



Movement of american lobster *Homarus americanus* associated with offshore mussel *Mytilus edulis* aquaculture

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ABSTRACT: Bivalve aquaculture sites attract a variety of large benthic species. Previous studies have shown that American lobster *Homarus americanus* are more abundant in mussel *Mytilus edulis* farms than in areas outside of them, suggesting that farms provide lobsters with adequate food and shelter. This study used acoustic telemetry to evaluate the influence of longline mussel farms on lobster movement behavior. In 2014, 60 lobsters were acoustically tagged on a boat and released in a mussel farm and at 2 reference sites outside the farm. Most lobsters (92%) left the monitored area within 1 d post-tagging; those released in reference sites moved northeast, whereas those released in the farm moved in random directions. Of the 16 lobsters that stayed or returned to the study area over the course of the 2 mo experiment, 10 displayed nomadic movements, 3 displayed small, local movements—presumably associated with foraging behavior, and 3 displayed both movements. The time lobsters spent within a site, distance travelled, and walking speed did not differ between the farm and reference sites. A second experiment was done in 2017 over 2 mo to evaluate tagging method ('on boat' and *in situ* tagging) effects on lobster movement behavior. The experiment followed movements by 50 lobsters, half for each treatment, and showed that tagging method can affect walking speed during the first 24 h, but had no impact on the residence time and the distance travelled by the lobsters.

KEY WORDS: Acoustic telemetry · *Homarus americanus* · Mussel aquaculture · Movement · Behavior · Tagging method

1. INTRODUCTION

Bivalve aquaculture has a variety of ecosystem-level effects. For example, the influence of suspended mussel (*Mytilus* spp.) aquaculture on the benthic environment has been studied with respect to enhanced organic loading from biodeposition of mussel feces and pseudofeces (Hatcher et al. 1994, Newell 2004, McKindsey et al. 2012, Lacoste et al. 2019). Organic loading from mussel biodeposition may lower oxygen concentrations in sediments below suspended

mussels (due to increased benthic respiration), increase sediment sulfide levels, reduce redox potentials, and alter nutrient fluxes at the sediment–water interface (Richard et al. 2006, 2007, McKindsey et al. 2011), as well as shift benthic infaunal community structure towards dominance by small, opportunistic species (Giles & Pilditch 2006, Callier et al. 2007). In addition, the most evident physical impact of mussel farming is commonly the accumulation of mussel shells and shell hash below suspended mussels (Wilding & Nickell 2013). Because fallen mussels

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provide food for many macrobenthic species, mussel farms often support a higher abundance (relative to areas outside mussel farms) of predatory and scavenger species, such as sea stars, crabs, and lobsters (Inglis & Gust 2003, D'Amours et al. 2008, Clynick et al. 2008, Wilding & Nickell 2013, Callier et al. 2018). The physical structure associated with suspended mussel aquaculture (longlines, dropper lines and anchor blocks) creates novel hard structure in commonly soft-bottom habitats that is colonized by sessile fouling organisms and may serve as shelter for a variety of mobile species (McKinsey et al. 2011). Thus, both an increase in food resources and physical structure complexity may act to concentrate mobile macrofauna in farm sites, which may also create within-farm variability in the abundance of attracted organisms (D'Amours et al. 2008, McKinsey et al. 2011, Wilding & Nickell 2013, Drouin et al. 2015). Drouin et al. (2015) showed that the spatial distribution of mobile macrofauna (lobster, crab, sea star, and flounder) in a mussel farm was related to the distribution of food resources (i.e. from fallen mussels or modified infaunal or macrofaunal communities) and the presence of anchor blocks throughout the farm and surrounding area.

To date, there has been little work on the consequences of these macrofauna concentrations on population dynamics (but see Inglis & Gust 2003). For lobster, their movement in relation to mussel farms needs to be studied to understand the extent to which farms may function as ecological traps, whereby their aggregation in farm sites may make them vulnerable to predation or exploitation by the lobster fishery. It is also possible that farms may have the opposite effect; that is, lobsters may find mussel farms so attractive that they remain within the confines of culture sites, making them thus inaccessible to the lobster fishery.

Crustacean movement was first studied using mark–recapture methods to better understand large-scale movements. However, acoustic telemetry is now often used to follow aquatic animal movements to address questions about behavior, habitat use, migration, management, and conservation issues (Hussey et al. 2015, Florko et al. 2021). Recent advances in telemetry methods have revealed finer-scale variations in movements including variation in movements among habitat types, foraging forays, territoriality, and reproductive activities (Pittman & McAlpine 2003). Notably, acoustic telemetry has been used to determine movements of rock crab *Cancer irroratus* (Comeau et al. 2012) and lobsters *Homarus gammarus* and *H. americanus* (Golet et al. 2006, Moland

et al. 2011, Skerritt et al. 2015). For *H. americanus*, telemetry has led to a better understanding of predator (Atlantic cod *Gadus morhua*)–prey interactions (McMahan et al. 2013), dispersal behavior (Bowlby et al. 2007), and the influence of bait in lobster trapping areas (Watson et al. 2009). To our knowledge, interactions between longline mussel aquaculture and *H. americanus* behavior have not been investigated.

To use acoustic telemetry to evaluate crustacean movement, a tag must be affixed to the animals, although various methods may be used to capture them prior to tagging (Florko et al. 2021). Many capture-based and acoustic tagging methods have been used for crustaceans: capture using baited lobster traps (Wiig et al. 2013) or *in situ* (Golet et al. 2006) and thereafter tagged on a boat (Skerritt et al. 2015) or in a laboratory (Moland et al. 2011). However, the capture, tagging, and release of animals may temporarily disturb them (Maynard & Robichaud 1986). To minimize potential disturbance effects, some studies have disregarded movement data until 1 wk post-tagging (Moland et al. 2011), whereas other studies excluded the first 48 h (Bowlby et al. 2007, Skerritt et al. 2015, Lees et al. 2020) or 24 h (Scopel et al. 2009), or did not exclude any data (Wiig et al. 2013), stating that there is no indication that manipulations impact behavior.

This study examines the impact of an offshore mussel farm on lobster movement behavior, based on the assumption that farms attract lobsters (Drouin et al. 2015). The study also evaluates the impact of tagging method on lobster movement behavior, where we contrast typical baited trap capture-surface tag-release ('on boat') methods to lobsters tagged by divers on the bottom (*in situ*). The evaluation of these 2 tagging methods was done to better understand the impact of tagging-related manipulations on lobster behavior (directly after the tagging and 24 h after), with the idea that *in situ* tagging is the least invasive method possible.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in Baie de Plaisance, Îles-de-la-Madeleine (47.3613°N, 61.7447°W), eastern Canada (Fig. 1), in the summers of 2014 and 2017. The farm area has a mostly sandy bottom with a mean water depth of 18 m (range: 15–22 m) (Fig. 1). The focal area was an offshore (3 km southeast of the coast) blue mussel *Mytilus edulis* farm that had been

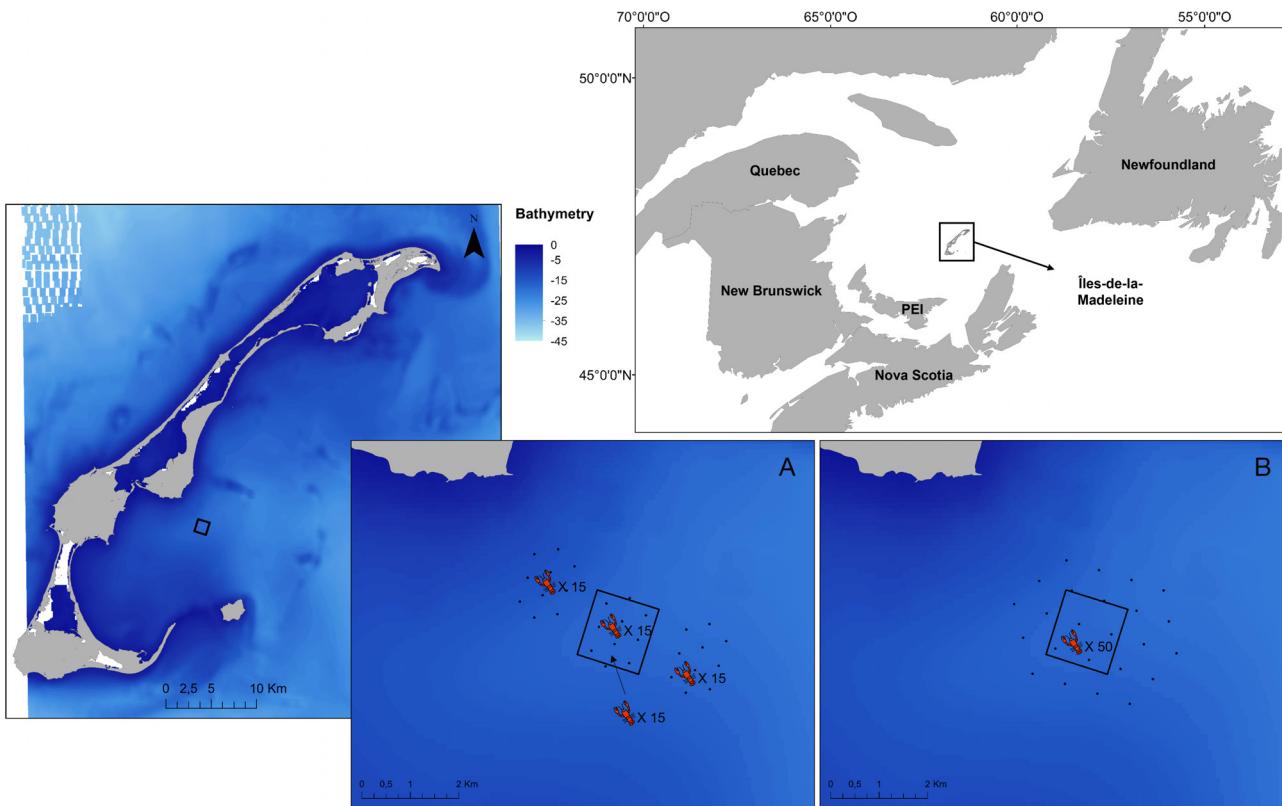


Fig. 1. Location of the studied mussel farm (black polygon) in the Baie de Plaisance, Iles-de-la-Madeleine, Canada, where (A) 60 lobsters in 2014 and (B) 50 lobsters in 2017 were acoustically tagged and released. The black dots represent the locations of the acoustic receivers

in operation for 3 yr when the experiment was initiated. The 2 km² farm site had 27 rows of 7 longlines (each 100 m long). Longlines within a row were separated by 90 m and adjacent rows were separated by 50 m. Mussel sleeves (3 m long) were suspended mid-water at about 10 m above the bottom with cement anchors spaced at about 5 m intervals in the areas with the oldest mussels. Age classes of mussels were arbitrarily distributed throughout the farm and no attempt was made to focus on lobsters in any specific area of the farm.

2.2. Acoustic telemetry design

Acoustic receivers (model VR2W, Innovasea) operating at 69 kHz were deployed in summer 2014 (88 d: June 28th to September 24th) and 2017 (90 d: July 24th to October 22nd). In 2014, 30 receivers were used to create 3 acoustic arrays: one within and 2 outside of the mussel farm for a total coverage of ca. 10 km² (Fig. 1A). In 2017, 24 receivers were used to cover the same mussel farm and surrounding area of

ca. 10 km² (Fig. 1B). Receivers were deployed by SCUBA divers and attached (with cable ties) to the top of 2 m long steel garden posts, which were driven halfway into bottom sediments. Distances between receivers (500 m—more conservative—in 2014 and 800 m in 2017) were based on the results of a 1 wk long range test in 2014 to determine optimal receiver spacing for meeting the objectives of each experiment.

Appropriate spacing of receivers is important to create arrays that are suitable for VEMCO Positioning System (VPS) analysis, an aquatic ultrasonic fine-scale positioning system used to track aquatic animals that was developed by Innovasea (Espinoza et al. 2011). It requires the use of 'sync' tags to synchronize receiver internal clocks (Espinoza et al. 2011) and reference tags to calibrate positioning accuracy. The positions of both types of tags needs to be known, and it is preferable to install sync tags 1 m above VR2W receivers (Innovasea pers. comm.). Accordingly, a sync tag (model V13, 36 mm long and 13 mm diameter, transmission delay between 500 and 700 s, Innovasea) was affixed 1 m above each receiver on a 2 m long buoyed polypropylene line

attached to the top of each post. A reference tag (model V13, 36 mm long and 13 mm diameter, transmission delay between 500 and 700 s, Innovasea) was placed in the centre of each acoustic array to further increase the precision of spatial data.

2.3. Acoustic tag deployments

2.3.1. 2014

A total of 60 lobsters (*Homarus americanus*, 32 males, 28 females) ranging in size from 63 to 122 mm (mean \pm SE = 82 \pm 1.41 mm) cephalothorax (CL) length was caught on July 15th, after the fishing season, and brought to the boat where they were fitted with acoustic transmitters (model V9, 26 mm long and 9 mm diameter, transmission delay between 60 and 120 s, Innovasea) operating at 69 kHz. Lobsters were collected using lobster traps and SCUBA diving to obtain the 60 lobsters required for the study, given tagging constraints (e.g. commercial size, same ratio male–female, and a clean carapace to indicate that the animal had recently molted). Acoustic transmitters (tags) were glued to lobster carapaces using LePage® Ultra Gel Control® Super Glue following carapace cleaning by rubbing with sandpaper and then swabbing with alcohol. Manipulations took about 3 min for each lobster, which was then released back into the study arrays on the seafloor within about 10 min of being captured. Returned lobsters were placed in plastic crates, transported to the bottom by divers to the same general area that they were captured (i.e. same GPS coordinates), and released. This approach reduced the likelihood of lobsters having to move large distances to return to their initial territories (Goldstein & Watson 2015). Fifteen lobsters were captured and released within the center of the mussel farm array and within each of the 2 reference arrays in which they were captured. An additional 15 lobsters were caught outside of the mussel farm and placed within the farm site (Fig. 1A).

2.3.2. 2017

A total of 50 lobsters was caught directly within the mussel farm on July 26th (Fig. 1B). Twenty-five lobsters (14 males and 11 females) ranging in size from 73 to 91 mm (mean \pm SE = 82 \pm 0.77 mm) CL were caught (using baited lobster traps), tagged, and released, as described for 2014. A further 25 lobsters (15 males, 10 females) ranging in size from 52 to 96 mm (mean \pm

SE = 74 \pm 2.40 mm) CL were tagged *in situ* by SCUBA divers. Tags were attached by cable ties directly on lobster claws as outlined by McMahan et al. 2013 (although lobsters were tagged out of the water in that study), an operation that took about a minute to complete, including measuring the animal.

2.4. Data analysis

A 2-way ANOVA was used to compare lobster size as a function of 'year' (2 levels: 2014 and 2017) and 'sex' (2 levels: male [M] and female [F]), and their interaction. Data were transformed (log-x) to satisfy the assumptions of ANOVA. Variation in lobster size in 2017 was evaluated as a function of 'tagging method' (2 levels: 'on boat' and *in situ*) and 'sex' using PERMANOVA (with 9999 permutations) using PRIMER 7 (Clarke & Gorley 2015) and PERMANOVA+ (Anderson et al. 2008), as data transformations were unable to constrain the data to meet the assumptions of ANOVA (Anderson 2001). The corresponding similarity matrix was constructed based on Euclidean distances built on square-root transformed data and homogeneity of multivariate dispersion evaluated using PERMDISP (Anderson et al. 2008).

2.4.1. Acoustic telemetry data preprocessing

Prior to analysis, data were filtered to identify detections with high positioning error (HPE) using a linear regression with the HPE and the error measure in meters (HPEm) (Skerritt et al. 2015, Lees et al. 2020). In 2014, less than 4 % of the synchronization tag data had a HPE $>$ 30 and the 95th quantile of HPE values was 25 (regression R² = 0.93). Lobster data were filtered to HPE $<$ 30, and the positional error was between 23 and 65 m with a mean (\pm SE) of 30.8 \pm 0.05 m (n = 32 511). For the 2017 data, less than 2 % of synchronization tag data were lost if the data were filtered with an HPE $<$ 30, and the 95th quantile of HPE values was 9 (regression R² = 0.97). Lobster data were thus filtered with an HPE $<$ 30 and the error in meters was between 2 and 30 m with a mean (\pm SE) of 4.02 \pm 0.02 m (n = 32 023).

Lobster movements were drawn using ArcGIS 10.2.1 (Esri) and Geospatial Modelling Environment tools (Beyer 2012). All data were projected in Universal Transverse Mercator (UTM) Zone 20. Residence time and distance travelled correspond to the cumulative time spent and cumulative distance travelled by each lobster in all study locations (farm site and

reference areas), respectively. Walking speed was estimated by dividing the distance interval from each step by the time interval from the same step.

2.4.2. Short-term (acclimation period) and tagging method effects

Data were separated into 2 periods: the first 24 h post-release (acclimation period) and movement thereafter (Cote et al. 2019). Analysis of short-term effects focused on the acclimation period, as the greatest impacts due to tagging are expected during this period. Data for all lobsters were used for the short-term analyses, including low detections, because these may indicate that lobsters left the study site quickly. Lobster movement direction was evaluated by polar plots and circular ANOVA with the R package 'Circular' (Agostinelli & Lund 2017), with uniformity in the acclimation period evaluated using the Rayleigh test (r ; a value of 0 means uniform dispersion around the circle and a value of 1 means complete concentration in one direction). Analyses were done for each group of lobsters in 2014 (i.e. those collected and returned to the 2 reference areas and the farm as well as those collected from outside of the farm and placed within it) and for the area directly within the farm and the area beyond it (or equivalent areas in the reference sites). Directional data from 2017 were analyzed by polar plot and uniformity tested with the Rayleigh test. A Watson's 2-sample test of homogeneity (Watson's U^2) was used to evaluate if the 2 samples come from the same distribution (i.e. travelled in the same direction) and if the calculated value is greater than the critical value, the null hypothesis of uniformity is rejected. Movement data from 2017 were compared for 'on boat' and *in situ* lobster tagging methods. The effect of the 'tagging method' (2 levels: 'on boat' and *in situ*) was also evaluated by comparing lobster movement behavior (i.e. direction, residence time in the farm, distance travelled, and walking speed) of the 2 groups ('on boat' vs. *in situ*). A 2-way ANOVA was used to determine the influence of the 'tagging method' and 'sex' (2 levels: M and F) on the distance travelled and walking speed. An initial model included 'size' as a covariate, but it was not significant and was thus removed. Assumptions of normality and homoscedasticity were verified prior to running ANOVAs, as outlined by Quinn & Keough (2002). Data were transformed (fourth-root: distance travelled) prior to analysis. Residence time was evaluated using PERMANOVA (with 9999 permutations) as data transfor-

mations were unable to constrain the data to meet the assumptions of ANOVA (Anderson 2001). The similarity matrix used to this end was constructed based on Euclidean distances. Homogeneity of multivariate dispersion was evaluated using PERMDISP and data transformed (log-x or fourth-root), when necessary. PERMANOVA analyses included 2 factors ('tagging method' and 'sex').

2.4.3. Long-term effects—general behavior

Analyses were divided between the acclimation and post-acclimation periods (movement after the first 24 h) to ensure that tagging-related impacts and biases related to 'where lobsters were released' were excluded from analyses. Only lobsters with more than 200 detections were included in the analyses, for a total of 16 in 2014 (range between 207 and 5116 detections) and 17 in 2017 (range between 204 and 4717 detections). Gaps in acoustic telemetry data can arise when lobsters leave and then reenter the acoustic telemetry array. To avoid including these large gaps and associated poor estimates of residence time, distance travelled, and walking speed, lobster trajectories were split into separate bursts if the time between detections was >12 h. Residence time, total distance travelled, and walking speed were analyzed within and outside the mussel farm. Variation in movement parameters was examined using 2-way ANOVA with the factors 'site' (4 levels: resident mussel farm, introduced mussel farm, east reference site, and west reference site) and 'sex' for the data from 2014. In 2017, as all lobsters were tagged and released on the same site, only the factors 'sex' and 'tagging method' were included in the model. The factor 'size' was initially included as a covariate in both analyses but was not significant and was thus removed. Assumptions of homoscedasticity were evaluated for each ANOVA analysis using the Bartlett test (Quinn & Keough 2002). Data were transformed, where necessary, to satisfy assumptions of ANOVA (log-x or square root). Data from the 2 years were not analysed together, given the many differences in the sampling design.

Classification of movement types in the post-acclimation period was done by calculating the net squared displacement (NSD) over time for each individual. NSD measures the square Euclidean distance between the starting location of a movement path and all subsequent locations of an individual over time (Turchin 1998). NSD can be used to determine individual movement tactics, e.g. migration, resi-

dency, nomadic, or dispersal. We did not consider migration tactics, because lobsters were not followed over all the seasons. Non-linear mixed-effect models were built to link theoretical expectations to movement data (Börger & Fryxell 2012) with nlme package and the NSD estimated with the AdehabitatLT for the R environment. Börger & Fryxell (2012) estimated mean squared displacement (MSD) as the mean of the squared distance at each step over a given time period. Compared to NSD, MSD provides smoother trajectories such that daily movements may be more readily distinguished (Singh et al. 2016). We thus used non-linear models to predict MSD. The model with the largest concordance correlation (CC) was retained to express the best fit with the movement data. As the fit between theoretical models and movement data is not always close, visual tactics may be used to identify best fit for NSD trajectories (Courtiot et al. 2018). According to the visual patterns described by Börger & Fryxell (2012), resident individuals were categorized by a relatively constant NSD, dispersed individuals by constant NSD before increasing rapidly to reach a plateau, and nomadic individuals by a linear increase of NSD over time (also see Bastille-Rousseau et al. 2016, their Fig. 1).

3. RESULTS

Variation in lobster size from all individuals captured due to 'year' and 'sex' was not significant, with a mean (\pm SE) carapace size of 80.06 ± 1.00 mm. In 2017, lobster size varied significantly as a function of the interaction between 'tagging method' and 'sex' (Table 1), with a mean (\pm SE) carapace size of 82.40 ± 0.77 mm for animals tagged 'on boat' and 74.20 ± 2.40 mm for those tagged *in situ*, and with females that were tagged *in situ* being smaller than males (66.90 ± 4.34 and 79.07 ± 2.02 , respectively).

3.1. Short-term (acclimation period) and tagging method effects

Most lobsters (55 of 60) in 2014 left the monitored site within 24 h post-tagging (Fig. 2A); only 5 stayed after the acclimation period and 11 returned to the acoustic array area over the ensuing 2 mo. Tagged lobsters in reference sites moved mostly northeast both within and outside of the 700 m radius area surrounding their release location ($r = 0.70$ and 0.74 respectively). In contrast, lobsters that were released within the mussel farm dispersed in more random

Table 1. Results of PERMANOVA evaluating the influence of 'tagging method' ('on boat' and *in situ*) and 'sex' on lobster size in 2017. Significant effects ($p < 0.05$) are highlighted in **bold**

Source	df	MS	F	p
Tagging method	1	3.8139	17.875	0.0002
Sex	1	1.8763	8.7937	0.0046
Tagging method \times sex	1	1.4571	6.829	0.0117
Error	46	0.21337		

directions immediately following release ($r = 0.34$). However, these lobsters also moved northeast once they left the farm site ($r = 0.5$) (Fig. 2B). Directionality of lobster movements within the mussel farm site and over an equivalent distance in reference areas (≈ 700 m linear distance) post-tagging differed significantly (circular ANOVA: $F_{1,58} = 11.05$, $p = 0.0015$), but did not differ between reference and farm sites beyond the first 700 m (circular ANOVA: $F_{1,57} = 0.9923$, $p = 0.3234$). In addition, movement direction of lobsters inside the farm site changed once they moved beyond the farm site, heading mostly northeast (circular ANOVA: $F_{1,57} = 7.135$, $p = 0.0098$). The time that lobsters spent within the mussel farm, and in an equivalent habitat in reference sites, did not differ during the first 24 hr post-tagging period (ANOVA $F_{1,58} = 0.193$, $p = 0.662$).

In 2017, 38 lobsters (76%) left the study site during the 24 h acclimation period. Of these, 19 were tagged *in situ* and 19 'on boat'. Most lobsters tagged 'on boat' moved in the SE and NE directions ($r = 0.52$), whereas lobsters tagged *in situ* dispersed in more random directions post-release ($r = 0.32$) (Fig. 3)—a significant difference in movement orientation (Watson's $U^2 = 0.2628$, critical value = 0.187). Residence time and distance travelled did not differ between lobsters tagged *in situ* and 'on boat' during the acclimation period (Table 2). In contrast, tagging method affected walking speed (Table 2), which averaged (\pm SE) 3.21 ± 0.39 km d $^{-1}$ for lobsters tagged *in situ* and 5.90 ± 0.75 km d $^{-1}$ for those tagged 'on boat'. As described in Section 2.4, lobster size was initially evaluated as a covariate for lobster movement speed, although the effect was not significant and was removed from subsequent analyses.

3.2. Long-term (post-acclimation period) effects

During the post-acclimation period, no lobsters were detected by the acoustic arrays beyond 39

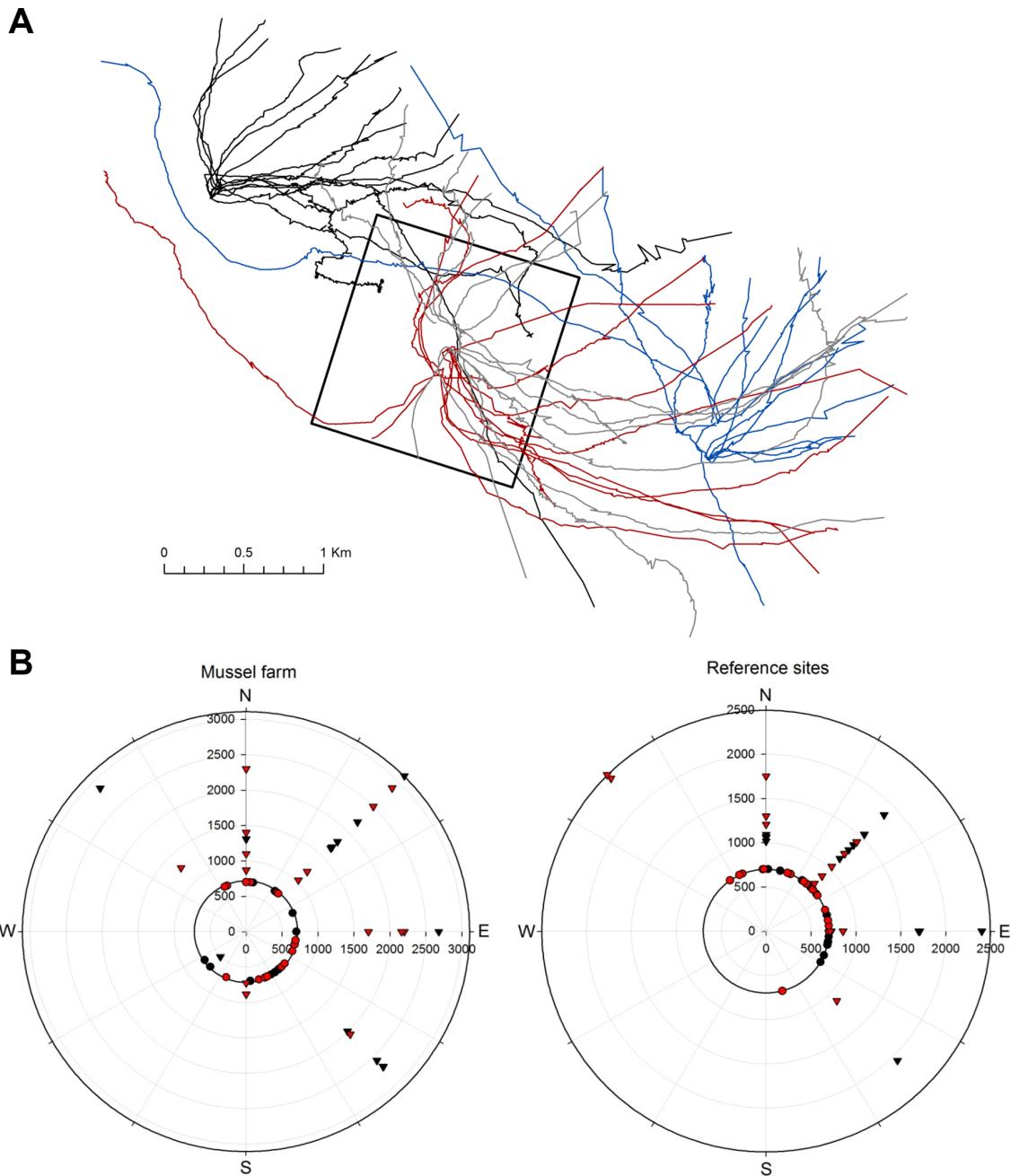


Fig. 2. (A) Raw movement data and (B) circular scatter diagrams representing the direction and distance traveled by 60 lobsters during the acclimation period (i.e. 24 h post-release) in the monitored area in 2014. (A) Movement tracks by lobsters collected from and returned to the east (black lines), west (blue lines), and farm (red lines) arrays; also depicted are lobsters collected from outside of the farm site but placed in the farm post-tagging (grey lines). (B) The inner circle (700 m radius) corresponds to the area covered by the mussel farm (and equivalent area in the reference sites), which is roughly equivalent to the distance between receiver arrays. Circles represent the direction of lobster movements within the farm (or equivalent reference sites) and triangles represent the direction of lobster movements outside of these sites. In reference area sites, black and red symbols represent lobsters in west and east reference sites, respectively. In the farm site, black and red symbols represent lobsters caught inside and outside of the mussel farm, respectively

and 51 d in 2014 and 2017, respectively (Fig. 4). Of the 16 lobsters detected during the post-acclimation period in 2014, 8 (7 M, 1 F) had been tagged and released in the western reference site and 1 (1 M) in the eastern reference site, 6 (4 M, 2 F) had been

captured and released in the farm, and 1 (1 F) had been captured outside the farm but released within the farm. Of these 16 lobsters, 10 (8 M, 2 F) displayed nomadic movements, 3 (2 M, 1 F) displayed residency movements (foraging behavior is charac-

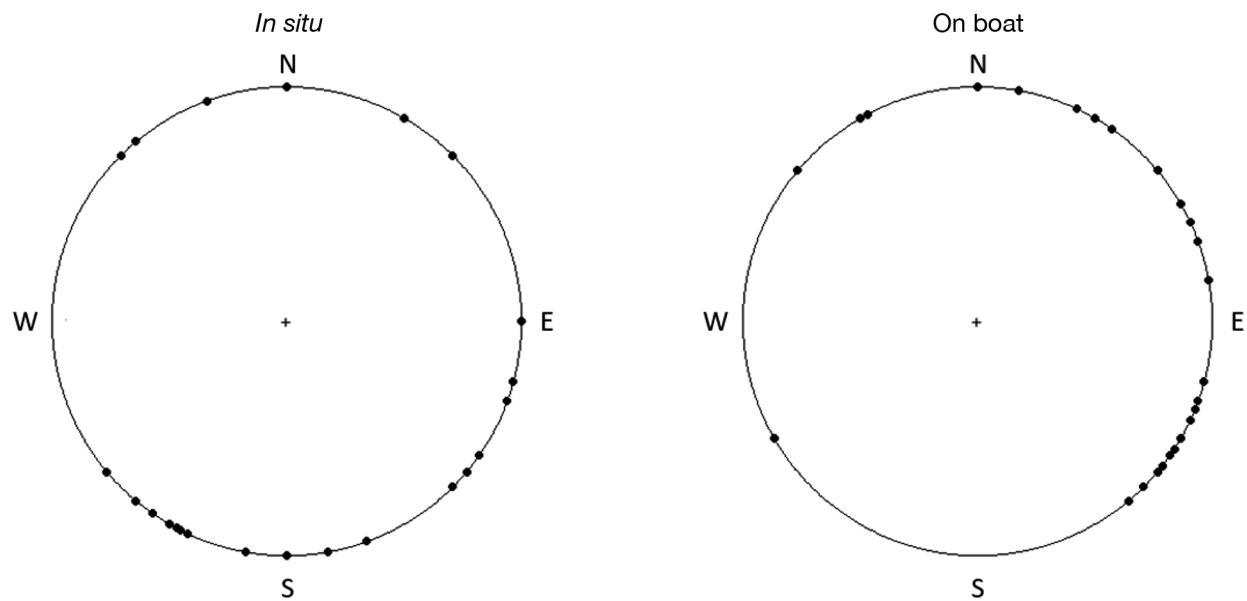


Fig. 3. Lobsters released at a center point and moving towards the edge of an acoustic array in 2017 according to tagging method. Dots represent individual lobsters (25 per tagging method) and their movement direction recorded 24 h following their release

Table 2. Results of PERMANOVA and ANOVAs evaluating the influence of 'tagging method' (*in situ* and 'on boat') and 'sex' on the lobster behavior during the 24 h acclimation period in 2017. Significant effects ($p < 0.05$) are highlighted in **bold**

Source	df	MS	F	p
PERMANOVA				
Residence time				
Tagging method	1	148.53	2.1392	0.1463
Sex	1	41.113	0.59215	0.4482
Tagging method \times sex	1	53.851	0.77561	0.3816
Error	46	69.43		
ANOVA				
Distance travelled				
Tagging method	1	0.0136	0.032	0.860
Sex	1	0.0039	0.009	0.925
Tagging method \times sex	1	0.1754	0.406	0.527
Error	46	0.4320		
Walking speed				
Tagging method	1	0.10151	8.294	0.006
Sex	1	0.00405	0.331	0.568
Tagging method \times sex	1	0.00772	0.630	0.431
Error	46	0.01224		

terized by shorter step lengths and large turn angles between steps; Turchin 1998), and 3 (2 M, 1 F) displayed both movement types (Fig. 5). In 2017, of the 17 lobsters detected during the post-acclimation period, 7 (5 M, 2 F) had been tagged *in situ* and 10 (4 M, 6 F) 'on boat'. Of these 17 lobsters, 14 (7 M and 7 F) displayed nomadic move-

ments, and 3 (2 M and 1 F) displayed nomadic and residency movements (Fig. 6).

The maximum distance travelled by an individual within the study area was 40.2 km (F, 90 mm CL) in 2014 and 30.6 km (F, 86 mm CL) in 2017. Cumulative residence times were relatively short, ranging from 0.33 to 11.90 d in 2014 and 1.18 to 29.68 d in 2017. On average, lobsters were detected by receivers in the mussel farm only 24 % of the total time that lobsters were detected in the entire study area in 2014. Average (\pm SE) walking speed was 5.66 ± 0.59 km d $^{-1}$ in 2014 and 3.91 ± 0.23 km d $^{-1}$ in 2017. Residence time, distance travelled, and walking speed did not vary between lobsters with respect to the factors 'site' and 'sex' in 2014 and 'tagging method' and 'sex' in 2017 (Tables 3 & 4, respectively).

4. DISCUSSION

Our results represent the first evaluation of the effect of longline mussel *Mytilus edulis* culture on lobster *Homarus americanus* movement behavior. Mussel culture seems to affect lobster movement directly after release; however, mussel culture had no significant effect on behavior post-acclimation. Both tagging methods likely affected lobster behavior, as indicated by most lobsters leaving the study sites within the first 24 h post-tagging. Neither size nor sex affected short- or long-term movement parameters.

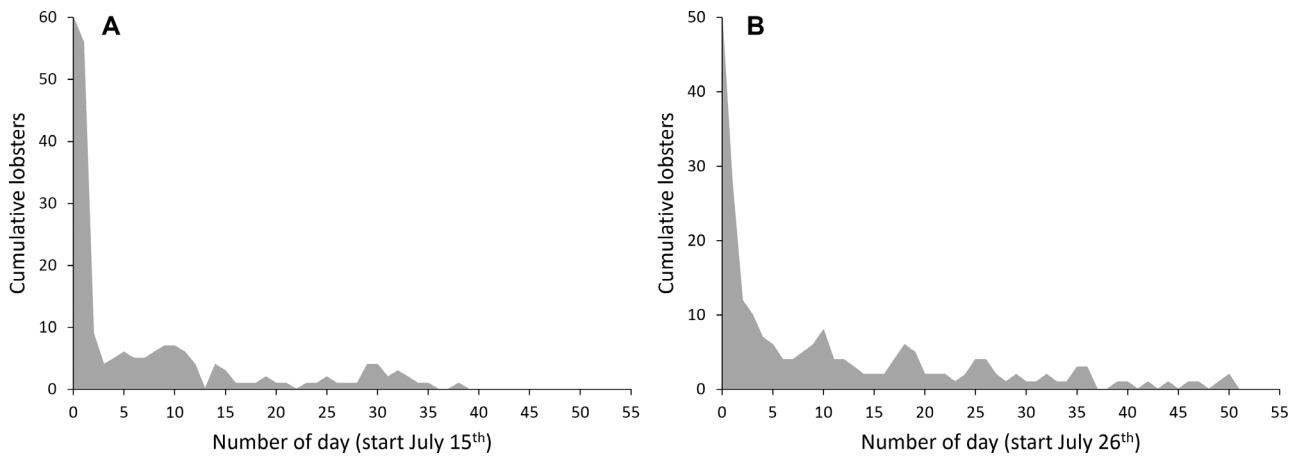


Fig. 4. Cumulative number of lobsters detected by the acoustic arrays during the 55 d following the start of the experiment in (A) 2014 and (B) 2017

4.1. Mussel farm—lobster interactions

Lobsters are commonly more abundant within mussel farms than in equivalent areas outside of farms (D'Amours et al. 2008, Drouin et al. 2015) and thus it was predicted that they would show some affinity to and remain within the farm, given the addition of appropriate food and shelter there (McKinsey et al. 2011). Contrary to our predictions, lobsters were not strongly associated to the habitat created by the off-shore longline mussel aquaculture site. In both years, most lobsters left the areas in which they were released immediately post-tagging, and this behavior may have been influenced by manipulations during tagging (Maynard & Robichaud 1986, Bowlby et al. 2007, Scopel et al. 2009, Moland et al. 2011, Skerritt et al. 2015, Lees et al. 2020). It also appears that the sandy benthic environment at the site caused their behavior there to be more nomadic than sedentary, suggesting that the study site was not a high-quality habitat for lobster. This is despite the observation of many lobsters being associated with farm-related structures (i.e. anchor blocks) in the site (Sean et al. 2022). Indeed, many authors have suggested that adult lobsters are more associated with hard, rather than soft-bottom, habitats (Lawton & Lavalli 1995, Tanaka & Chen 2015), and lobsters inhabiting rocky substrates typically show more sedentary behaviors than those observed in the present study (Tremblay et al. 2003, Goldstein & Watson 2015). Although lobsters may display considerable shelter fidelity with the same individuals being reported to inhabit a given shelter over extended periods (Cobb 1971, Ennis 1984, Karnofsky et al. 1989), such work has focused on mostly hard- or mixed-bottom locations. Post-tagging, lobsters may have either not found

their shelters upon being returned to the area they were caught in post-tagging or other lobsters could have taken over their shelters in the interim, perhaps explaining the animal's more randomly oriented movements until they left the farm site (there is commonly 1 or 2 lobsters associated with each anchor block in the farm site). Such movement behavior could be explained by intraspecific competition among lobsters, due to the relatively high density of lobsters inhabiting the mussel farm (O'Neill & Cobb 1979). Lobsters released in the mussel farm may have found that appropriate lodges were occupied by resident lobsters and thus kept travelling through the area. However, this is not true for lobsters tagged *in situ* in 2017, as they were tagged in their 'burrows'—commonly simple depressions dug by them into the sandy bottoms or below an aquaculture anchor block. These lobsters also mostly left the study area within a day, suggesting that their not re-finding their burrows was not the cause of their leaving the study area.

Lobsters are known to undertake seasonal migrations along the coast of Îles-de-la-Madeleine, with animals migrating onshore and into lagoons during the spring (May–June) and heading offshore in the fall (October) (Munro & Therriault 1983). This migration pattern supports the findings of Hardy et al. (2008) and Cooper & Uzmann (1971), who found that adult lobsters tend to move inshore in the summer, when coastal waters warm more rapidly than offshore waters, and then offshore in the fall, when coastal waters rapidly cool and fall storms arrive. In addition to lobsters preferring shallow waters during the summer, they are particularly abundant in rocky habitats during this season (Hardy et al. 2008). The bottom under the mussel farm in the study was

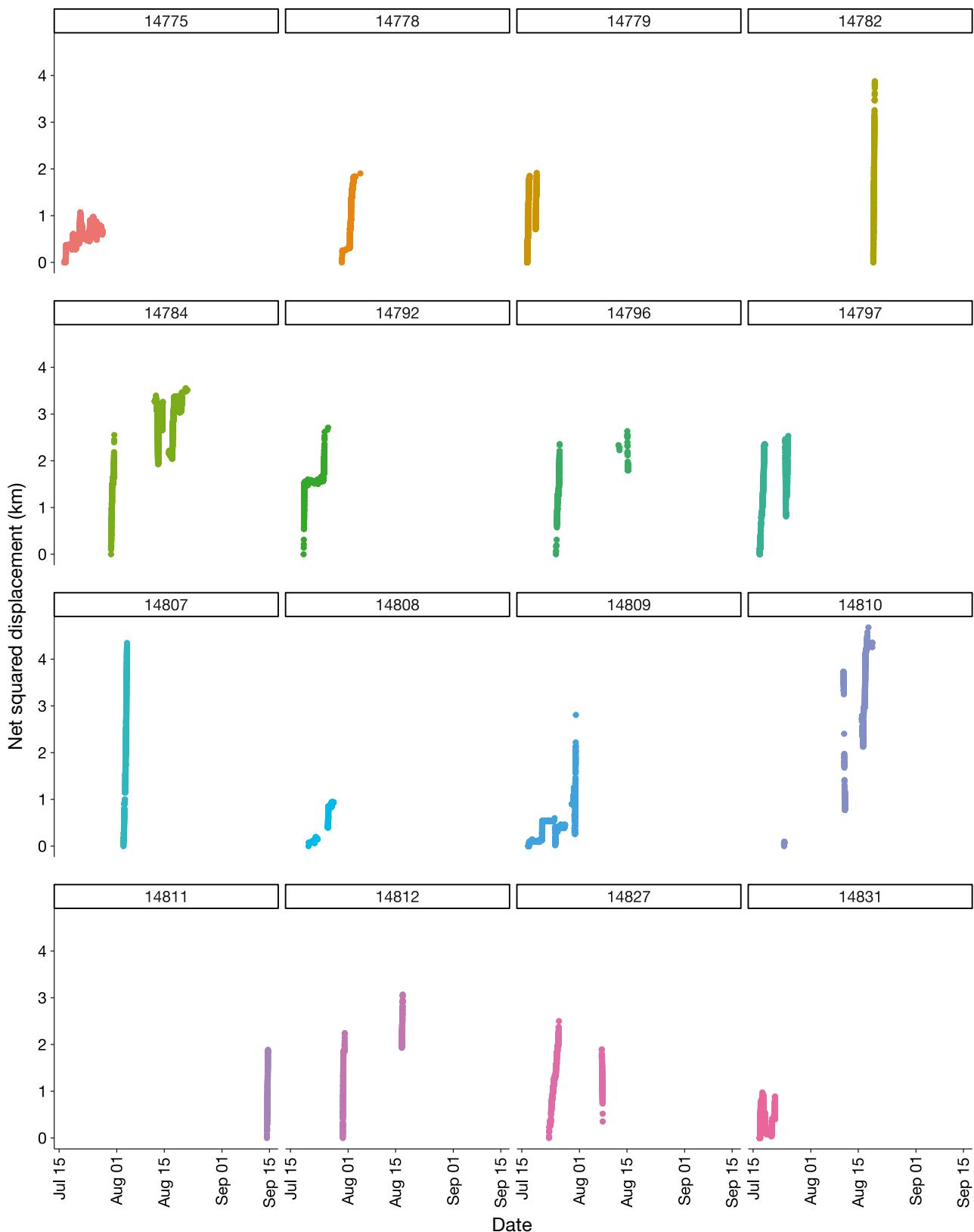


Fig. 5. Net squared displacement for each lobster that stayed or returned to acoustic arrays during post-acclimation in 2014 ($n = 16$). Numbers above each panel are individual lobster IDs

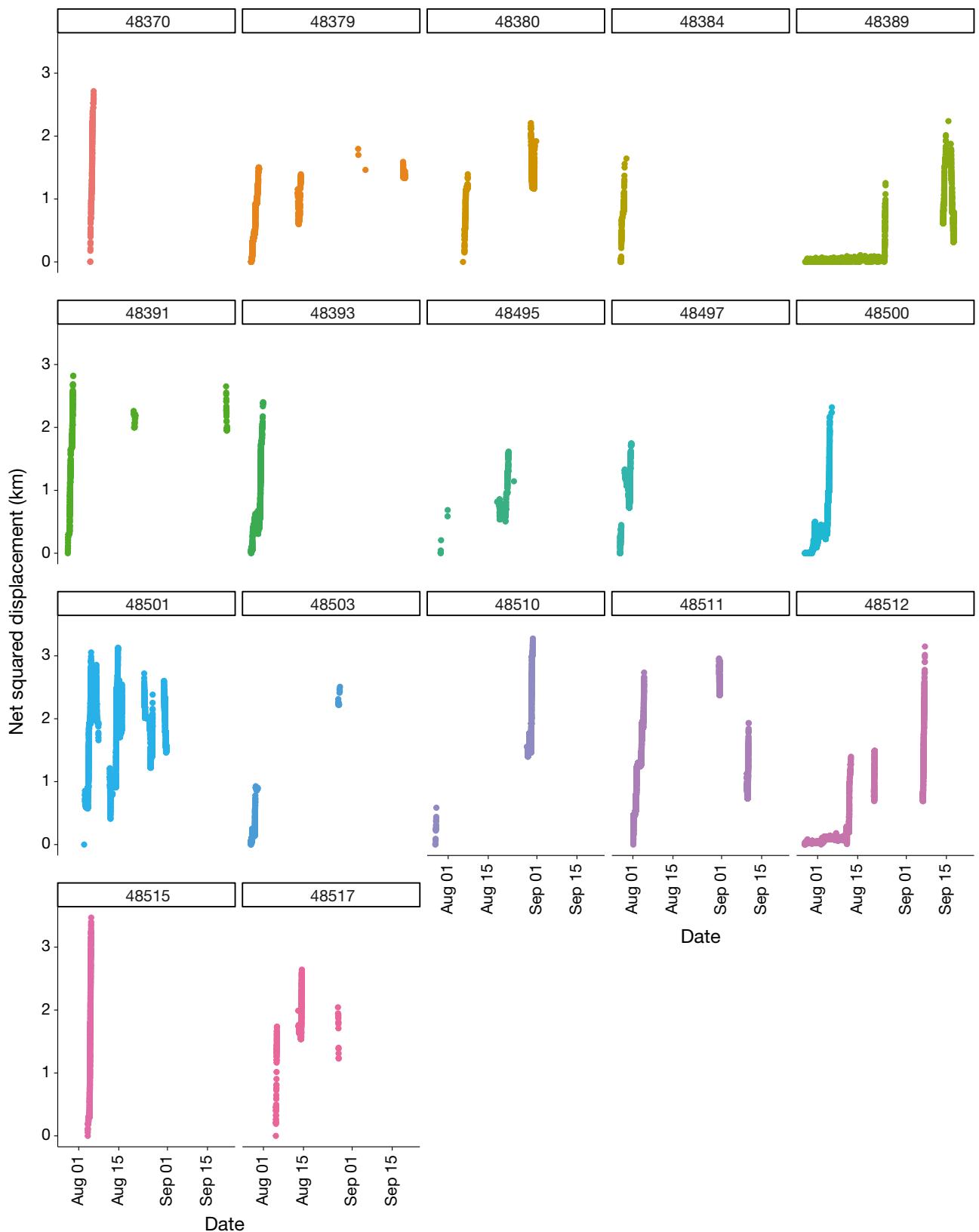


Fig. 6. Net squared displacement for each lobster that stayed or returned to acoustic array during post-acclimation in 2017 ($n = 17$). Numbers above each panel are individual lobster IDs

Table 3. Results of 2-way ANOVAs evaluating the effects of 'site' (west, east, resident farm, and introduced farm) and 'sex' on residence time, total distance travelled, and average walking speed during post-acclimation in 2014

Source	df	MS	F	p
Residence time				
Site	3	0.645	0.605	0.6266
Sex	1	0.348	0.327	0.5802
Site × sex	1	4.125	3.872	0.0774
Error	10	1.065		
Distance travelled				
Site	3	0.2232	0.472	0.7084
Sex	1	2.2885	4.842	0.0524
Site × sex	1	1.2885	2.726	0.1297
Error	10	0.4727		
Walking speed				
Site	3	0.2791	1.243	0.345
Sex	1	0.4381	1.951	0.193
Site × sex	1	0.4523	2.014	0.186
Error	10	0.2245		

mostly sandy and thus probably less attractive to lobsters during the summer. Seasonal, temperature-dependent, migrations along the coastline may thus account for the observed dispersal patterns of the lobsters that were released within the study area and suggests that other movement behaviors might occur at other times of the year. However, the generally northeast movement of tagged lobsters outside of the farm area relative to the more random directional movement of lobsters released within the farm site cannot be explained by such seasonal migrations. It is assumed that some factor or factors in the farm site at the time of release may have affected their movements. The main differences between the farm site and the reference sites include the provision of abundant physical structure in the form of anchor blocks and mussels that have fallen from lines (McKinsey et al. 2011) and the much greater abundance of potential lobster prey in the farm site, including common sea star *Asterias rubens*, rock crab *Cancer irroratus*, northern moon snail *Polinices heros*, and hermit crab *Pagurus pubescens* (Sean et al. 2022).

Whatever the factor responsible for this difference in movement behavior post-tagging, its impact seemed to be less important later in the summer. Lobsters returning to the farm or reference sites at that time displayed 2 types of movement: rapid excursions (nomadism), and small local movements that are associated with foraging behavior. Lobsters displayed nomadic movements within the study area over a variety of distances and time periods, only to change course and

Table 4. Results of 2-way ANOVAs evaluating the effects of 'tagging method' and 'sex' on residence time, total distance travelled, and average walking speed during post-acclimation in 2017

Source	df	MS	F	p
Residence time				
Tagging method	1	0.0132	0.013	0.913
Sex	1	0.1153	0.109	0.747
Tagging method × sex	1	0.0657	0.062	0.807
Error	13	1.0587		
Distance travelled				
Tagging method	1	0.2418	0.372	0.553
Sex	1	0.1778	0.273	0.610
Tagging method × sex	1	0.4003	0.615	0.447
Error	13	0.6505		
Walking speed				
Tagging method	1	0.03902	0.512	0.487
Sex	1	0.08554	1.122	0.309
Tagging method × sex	1	0.01096	0.144	0.711
Error	13	0.07628		

travel rectilinearly in another, seemingly random direction, as reported by Turchin (1998). American lobsters are known to periodically make long excursions to new areas, or 'neighborhoods,' and may stay in a given area for a week or so, and then move rapidly to another area a short distance away (Scopel et al. 2009). Some lobsters were observed to display foraging movement behavior (small steps, several turning angles). This behavior was not observed more frequently within the mussel farm than in reference sites, suggesting that the aquaculture site did not offer better feeding resources than do surrounding areas, notwithstanding the much greater abundance of potential food items within the farm relative to reference sites around it. However, small-scale modification of movement behavior may not be detectable using VPS analysis, given the precision of position locations (on the order of 4 and 30 m, depending on the year).

4.2. Tagging methods

Many methods have been used to tag and evaluate the movement of lobsters in past studies, each of which may influence post-manipulation behavior. As for many past studies (e.g. Tremblay et al. 2003, Wiig et al. 2013, Withy-Allen & Hovel 2013, Goldstein & Watson 2015), lobsters in 2014 were trapped/captured, tagged, and released by divers or from the surface in the same area they were caught. This general procedure may somehow impact lobster movement

behavior post-tagging, potentially involving extensive post-release movements (Scopel et al. 2009). Indeed, tagged lobsters in other studies have been returned to their habitat by placing them in disabled traps (artificial shelters) deployed on the seafloor so that the lobsters can leave the traps and return to their shelters in their preferred timeframe (Goldstein & Watson 2015).

In 2017, lobsters were acoustically tagged using one of 2 methods—one that could be considered quite stressful (cage capture, surface tagging, and on-bottom release following transport to the bottom from the surface in a plastic basket) vs. direct tagging *in situ* by SCUBA divers. Overall, both groups had similar movement behavior, quickly leaving the study site (notwithstanding a significant effect on walking speed, such that surface-tagged individuals moved more quickly than those tagged *in situ* in the post-acclimation period). Lobsters are known to undertake some movements at different speeds: e.g. local meandering vs. medium distance and rapid excursions (including longer migrations) (Watson et al. 1999). According to Watson et al. (1999), lobsters can easily travel at speeds of 1 to 4 km d⁻¹ during rapid excursions, even if local or slower movements are more typical. These authors compared walking speed with other studies and found that offshore lobsters seemed to move faster than inshore lobsters. In the present study, lobsters moved fast enough to indicate rapid excursions after both tagging methods. Although walking speed differed significantly with respect to tagging method, mean walking speeds observed during the acclimation period suggest that most lobsters were moving quickly.

Several studies have suggested that data from the first days of acoustic telemetry studies be removed from movement behavior analyses (Bowlby et al. 2007, Moland et al. 2011, Skerritt et al. 2016). Other factors may also influence post-manipulation lobster behavior, including the habitat type to which they are returned (i.e. substrate type, availability of shelter) and biological conditions (e.g. competition intensity, food availability, seasonal effects). Other lobster behavior studies have observed post-handling reactions of lobsters, which typically involve extensive post-release movements and lobsters appearing to move directly towards deeper water (see Scopel et al. 2009, keeping in mind that this work was done in a 3125 m² mesocosm). In the present study, lobsters tagged 'on boat' moved mostly northeast and southeast, with a higher walking speed during the acclimation period than the *in situ* lobsters, a movement behavior that would take them to deeper water.

4.3. Offshore mussel farm dynamics

A previous study done in Îles-de-la-Madeleine lagoons suggested that mussel aquaculture attracts American lobsters, as they are much more abundant within farms than outside of them (Drouin et al. 2015). It is also apparent that lobsters, particularly larger ones, consume fallen mussels, whereas the younger lobsters consume more rock crabs (Sardenne et al. 2019), both of which are more abundant within a farm site than outside it (Sean et al. 2022). Although farms in inshore and offshore locations provide similar habitat structures (in the form of cement anchor blocks) and enhance lobster prey availability, their effects on the bottom may differ via several mechanisms. Specifically, mussel lines were spaced 50 m apart in the offshore study farm, whereas line spacing is typically less than half that distance in inshore farms. For example, spacing between mussel longlines is 12 and 20 m in farms in Iles-de-la-Madeleine lagoons (Callier et al. 2007) and averages 12–13 m in farms in Prince Edward Island, Canada (Drapeau et al. 2006). Offshore aquaculture sites are also typically deeper than sites in protected embayments (e.g. 18–20 m in the studied farm vs. 5–8 m in the 2 afore mentioned locations) and typically have coarse sandy substrate, as opposed to muddy or sandy mud substrates in the lagoon and near-shore mussel farms. Likewise, mussel socks are about 10 m above the bottom in the offshore mussel farm evaluated in this study but are typically about 1 m or (commonly) less off the bottom in the aforementioned areas (C. W. McKinsey pers. obs.). In addition, given the wider spacing and relatively stronger hydrodynamic conditions in offshore sites, effects related to benthic loading on infaunal communities are less perceptible in more exposed offshore conditions (Drapeau et al. 2006, McKinsey et al. 2011, Wilding & Nickell 2013, Lacoste et al. 2018). Together, differences in farm structure configuration and depth may make offshore sites less attractive to lobsters than mussel farms in bays and lagoons.

4.4. Acoustic telemetry error sensitivity

By default, acoustic telemetry has associated inaccuracies, although newer methodologies are reducing these (Orrell & Hussey 2022). The error observed in this study varied considerably between years, with the 2014 data having a larger associated error than observed in 2017. Many factors may explain this difference. Data quality and quantity may be impacted

by environmental factors, such as noise and temperature, and the system properties, such as clock resolution and positioning method used (Melnychuk 2012). As the arrays were deployed by the same team and at the same time of the year in both years, the environmental conditions probably explain little of the variation in error between the years. A potential confounding factor may be that data from the 3 sites (the farm and the 2 reference sites) in 2014 were analyzed together, whereas there was a single array deployed in 2017 which was analyzed as such (Innovasea pers. comm.). Communication of receivers between the 3 sites may have been less efficient, perhaps impacting time synchronization and thus blurring tag position and increasing error sensitivity (Innovasea pers. comm.). Although positions in 2014 were less precise, patterns of lobster movement were clear enough to be analyzed and discussed in this study.

5. CONCLUSION

Mussel farming is generally considered to attract a variety of scavenging macrobenthic species, such as lobster, crabs, and sea stars. However, although previous studies have observed a greater abundance of lobster under mussel farms, the studied farm did not seem to attract or retain the lobsters. Indeed, other than short-term effects on lobster movement immediately following tagging, lobster movements in and around the study area seemed to be operating at a spatial scale larger than the farm site.

Acknowledgements. We are grateful to Frédéric Hartog, Olivia Lacasse, Kathleen MacGregor, Jean-Daniel Tourangeau-Larivière, Paul Robichaud, François Roy, and Anne-Sara Sean for help in project planning and field assistance. This study was supported by Fisheries and Oceans Canada (Aquaculture Collaborative Research and Development Program, project Q-13-01-00) in collaboration with Resources Aquatiques Québec (RAQ). We are grateful to the Ocean Tracking Network for the loan of some equipment. We also thank the mussel farmer, Christian Vigneau, from Les Cultures du Large, who kindly advised on the project and field work.

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Editorial responsibility: Pablo Sánchez Jerez,

Alicante, Spain

Reviewed by: G. I. van der Meer and 1 anonymous referee

Submitted: January 21, 2022

Accepted: May 27, 2022

Proofs received from author(s): July 15, 2022