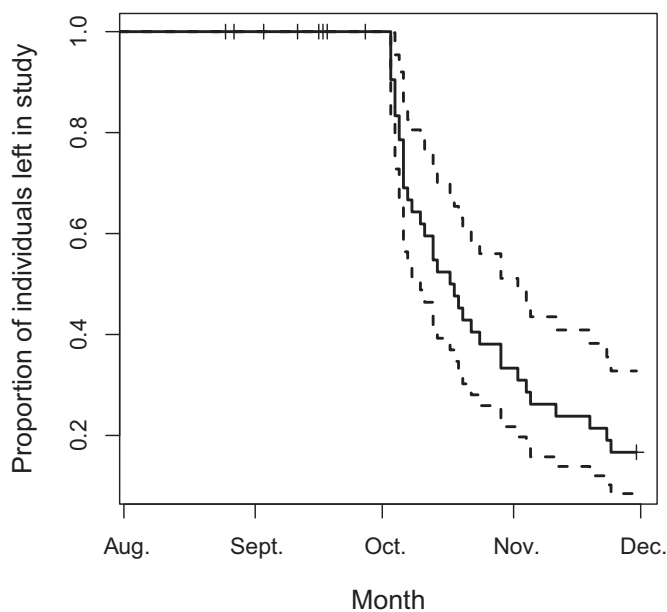
This study reveals spatial interactions between lobsters and lobster fishers in a coastal habitat. By applying the method of acoustic telemetry, we were able to monitor fine-scale behaviour of individual lobsters in their natural habitat in relation to commercial and recreational fishing activity. The fishing mortality exerted on the sample population was high, with an overall bimonthly survival probability of  $\approx 17\%$ . Also, there was marked spatial heterogeneity in fishing activity and lobster survival. Individuals with home ranges located away from the most popular fishing grounds had a considerably higher survival probability compared with individuals that experienced a higher trap exposure. This shows that even on a very fine spatial scale ( $< 1$  km), fishing — and the effects of fishing on target populations — may be nonrandom. We discuss the potential ecological, evolutionary, and management implications of these findings.

Most lobsters were harvested close to their original tagging position (see Table 1; Fig. 3) and mostly within the area we had estimated as their respective home range. Although the present study was relatively short in duration, this indicates that lobsters show high site fidelity and do not wander far from their respective core areas. In a longer-term study, Moland et al. (2011b) found that 95% of European lobsters monitored exhibited strong site fidelity for up to 1 year. Smith et al. (2001) found that while most lobsters were caught near their tagging location, some individuals were

**Fig. 5.** Short-term home ranges for the seven European lobsters surviving the 2011 fishing season (1 October – 30 November) estimated from acoustic monitoring. Stars mark the GPS locations of all lobster traps registered during the fishing season (see also Fig. 4).



**Fig. 6.** Kaplan–Meier survival curve for 50 male lobsters larger than MLS fitted with acoustic transmitters in August 2011. Broken lines denote the 95% confidence interval. Vertical hatch lines indicate censoring ( $n = 8$ ) due to tag loss (moulting) or tag malfunction prior to the fishing season.



**Table 2.** Correlations among behavioural traits, individual traits, and trap exposure.

Trait	HR	SF	ETE	TL	CL
HR	1	0.0727	0.1036	0.0899	0.0895
SF	0.0727	1	0.0069	0.0094	0.0044
ETE	0.1036	0.0069	1	0.0196	0.0284
TL	0.0899	0.0094	0.0196	1	0.9153
CL	0.0895	0.0044	0.0284	0.9153	1

**Note:** HR, home range (UD95); SF, degree of site fidelity; ETE, experienced trap exposure; TL, total length; CL, carapace length.

**Table 3.** Logistic regression modelling of lobster survival during the 2011 fishing season (1 October – 30 November).

Model	Structure	Deviance	No. of parameters	AIC
1	HR + SF + ETE	26.591	3	34.591
2	HR + SF	35.026	2	41.026
3	HR + ETE	26.593	2	32.593
4	SF + ETE	28.115	2	34.115
5	HR	35.893	1	39.893
6	SF	35.126	1	39.126
7	ETE	28.761	1	32.761

**Note:** Structure, model structure; AIC, Akaike's information criterion score. Explanatory variables: HR, home range (UD95); SF, degree of site fidelity; ETE, experienced trap exposure. For details, see Materials and methods section.

found to exhibit a more exploratory character. Leptokurtic distributions in movement distances are a common feature in mobile animals, which may be explained by intrapopulation variation in boldness and exploration (Fraser et al. 2001).

In our estimations of short-term home-range kernels, the same smoothing parameter was applied to all individuals. Attempts at using least-squares cross-validation in choosing a unique smoothing parameter for each individual did not yield a clear advantage (e.g., clearly less fragmented home ranges) compared with a fixed kernel method. Negatively, it caused a bias by giving some lobsters an artificially large home range and for others an artificially small and more fragmented home range. In practical terms, this bias gave individuals with a larger  $h_0$  value a higher count of traps within their home range than individuals with small  $h_0$  values. Choosing a fixed smoothing parameter for all individuals gave a reasonably fair basis for comparing home-range sizes and number of traps accumulated within the home range of each lobster.

According to Moland et al. (2011b), male lobsters ( $n = 8$ ) in the nearby Flødevigen lobster reserve had a mean home-range (UD95) size of  $21\,250 \pm 2224 \text{ m}^2$  SE over a monitoring period lasting up to 318 days, which greatly contrasts the larger home ranges found in the present shorter-term study (mean  $170\,660 \pm 20\,635 \text{ m}^2$  SE). The observed differences are most likely due to the different tracking methods used in each study. Home-range estimates reported in Moland et al. (2011b) were based on manual tracking in which a single position was obtained per individual during daytime every 5 days and as a result were likely biased low. The acoustic monitoring array used in the present study may have produced larger home ranges because a number of 30 min centres of activity (see Data analyses above) were “pulled” towards receiver station positions. This would occur whenever transmitted signals were recorded by a single receiver only over an extended time period. In such cases, one or multiple 30 min average positions would land on the position of the receiver station. Home-range sizes, as estimated in the present study, were thus partially dictated by the configuration of receiver stations and were likely biased high. However, this attribute of the study design was shared among the study animals. A marked strength of the present study was the high sample size, continuous monitoring of individuals in range of receivers, and the relatively large area under surveillance.

Home-range shape also varied greatly among individual lobsters (see Figs. 3 and 5). This variation may be explained by different movement patterns among individuals. Moland et al. (2011b) reported repeated “commuting behaviour”, described as instances where lobsters were found to alternate between two core areas. Bathymetry could also play a role, if lobsters repeatedly moved along certain features of the sea floor. Both phenomena will result in elongate home-range shapes. Wider home-range shapes might be a result of a more uniform space use within an area without bathymetric features that hampered or channelled lobster movement. Home ranges estimated for lobsters residing at the edge of the monitoring array will have shapes that to some degree are dictated by this cut-off in study area. However, we were aware of this when designing the array and placed the perimeter where it would include, rather than intersect, favourable habitat patches.

The overall fishing pressure (accumulated trap density) was highest around the outer laying skerries and islands surrounded by rock habitat (see Fig. 5). We assume that this pattern reflect fishers' perception of these areas as favourable lobster habitat. In fact, from interacting with fishers during this and other studies, we know that the outer exposed areas are preferred and fished more intensively when weather conditions allow small boats to operate. In general, we found that lobsters with home ranges in areas with high relative fishing pressure were harvested while individuals who experienced less fishing pressure survived ( $p = 0.046$ ; Table 2). However, Jury et al. (2001) found that only 6% of American lobsters (*Homarus americanus*) that entered a trap were

subsequently caught and concluded that lobster traps are ineffective and catch only a small proportion of lobsters present in a certain area. Other studies strengthen this theory (Lovewell et al. 1988; Watson et al. 2009). Lobsters above minimum landing size (MLS) may easily escape from traps unless they have entered the innermost “parlour” chamber. Only these individuals, or those present in the bait chamber (kitchen) at the moment of hauling, are caught. Another important factor behind the observed low effective catch rate is saturation of traps (e.g., if a lobster is already caught in a trap, it is less likely that another will enter; Addison 1995). The same study also noted that interaction between conspecifics and other species outside the traps have a major impact on an individual's catchability. In the present study, the fishing mortality of the 42 lobsters at large with transmitters at the onset of the fishing season was 83.3% (see Fig. 6). Mortality was highest during the first 2 weeks of the season, coinciding with the largest number of traps observed early in the fishing season (see Fig. 4). To our knowledge, no other studies have reported a mortality rate this high in any lobster species. In comparison, mark-recapture studies done by Smith et al. (2001) and Bannister and Addison (1986) on European lobster in southern UK reported mortality rates of 26%–52% and 35%–55%, respectively. Both studies reported much larger sample sizes than used in the present study, and their estimates may thus be more representative for a lobster population as a whole. It is also important to note that the lobster population in southern England has not plummeted as the Norwegian population has, and this may also have had an effect on the different results obtained.

A bias in our mortality estimate is likely due to the fact that all lobsters in our sample population were caught by the use of lobster traps during the month of August, 1–2 months prior to the onset of the fishing season (1 October), meaning that their catchability — or willingness to enter traps — was confirmed prior to the study. This “selectivity of traps problem” and the resultant bias is a recurring paradox in lobster research (e.g., Smith and Tremblay 2003; Bowlby et al. 2007). Further, we do know that by setting traps, one also trains lobsters to walk into them. This effect is believed to maintain an unnaturally large American lobster population in the Gulf of Maine (Saila et al. 2002; Steneck et al. 2012). This applies especially to berried females, which are protected — and thus released upon capture — and individuals below MLS that are either released or may leave traps via escape vents. Both groups are thus rewarded by a free meal when entering traps. Ideally, a proportion of the lobsters studied herein should have been caught by other means, such as diving or fyke nets. In a recent 14-year mark-recapture study, Moland et al. (2013b) showed that annual recapture probability (= catchability) of European lobster was usually lower than 50% for both males and females, meaning that less than half of the population studied was willing to enter traps in a given year. However, provided a mortality rate of  $\approx 83\%$  as estimated in this study is representative of a given catchable portion of a lobster population, it would mean that after just a few years, fishers would deplete the catchable part of a population completely and thus artificially suppress lobster populations so that they mainly consist of individuals below the minimum legal size. It is accepted that regulations on minimum size and protection of egg-bearing females (common in managed lobster fisheries) select for early maturation and slow growth, because mortality increases with size (Caputi et al. 2010).

In conclusion, our study shows that individual lobster behaviour and exposure to a coastal fishery vary on a small geographical scale (<1 km). We also show that such a coastal fishery can be highly effective, in our case removing as much as 83% of the tagged population. Fisheries-induced selection may favour individuals that establish home ranges in habitats where fishing activity is less intense. However, the high rate of removal of individuals in high quality (high fishing pressure) habitats might result in a high rate of movement of “beta-males” from the low



quality (low fishing pressure) habitats. This movement might give these individuals breeding opportunities they would not have had in low quality habitats, which might partially offset the removals of the established “alpha-males” in high quality habitats. Future studies aimed at pinpointing criteria for male lobster success (fitness) in harvested versus protected states are needed to understand the consequences of fine-scale geographic differences in survivorship upon population-level processes.

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