



Influence of an Offshore Mussel Aquaculture Site on the Distribution of Epibenthic Macrofauna in Îles de la Madeleine, Eastern Canada

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Mussel farming influences benthic environments by organic loading and the addition of physical structure within aquaculture leases. This study evaluated near-field (distance to mussel aquaculture structures, line-scale) and bay-scale (inside vs. outside a blue mussel, *Mytilus edulis*, farm) effects of an offshore mussel farm in Îles de la Madeleine (Canada) on epibenthic macrofaunal communities. Benthic communities were evaluated by underwater visual counts using SCUBA in June and July 2014. The mussel farm influenced benthic communities at line- and bay-scales. Overall, crabs (*Cancer irroratus*, *Pagarus pubescens*, *Pagarus acadianus*), sea stars (*Asterias rubens*), Northern moon snails (*Polinices heros*), and American lobsters (*Homarus americanus*) were more abundant in farm sites than outside of farm sites and ocean quahogs (*Arctica islandica*) were more abundant outside. No clear spatial trend was observed for winter flounder (*Pseudopleuronectes americanus*) and the sand dollar (*Echinarachnius parma*) but both species differed (flounder) or showed a trend to differ (sand dollar) between sampling dates. Spatial structure in the distribution of macrofauna was evident within the aquaculture lease as most species were more abundant directly below and close to mussel lines and anchor blocks. There was no spatial structure in non-farm sites. Further investigation is needed to evaluate if mussel farms serve as ecological traps for the species that congregate within them. The long-term effects of the observed spatial effects of offshore mussel culture on macrofauna fitness remains unknown.

Keywords: offshore mussel aquaculture, *Mytilus edulis*, *Homarus americanus*, *Cancer irroratus*, benthic macrofauna, spatial variation

INTRODUCTION

Declining wild stocks and increasing demand for seafood have led to a rapid expansion of the aquaculture industry and concerns of its potential impact on the environment. Bivalve aquaculture has various near- and far-field effects on marine ecosystems. Far-field effects are mostly limited to effects on water column processes, such as alteration of plankton communities

(Prins et al., 1997) and hydrodynamic processes (Plew et al., 2005). Although near-field effects (i.e., within-and immediately surrounding farms) may occur in the water column due to hydrodynamic modifications and farmed bivalves grazing on plankton (see review in Weitzman et al., 2019), most research on near-field effects of bivalve culture has focused on the benthic environment with an emphasis on infaunal and epibenthic macrofaunal communities, sediment structure, and nutrient fluxes and benthic respiration (Souchu et al., 2001; Giles et al., 2006; McKindsey et al., 2011).

The effects of bivalve culture on benthic macrofauna may be evident at several spatial scales. At a bay-scale, culture sites may differ from non-culture sites in the same general area and, at the farm-scale, communities may differ between farm areas at different stages of production (e.g., Toupoint et al., 2008; Drouin et al., 2015). At a smaller spatial scale (line-scale), communities close to or directly below culture gear may differ from those further from such structures (McKindsey et al., 2012; Drouin et al., 2015). In all cases, variations in benthic communities among locations are largely due to two main mechanisms: the addition of physical structure to the environment and organic loading effects.

As suspended bivalve culture is commonly done above unvegetated soft-bottom habitats, culture gear adds considerable physical structure and complexity to an environment that is largely devoid of three-dimensional surfaces (Dumbauld et al., 2009; Forrest et al., 2009; McKindsey et al., 2011). The introduction of aquaculture gear (e.g., ropes and anchor blocks) modifies habitat characteristics and may attract vagile organisms directly (as shelter) or indirectly (as substrate for sessile hard-bottom prey) (Drouin et al., 2015). When fouled, aquaculture structures may increase the abundance and diversity of fauna in farm sites relative to non-farm sites (Saranchova and Flyachinskaya, 2001; Miron et al., 2002; D'Amours et al., 2008) but not necessarily the productivity of these species (Clynick et al., 2008). Bivalve fall-off also alters the habitat of otherwise flat, soft bottoms, adding physical structure through the addition of living hard-bodied organisms and shell debris, although this effect is most likely to occur in mussel farms as other bivalves (e.g., oysters and scallops) are most typically grown in baskets or other structures and do not fall from culture structures to the extent that mussels do.

Many studies of the effects of bivalve culture on the benthic environment have focused on the accumulation of biodeposits (organic material in feces and pseudofeces) from farmed bivalves (Matisson and Lindén, 1983; Callier et al., 2008; Weise et al., 2009). In general, this type of organic loading may alter benthic infaunal and epifaunal communities. This, in turn, may influence the types of larger animals that may feed on these communities (McKindsey et al., 2011; Froehlich et al., 2017). However, as noted by Cranford et al. (2006) and Fréchette (2012), organic loading also occurs in the form of fallen mussels (and associated fauna). Casual observations (authors' pers. obs.) show that there are often notable quantities of fallen mussels on the seabed within mussel farm sites, particularly directly below and close to culture structures, in eastern Canada. This has also been reported elsewhere around the world where mussels are farmed

(e.g., Kaspar et al., 1985; Freire and González-Gurriarán, 1995; Inglis and Gust, 2003; Wilding and Nickell, 2013). Fallen mussels represent a direct input of food and may act as a trophic subsidy for the animals that live in and around culture sites with scavengers and opportunistic predators likely benefiting from this novel prey source. Evidence of this trophic link was provided by Freire and González-Gurriarán (1995), who documented a greater proportion of mussels in the diet of crabs located in a Spanish mussel farm area than comparable areas outside of it. More recently, Sardenne et al. (2019) used lab and field studies to determine that large lobsters fed mainly on mussels from a mussel farm.

At the bay-scale, predators and scavengers are commonly more abundant within mussel farms than outside of them because of the greater abundance of physical structure and trophic interactions (i.e., modified benthic communities and the addition of prey through fall-off of farmed and associated species). At the farm-scale, predators and scavengers may be more abundant in some areas than others as the level of fall-off and physical structure in areas is a function of the stage of production (e.g., fall-off is greater and more anchor blocks are deployed to maintain culture structures in place for larger mussels). Farm-related physical structures, such as anchor blocks, ropes, associated farmed animals, and fall-off are not randomly distributed in farm sites – they occur in well-defined rows. Accordingly, vagile macrofauna have been observed to be more abundant in the vicinity of culture structures and fallen mussels than in areas between mussel lines, thus accounting for line-scale variation in species abundances (Inglis and Gust, 2003; D'Amours et al., 2008; Wilding and Nickell, 2013; Drouin et al., 2015).

Numerous studies have documented that the abundance of vagile predators and scavengers (e.g., crustaceans, sea stars, and gastropods) is increased within bivalve culture sites, particularly mussel farms (Romero et al., 1982; Inglis and Gust, 2003; D'Amours et al., 2008; Callier et al., 2018; Barrett et al., 2019). These studies have mostly focused on mussel farms in shallow, protected embayments. However, the expansion of the aquaculture industry is increasingly leading to the development of offshore farm sites as the inshore industry is becoming saturated in some areas and conflicts with other users increase (Jansen et al., 2016; Mascorda Cabre et al., 2021). According to Jansen et al. (2016) and Mascorda Cabre et al. (2021), cultivation of lower trophic species, such as bivalves and specifically mussels, has a high biological and economic potential for offshore production and this type of aquaculture will most likely expand in the future. Offshore sites have a different architecture (e.g., cultured bivalves being suspended higher off the bottom, longlines with greater spacing between them) and the general environment is different from that of enclosed embayments (e.g., commonly stronger currents, colder waters, deeper areas, different species). Such differences may affect interactions between bivalve culture and benthic communities. Few studies have concentrated on the distribution of vagile epibenthic macrofauna in offshore sites, including those for mussel farms (Froehlich et al., 2017). In the context of marine spatial planning, it is important to quantify the effects of offshore aquaculture on capture fisheries (and ecologically important)

species to better predict if farms result in net gains or losses for impacted populations (Clavelle et al., 2019). Indeed, Barrett et al. (2022) recently suggested that non-fed aquaculture may increase productivity of associated species, providing a more holistic view of the costs and benefits of aquaculture production in support of decision-making and the development of sustainable aquaculture (Weitzman, 2019).

The general objective of this study was to evaluate the effects of offshore suspended mussel *Mytilus edulis* aquaculture on the spatial distribution of vagile epibenthic macrofauna. Two hypotheses were evaluated: (1) that the abundance of epibenthic macrofauna is greater within farm sites relative to non-farm sites (hereafter, reference sites—bay-scale variation), and (2) that the abundance of epibenthic macrofauna within farm sites increases with proximity to farm infrastructure (e.g., mussel longlines and anchor blocks—line-scale variation). Sampling was done twice to evaluate if the benthic communities display temporal variation.

MATERIALS AND METHODS

Study Sites

The study was done in Baie de Plaisance (N 47°21', W 61° 44'), îles de la Madeleine, Québec, Canada (Figure 1). The mussel lease covers an area of approximately 2.5 km², 4 km offshore, where 187 longlines are deployed primarily for mussel aquaculture but the area also supported limited oyster aquaculture. Longlines are 100 m long and are anchored at each end by cement blocks or screw anchors, suspended off-bottom by variable numbers (depending on grow-out stage) of 40 cm spherical buoys and ballasted by ca. 10 concrete anchor blocks (typically about 30 × 30 × 40 cm high) spaced at ca. 10 m. Rows of longlines are spaced 50 m from adjacent ones and individual longlines within rows are separated by 70 m. The site is about 20 m deep and 2 m-long mussel socks are suspended from longlines ca. 10 m above the bottom. The studied area experiences a tidal range of 0.60 m and water temperature can reach 20°C in summer and drop below 0°C during the winter (December to April). The

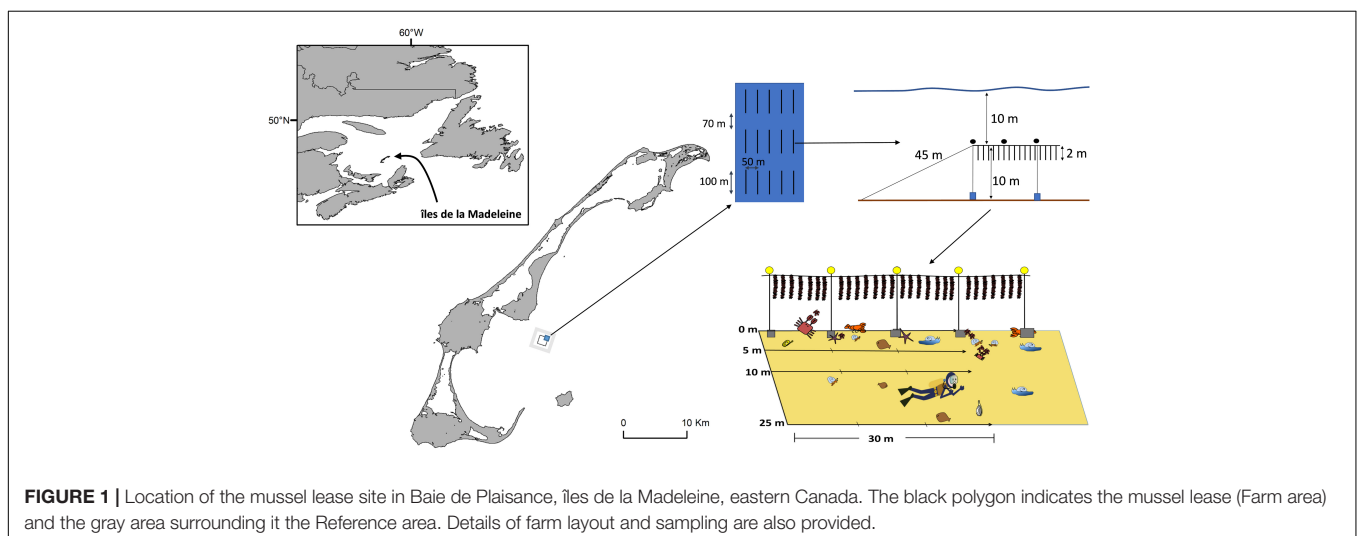
bottom is characterized by a very flat sandy substratum with little physical heterogeneity. In all sites, underwater visibility was typically >5 m. Up to 85% of the mussel lease is used at a time and contains mussels at different stages of production.

Sampling Protocol

Sampling was done at two different periods, June 8–14 and July 19–23, 2014. Two areas were studied, one inside (Farm area) and one outside (Reference area, encompassing all areas surrounding the farm and > 500 m to about 1 km distant from it) the offshore mussel farm site. At each area and each period, 8 stations were chosen haphazardly to cover the surface of the mussel farm (concentrating on longlines with 2-year-old mussels) and non-farm areas, for a total of 32 sampling stations. As described by D'Amours et al. (2008), two SCUBA divers made underwater visual counts along transects. The first diver swam near the bottom holding a 2 m pole equipped with a compass and swam transects along the same bearing that mussel lines were oriented while deploying a measuring tape. The second diver identified, counted, and noted epibenthic macroinvertebrates and fish by swimming directly above the bar guided by the first diver. All taxa were distinct and a clear distinction between hermit crabs was made; large hermit crabs were identified as *Pagurus pubescens* and small hermit crabs as *Pagurus acadianus*. Inside the farm, benthic macrofauna were noted along 30 m transects, divided into contiguous ($n = 3$) 10 m segments, parallel to mussel lines at each of 4 distances from them: 0 m (directly under mussel lines), and at 5, 10, and 25 m away from them (i.e., directly between two adjacent longlines). Transects evaluated in non-farm stations were done following the same pattern and orientation of four transects, with the exception that there was no mussel line, to evaluate if spatial structure of benthic communities differed between farm and reference areas.

Data Analysis

Temporal, bay- and line-scale variation in abundances and taxonomic richness were evaluated using 4-way mixed effect

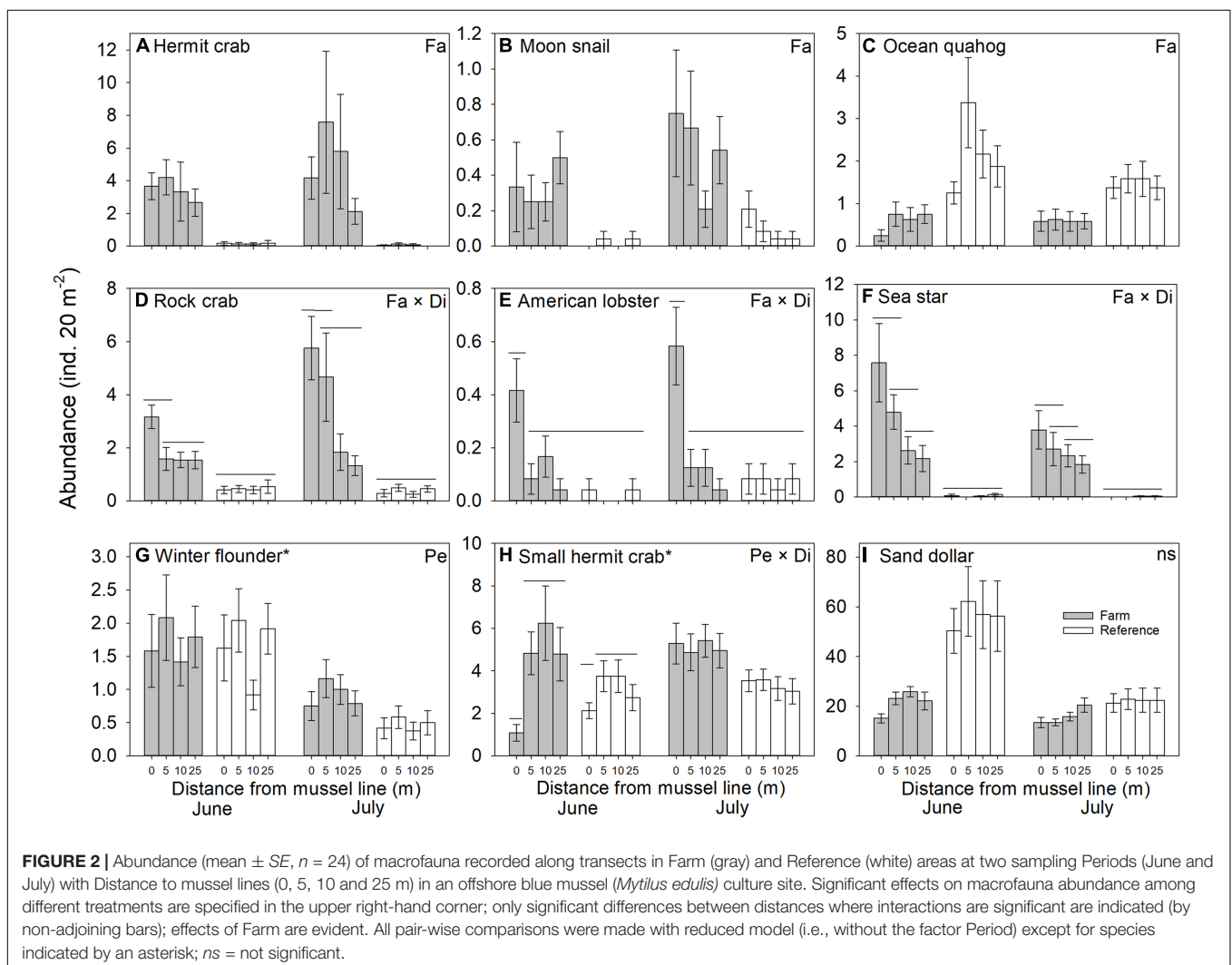


models with the factors Farm (fixed; farm area or reference area), Period (random; June or July), Distance (fixed; from mussel line: 0, 5, 10, and 25 m) and Site (random; nested in Farm and Period) and the interactions among these factors. Samples from contiguous transect are considered as replicates nested within each Distance in a given Site. The assumptions of normality and homoscedasticity for parametric analyses were verified by visual evaluation of residuals and Cochran's test and were never met, despite trying various data transformations. Thus, all univariate models (i.e., for abundances of each species, total abundance, and richness) were evaluated using PERMANOVA with PRIMER 7 + PERMANOVA based on Euclidean distances ($n = 4,999$ unrestricted permutations) as suggested by Anderson (2001). All univariate analyses (with the exception of winter flounder and small hermit crabs) showed that the factor Period and its interactions with other factors were not significant ($P > 0.2$) and thus this factor was removed from the analyses and the reduced model rerun for all species other than winter flounder and small hermit crabs. Significant factors were further examined using appropriate pairwise comparisons.

Variation in multivariate community structure was visualized using non-metric multidimensional scaling (MDS) and evaluated using PERMANOVA (fourth-root transformation of abundance data and based on Bray Curtis similarity distances, $n = 4,999$ unrestricted permutations). PERMDISP was performed on the same Bray-Curtis matrix to evaluate variation in multivariate dispersion among *a priori* groups (i.e., contrasting variation in multivariate community structure between outside and inside of the farm and among distance classes within the farm). Likewise, species accounting for differences between Farm and Reference areas and between distances within the farm were identified using SIMPER.

RESULTS

Epibenthic macrofaunal communities were dominated by sand dollars *Echinarachnius parma* (70.5%), small hermit crabs *Pagarus acadianus* (9.59%), large hermit crabs *Pagarus pubescens* (5.2%), sea stars *Asterias rubens* (4.3%), Atlantic rock crabs



Cancer irroratus (3.8%), ocean quahogs *Arctica islandica* (2.9%), winter flounders *Pseudopleuronectes americanus* (2.9%), Northern moon snails *Polinices heros* (0.6%), and American lobsters *Homarus americanus* (0.3%). Other vagile organisms were occasionally observed, mostly within mussel farms and directly on anchors blocks (data not shown), such as sea ravens *Hemitriptera* sp. and sculpins *Myoxocephalus* sp., although they were not considered in the present study due to their rarity.

Univariate Analyses

Variation in abundance was observed between farm and reference sites for seven of the nine epibenthic species evaluated. The abundance of large hermit crabs, Northern moon snails, and ocean quahogs varied significantly between farm and reference areas, being more abundant in farm than reference sites, with the exception of ocean quahog, which was more abundant in reference than in farm sites (Figure 2 and Table 1). The abundance of American lobster, Atlantic rock crab and common sea star showed significant 2-way interactions between Farm and Distance. Atlantic rock crab and sea star abundance increased significantly with proximity to longlines, whereas American lobster abundance was greater at 0 m than at other distances from the longlines (Figure 2 and Table 1). Winter flounder was significantly more abundant in June than July but did not show any spatial variation in abundance (Figure 2 and Table 2). The abundance of small hermit crabs varied as a function of the Period × Distance interaction (Figure 2 and Table 2) such that its abundance decreased with proximity to longlines—being least

abundant at 0 m in June—but no trend was observed in July. Despite a fairly clear trend in the abundance of sand dollars (Figure 2 shows that sand dollar abundance in reference sites in June to be about twice that observed in farm sites and of reference sites in July), this effect was not statistically significant (Table 1), likely due to very high variability among sites. Overall, taxonomic richness was significantly greater inside the mussel farm than in the reference sites (Figure 3 and Table 1). There were no statistically significant patterns for total abundance, again most likely due to the abundance of sand dollars among sites. When the abundance of this species is removed from the calculation of “total abundance,” the abundance of all other species combined is greater in Farm sites than Reference sites (Figure 3 and Table 2), mirroring the overall trends observed for most individual species.

Multivariate Analyses

Macrofaunal community structure varied as a function of the Farm × Distance interaction (Table 2), with communities from farm and reference areas differing. Within the farm, communities directly under the mussel lines differed from those at other distances (i.e., 0 m ≠ 5 m = 10 m = 25 m) and were most different from those in reference sites. In both periods, MDS plots (Figure 4) show clear farm-scale effects where Farm sites differ from Reference sites with little overlap between site points. Multivariate dispersion differed between farm and reference sites, with variation among replicate contiguous transects being greater inside of the farm than outside of it (\bar{x} = 25.026 and 20.642 for dissimilarity outside and inside of the farm, respectively,

TABLE 1 | Results of PERMANOVA analysis (reduced model; untransformed data) for variation in the abundance of American lobster *Homarus americanus*, Atlantic rock crab *Cancer irroratus*, hermit crab *Pagurus pubescens*, common sea star *Asterias rubens*, northern moon snail *Polinices heros*, sand dollar *Echinarachnis parma* and ocean quahog *Arctica islandica*, total abundance, taxonomic richness, and multivariate community structure to test the blue mussel (*Mytilus edulis*) culture lease effects of Farm (Farm vs. reference), Distance (from mussel line: 0, 5, 10, and 25 m) and Site (1–32) and their interactions.

Source of variation	<i>Homarus americanus</i>				<i>Cancer irroratus</i>			<i>Pagurus pubescens</i>			<i>Asterias rubens</i>		
	df	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)
Farm (Fa)	1	2.19	22.093	0.002	490.51	10.741	0.001	1604.8	5.231	0.001	1134.4	13.222	0.001
Distance (Di)	3	1.093	9.289	0.001	45.622	4.598	0.001	51.912	1.486	0.246	63.965	5.229	0.002
Si(Fa)	30	0.099	0.928	0.566	45.666	11.621	0.001	306.78	8.193	0.001	85.797	11.634	0.001
Fa × Di	3	0.961	8.168	0.001	48.955	4.934	0.001	49.579	1.419	0.239	66.299	5.42	0.002
Si (Fa) × Di	90	0.118	1.102	0.274	9.922	2.525	0.001	34.94	0.933	0.709	12.232	1.659	0.002
Res	256	0.107			3.93			37.443			7.375		
Total	383												

	<i>Polinices heros</i>			<i>Echinarachnis parma</i>			<i>Arctica islandica</i>			Taxonomic richness			
	df	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)	MS	Pseudo-F	p (perm)
Farm (Fa)	1	13.878	5.713	0.004	41003	3.013	0.070	145.04	8.686	0.005	217.5	20.275	0.001
Distance (Di)	3	0.704	1.212	0.308	670.73	2.431	0.066	8.438	1.211	0.332	1.718	1.034	0.375
Si(Fa)	30	2.429	5.585	0.001	13608	57.396	0.001	16.699	11.853	0.001	10.728	7.758	0.001
Fa × Di	3	0.343	0.59	0.635	186.78	0.677	0.577	4.021	0.577	0.673	0.926	0.558	0.668
Si (Fa) × Di	90	0.581	1.336	0.043	275.94	1.164	0.179	6.97	4.947	0.001	1.661	1.201	0.134
Res	256	0.435			237.09			1.409			1.383		
Total	383												

Values in bold indicate statistically significant ($\alpha = 0.05$) effects. Pseudo-F (F) and permutationally-derived probability (P) values, respectively, were calculated using PERMANOVA.

TABLE 2 | Results of PERMANOVA analysis (full model; untransformed data for univariate metrics but fourth-root transformed data for multivariate community structure) for variation in the abundance of winter flounder *Pseudopleuronectes americanus* and small hermit crab *Pagurus acadianus*, multivariate community structure, total abundance and total abundance without sand dollar *Echinarachnius parma* to test the effects of Farm, Period, Distance, Site and their interactions.

Source of variation	Pseudopleuronectes americanus			Pagurus acadianus			Multivariate community structure			Total abundance (N)			Total abundance (N) (without sand dollars)			
	df	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	MS	Pseudo-F p (perm)	
Farm (Fa)	1	7.315	2.293	0.274	208.570	20.179	0.243	54948.000	37.962	0.254	9272.800	0.384	0.482	92095.000	58.762	0.234
Period (Pe)	1	91.065	5.534	0.018	30.940	0.313	0.551	7528.300	2.315	0.040	38420.000	2.617	0.100	11863.000	2.848	0.024
Distance (Di)	3	5.107	1.837	0.317	46.961	0.818	0.699	1244.700	4.089	0.020	796.460	1.482	0.397	1790.700	4.114	0.022
Fa x Pe	1	3.190	0.194	0.687	10.336	0.104	0.768	1447.800	0.445	0.824	24146.000	1.644	0.229	1567.300	0.376	0.827
Fa x Di	3	1.100	6.005	0.094	19.225	1.552	0.325	1255.500	20.974	0.004	106.110	1.152	0.473	1917.400	26.927	0.011
Pe x Di	3	2.780	1.606	0.208	57.433	3.536	0.008	304.410	0.655	0.743	537.300	1.644	0.183	435.270	0.536	0.809
Si (Fa x Pe)	28	16.454	7.998	0.001	98.916	11.315	0.001	3251.900	11.311	0.001	14683.000	41.929	0.001	4165.400	8.223	0.001
Fa x Pe x Di	3	0.183	0.106	0.961	12.385	0.762	0.507	59.857	0.129	0.986	92.114	0.282	0.844	71.209	0.088	0.987
Si (Fa x Pe) x Di	84	1.731	0.841	0.802	16.245	1.858	0.001	465.020	1.618	0.001	326.800	0.933	0.666	812.070	1.603	0.001
Residual	256	2.057			8.742			287.490			350.190			506.550		
Total	383															

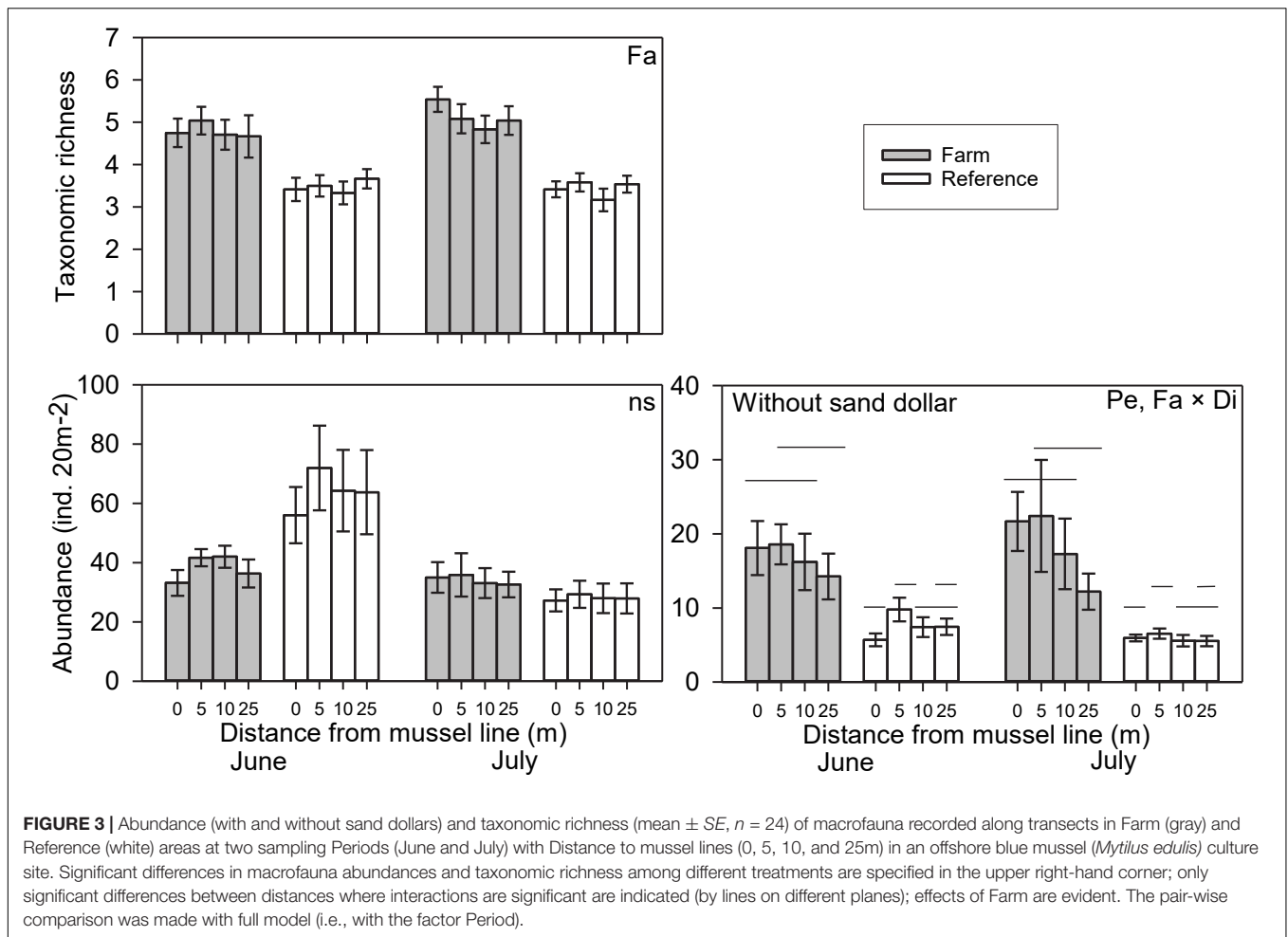
Values in bold highlight statistically significant ($\alpha = 0.05$) effects. Pseudo-F (F) and permutationally-derived probability (P) values, respectively, were calculated using PERMANOVA.

$F_{(1, 382)} = 21.225, p = 0.001$]. In contrast, multivariate dispersion within the farm did not differ among distances [$F_{(3, 39)} = 0.128, p = 0.961$]. In all contrasts among distance classes within farms, sea stars, small and large hermit crabs, flounders, and rock crabs, together, accounted for between 71 and 77% of the observed dissimilarity in community structure among distances, with the contribution of the various species differing depending on the contrast.

DISCUSSION

This study shows that offshore suspended mussel aquaculture in Îles de la Madeleine influences the distribution and abundance of epibenthic macrofauna at both the bay- and line-scale, although the effects varied among species and, at times, between sampling periods. Community structure analyses highlighted three distinct species assemblages: outside the farm sites, within the farm sites but not below mussel lines, and directly below mussel lines. This was reflected by the distribution of most species, except for winter flounder and sand dollars, whose abundance did not vary between farm and reference sites, most of which (except for ocean quahogs, which is actually an infaunal species) were most abundant in farm sites and many of which were more abundant directly below mussel lines than between them. Taxonomic richness and total abundance (less sand dollars) were also greater in farm areas than non-farm areas. This increased taxonomic richness and total abundance likely homogenized benthic communities within the farm relative to those outside of the farm, as evidenced by the decreased multivariate dispersion of samples from farm sites relative to those from reference sites.

Two main mechanisms likely account for the spatial distribution of the vagile macrobenthic organisms observed in the present study (see review in McKindsey et al., 2011). First, effects on trophic structure (increased input of prey resulting from fallen mussels and associated fouling organisms may attract predators, as may biodeposit-enriched and modified infaunal communities). Second, the addition of physical structure to the benthic environment in the form of anchor blocks and fallen mussels alters the seabed by creating colonization surfaces and increasing possible shelter or refuges for a variety of organisms. While other studies have focused on a few species (e.g., Freire and González-Gurriarán, 1995; Inglis and Gust, 2003; Wilding and Nickell, 2013), we focused on entire local macrofaunal communities to allow more general conclusions to be drawn. Given that the impact of this offshore mussel farm on benthic infauna is quite limited (Lacoste et al., 2018) and that lobster, but not crabs, sea stars, or flounders are impacted by the presence of anchor blocks alone without the presence of mussels (Drouin et al., 2015), we assume that observed impacts on species distributions of most species are likely mostly attributable to the presence of fallen mussels as a food source. That is, a simple trophic effect (i.e., the supply of food in the form of fallen mussels to scavengers or predators; Forget et al., 2020) is likely the main reason for the increased abundance of several taxa in farm sites, particularly close to mussel lines within the farm. Mussels are considered the main prey of rock crabs in coastal

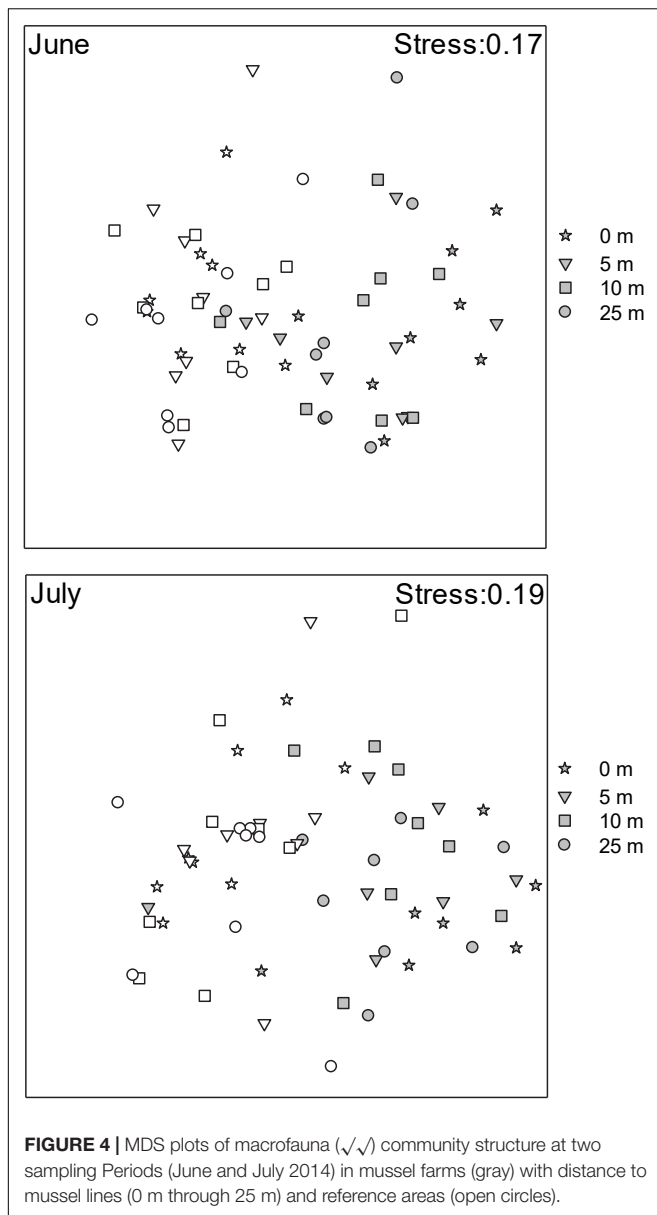


areas (Drummond-Davis et al., 1982). Given that many mussels fall from culture structures during grow-out, particularly more or less directly below mussel longlines (Wilding and Nickell, 2013), this provides a great trophic advantage to crabs in the area, logically concentrating them where the mussels have fallen. Romero et al. (1982) noted a greater abundance of various crabs in areas with mussel rafts relative to areas without them, suggesting that they are attracted to aquaculture sites where they feed on fallen cultured mussels and associated epifauna. As noted by Hudon and Lamarche (1989), mussels may account for an important fraction of American lobster diet due to their high calorific value. Moreover, a great proportion of the diet of large lobsters is mussels in an area with available farmed, but few wild, mussels (Sardenne et al., 2019). However, rock crabs play a key role in the growth, condition and ovary development of American lobsters of all sizes due to their high protein content and ratio of amino acids (Gendron et al., 2001), likely accounting for the finding that smaller lobsters feed mostly on rock crabs associated with mussel farms (Sardenne et al., 2019). In contrast, Sainte-Marie and Chabot (2002) found that larger lobsters preyed on large, vagile, nutritious prey, such as crustaceans, although this latter work was done in an area that lacked nearby mussel aquaculture sites. Together, this suggests that lobsters are, in part,

more abundant in farm sites, particularly close to mussel lines, because of both the abundant prey and the addition of physical structure in the form of anchor blocks.

Sea stars were orders of magnitude more abundant in farm sites than in reference sites, showing the great attractiveness of the farm for these animals. Increased abundance of sea stars within mussel sites associated with mussel lines was also reported by Inglis and Gust (2003) and Barrett et al. (2020) for *Coscinasterias muricata* and D'Amours et al. (2008) for *Asterias* sp. Gaymer et al. (2004) showed that mussels (*M. edulis*) are the preferred prey of *Asterias* sp., again suggesting a trophic link. Similarly, Wilding and Nickell (2013) reported a negative correlation between sea star abundance and distance to mussel lines and related this to mussel fall-off. However, sea stars may also recruit in large quantities to mussel lines (Barkhouse et al., 2007) and this too could, in part, account for the greater abundance of these animals in the farm relative outside of it.

Large hermit crabs and Northern moon snails were more abundant in mussel farm sites relative to reference sites. Hermit crabs are omnivorous detritivores (Hazlett, 1981) and thus likely able to take advantage of the general increase of detritus in farm areas due to incomplete consumption of fallen mussels and associated organisms by other macropredators in the site.



In contrast, Northern moon snails are active foraging predators of molluscs (Commito, 1982) that readily feed on mussels if found in their environment (Kenchington et al., 1998) and thus were likely more abundant in the farm site because of the great concentration of fallen mussels in the area. Other authors reported similar findings of increased abundance of predatory gastropods in Eastern Canada (Grant et al., 1995; D'Amours et al., 2008).

Although small hermit crabs were, overall, more abundant in mussel farm sites than reference sites, they displayed line-scale variation in abundance in June, when they were less abundant directly below mussel lines than at other distances and locations. Small hermit crabs are vulnerable to dexterous predators, including larger hermit crabs, brachyuran crabs (e.g., rock crabs) and lobsters (Angel, 2000) and these predators

were particularly more abundant in farm sites close to mussel longlines, potentially explaining their line-scale variation in abundance. Similarly, Drummond-Davis et al. (1982) found that *P. acadianus* is the most frequently consumed prey by rock crabs in kelp beds in Nova Scotia. Although more food is available in farm sites (e.g., fallen mussels, associated organisms), small hermit crabs may avoid such areas since predation risks are elevated, illustrating a behavior defined by Kerfoot and Sih (1987) whereby aquatic prey adjust to spatial and temporal variation in predation risk.

In contrast to the positive association of animals to the mussel culture site, both ocean quahogs and sand dollars tended to be less abundant in the farm than outside of it. In both cases, this may be due to the increased abundance of predators in the farm, which may also prey on these two species. Predators of ocean quahogs include invertebrates such as brachyuran crabs (e.g., *C. irroratus*) (Stehlik, 1993), crustaceans (Kraus et al., 1992), sea stars (Kennish et al., 1994), and teleost predators such as sculpins (*Myoxocephalus* sp.) (Langton and Bowman, 1980), all which were most abundant in farm sites. Likewise, predators of sand dollars include sea stars, common rock crabs, and benthic fish (i.e., winter flounder) (Jalbert et al., 1989; Himmelman and Dutil, 1991; Gaymer et al., 2004). Most of these predators were more abundant in farm sites than reference sites. In addition to predation, mortality of ocean quahogs may also occur due to increased sedimentation (Anger et al., 1977). Thus, organic loading from biodeposition below mussel lines may, in part, explain the decreased abundance of these bivalves in farm sites. Sand dollars are more mobile than ocean quahogs and commonly burrow in sediments (Cabanac and Himmelman, 1996), suggesting that increased sedimentation may not account for the observed trends in sand dollar abundance.

The presence of physical structure in marine habitats allows for a greater abundance of organisms and species richness compared to less complex habitats (Gratwicke and Speight, 2005). Anchor blocks, ropes and other aquaculture items, including fallen mussels and shell debris, may create a more heterogeneous benthic environment and modify community richness and biomass (Chesney and Iglesias, 1979). It may also decrease the abundance of species that require flat homogeneous substrata, such as sand dollars and ocean quahogs. Significant variation at the line-scale was observed for many taxa. American lobsters were most abundant directly under the mussel line, most often associated with anchor blocks, whereas the abundance of rock crabs and sea stars increased with proximity to mussel lines and Northern moon snails and large hermit crabs showed the same trend. However, the relative importance of trophic and physical structure effects on the distribution of taxa within farms is difficult to resolve. Drouin et al. (2015) did an experiment to separate these factors and found that the association of American lobster with mussel lines is likely primarily due to the presence of anchor blocks but suggested that the abundance of food in mussel farm areas further increased their abundance. As American lobsters cannot quickly bury themselves in sand, they seek protection from other shelters in their environment (Hudon and Lamarche, 1989). In contrast, Drouin et al. (2015) also suggested that rock crabs, which are less dependent on shelter and

physical structure (Fogarty, 1976; Cobb et al., 1986; Gendron and Fradette, 1995), likely benefit from fallen mussels, thus explaining the line-scale distribution of this species.

Overall, the distribution of winter flounder does not appear to be influenced by mussel leases as no clear trend was observed except for a temporal variation. Similarly, Clynick et al. (2008) found no difference in the abundance of winter flounder in farm sites relative to reference sites. Winter flounder is a habitat generalist that occurs on a variety of shallow substrates and sediment types (Sogard and Able, 1991). According to Worobec (1984), juveniles prey opportunistically on small infaunal organisms, crustaceans, and other appropriate food as they grow. Only winter flounder was observed to vary temporally in the present study. However, the abundance of other taxa also likely vary temporally but the sampling regime employed (sampling twice at the beginning of summer) was not appropriate to detect such temporal variation.

The present study suggests that most epibenthic macrofauna taxa have a positive response to suspended mussel aquaculture in the studied offshore area. By itself, the addition of aquaculture structural features likely increase local productivity, diversity, and biomass, which are typically greater on hard-substrates (Cowles et al., 2009). Mussel fall-off from longlines likely increases the abundance of many predators in the farm site. Beyond the simple aggregative effect of predators due to fall-off, the impact of such a transfer of trophic energy from the pelagic environment (plankton) and intermediary (mussel filtration and fall-off) to the benthic environment on the animals that live there is poorly understood. Observational and modeling work on benthic scallop culture (Kluger et al., 2016a,b) suggests that the addition of farmed bivalves to the bottom increases the abundance of their predators at the bay-scale, thus benefiting fisheries of any such species, whereas this increased abundance of predators also negatively impacts non-predatory species that are normally present. However, the increased abundance of predators in farm sites may also cause farms to act as ecological traps for these animals if fishing effort is directed in or around them (Fernandez-Jover et al., 2008; Dempster et al., 2009). Although a recent review (Barrett et al., 2022) suggests that such aggregations of wild animals may enhance the productivity of farm environments relative to otherwise equivalent environments, the impact of mussel farms on the fitness of these animals is unknown. Wang and McGaw (2016) suggest that a mussel-only diet is not suitable for lobsters because of low levels of amino acids such as asparagine, alanine and glutamic acid and the carotenoid astaxanthin in mussel flesh. Further studies are needed to obtain a more holistic understanding of the interactions between mussel aquaculture and associated macrofauna to ensure the ecological sustainability of the industry and better understand its effects on the fishing industry and the fisheries species themselves.

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CONCLUSION

Marine aquaculture of many types is expanding into offshore areas to provide seafood products while limiting environmental impacts and conflict between users of the limited space in coastal zones (Froehlich et al., 2017). In the context of marine spatial planning, a better understanding of the interactions between aquaculture and fisheries is of great importance (Clavelle et al., 2019) and may be used to limit the impacts of these two activities on one another (Gentry et al., 2017; Lester et al., 2018). It is hoped that the clear evidence of increased abundance of many macrobenthic species in the examined îles-de-la-Madeleine offshore mussel farm will contribute to a more holistic (Weitzman, 2019) understanding of offshore mussel farm effects to support logical marine spatial planning.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

A-SS, AD, PA, and CM contributed to the design and concept of the study. A-SS, AD, and CM contributed to field missions, statistical analysis of the data, and writing the manuscript. AD, PA, and CM obtained funding to complete the work. All authors reviewed and edited the manuscript contributing to the final version.

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