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Movement of American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* around mussel farms in Malpeque Bay, Prince Edward Island, Canada

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ABSTRACT: A worldwide increase in aquaculture has focussed attention on the interactions between aquaculture activities and the surrounding habitats and ecosystems. In Atlantic Canada, mussel aquaculture occurs alongside static-gear fisheries for American lobster *Homarus americanus* and rock crab *Cancer irroratus*. Current knowledge gaps surround how lobsters and crabs utilise aquaculture sites and the potential impacts of this use on wild fisheries. During 2015 and 2016, at 3 mussel farms within Malpeque Bay, Prince Edward Island, Canada, a combination of diver surveys and acoustic telemetry positional arrays were used to investigate differences in the abundance of lobsters between farms and adjacent reference sites, the number and duration of lobster visits to a mussel farm, and the fine-scale movements of lobsters and crabs inside and outside of mussel farms. Although lobster abundance at mussel farms varied from June–September, abundance only differed between the farms and their associated reference sites in June. Disturbance due to handling may have led some lobsters in the acoustic telemetry study to leave the mussel farm after tagging; however, those that remained crossed the farm boundary frequently, and there was little evidence that the farm was a refuge for lobsters. Both lobsters and crabs appeared to move at significantly slower speeds inside the mussel farm, suggesting that both species used the mussel farms for foraging and/or sheltering; this was particularly evident for the rock crab. The results of this multi-approach field study are informative for spatial planning and provide important insight into how commercially and ecologically important species use aquaculture facilities.

KEY WORDS: Acoustic telemetry · Marine invertebrates · Aquaculture · Movement · Behaviour · Foraging

1. INTRODUCTION

Aquaculture production is increasing worldwide and today accounts for a greater proportion of the fisheries biomass destined for human consumption than traditional capture fisheries (FAO 2018). However, this growth has also led to concerns about the interactions of the industry with the natural environment (Barrett et al. 2019, Weitzman & Filgueira 2019) as well as other industries that occur in the same water bodies, particularly fisheries (Soto et al. 2008). In response to these concerns, the Ecosystem Approach to Aquaculture (Soto et al. 2008, Brugère et al. 2019) was developed to provide an integrative

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framework for the aquaculture sector, whereby aquaculture activities must adhere to local environmental and economic objectives. In eastern Canada, mussel aquaculture farms may overlap with lobster *Homarus americanus* and rock crab *Cancer irroratus* fisheries (~16 777 t of *H. americanus* and ~888 t of *C. irroratus* was landed in Prince Edward Island [PEI], Canada, in 2020; Department of Fisheries and Communities 2020). Ouellette et al. (2016) and Sonier et al. (2018) indicated that the lobster fishing industry has concerns about expansion of the mussel industry. Although concerns often focus on the potential for lobster larvae to be consumed by mussels while filter-feeding (e.g. Davenport et al. 2000, Gendron et al. 2003), fishers also express concern about the fished adult stages and mussel farms' potential effects on the animals' distributions (i.e. the possibility of the animals remaining within farms and thus not available to the fishery) and behaviour.

Mussel farming may have a considerable impact on the ecosystems in which it is carried out, including impacting the benthic environment in which lobsters and crabs are intimately associated (McKindsey et al. 2011). The addition of considerable physical structure in the form of anchors, and food in the form of fallen mussels and associated fauna from farm structures, create conditions that attract a large number of scavenging animals, including lobsters and crabs but also sea stars, predatory snails, etc. (Inglis & Gust 2003, D'Amours et al. 2008, Callier et al. 2018). Evidence of such aggregations within mussel farms throughout eastern Canada (Clynick et al. 2008, D'Amours et al. 2008, Drouin et al. 2015, Sean et al. 2022) suggests that lobsters and crabs may indeed remain within or closely associated with mussel farms, as both species likely find suitable shelter and significant trophic subsidies there. For example, McKindsey et al. (2011) calculated that up to 60 000 anchors — mostly cement blocks — may be deployed at any time in Tracadie Bay, close to Malpeque Bay, providing additional sheltering habitat for lobsters and crabs. Great quantities of mussels and associated fouling organisms may fall from farm structures to the bottom through self-thinning processes. For example, Comeau et al. (2015) estimated that 89% of seed mussels are lost due to fall-off over a 2 yr production cycle in PEI. In some areas, inputs due to fall-off may account for the greatest fraction of organic loading to the seafloor (Fréchette 2012) and attract a variety of predatory and scavenging species. Recent work has shown that as lobsters grow in farm areas, they switch from a diet dominated by crabs (Gendron et al. 2001) to one dominated by mussels (Sardenne et al. 2019). Similarly, rock crab diets are commonly composed of mussels in coastal areas (Drummond-Davis et al. 1982), and crabs commonly increase the proportion of mussels in their diets inside of mussel farm areas (Freire et al. 1990), although such a diet shift does not seem to impact crab metrics such as growth and moulting (Drolet et al. 2022). Together, these findings lend support to the idea that mussel farms may attract crustaceans, and as a result, alter their movements, foraging behaviour, and habitat use. A number of studies have shown that lobsters and crabs may modify their movements and behaviour based on benthic conditions (Richards 1992, Holsman et al. 2006, Skerritt et al. 2015, Tanaka & Chen 2016, Carloni & Watson 2018, Florko et al. 2021). Given the addition of benthic structure and foraging resources associated with mussel farms, it may be expected that lobsters and crabs alter their movements in areas below and surrounding farms.

However, little work has addressed how such changes may have bottom-up effects that impact fisheries species (but see Gibbs 2004, Byron et al. 2011, Barrett et al. 2022, Lavoie et al. 2022, Theuerkauf et al. 2022). Several authors have suggested that similar attractive devices may have negative consequences on fish and crustaceans, as the aggregation of fisheries species may lead to overfishing (Dagorn et al. 2013, Wilhelmsson & Langhamer 2014, Swearer et al. 2021). Indeed, in areas where lobster fishing overlaps with mussel farms, fishers often set up their cages immediately outside of farm sites. Work done elsewhere on lobster interactions with mussel farming (Lavoie et al. 2022) showed that the animals had little affinity to offshore mussel farms and did not alter their behaviour other than immediately following release. The impact of lobster and crab behaviour in coastal embayments, such as those in PEI, remains unstudied.

As part of a long-term research strategy to better understand the cascading effects of mussel culture on fisheries species, this study examined the spatial distribution (visual SCUBA surveys) and movement/behaviour (acoustic telemetry) of lobsters and rock crabs within and around mussel culture sites in Malpeque Bay, PEI, Canada, to evaluate their availability to the fishery. Specific objectives were to provide information on various lobsters and crab attributes in farm sites relative to non-farm sites regarding (1) population structure (i.e. size class and sex distributions), (2) movements and behaviours, and (3) the affinity of lobster and crabs to mussel farm sites.

2. MATERIALS AND METHODS

2.1. Study area

The study was done in Malpeque Bay, PEI, eastern Canada (46.5356° N, 63.8027° W) from 15 June to 28 September 2015, and 7 June to 8 September 2016 (Fig. 1). The bay is ca. 224 km^2 and characterised by shallow areas (mean depth: ~4.5 m) of low tidal amplitude (maximum: ca. 0.55 m). It is dominated by soft bottom areas, varying from mud to more compacted sediment with cobble. The bay is usually covered by ice from December to April, and water temperature may reach 26°C during the summer. Over the sampling period, about 7 % of the bay was leased for bivalve aquaculture (Filgueira et al. 2015), mainly blue mussels *Mytilus edulis* growing in suspended mesh socks attached to long lines. Fishing activity is concentrated across the mouth of the bay and in the middle of the bay between Marchwater (MW) and Richmond Bay (RB) farms. At-sea-sampling estimated catch-per-unit-effort (CPUE) of commercial-sized lobsters (>72 mm carapace length [CL]) in the immediate vicinity of the farms is between 500 and 1100 g per trap hauled (Ouellette et al. 2016).

2.2. Mussel farm transect surveys

Three mussel farms — MW (ca. 2.71 km^2), Bentick Cove (BC; ca. 0.20 km^2), and RB (ca. 0.10 km^2; Fig. 1) — were selected to assess the density and individual size structure of lobsters within farm areas and at surrounding reference areas (i.e. >300 m from mussel farms). MW is in the northeast area of the bay in a sub-basin with connectivity to the main water body through a narrow channel defined by small islands and shallow areas (Filgueira et al. 2015). BC and RB are within the main water body situated on the southwest and southern edge of the bay (Fig. 1). Lobster density and size structure were evaluated at each site on 3 occasions: 6–16 June, 8–14 July, and 24–26 September 2015 (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/q015p179_supp.pdf). At each of the 3 sites, demographic information was collected for lobsters along 5 transects (60 m long × 2 m wide = 120 m^2) by SCUBA divers inside the mussel farm and 5 others in adjacent reference habitat (>300 m from a lease boundary). In mussel farms, transects were placed perpendicular to mussel long lines, and all lobsters present along a transect were caught and placed in a collection bag and subsequently sexed, measured (CL), and counted while on board the dive boat. Lobsters were returned at the surface at their capture location after processing. Some lobsters observed along the transects could not be caught but were noted in the data as 'undetermined' (i.e. without sex and length data).

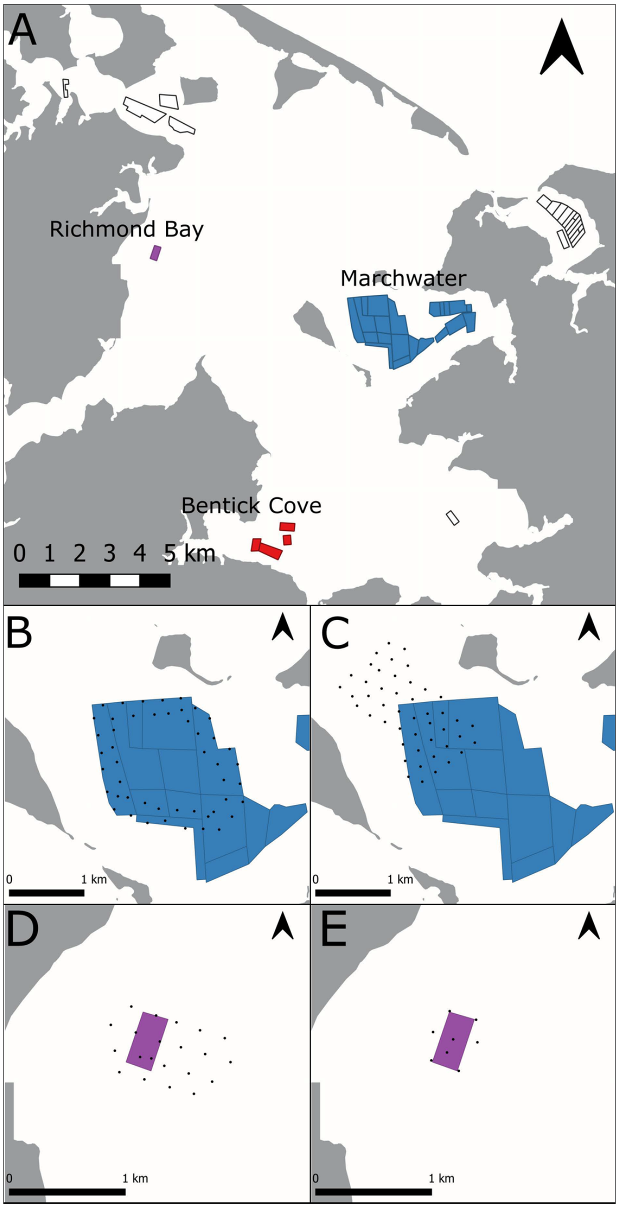

Fig. 1. (A) Location of the 3 study sites (BC: Bentick Cove, red polygon; RB: Richmond Bay, purple polygon; MW: Marchwater, blue polygon; additional mussel farms which were not included in the study, white polygons) in Malpeque Bay, Prince Edward Island, eastern Canada (46.5356° N, 63.8027° W) and (B–E) spatial arrangement of the receiver arrays. (B) Retention of lobsters within the MW mussel farm during the fishing season (n = 42) and (C) fine-scale movement of lobsters after the fishing season (n = 32). Fine-scale movement of (D) lobster after the fishing season at RB in 2015 (n = 30) and (E) rock crabs in 2016 (n = 20). Black dots: receivers

2.3. Acoustic telemetry design

2.3.1. Retention within the mussel farm during the fishing season

Three field experiments were undertaken at the MW (Fig. 1B,C) and RB (Fig. 1D,E) study sites. The first field experiment (Expt 1) quantified the time lobsters spent inside and outside the mussel farm at the MW site during the 2015 fishing season (15 June to 9 July 2015). A double gate of 45 receivers (VR2W — 69 kHz, Innovasea) was set up in MW, each separated by 250 m from its closest neighbour to ensure a detection probability of 0.8. The optimal distance between receivers was determined by a range test. The range test placed receivers and tags with a fixed transmission delay at increasing distances from each other. The frequency of detections logged by each receiver was modelled as a function of distance, and the resulting detection function was used to determine the appropriate distance between receivers using the VEMCO Range Test Software (VEMCO 2015). A double gate was used so that the position of the lobster, and thus its direction of travel through the gate, could be quantified. The gate was deployed around the edge of part of the mussel farm; the perimeter of the encircled study site was 6.19 km, delimiting an area of 2.65 km^2 (Fig. 1B). Due to a limited number of receivers, a small active area of mussel culture in the southeast area of the mussel farm was not encircled by the receiver gate (Fig. 1B). Each receiver was fixed to one end of a steel bar (T-shaped; length 1.8 m), with the other half buried in the sediment. This anchoring method minimised the addition of structure on the seabed, which is known to attract lobsters and may bias results (see Drouin et al. 2015). Receivers were moored using the same method for Expts 2 and 3 (Section 2.3.2).

Inside the mussel farm delimited zone, 42 intermoult, commercial-sized lobsters (≥72 mm CL) were caught by divers and brought back on the boat to be sexed, measured, and tagged with transmitters (V9; 69 kHz, Innovasea) with a 90 s nominal delay. All acoustic transmitters were attached to the carapace using LePage® Ultra Gel Control® Super Glue on a previously dried and sanded area that had been cleaned with an ethanol solution. Lobsters were kept onboard and sheltered from the sun until the glue was dry (≤15 min) and then released at the surface at the position where they were captured. Lobster movements were recorded for 23 or 24 d, i.e. from 15 June (14 lobsters) or 16 June (28 lobsters) until 9 July (first day of receiver removal).

2.3.2. Behaviour and habitat use inside and outside of the mussel farms

The objective of the second field experiment (Expt 2) was to investigate fine-scale lobster movement and habitat use during the 2015 post-fishing season; i.e. when no lobster traps were present in the bay (11 July through 28 September 2015) at both the MW and RB sites (Fig. 1C,D). At each site, receivers were deployed in a continuous array with a detection area of 2.07 km^2 in MW (47 receivers) and 0.92 km^2 in RB 2015 (20 receivers). Arrays covered either the entire mussel farm (RB) or a fraction of the farm (MW); in both cases, a similar area of adjacent benthic habitat was also covered. A total of 32 (mean ± SE: 64.3 ± 1.2 mm CL) and 30 lobsters (mean: 64.3 ± 1.0 mm CL) were tagged after the 2015 fishing season in MW and RB, respectively. Half of the lobsters were caught and released in the mussel farms and the other half in the non-farm adjacent habitats (Fig. 1C,D). Lobster tags had a nominal delay of 90 s and were attached using the same methods as Expt 1 (Section 2.3.1).

The purpose of the third field experiment (Expt 3) was to assess fine-scale crab movement and habitat associations at RB during the 2016 post-fishing season (7 June to 9 September 2016) using 7 receivers with a detection area of 0.72 km^2. As in 2015, the array covered both the mussel farm and the adjacent soft-bottom habitat (Fig. 1E). A total of 20 rock crabs (mean ± SE: 67.01 ± 5.6 mm carapace width) were caught inside the RB mussel farm and tagged using the same method and then released at the surface inside the mussel farm. Crab tags had a nominal delay of 60 s and were attached using the same methods as Expt 1 (Section 2.3.1).

2.4. Acoustic telemetry data pre-processing

In order to identify detections with high positional error, the relationship between 2 measures of horizontal position error, HPE and HPEm, was assessed for all 3 field experiments using linear regression (Coates et al. 2013, Skerritt et al. 2015). HPE is a relative measure of error sensitivity; as such, a calculated position with a high HPE provides less information on the position of an animal compared to a position with a lower HPE. HPEm is the measured error between a calculated position and its known location; e.g. a GPS position of a transmitter (for full definitions see Smith 2013). At MW and RB during 2015, <1% of all synchronisation tag data had an HPE value >30; in RB in 2016, <1% of HPE values were >38. Data were filtered to remove HPE > 30; in all cases, $r^2 > 0.95$. All lobster and crab data were subsequently filtered to HPE ≤ 30 prior to analysis, with the exception of the MW generalized estimating equation (GEE) analysis (see Section 2.5.3). The positional error in all field experiments was between 2 and 34 m (field Expt 1, MW: mean: 3.19 ± 0.01 m, n = 41 576; field Expt 2, MW: mean: 4.27 ± 0.03 m, n = 13 561, RB 2015: mean: 6.53 ± 0.02 m, n = 92 202; field Expt 3, RB 2016: mean: 3.08 ± 0.004 m, n = 254 395).

2.5. Data analysis

2.5.1. Spatial variation in abundance

Lobster abundance data from transects were converted to number of individuals per 100 m^2. Variation in lobster abundance inside and outside of the mussel farm was analysed using a 3-way ANOVA design (crossed factors) with the fixed factors 'site' (3 levels: BC, RB, and MW), 'habitat' (2 levels: mussel farm and reference), and 'month' (3 levels: June, July, and September). An additional 3-way ANOVA (crossed factors) was used to evaluate variation in size as a function of site, habitat, and month. Assumptions of normality (Shapiro test) and homoscedasticity (Levene's test) were assessed (Quinn & Keough 2002). Both abundance and size data violated normality assumptions, and abundance data was non-equal between groups; therefore, abundance and size data were $\log(x + 1)$ transformed prior to analysis. The sex ratio of lobsters was analysed using a generalized linear model with a binomial distribution and logit link function. The model included a 2-way interaction between site and habitat with month as a main effect; a 3-way interaction could not be fitted due to model singularity. Tukey's HSD was used to adjust for multiple comparisons.

2.5.2. Retention within the mussel farm during the fishing season

During the fishing season at MW, lobster retention inside the mussel farm perimeter was calculated in hours according to the time a lobster was detected on the inside or outside of the receiver gate. Firstly, a polygon of the gated mussel farm was created using the receiver locations. Lobsters were then identified as being inside the mussel perimeter if their detected position intersected the polygon; positions that did not intersect the polygon were used to confirm that the lobster had left the mussel farm. Both the number of entries and exits from the mussel farm and the length of time spent inside and outside as a proportion of the total tracked time were calculated; the direction of entry or exit was also identified. The time inside and outside the mussel perimeter was calculated each time a lobster crossed the perimeter while exiting or re-entering the mussel farm, and the time spent outside the mussel farm was defined as the time between the first detection on the outside of the mussel farm and the first detection upon re-entering the mussel farm. If the lobster did not cross the perimeter again, the time inside or outside was determined as the difference in time between the first and last detection. The number of lobsters inside the mussel farm in the days following tagging was calculated as the cumulative total number present per day; lobsters that were present for part of a day were counted, and lobsters that entered and exited the perimeter multiple times were only counted once per day. The dates that lobsters left the farm were compared to those of simulated random walks to identify if lobsters left the mussel farm early due to a potential disturbance effect. These simulated random tracks were created in the R library 'adehabitatLT' (Calenge 2006) using bivariate Brownian motion (i.e. a simulated lobster could move in any direction), and the scaling factor that controls dispersion was inferred using the observed step lengths of tagged lobsters as they crossed the perimeter ($h = 6$). Simulated tracks began at each of the observed release locations. Each time step was equivalent to 5 min, and trajectories were 153 d in length. This is longer than the 23 d of the observed tracks but was required to give the simulated lobsters adequate time to leave the mussel perimeter and avoid truncating the distribution of expected values. Using a null model approach, 999 replicate tracks were generated for each lobster by randomising the turn angle and step lengths of the simulated track. The observed exit date was then compared to the expected exit date via a permutation test.

2.5.3. Behaviour and habitat use inside and outside the mussel farm

Sheltering behaviour inside and outside the farm. Sheltering and burrowing under rocks and boulders is central to lobster behavioural and reproductive ecology (Cobb 1971). Likewise, rock crabs can also seek shelter under rocks and boulders to avoid predation, although they do not excavate burrows as is typical for lobsters (Fogarty 1976). If lobsters and crabs are sheltering amongst farm infrastructure, such as under concrete blocks, it may prevent a signal from an acoustic transmitter reaching a receiver, thereby creating gaps in data collection. By analysing these gaps in detection, it can be possible to identify if lobsters and crabs are sheltering under farm infrastructure. GEEs, using the R library 'geepack' (Halekoh et al. 2006), were used to model gaps in the detection of lobsters and crabs and investigate the presence of temporal and spatial patterns in detections. All data were included in the GEE analysis regardless of HPE so as not to create additional gaps in the data. However, the first 24 h of tracking data was excluded to minimise the impact of tagging on behaviour (Lavoie et al. 2022), and only lobsters that were tracked for at least 24 h were included in the analyses. Gaps in acoustic telemetry data can also arise when lobsters leave and then re-enter the acoustic telemetry array. To avoid including these large gaps in the analysis, lobster trajectories were first split into separate tracks if the time between detections was >12 h or if detections were >50 m apart; in addition, only detections that occurred within 150 m of the outside of the receiver array were included. Gaps in the detection data were then input at the mean transmission delays of the V9 acoustic tags used: 90 s resolution for lobsters and 60 s for crabs. These 'missed detection' inputs were coded as '1' while observed detections, i.e. real detections of lobsters and crabs, were coded as '0'. This vector of ones and zeros formed the response variable 'detection'. Model covariates were 'location', a 2-level factor identifying if an animal was inside or outside a mussel farm, 'time from high tide' as sine and cosine functions, and 'time of day', an integer from 0–23. Models had a binomial error structure with a logit link. Animal ID was included as a random effect, and observations were time-ordered within each ID. An autoregressive correlation structure was included. To make the analyses more tractable, lobster data (MW 2015 and RB 2015) were subsampled to 15 min resolution. There were considerably more crab detections (RB 2016), as fewer crabs left the receiver array and, as a result, data were subsampled to 60 min resolution. If a significant effect was found, the analysis was repeated using synchronisation tags to check that the effect was related to lobster or crab behaviour and not due to the detection performance of the acoustic receiver array. Gaps in synchronisation tag data were filled at 8 min intervals, the minimum sampling period for the synchronisation tag, and subsampled to 64 min.

Distribution and movement of lobsters and crabs inside and outside the mussel farm. Trajectories were cleaned (first 24 h removed) and separated as described in the GEE analysis. Data were then filtered to remove positions with HPE > 30 to eliminate locations with high positional error. Speed estimates were calculated as step length / time step. Using the R library 'raster' (Hijmans 2020), detections were aggregated to create 50 × 50 m geospatial grids (rasters) of the mean number, mean speed, and standard deviation of the speed per cell for both lobsters and crabs. The difference in density of crabs inside and outside the farm was not tested, as crabs were only released inside the receiver array whereas lobsters were released both inside and outside the farm. Rasters were then randomly sampled without replacement 999 times to create a distribution of mean values; cells could be drawn from inside or outside the mussel farm. The number of cells sampled to calculate the mean at each draw was equal to the number of cell values within the mussel farm so that the calculated means and standard deviations were comparable. These distributions were then compared to the mean observed values within the mussel farm via a 2-sided permutation test in the R library 'ade4' (Bougeard & Dray 2018).

3. RESULTS

3.1. Spatial variation in abundance

A total of 433 lobsters (173 females [F], 222 males [M], and 38 undetermined) were observed along transects in 2015. By combining data for the 3 sites and months, 232 lobsters (85 F, 120 M, and 27 undetermined) were observed under the mussel farms and 201 lobsters (88 F, 102 M, and 11 undetermined) were observed in corresponding reference areas (Fig. 2). Overall, fewer lobsters were observed in BC (n = 27 total) than in RB (n = 159) and MW (n = 247; Fig. 3), and lobster abundance varied significantly between study sites when data were aggregated; i.e. reference site and farm data combined for each sampling month (Table 1). Lobster abundances differed significantly as a function of the site × habitat and habitat × month 2-way interactions (Table 1). In June, the abundance at the RB mussel farm was significantly higher than in the reference area, but there were no differences between mussel farms and reference sites in July and September (Fig. 3).

The mean (±SE) CL of lobsters was 49.56 ± 0.86 mm for F (n = 173) and 50.79 ± 0.71 mm (n = 222) for M (excluding 38 that were not captured or sexed during

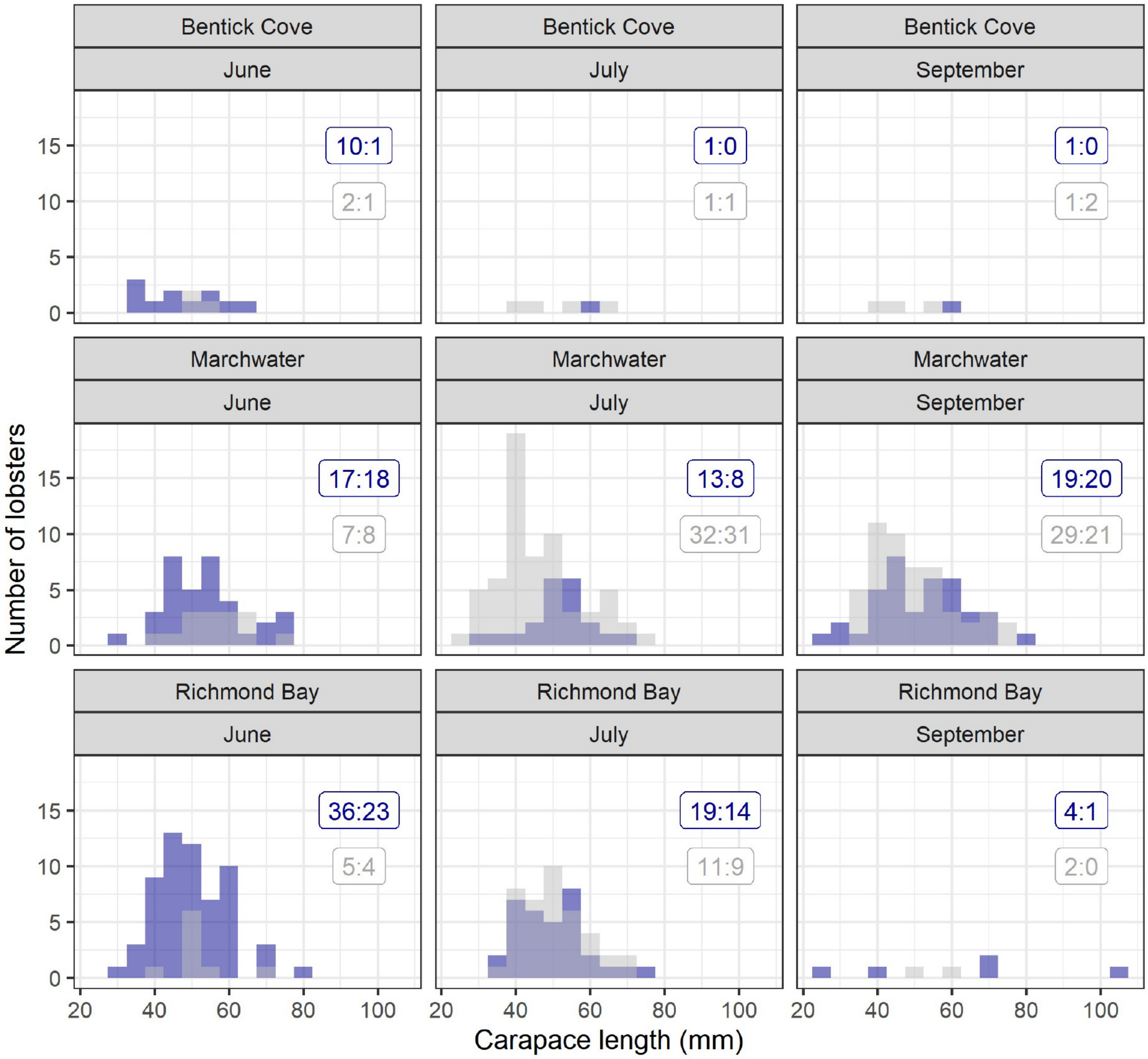

Fig. 2. Size–frequency distribution of lobsters in mussel farm (blue) and reference (grey) areas at Bentick Cove, Richmond Bay, and Marchwater, in June, July, and September. The sex ratio (males:females) is noted for mussel farm and reference areas at each site and sampling period

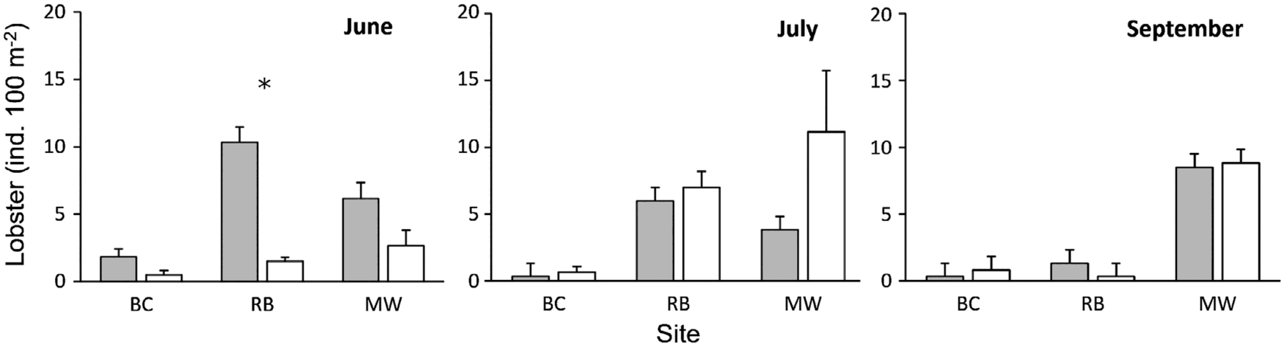

Fig. 3. Lobster abundance (mean ± SE) in mussel farm (grey) and reference (white) areas at each site (BC: Bentick Cove; RB: Richmond Bay; MW: Marchwater) during the 3 sample periods (June, July, and September 2015). Individual means were calculated per 100 m^2. Asterisk above the bar represents a significant difference between reference and mussel farm areas according to Tukey's HSD ($p < 0.05$)

Table 1. Results of 3-way ANOVA evaluating the effects of site (Bentick Cove, Richmond Bay, and Marchwater), habitat (mussel farm and reference areas), and month (June, July, and September) on lobster abundance. Significant effects ($p < 0.05$) are indicated in **bold**; subscripts = degrees of freedom

Source	MS	*F*	p
Site (S)	13.95	40.25_2	**<0.001**
Habitat (H)	0.82	2.36_1	0.129
Month (M)	1.21	3.49_2	**0.036**
S × H	0.82	2.36_2	0.102
S × M	2.82	8.13_4	**<0.001**
H × M	3.24	9.35_2	**<0.001**
S × H × M	0.17	0.49_4	0.746
Error	0.35		

transect sampling and 1 F that was not measured). Only 15 lobsters measured greater than 72 mm CL — the legal size for the fishery. None of the 2-way interactions for lobster size (site × zone, $F = 2.76_2$, p = 0.06; site × month, $F = 1.98_4$, p = 0.10; zone × month, $F = 1.95_2$, p = 0.14) or the 3-way interaction (site × zone × month, $F = 1.04_4$, p = 0.39) were significant. When interaction terms were removed, the main effects remained non-significant (all p > 0.09).

Sex ratios did not differ significantly between months (all p > 0.70), and no contrasts of interest for the 2-way interaction site × habitat were significant (Tukey's HSD; all p > 0.13); i.e. mussel farm vs. reference site at the same farm, mussel farms compared between sites, or reference sites compared between sites. The model was subsequently rerun without the site × habitat interaction term, but the main effects of site and habitat remained non-significant (all p > 0.10).

3.2. Retention within the mussel farm during the fishing season

There were 42 lobsters (10 F, 2 ovigerous females [F_{ov}], and 30 M) tagged and released at 14 locations within the mussel perimeter during the fishing season, and 2 lobsters were not detected by the receiver gate or by the receiver arrays deployed after the fishing season (1 F_{ov} and 1 M). The mean (±SE) CL of tagged lobsters was 77.16 ± 2.05 mm for the females and 78.56 ± 1.57 mm for the males. There were 41 805 detections; 0–11 517 per lobster (mean: 995.36 ± 298.74, n = 42). The 40 lobsters that were detected by the array were tracked between 0.03 and 23.7 d. All lobsters were initially detected inside the perimeter,

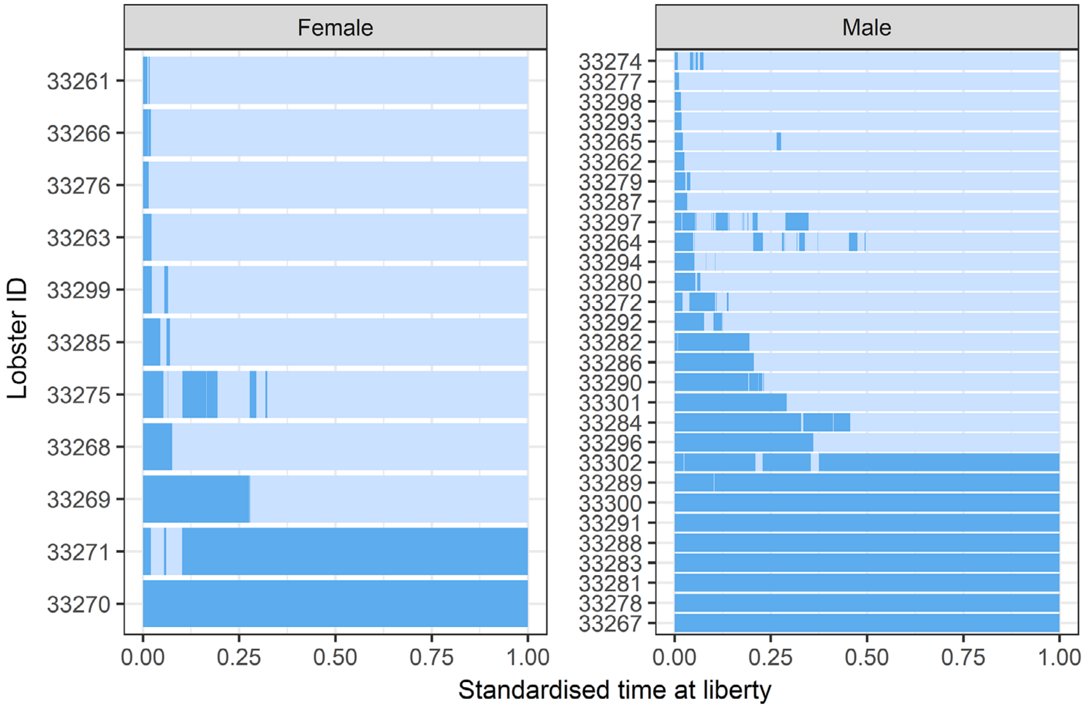

Fig. 4. Time spent inside and outside the mussel farm perimeter by male and female lobsters during the fishing season at Marchwater in June and July 2015 as a proportion of time from release until the removal of the receiver gate. Dark blue: inside mussel farm; light blue: outside mussel farm. Due to the scale of the graph, short periods spent inside or outside the farm may not be visible. Lobster ID corresponds to unique acoustic transmitter IDs

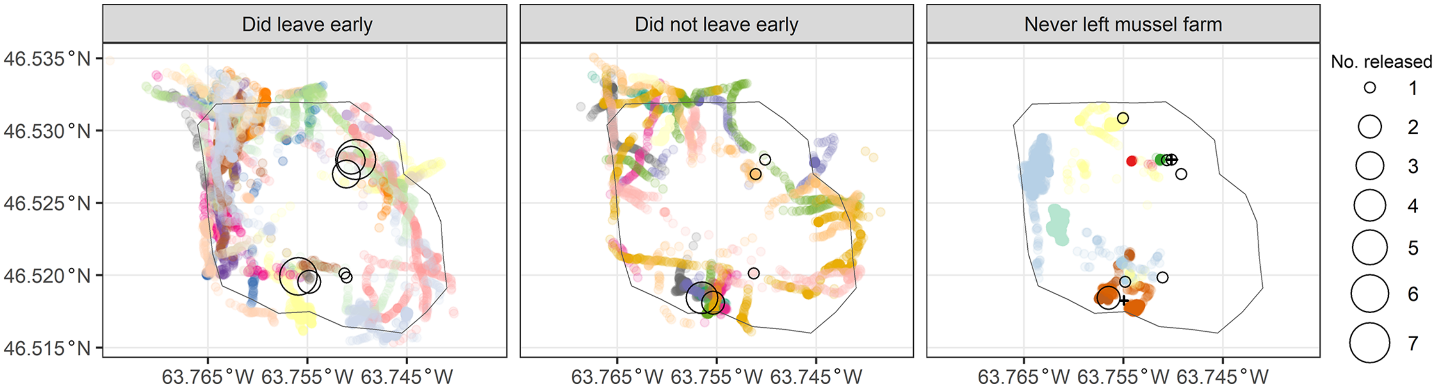

Fig. 5. Observed lobster movements across and within the Marchwater mussel farm receiver gate in 2015 (n = 42). The labels 'Did leave early' and 'Did not leave early' refer to the results of the permutation test to identify lobsters that left the farm earlier than would be expected under random movement ($p < 0.05$ and $p > 0.05$, respectively). The label 'Never left mussel farm' refers to lobsters that remained in the mussel farm for the duration of the study. Colours: individual lobsters; circles: release locations of lobsters that were detected by the receiver gate; crosses: release locations of lobsters that were not detected (n = 2)

except 1 lobster that was first detected on the outside. A total of 18 lobsters exited the mussel farm within the first 24 h post-tagging; 10 of these lobsters did not re-enter the mussel farm. The proportion of tagged lobsters present within the mussel farm decreased to 50% 5 d after tagging; 8 lobsters remained within the perimeter for the duration of the study (1 F and 7 M; Fig. 4). The majority of animals (n = 21, 7 F and 14 M) exited and re-entered the farm multiple times, crossing the perimeter between 3 and 130 times; 7 lobsters (2 F and 5 M) crossed the perimeter 9 times or more while apparently utilising habitat surrounding the perimeter edge (Fig. 4). The duration of visits ranged from 0.001–23.8 d inside the perimeter and from 0.001–23.3 d outside the mussel perimeter. Half of the tagged lobsters (n = 21) initially exited the mussel perimeter at its north-westerly edge (between 270 and 360°), 10 exited at its south-westerly edge (between 180 and 270°), 6 exited at the north-easterly edge (between 0 and 90°), and 2 exited at the south-easterly edge (between 90 and 180°; Fig. 5). During the study, only 2 male lobsters crossed the receiver gate into the active area of the mussel farm. Thirty lobsters subsequently re-entered the perimeter from the similar direction by which they left, 20 re-entered from the north-westerly edge, 6 from the south-westerly edge, 4 from the north-easterly edge, and 1 from a south-easterly edge; 1 lobster entered from a different direction.

Simulated tracks were created for the 32 lobsters that spent time inside and outside of the mussel farm. Lobsters were released at 8 different release locations (Fig. 5). Results of the permutation test identified 9 lobsters that did not exit the mussel farm earlier than would be expected under random movement ($p > 0.05$). Of these 9 lobsters, 6 were released at 2 locations close to the southern edge of the mussel farm; they were the only lobsters released at these locations and remained within the mussel farm between 0.23 and 6.30 d (Fig. 5). The 3 other lobsters were released at different locations at the northeast and southeast edge of the mussel farm and remained within the mussel farm between 4.58 and 8.60 d, which was on average 6.24 ± 0.07 d longer than lobsters that were released at the same locations but that left the mussel farm earlier than expected under random movement (Fig. 5).

3.3. Behaviour and habitat use inside and outside the mussel farm

3.3.1. Sheltering behaviour inside and outside the mussel farm

In MW (9 lobsters), there was a significant negative effect of location on the number of missed lobster detections ($\beta_{\text{Outside}} \pm \text{SE} = -0.741 \pm 0.296$, $p = 0.012$, $n = 3216$), suggesting that lobsters were more detectable outside farm areas. There was no significant effect of time from high tide on missed lobster detections ($p = 0.340$ and $p = 0.441$, sine and cosine respectively[1]), or on the time of day ($p = 0.696$). There was a small significant effect of the time of day on the number of missed receiver detections ($\beta \pm \text{SE} = 0.003 \pm 0.001$, $p = 0.019$,

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[1] It is the linear combination of the sine and cosine functions that produce a sine wave with a phase shift and scaled amplitude that models the periodicity; therefore, both functions have to be significant

n = 73 281), but there was no significant effect of location on the detectability of the receiver (p = 0.799) and no significant effect of time from high tide (p = 0.019 and p = 0.135, sine and cosine, respectively).

In RB 2015 (10 lobsters), there was no significant effect of location (p = 0.913, n = 1601), time from high tide (p = 0.884 and p = 0.402, sine and cosine, respectively), or time of day on the number of missed lobster detections (β ± SE = 0.023 ± 0.012, p = 0.891).

In RB 2016 (17 crabs; 3 crabs were not detected beyond 24 h), there were no significant effects of location (p = 0.660, n = 19 999), time from high tide (p = 0.320 and p = 0.0.380, sine and cosine, respectively), or time of day (p = 0.410) on the number of missing crab detections.

3.3.2. Distribution and movement of animals inside and outside the mussel farm

In July 2015, 31 of the 32 tagged lobsters were detected and tracked for 0.09–71.9 d in MW (mean ± SE: 8.1 ± 2.9 d; 1 M was released outside the farm but was not detected by the acoustic array after release). A total of 19 lobsters left the acoustic array within the first day and did not return. Thirteen lobsters (10 M, mean CL: 64 ± 1.50 mm; 3 F, mean CL: 60 ± 2.16 mm) remained or returned to the study site 24 h or more after tagging. After removing data from within 24 h post-tagging and detections with an HPE > 30, these 13 lobsters were detected 9–2460 times (mean: 678 ± 220). The direction of lobster movement was similar to that observed during the fishing season in MW, with the majority of lobsters exiting at the northwest corner of the mussel farm (Figs. 5 & 6A). Lobster movements within the mussel farm appear to indicate increased turning and small areas of concentrated detections, whereas movements outside the farm were more directional (Fig. S2). The lobsters moved slower and at more constant speeds inside the mussel farm than outside (p < 0.001 and p < 0.001; Table 2, Fig. 6D,G), but the density of lobsters inside and outside the mussel farm did not differ significantly (p = 0.053; Table 2, Fig. 6A).

In RB during 2015, 30 lobsters were tracked for 0.001–33.7 d (mean ± SE: 6.1 ± 1.8 d); one lobster was excluded as there were insufficient detections that met the processing criteria. After release, 7 of the 8 lobsters that were released inside the mussel farm were detected outside the mussel farm within first 24 h. Similarly, of the 22 lobsters that were released outside the mussel farm, 9 were detected inside the mussel farm within 24 h after release. Ten lobsters were present within the telemetry array 24 h after they were released (6 M, mean CL: 62.2 ± 2.55 mm; 4 F, mean CL: 66.2 ± 2.46 mm). After removing data gathered within 24 h of release and detections that had an HPE > 30, these remaining lobsters were tracked between 1.3 and 23.2 d (mean: 9.7 ± 2.2 d). The number of detections per lobster ranged from 117–3187 (mean: 635 ± 292). Lobster movement within the RB mussel farm was concentrated to the northwest, close to several release sites (Figs. 6B & S2). Lobsters moved at a significantly slower and more consistent speed inside the mussel farm compared to outside (p = 0.010 and p = 0.048; Table 2, Fig. 6E,H), but there was no significant difference between the density of lobsters inside the mussel farm and those outside the mussel farm (p = 0.896; Table 2, Fig. 6B).

Starting in June 2016, 20 crabs were tracked between 0.1 and 93.4 d (mean ± SE: 52.6 ± 9.3 d). Eighteen crabs remained within the study area 24 h after tagging (10 M, mean CW: 68.0 ± 1.89 mm; 8 F, mean CW: 64.6 ± 1.70 mm). After data that was gathered within the first 24 h after release and detections with HPE > 30 were removed, crabs were tracked for 0.2–92.4 d (mean: 57.3 ± 9.3 d). The number of detections per crab ranged from 19–40595 (mean: 14036 ±

Table 2. Permutation tests of the mean number of lobsters, and the mean speed of lobsters or crabs per 50 × 50 m. MW: March water; RB: Richmond Bay

Model	Study site and year	n	Observed	Expected	Variance	p
Mean number of lobsters 50 × 50 m	MW 2015	188	1.245	1.309	0.001	0.053
	RB 2015	57	1.491	1.504	0.007	0.896
Mean speed of lobsters or crabs per 50 × 50 m	MW 2015	182	0.059	0.068	<0.001	0.001
	RB 2015	57	0.073	0.091	<0.001	0.010
	RB 2016	69	0.015	0.027	<0.001	0.001
Standard deviation of the speed of lobsters or crabs per 50 × 50 m	MW 2015	163	0.013	0.018	<0.001	0.001
	RB 2015	54	0.015	0.025	<0.001	0.048
	RB 2016	69	0.010	0.018	<0.001	0.002

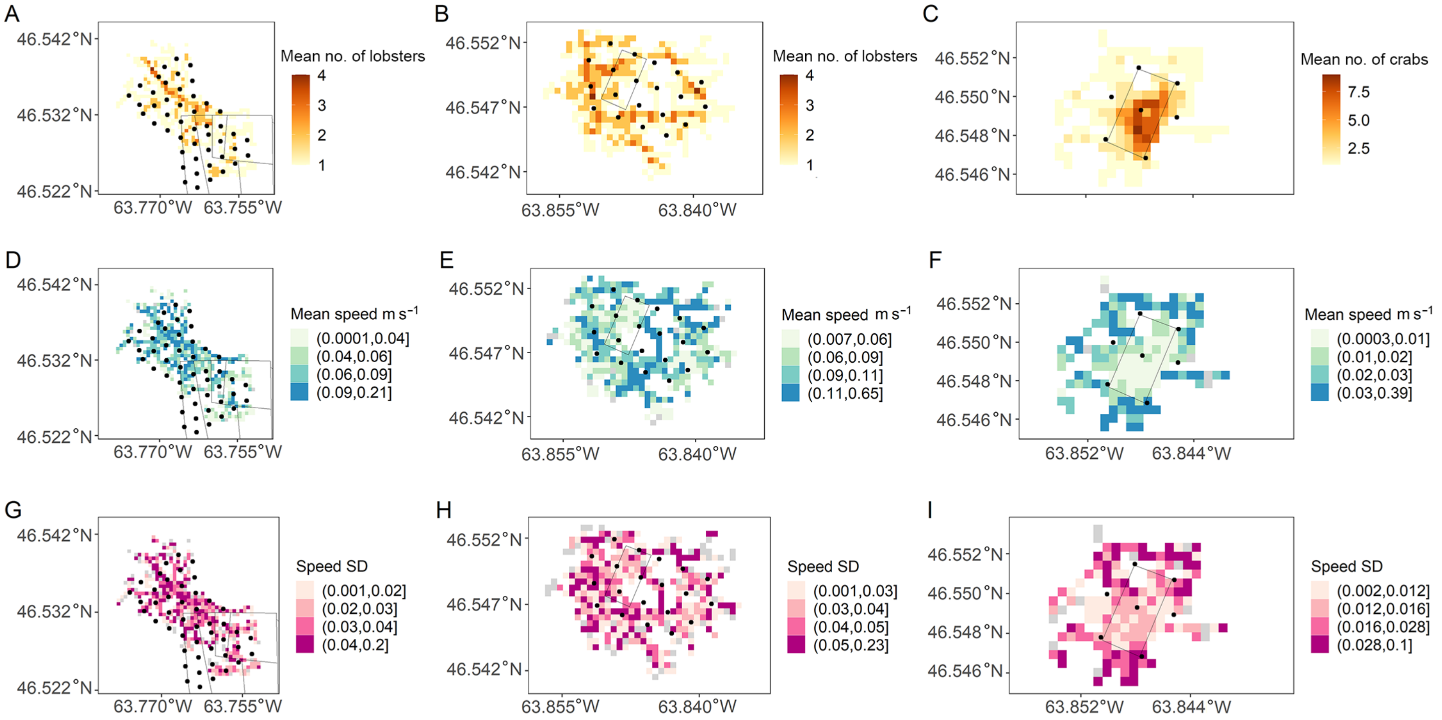

Fig. 6. Fine-scale acoustic tagging Expts 2 and 3 at (A,D,G) Marchwater 2015 (lobsters), (B,E,H) Richmond Bay 2015 (lobsters), and (C,F,I) Richmond Bay 2016 (crabs), showing (A–C) mean number of animals, (D–F) mean speed of animals, and (G–I) standard deviation of mean speeds. Raster grids: ~50 × 50 m; grey cells: NA. Black dots: receiver locations; black outlines: mussel farm boundaries

3331). Crab movements within the mussel farm were concentrated in small areas that were interconnected with more directional movement (Fig. 7). Crabs moved at a significantly slower and more constant speed inside the farm than outside ($p = 0.001$; Table 2, Fig. 6F,I).

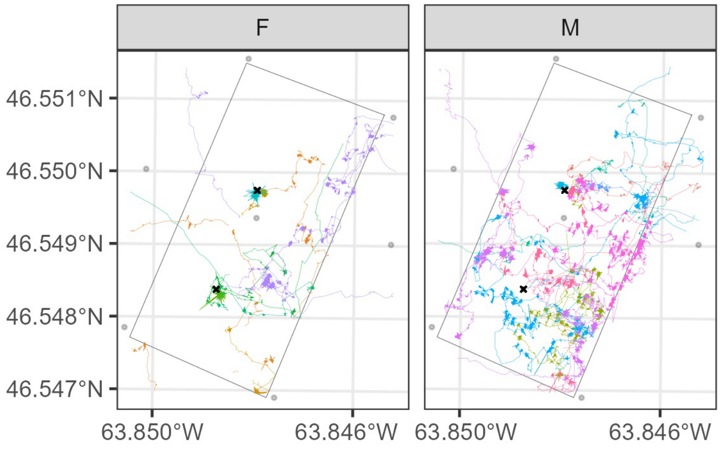

Fig. 7. Close-up of view of crab tracks in Richmond Bay in 2016 as part of Expt 3. F: female; M: male. Grey circles: acoustic telemetry receivers; grey outline: mussel farm perimeters; black crosses: release locations. Each colour represents a different individual

4. DISCUSSION

There was little evidence that mussel farms in this study act as refuges or ecological traps (Swearer et al. 2021) for lobsters during the fishing season. Although there was increased abundance at the RB mussel farm in June and July compared to September, acoustic telemetry at MW and RB during and after the fishing season indicated lobsters move frequently between mussel farms and the surrounding areas throughout the summer months. In 2016, there was a much clearer distinction in habitat use between inside and outside of the RB mussel farm for the tagged crabs, where the majority of crabs remained inside the mussel farm and were observed moving slowly while apparently foraging on fallen mussels and detritus directly under mussel socks. Although there was some indication of sheltering by lobsters at MW farm, there was no evidence of sheltering at the RB farm for lobsters or crabs, suggesting a site-specific effect and possible differences in site use between the species (e.g. Drouin et al. 2015)

4.1. Spatial variation in abundance

While there was some evidence of seasonal change in the abundance of lobsters at the RB mussel farm between summer and early fall, variation in abundance between farms and reference sites was only observed in June, when abundance was higher in the mussel farm. Lobsters are highly mobile, with mean daily movements of ~500 m (Scopel et al. 2008) and were therefore capable of moving between farms and from farms to adjacent reference sites during the project. Differences in abundance in macrofaunal communities have been detected between farms and surrounding areas at distances <50 m, with abundance typically highest directly under mussel lines (e.g. D'Amours et al. 2008, Drouin et al. 2015, Sean et al. 2022). However, distributions will likely differ among mussel farms in relation to the availability of surrounding favourable habitat. The substrate at RB was considered the most favourable for lobsters, with surrounding areas providing habitat for all life stages and size groups of lobsters as well as higher CPUE (Ouellette et al. 2016). RB was also the smallest of the 3 study sites, and it is possible that it attracted lobsters from a similar distance as the other farms, but due to its smaller size and proximity to harder substrate, resulted in a higher density of lobsters. In comparison, lobster abundance was lowest at BC in all months, potentially due to its slightly muddier substrate.

4.2. Retention within the mussel farm during the fishing season

The majority of lobsters left the mussel farm earlier than expected after their release within the MW mussel farm. A release location close to the boundary of the mussel farm may have resulted in 6 of the lobsters leaving. However, release location did not always influence the length of time lobsters remained in the mussel farm. A small number of lobsters released in the northeast and southeast parts of the site remained in the site longer than expected despite sharing their release location with lobsters that did leave early. The southeast corner of the mussel perimeter gate that neighboured additional mussel culture was not well utilised by the lobsters, with lobsters preferring to exit and re-enter the farm from the northwest corner where they could likely utilise a deeper channel (~7 m depth) to access mixed substrate in the centre of the bay (Filguerira et al. 2015). Lobsters crossed the farm perimeter multiple times during the study, and it is not clear whether this initial exiting of the mussel farm was due to disturbance from handling or due to lobsters routinely accessing resources outside the farm, such as rocky habitat, and then returning to forage within the mussel farm. Lobster traps are placed directly outside the farm areas in the hope of catching lobsters that are within the farm (Ouellette et al. 2016); therefore, during the fishing season, it is possible that lobsters are exiting the MW farm in the direction of the traps due to odour plumes emitting from outside the farm. However, this pattern of movement was also observed in the telemetry data after the fishing season, when no lobster traps were present (Fig. 6A), so it is probably more related to the bathymetry of the site than any attractant effect of the baited traps.

4.3. Behaviour and habitat use inside and outside the mussel farms

Lobsters tagged in MW after the 2015 fishing season were also significantly less detectable inside the mussel farm than outside. Although these gaps were not related to the time of day, they could indicate that lobsters were sheltering under the large amount of mussel farm infrastructure (D'Amours et al. 2008, Drouin et al. 2015); as there was no difference in the detection of synchronisation tags inside or outside of the mussel farm, this pattern in detection is more likely attributed to lobster behaviour. It should also be noted that no significant difference in detectability between the inside and outside of the farm was identified for either the lobsters or crabs in RB in 2015 and 2016, despite both spending time around and within farm structures. In addition, lobsters and crabs at both sites in 2015 and 2016 moved more slowly and at more constant speeds inside the mussel farms compared to outside. As lobsters are known to shift their diet towards mussels when in proximity to mussel farms (Sardenne et al. 2019), these slower movements could indicate foraging behaviour; restricted movement associated with foraging was particularly evident for crab tracks (Fig. 7). Therefore, it is unlikely that the difference in detectability in MW was simply due to lobsters passing between farm infrastructure while foraging, as a difference in detectability would also have been observed at RB in 2015 and 2016. A possible reason for the difference in detectability at MW could be that the substrate within and surrounding the farm is predominantly soft sediment; therefore, natural shelters are limited and thus farm structures are more likely to be utilised for lobster shelters. In RB, adjacent rocky habitat provides natural sheltering opportunities in addition to the farm structures, and therefore shelter availability did not differ inside compared to outside the farm. There was no significant difference in the density of tagged lobsters per 50 m^2 inside or outside the farm during 2015 in either MW or RB.

Mussels are a principal part of the coastal rock crab diet (Drummond-Davis et al. 1982), and crabs have been known to increase the proportion of mussels in their diet inside farmed areas (Freire et al. 1990), so it is perhaps not surprising that most crabs released within the farm remained there. Slower and more constant speeds within the mussel farm could indicate foraging movements. The spacing between the small clusters of crab detections within the mussel farm is similar to the spacing of the mussel long lines within the farm and likely results from the crabs' slow movement and repeated foraging on fallen mussel debris (Fig. 7). There is also a noticeable absence of crab detections in the northwestern corner of the farm in 2016. During this time there were no active mussel lines in that area and therefore no foraging opportunities to attract the crabs tagged in this study.

5. CONCLUSIONS

The global increase in aquaculture has created a large amount of seabed-associated infrastructure, which, depending on its location, can create shelter and provide habitat for *Homarus americanus*. In addition, falling mussels and associated fouling organisms from mussel lines provides increased scavenging opportunities for benthic consumers, potentially changing the distribution of mobile macro-invertebrates. Results from this multi-approach field study suggest that lobsters are indeed utilising the mussel farms within Malpeque Bay for foraging and sheltering and that they entered and exited the mussel farms frequently, sometimes multiple times a day. It is, therefore, unlikely that lobsters would remain in the farm and be unavailable to the fishery. Further work is required to understand how these additional foraging resources impact the catchability of lobsters when they exit the mussel farm and become available to the fishery. However, it did appear that scavenging crabs may be more likely to remain within the mussel farms, exploiting fallen mussels and associated organisms. These findings will inform spatial planning and fisheries management strategies where aquaculture and wild fisheries co-occur. While there was no conclusive short-term effect of mussel farms on the distribution of lobsters within Malpeque Bay during the summer months, the physical space attributed to aquaculture activities remains unavailable to the wild fishery. Future planning applications could consider the wider distribution and availability of habitat, particularly cobble habitat, relative to designated and proposed aquaculture facilities (Ouellette et al. 2016) to fully understand the possibility for changes in distribution and connectivity.

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LITERATURE CITED

Barrett LT, Swearer SE, Dempster T (2019) Impacts of marine and freshwater aquaculture on wildlife: a global meta-analysis. Rev Aquacult 11:1022–1044

Barrett LT, Theuerkauf SJ, Rose JM, Alleway HK and others (2022) Sustainable growth of non-fed aquaculture can generate valuable ecosystem benefits. Ecosyst Serv 53: 101396

Bougeard S, Dray S (2018) Supervised multiblock analysis in R with the ade4 package. J Stat Softw 86:1–17

Brugère C, Aguilar-Manjarrez J, Beveridge MCM, Soto D (2019) The Ecosystem Approach to Aquaculture 10 years on — a critical review and consideration of its future role in blue growth. Rev Aquacult 11:493–514

Byron C, Link J, Costa-Pierce B, Bengtson D (2011) Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modeling: Narragansett Bay, Rhode Island. Ecol Model 222:1743–1755

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Callier MD, Byron CJ, Bengtson DA, Cranford PJ and others (2018) Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. Rev Aquacult 10:924–949

Carloni JT, Watson WH (2018) Distribution of ovigerous American lobsters near the Isles of Shoals, New Hampshire. Bull Mar Sci 94:555–570

Clynick BG, Archambault P, McKindsey CW (2008) Distribution and productivity of fish and macroinvertebrates in aquaculture sites in the Magdalen islands (Québec, Canada). Aquaculture 283:203–210

Coates JH, Hovel KA, Butler JL, Klimley AP, Morgan SG (2013) Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. Mar Ecol Prog Ser 486:189–201

Cobb JS (1971) The shelter-related behavior of the lobster, *Homarus americanus.* Ecology 52:108–115

Comeau LA, Filgueira R, Guyondet T, Sonier R (2015) The impact of invasive tunicates on the demand for phytoplankton in longline mussel farms. Aquaculture 441: 95–105

D'Amours O, Archambault P, McKindsey CW, Johnson LE (2008) Local enhancement of epibenthic macrofauna by aquaculture activities. Mar Ecol Prog Ser 371:73–84

Dagorn L, Holland KN, Restrepo V, Moreno G (2013) Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? Fish Fish 14:391–415

Davenport J, Smith RJJW, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. Mar Ecol Prog Ser 198:131–137

Department of Fisheries and Communities (2020) Fishery statistics. https://www.princeedwardisland.ca/en/information/fisheries-and-communities/fishery-statistics (accessed 25 November 2022)

Drolet D, Riley C, Robert S, Estrada R, Gianasi BL, McKindsey CW (2022) Effect of aquaculture-related diets on the long-term performance and condition of the rock crab, *Cancer irroratus.* Front Mar Sci 9:865390

Drouin A, Archambault P, Clynick BG, Richer K, McKindsey CW (2015) Influence of mussel aquaculture on the distribution of vagile benthic macrofauna in Îles de la Madeleine, eastern Canada. Aquacult Environ Interact 6:175–183

Drummond-Davis NC, Mann KH, Pottle RA (1982) Some estimates of population density and feeding habits of the rock crab, *Cancer irroratus*, in a kelp bed in Nova Scotia. Can J Fish Aquat Sci 39:636–639

FAO (2018) The state of world fisheries and aquaculture 2018 — Meeting the sustainable development goals. FAO, Rome

Filgueira R, Guyondet T, Bacher C, Comeau L (2015) Informing marine spatial planning (MSP) with numerical modelling: a case-study on shellfish aquaculture in Malpeque Bay (Eastern Canada). Mar Pollut Bull 100: 200–216

Florko KRN, Davidson E, Lees R, Hammer KJ and others (2021) Tracking movements of decapod crustaceans: a review of a half-century of telemetry-based studies. Mar Ecol Prog Ser 679:219–239

Fogarty MJ (1976) Competition and resource partitioning in two species of *Cancer* (Crustacea, Brachyura). MSc thesis, University of Rhode Island, Kingston, RI

Fréchette M (2012) Self-thinning, biodeposits, and organic matter input to the bottom in mussel suspension culture. J Sea Res 67:10–20

Freire J, Fernández L, González-Gurriarán E (1990) Influence of mussel raft culture on the diet of *Liocarcinus arcuatus* (Leach) (Brachyura: Portunidae) in the Ría de Arousa (Galicia, NW Spain). J Shellfish Res 9:45–57

Gendron L, Fradette P, Godbout G (2001) The importance of rock crab (*Cancer irroratus*) for growth, condition and ovary development of adult American lobster (*Homarus americanus*). J Exp Mar Biol Ecol 262:221–241

Gendron L, Weise AM, Fréchette M, Ouellet P, McKindsey CW, Girard L (2003) Evaluation of the potential of cultured mussels (*Mytilus edulis*) to ingest stage I lobster (*Homarus americanus*) larvae. Can Ind Rep Fish Aquat Sci 274:1–20

Gibbs MT (2004) Interactions between bivalve shellfish farms and fishery resources. Aquaculture 240:267–296

Halekoh U, Højsgaard S, Yan J (2006) The R package geepack for generalized estimating equations. J Stat Softw 15:1–11

Hijmans RJ (2020) raster: geographic data analysis and modeling. R package version 3.4-5. https://CRAN.R-project.org/package=raster

Holsman KK, McDonald PS, Armstrong DA (2006) Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. Mar Ecol Prog Ser 308:183–195

Inglis GJ, Gust N (2003) Potential indirect effects of shellfish culture on the reproductive success of benthic predators. J Anim Ecol 40:1077–1089

Lavoie MF, Simard É, Drouin A, Archambault P, Comeau LA, McKindsey CW (2022) Movements of American lobster (*Homarus americanus*) associated with offshore mussel (*Mytilus edulis*) aquaculture. Aquacult Environ Interact 14:189–204

McKindsey CW, Archambault P, Callier MD, Olivier F (2011) Influence of suspended and off-bottom mussel culture on the sea bottom and benthic habitats: a review. Can J Zool 89:622–646

Ouellette M, Comeau M, LeBlanc A, Comeau B (2016) Characterization of the American lobster (*Homarus americanus*) habitat and fishery to inform marine spatial planning in Malpeque Bay, PEI. Can Sci Advis Sec Res Doc 2016/025

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Richards RA (1992) Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). J Exp Mar Biol Ecol 156: 187–197

Sardenne F, Forget N, McKindsey CW (2019) Contribution of mussel fall-off from aquaculture to wild lobster *Homarus americanus* diets. Mar Environ Res 149: 126–136

Scopel DA, Golet WJ, Watson WH III (2009) Home range dynamics of the American lobster, *Homarus americanus*. Mar Freshw Behav Physiol 42:63–80

Sean AS, Drouin A, Archambault P, McKindsey CW (2022) Influence of an offshore mussel aquaculture site on the distribution of epibenthic macrofauna in Îles de la Madeleine, eastern Canada. Front Mar Sci 9:859816

Skerritt DJ, Robertson PA, Mill AC, Polunin NVC, Fitzsimmons C (2015) Fine-scale movement, activity patterns and home-ranges of European lobster *Homarus gammarus.* Mar Ecol Prog Ser 536:203–219

Smith F (2013) Understanding HPE in the VEMCO positioning system (VPS). https://go.innovasea.com/understanding-hpe-vps.pdf

Sonier R, Filgueira R, Daoud D, Comeau LA (2018) Feeding pressure of *Mytilus edulis* and *Styela clava* on phytoplankton and zooplankton, including lobster larvae (stages I and IV). Can Tech Rep Fish Aquat Sci 3263:1–19

Soto D, Aguilar-Manjarrez JCB, Angel D, Bailey C and others (2008) Applying an ecosystem-based approach to aquaculture: principles, scales and some management measures. In: Soto D, Aguilar-Manjarrez J, Hishamunda N (eds) Building an ecosystem approach to aquaculture. FAO/Universitat De Les Illes Balears expert workshop, 7–11 May 2007, Palma De Mallorca. FAO Fisheries and Aquaculture Proceedings, Vol 14. FAO, Rome, p 15–35

Swearer SE, Morris RL, Barrett LT, Sievers M, Dempster T, Hale R (2021) An overview of ecological traps in marine ecosystems. Front Ecol Environ 19:234−242

Tanaka K, Chen Y (2016) Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. Fish Res 177:137−152

Theuerkauf SJ, Barrett LT, Alleway HK, Costa-Pierce BA, St. Gelais A, Jones RC (2022) Habitat value of bivalve shellfish and seaweed aquaculture for fish and invertebrates: pathways, synthesis and next steps. Rev Aquacult 14:54−72

VEMCO (2015) VEMCO range test software manual. https://go.innovasea.com/range_test_manual.pdf

Weitzman J, Filgueira R (2019) The evolution and application of carrying capacity in aquaculture: towards a research agenda. Rev Aquacult 12:1297−1322

Wilhelmsson D, Langhamer O (2014) The influence of fisheries exclusion and addition of hard substrata on fish and crustaceans. In: Shields MA, Payne AIL (eds) Marine renewable energy technology and environmental interactions. Springer Science + Business Media, Dordrecht, p 49−60

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