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Influence of mussel aquaculture on the distribution of vagile benthic macrofauna in îles de la Madeleine, eastern Canada

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ABSTRACT: We examined spatial variation in the abundance of 4 benthic vagile species in a lagoon with blue mussel *Mytilus edulis* aquaculture (inside vs. outside of the mussel lease; among areas with 1 yr old, 2 yr old and harvested mussels; and with distance from mussel lines). American lobster *Homarus americanus*, Atlantic rock crab *Cancer irroratus*, common starfish *Asterias rubens* and winter flounder *Pseudopleuronectes americanus* were all at least 3 times more abundant in the farm area with 2 yr old mussels, where mussel fall-off is more frequent, than in areas outside of the farm or other areas within the farm. A strong association of lobsters with mussel line structures was observed, where most individuals were observed directly under the mussel lines, close to anchor blocks, in the areas with 1 yr old, 2 yr old and harvested mussels (58, 42 and 57%, respectively). Mussel farms influence the distribution of benthic macrofauna at a number of spatial and temporal scales, and this may be due to a number of mechanisms, depending on the species. An *in situ* experiment was done to separate the influence of anchor blocks and mussel fall-off on the distribution of lobsters, crabs, starfish and flounders. Results of the manipulative experiment highlighted the importance of shelter structures over a short-term period for lobsters, but not for the other 3 species. Conclusions from the observations and the manipulative experiment suggest that lobster distribution is a function of both physical structure and feeding opportunities, whereas the distribution of the other species was mainly due to trophic effects.

KEY WORDS: *Mytilus edulis* · *Homarus americanus* · *Cancer irroratus* · *Asterias rubens* · *Pseudopleuronectes americanus* · Spatial variation · Environmental impact

INTRODUCTION

Bivalve aquaculture is known to influence the benthic environment within—and in the areas immediately surrounding—farm areas, with impacts on benthic habitats largely attributed to the accumulation of organic matter related to bivalve filter-feeding and waste production. Biodeposition (mainly from faeces and pseudo-faeces from the farmed bivalves and associated species) generates enrichment responses on sediment biogeochemistry and infaunal assemblages as described by the organic enrichment response model of Pearson & Rosenberg (1978). Studies have also shown indirect physical effects of bivalve culture, whereby hydrodynamic alterations brought about by aquaculture structures may alter sediment dynamics and thus associated benthic communities (e.g. Ottman & Sornin 1985, Cayocca et al. 2008, Forrest et al. 2009, Grant et al. 2012). Although bivalve culture may also affect larger and more vagile macrofauna, comparatively few studies have documented these patterns and the mechanisms behind them.

Studies on larger and more mobile macrofauna species have observed that scavengers and other preda-

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tors (crabs, starfish, and gastropods) are more abundant in aquaculture areas (Romero et al. 1982, Inglis & Gust 2003, D′Amours et al. 2008, Wilding & Nickell 2013) or found no difference in macrofauna community structure between farmed and unfarmed areas (Chesney & Iglesias 1979, Clynick et al. 2007). Simple trophic mechanisms, whereby scavenging species are seen associated with fallen farmed bivalves, are usually invoked to explain the observed patterns of greater abundance in farm areas relative to non-farm areas. Indeed, in some cases fall-off of farmed mussels may represent the greatest input of organic matter to the seabed (Fréchette 2012), a habitat in which such a food source is not generally found (i.e. compared to adjacent soft bottom habitats). The existence of a trophic mechanism is also supported by the studies by Freire et al. (1990) and Freire & González-Gurriarán (1995), who showed that crabs in mussel culture areas increase the proportion of mussels in their diets relative to that of crabs in areas outside of mussel farms. A trophic mechanism also supports observations of variation in the distribution of macrofauna within farms. Mussel fall-off is concentrated directly below mussel lines, where starfish and other vagile macrofauna were observed to be more abundant than in areas between mussel lines (D′Amours et al. 2008, Wilding & Nickell 2013). Such mussel line-scale variation in the distribution of macrofauna could explain why some studies failed to observe spatial patterns in the abundance of vagile macrofauna. For example, Clynick et al. (2008) found no consistent effect of longline mussel culture on the abundance of vagile macroinvertebrates and fishes, but their sampling method (small beam trawl sampling parallel to longlines) could not have sampled those organisms that lived closer to or directly below mussel longlines. Given that mussel fall-off has been shown to increase with increasing size of mussels (Léonard 2004, Fréchette 2012), it may be predicted that the abundance of scavengers and other predators may be greatest in areas with older mussels, creating farm-scale variation in the abundance of macrofauna. Indeed, Inglis & Gust (2003) have reported such variation for the abundance of starfish among farm areas in New Zealand.

A neglected effect of off-bottom and suspended bivalve culture is how the introduction of a large amount of physical structure (ropes and anchor blocks) affects benthic communities by modifying habitat characteristics, such as physical complexity, currents, sediment dynamics (accretion and scouring) and sedimentation rates (McKindsey et al. 2011). Bivalve farming typically occurs in, on, or above unvegetated soft-bottom habitats, and adding physical structures creates novel, and more structurally complex, types of habitat that may provide shelter to species that would not ordinarily be present. This is evident for species that require hard surfaces to settle and grow upon but may also be true for vagile thigmophilic and sciaphilic species. Casual observation (authors' pers. obs.) suggests that lobsters *Homarus americanus* in different areas in eastern Canada are more abundant in suspended mussel culture areas than in otherwise similar areas outside of mussel farms, often congregating under anchor blocks within farms. Food enhancement (i.e. mussel fall-off from culture structures) may account for this pattern, but the provision of habitat structure (i.e. anchor blocks) may also directly influence their distribution.

We investigated the influence of suspended blue mussel *Mytilus edulis* aquaculture on fish and vagile macroinvertebrates and the mechanisms that determine their distribution within an aquaculture area. Specifically, 3 hypotheses were tested using observational studies: (1) macrofauna is more abundant in mussel farms relative to areas outside of mussel farms (bay-scale variation); (2) the abundance of macrofauna varies within mussel farms, such that areas of different stages in the farm husbandry cycle have different abundances of macrofauna, with areas with the largest mussels having the greatest abundance of macrofauna (farm-scale variation); and (3) macrofauna display small-scale variation in abundance such that they are most abundant close to mussel longlines and anchor blocks (line-scale variation). In addition, we conducted a manipulative field experiment to determine the mechanism (food or shelter) that brings about the observation that vagile macrofauna are more abundant in mussel areas than reference areas by adding mussels and/or blocks in field areas at rates similar to those observed in an operating farm.

MATERIALS AND METHODS

Study location

The mussel farm studied, which is in Grande-Entrée Lagoon (47° 37′ N, 61° 31′ W) in the north-eastern portion of îles de la Madeleine, Quebec, Canada (Fig. 1), has been in operation since 1982 and produces about 180 t of mussels annually (Callier et al. 2007). The shallow boundaries of the lagoon are dominated by eelgrass, while the deeper area where the mussel farm is located (5 to 7 m) is characterised

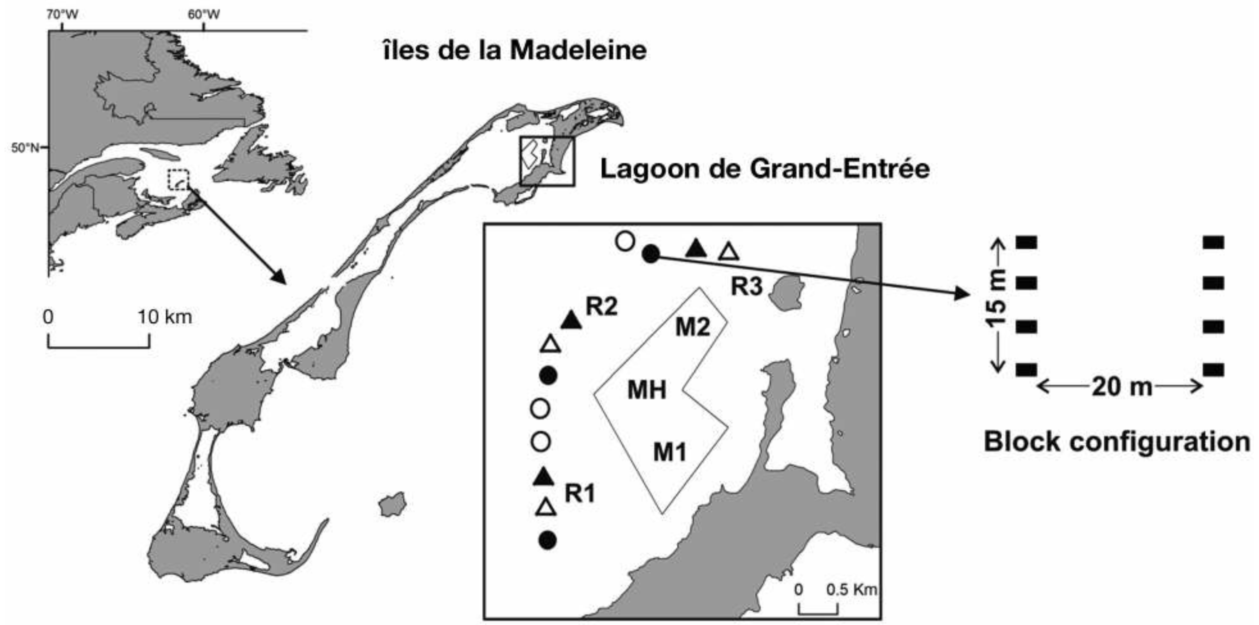

Fig. 1. Location of the blue mussel *Mytilus edulis* farm (polygon) in lagune de Grand-Entrée, îles de la Madeleine, eastern Canada. The location of reference areas (R1, R2, R3), areas with 1 yr old mussels (M1), 2 yr old mussels (M2), and where mussels were harvested (MH) in the observational part of the study are indicated within and around the mussel farm. Circles and triangles indicate the 12 sample sites used for the experimental part of the study. Black circles refer to sites with blocks, white circles to sites with blocks and mussels, black triangles to sites with mussels and white triangles to reference sites (neither blocks nor mussels). The block configuration within experimental sites where they were involved is illustrated with black rectangles as concrete blocks

by a sandy substrate. This region is characterised by low tidal amplitude (0.60 m). Water temperature can exceed 20°C in summer and decrease below 0°C during the winter (December to April). The mussel lease covers an area of approximately 2.5 km^2, where mussels are cultured on longlines (spaced at 20 m) in a 2 yr grow-out cycle. Mussel lines are typically suspended between ca. 2 m from the surface and the bottom.

Observational sampling strategy

Variation in the abundance of vagile macroinvertebrates and benthic fish inside and outside the aquaculture lease was evaluated between 30 July and 2 August 2006. Sampling was done in each of 3 reference (R1, R2, R3) areas, each about 0.25 km^2, located outside the mussel farm (>500 m) and 3 areas of the same size inside the mussel farm (bay-scale variation). This sampling strategy included all parts of the deep basin within the lagoon. In each of these 6 areas, fauna was visually counted by SCUBA divers along 4 transects (each 100 m long) that were placed perpendicular to the mussel lines in mussel areas using a 2 m pole to delimit the survey to 1 m either side of the transect, as described by D'Amours et al. (2008). As each area inside the mussel farm represented a given stage of the mussel culture cycle, farm-scale variation was evaluated by comparing abundances noted along the 4 visual transects in each farm area (Fig. 1: M1: lines with 1 yr old mussels, M2: lines with 2 yr old mussels and MH: harvested lines). Within farm areas, line-scale variation in lobster abundance was evaluated by noting the position of each lobster observed along transects relative to mussel lines (by noting the position of each along a measuring tape that served as the transect).

Manipulative experiment to isolate responsible mechanism(s)

A manipulative experiment was conducted from 16 June to 23 July 2007, to evaluate the relative importance of physical habitat (cement blocks, used as compensation weights to anchor the longline legs to the bottom) and feeding opportunities (mussels) to the pattern of abundance of macrofauna within the mussel farm. Replicate setups of the resulting 4 orthogonal treatments were randomly distributed within 12 sites around the mussel farm (i.e. 3 replicates for each treatment): (1) blocks (Blo), (2) mussels (Mu), (3) blocks and mussels (BloMu) and (4) reference (Ref). All sites were characterised by a similar sandy bottom and depth (6 m), and were separated by at least 300 m. Treatments with blocks (Blo and BloMu) consisted of 8 concrete blocks (0.3 × 0.3 × 0.3 m) placed every 5 m along 2 parallel axes 20 m apart to mimic the same pattern observed in the culture areas (Fig. 1). Treatments with supplemented mussels (Mu and BloMu) had mussels added at a rate of 3.4 kg of mussels every 3 d, a rate equivalent to that observed from natural fall-off under mussel lines with 2 yr old mussels in a mussel farm in a neighbouring lagoon in îles de la Madeleine (Léonard 2004), using the same configuration. Reference sites were simply identified by a buoy. All sites were sampled 2 times before and 3 times after setting up the experiment. On the second sampling date (before), the survey was done during the night, when lobsters are known to be more active (Golet et al. 2006), but because no difference in abundance was found between day and night sampling and to simplify the survey process, all subsequent observations were made during the day. One site with blocks (Blo) was lost after the third sampling date because of the loss of the buoy marking the site. The abundance of lobsters and other conspicuous organisms were counted by SCUBA divers along transects corresponding to the 2 axes (15 m) with blocks and/or where mussels were placed, or in the Ref sites, as outlined above for the observational part of this study.

Data analysis

Variation in the abundance of organisms inside and outside of the mussel farm, and the distribution of lobsters inside the mussel farm, were evaluated using analysis of variance (ANOVA). The general model to evaluate species abundances at the bay and farm scales consisted of 3 reference and 3 farm Areas (reference: R1, R2 and R3; farm: M1, M2 and MH) nested within bay Zone (outside of the farm or within the farm). Line-scale variation in lobster abundance within the farm was evaluated with a 2-way random block model with the orthogonal factors Areas (M1, M2 and MH) and Distance (distance classes 0–1 m through 9–10 m), such that n = 10 for each distance class within each transect, with all data pooled for a given distance class within a transect (Station) and Stations as the blocking factor. Assumptions of normality and homoscedasticity were assessed by visual examination of the residuals (plot of residuals over predicted mean) and Cochran's test. Data were transformed when necessary to satisfy the assumptions of ANOVA: data for American lobster and common starfish were sqrt(x+1)-transformed and those for Atlantic rock crab were ln(x+1)-transformed prior to analysis. When main effects were significant, *a posteriori* comparisons were made using the Tukey HSD tests or the LSD test. For the manipulative experiment, fish and invertebrate abundances were analysed using a crossed mixed-effects model with repeated measures design with Block (with or without), Mussel (with or without) and Period (2 dates before and 3 dates after installing the experimental setup) considered as fixed factors and Site and Date considered as random factors nested in the factors Block × Mussel and Period, respectively. The covariance among repeated measures was modelled using the compound symmetry covariance structure. All data for the manipulative experiment were sqrt(x+1)-transformed prior to analysis.

RESULTS

Spatial variation in species abundances

Four species were common both inside and outside of the aquaculture lease. In total, 140 American lobsters *Homarus americanus*, 348 Atlantic rock crabs *Cancer irroratus*, 1174 common starfish *Asterias rubens* and 75 winter flounder *Pseudopleuronectes americanus* were noted along the transects. Only lobsters were, overall, significantly more abundant in farm areas than reference areas, but the abundance of all species varied among farm areas (Fig. 2, Table 1). Indeed, all species exhibited significant farm-scale variation such that they were all significantly more abundant in the M2 area relative to the other areas within the farm zone. Lobsters also displayed line-scale variation in their abundances as, within all 3 areas inside the farm lease, about half of all lobsters observed were directly under mussel lines (Table 2, Fig. 3).

Manipulative study

Lobster abundance was low and similar at the 12 sites in the period before the sites were manipulated (i.e. the addition of mussels and/or blocks; Fig. 4). The number of lobsters increased significantly after the experimental manipulations were initiated, but only for treatments where blocks were added (Table 3, Fig. 4). In both treatments involving blocks, lobsters were mostly observed in the vicinity

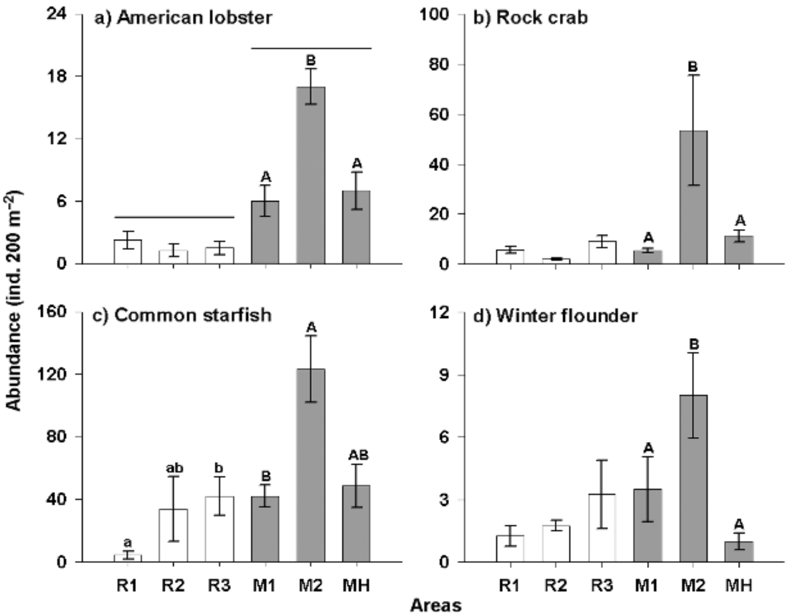

Fig. 2. Abundance (mean ± SE, n = 4) of common species recorded along transects in reference (in white: R1, R2, R3) and farm areas (in grey) with 1 yr old blue mussels *Mytilus edulis* (M1), 2 yr old mussels (M2) and where mussels had been recently harvested (MH). Species: American lobster *Homarus americanus*, Atlantic rock crab *Cancer irroratus*, common starfish *Asterias rubens*, and winter flounder *Pseudopleuronectes americanus*. Significant differences between areas are indicated by non-adjoining bars, and different letters (upper and lower case for farm and reference areas, respectively) indicate significant differences between areas within Zones (see Table 1)

of the blocks (92% Blo, 89% BloMu). The abundance of Atlantic rock crabs was higher at sites with blocks, but this effect was present both before and after the beginning of the experimental manipulations (Table 3, Fig. 4). The abundance of crabs also varied among sampling dates within Periods (Table 3, Fig. 4). The abundance of common starfish and winter flounder did not vary with the presence of blocks or mussels, either before or after the establishment of the experimental set-ups (Table 3, Fig. 4). The abundance of common starfish varied between sampling dates and an LSD post hoc test showed abundance was significantly lower at the sampling week before the beginning of the treatments (Table 3, Fig. 4).

DISCUSSION

This study shows a clear influence of mussel aquaculture on the abundance of fish and vagile macroinvertebrates. At the bay scale, there was a greater abundance of American lobsters and a trend for a greater abundance of rock crabs and common starfish in farm areas relative to areas outside of the farm. Within the farm, this effect was most pronounced in the area where older mussels were cultivated, showing farm-scale effects. Moreover, a strong association of lobsters with mussel line structures was observed, where most individuals were observed directly under the lines, using anchor blocks as shelter (data not shown). Most bay-scale studies on large vagile macrofauna in mussel culture have reported greater abundances of predators or scavengers in mussel farms relative to areas outside of mussel farms (see review by McKindsey et al. 2011). D'Amours et al. (2008) noted greater abundances of starfish, moon snails and rock crabs within mussel farms relative to areas outside of farms and that some species, including winter flounder and American lobster, were only observed in farm areas. In addition to a greater abundance of starfish in mussel farms relative to reference areas, Inglis & Gust (2003) also observed that starfish abundance was correlated with recent harvest history. This is in agreement with the farm-scale variation observed in the present study, where all organisms were more abundant in stations with 2 yr old mussels relative to farm stations where mussels were recently harvested and stations with 1 yr old mussels. This spatial variation within the farm also suggests that the distribution of vagile species varies temporally as a function of harvesting and as the crop is growing. As for the line-scale effects observed for lobsters in the present study, Wilding & Nickell (2013) also

Table 1. ANOVA results for comparing the abundance of conspicuous vagile macrobenthic species (see Fig. 2) in areas inside and outside of the mussel (*Mytilus edulis*) culture zone and at different stages of production inside the mussel farm (Areas: R1, R2, R3, M1, M2, MH; see Fig. 1). Values in **bold** highlight statistically significant (α = 0.05) effects

Source of variation	df	American lobster			Atlantic rock crab			Common starfish			Winter flounder		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Zone	1	15.81	9.65	**0.036**	5.57	2.27	0.206	78.44	3.55	0.133	26.04	0.95	0.384
Area (Zone)	4	1.64	6.54	**0.002**	2.45	7.53	**0.001**	22.12	4.82	**0.008**	27.33	4.20	**0.014**
Residual	18	0.25			0.33			4.58			6.51		

Table 2. ANOVA results for variation in the abundance of American lobsters *Homarus americanus* in different areas of the mussel (*Mytilus edulis*) culture lease (M1, M2, MH; see Fig. 1) and proximity to mussel longlines (Distance: 0–1 m through 9–10 m from mussel longlines), and the interactions between these 2 factors. Values in **bold** highlight statistically significant ($\alpha = 0.05$) effects

Source of variation	df	MS	*F*	p
Area	2	3.15	7.6	**0.012**
Transect(Area)	9	0.42	1.6	0.143
Distance	9	4.17	15.6	**<0.001**
Distance × Area	18	0.32	1.2	0.291
Residuals	81	0.27		

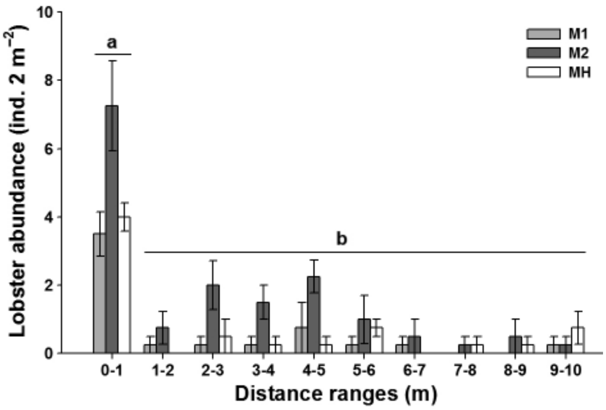

Fig. 3. Abundance of lobsters *Homarus americanus* found along transects relative to their distances from mussel lines in areas with 1 yr old mussels *Mytilus edulis* (M1), 2 yr old mussels (M2) and where mussels had been harvested (MH), from the mussel lines (0–1 m) to the midpoint between 2 mussel lines (9–10 m). Different letters and lines above bars indicate significant differences in lobster abundance among distances

observed a close association between starfish abundances and mussel lines. Likewise, D'Amours et al. (2008) observed that most macrofauna in mussel farms was directly below mussel lines and not between them.

Results from the observational and manipulative experiments suggest that the mechanisms (habitat structure or trophic interaction) that result in spatial variation in abundance vary among species. Lobster abundance increased quickly at sites with experimental treatments with concrete blocks after they were installed, whereas the addition of mussels did not alter lobster abundance. This observation, along with the observation that lobsters are found in greater abundances in all farm areas relative to reference areas, suggests that the provision of physical structures to the otherwise homogeneous benthic

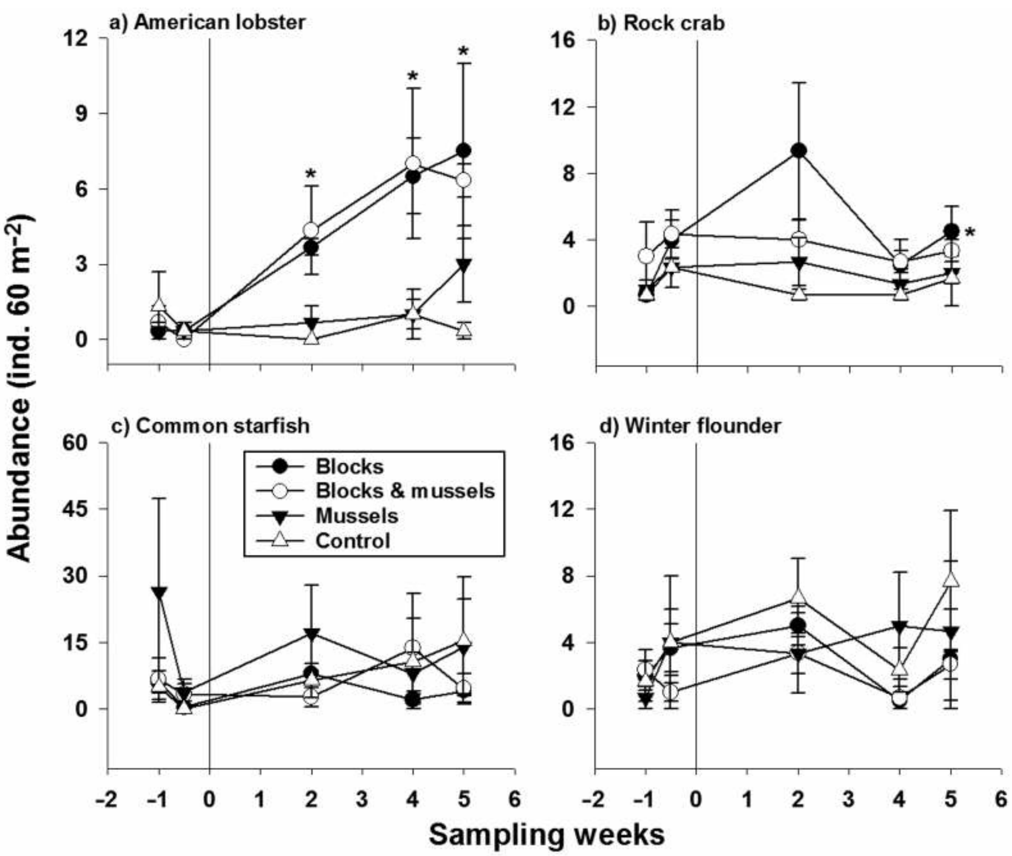

Fig. 4. Influence of Blocks and Mussels on the abundance of vagile benthic macrofaunal species abundances (mean ± SE, n = 3 or 2) over 5 sampling dates. The vertical black line at '0' wk indicates when the manipulative portion of the experiment was initiated

Table 3. Influence of shelter (Block) and food (Mussel) on the abundance of 4 vagile benthic macrofaunal species (see Fig. 2 for scientific names), before and after (Period) the addition of the different treatments, at different sites (Site), over different sampling dates (Date). Treatment and Period are fixed factors. Values in **bold** highlight statistically significant effects obtained with SAS PROC MIXED (type III fixed effects model) using the random effect Site(Block × Mussel) as between subjects error

Source of variation	df	American lobster		Atlantic rock crab		Common starfish		Winter flounder	
		F	p	*F*	p	*F*	p	*F*	p
Block	1	33.03	**0.0004**	7.39	**0.0263**	0.37	0.5588	0.34	0.5775
Mussel	1	0.04	0.8444	0.04	0.8542	0.27	0.6153	1.47	0.2597
Block × Mussel	1	0.69	0.4315	0.04	0.8495	0.19	0.6774	0.17	0.6940
Period	1	28.71	**<0.0001**	1.04	0.3151	2.07	0.1609	1.74	0.1971
Date(Period)	3	1.61	0.2078	2.96	**0.0479**	3.47	**0.0281**	1.96	0.1419
Block × Period	1	20.11	**<0.0001**	1.57	0.2201	0.05	0.8219	1.94	0.1743
Mussel × Period	1	0.54	0.4698	0.62	0.4379	1.55	0.2230	0.28	0.6037
Block × Mussel × Period	1	0.51	0.4795	0.96	0.3356	0.29	0.5967	0.19	0.6682
Block × Date(Period)	3	0.01	0.9975	0.64	0.5934	0.08	0.9724	0.88	0.4601
Mussel × Date(Period)	3	0.30	0.8247	0.37	0.7746	0.39	0.7601	0.54	0.6592
Block × Mussel × Date(Period)	3	0.47	0.7040	0.85	0.4777	1.52	0.2297	0.40	0.7574
Residual	30								

environment in the lagoon is likely the main mechanism accounting for increased lobster abundance in mussel farms. Newly settled and juvenile American lobsters are dependent on shelter until they reach a critical size, and they trade off energetic considerations against risk of predation until they start to expand their foraging range (Wahle 1992, Factor 1995). The association with shelter becomes less important as lobsters grow and become more vagile, except during times of moulting and mating (Wahle & Steneck 1992, Factor 1995). However, this study showed that adult lobsters also exert a strong selection for shelter and, when provided anchor blocks, were more often than not observed to shelter there (data not shown). The use of refuges is a typical anti-predator strategy, and the presence of predators is known to influence shelter use by both juvenile and adult lobsters (Spanier et al. 1998, McMahan et al. 2013). In the general study area, benthic fish such as sculpin and cod and larger lobsters are likely the main predators of adult lobsters (Sainte-Marie & Chabot 2002), although the former 2 are not common in the studied lagoon.

Although the observational study showed that the abundance of crabs, starfish and winter flounder was greatest in the M2 area in the mussel farm, the manipulative study indicated that the provision of physical structure did not influence the distribution of these species and is likely not the main mechanism that accounts for their spatial distribution within the studied bay. In contrast to lobsters, rock crabs seem less dependent on physical structure. Rock crabs may bury themselves in mud or sand, or hide under stones or rocks and not demonstrate fidelity to shelter (Gendron & Fradette 1995). Winter flounder is a cryptic species, with a morphology adapted to the lack of cover in soft bottom areas (Caddy 2008, Pappal et al. 2012), and thus changes in bottom complexity related to adding anchor blocks might not directly influence this species. Likewise, while commonly associated with hard bottoms, starfish may also be major predators on soft-bottom communities when hydrodynamic conditions permit (e.g. Gaymer et al. 2004), such as in enclosed bays where mussel farming is typically done, and thus are not reliant on hard substrates.

The results of the observational part of this study suggest that variations in the spatial distributions of rock crabs and starfish are likely due to trophic effects. However, as results from the manipulative part of the present study were inconclusive for these species, such effects likely occur over greater temporal or spatial scales than those considered. In addition, because mussel treatments were not applied daily, the importance of this factor may have been underestimated. Mussel fall-off from culture structures may be significant. For example, Léonard (2004) measured mussel fall-off in the lagoon south of the present study area at about 130 g m^{-2} d^{-1}, and Mallet & Carver (1991) suggested that up to 35 to 50% of mussels may be lost through fall-off. Mussels are among the main prey items of rock crabs in coastal areas and in the general study area (Drummond-Davis et al. 1982, Hudon & Lamarche 1989). Romero et al. (1982) observed a greater abundance of various crab species in areas with mussel rafts than in areas without them in the Ría de Arousa, Spain, and stomach content analysis of crabs in the same region showed crab diets shift to include more mussels in farm areas (Freire et al. 1990, Freire & González-Gurriarán 1995). Likewise, mussels are the preferred prey of many starfish (Penney & Griffiths 1984, Gaymer et al. 2001), and aggregations of starfish have often been noted with fallen mussels at mussel farm sites (Olaso Toca 1982, D'Amours et al. 2008, Wilding & Nickell 2013), suggesting that they are attracted to mussel farms for the abundant prey they offer. The importance of mussel drop-off to the distribution of rock crabs and starfish is further supported by the observation that both of these organisms were most abundant in the area where mussel fall-off is greatest (the area with 2 yr old mussels).

The observed spatial variation in the abundance of winter flounder may also be due to a trophic link. Biodeposition from mussel farms often increases the abundance of opportunistic organisms, such as small polychaetes (see review by McKindsey et al. 2011). This changed infaunal community may have cascading effects on other trophic levels, such as benthic fish and vagile macroinvertebrates. For example, Iglesias (1981) suggested that benthic fish feed on the infaunal communities below mussel rafts in Spain. Winter flounder, which were most abundant in the farm area with 2 yr old mussels in the present study, prey heavily on small infaunal species and crustaceans when they are young (Worobec 1984, Stehlik & Meise 2000). Becker & Chew (1987) showed that some flatfish in disturbed areas select for *Capitella capitata*, an indicator species for organic loading and also the dominant species in the area with 2 yr old mussels in the studied mussel farm (Callier et al. 2007). Together, this suggests that winter flounder abundances may have been greatest in the farm area with 2 yr old mussels, as it provided them an indirect trophic advantage.

Farm-scale variation in the abundance of lobsters also suggests that a trophic mechanism may be involved for this species. In the study area, although mussels in natural systems may account for the greatest fraction of lobster diets (Hudon & Lamarche 1989), rock crabs are important to the growth and development of all sizes of lobsters (Gendron et al. 2001), with larger lobsters preying primarily on rock crabs (Sainte-Marie & Chabot 2002). Thus, the greater abundance of rock crabs within the farm area with 2 yr old mussels may be due to mussel fall-off being greatest in this area, with lobster abundance being greatest there because of the increased abundance of both of these prey species.

Future studies should examine the movement of populations of vagile macrofauna within and around mussel farms to identify the effect on aggregation or biomass redistribution of these species on fisheries. For example, although lobsters are not fished within the studied lagoon, lobsters are fished in the bays of nearby Prince Edward Island, where fishing effort is often concentrated around mussel culture areas in these bays (C. W. McKindsey pers. obs.). Thus, mussel culture areas may act as ecological traps for lobsters, much as Dempster et al. (2009) suggested may occur for wild fish that aggregate around finfish farms if this behaviour increases their vulnerability to capture. Links between changes in benthic prey assemblages due to farm-induced nutrient loading (mussel fall-off and biodeposition) and higher trophic levels need to be better understood.

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