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Farmed mussel biodeposit production and dose-dependent influence on benthic communities

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Abstract. Much work has examined the influence of benthic loading from suspended bivalve culture on benthic infaunal communities. However, little effort has been directed at determining the production of biodeposits and dose-dependent effects of biodeposition on such communities. A study was done to determine the mussel size-dependent production of biodeposits in situ and characterize biodeposit sedimentation dynamics. Based on the results of this study, an in situ manipulative experiment was done to evaluate the dose-dependent response of biodeposition on sandy benthic infaunal community structure. Benthic communities sampled with sediment cores were used to create mesocosms which were exposed over 50 days to 7 different levels of mussel biodeposition by varying the densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels, equivalent to 0, 127, 255, 382, 510, 637 and 764 mussels m-2). Benthic communities responded as would be predicted from the Pearson & Rosenberg (1978) model of organic enrichment. The abundance and biomass of opportunistic species (Capitella sp.) were observed to increase in the mesocosms exposed to the highest mussel density. Sensitive species such as Tellina agilis and Pherusa plumosa tended to decrease in abundance and biomass with increasing mussel density. These results are discussed with respect to their importance to predictive ecological modelling for bivalve aquaculture.

Keywords: mussel aquaculture, biodeposit production, organic enrichment, benthic effects, mesocosm, AMBI

Highlights related to the theme objective:
- Mussel biodeposit production and settlement dynamics determined for dispersal estimates
- Evaluation of dose-response effects of farmed mussel biodeposition on benthic communities

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Introduction

Bivalve aquaculture production is growing worldwide and concerns about its impact on the environment are increasing. Environmental influences of bivalve aquaculture are mainly related to the filtration of the plankton and seston (Dame, 1996) and the production of organically-rich faeces and pseudofaeces by the bivalves that may accumulate on the bottom (e.g., Mattsson and Lindén, 1983). Although numerous models have been developed to determine production carrying capacity (i.e., maximizing production) (e.g., Campbell and Newell, 1998), less effort has been directed at modelling effects of bivalve biodeposition on the benthos. There is thus a need to determine the benthic environmental carrying capacity of sites for bivalve aquaculture, i.e., "the maximum level of production which is possible without having an unacceptable ecological impact" (see review by McKindsey et al., 2006).

The extent and intensity of benthic effects depend on many factors, including

the age and size of culture operations, species being cultivated, bivalve density, local hydrodynamic conditions and topography, which vary considerably between sites, making general conclusions about the influence of bivalve culture on the benthic environment difficult to establish. The accumulation and decomposition of biodeposits from bivalve culture may affect the abundance, biomass and diversity of benthic communities, generally according to the Pearson and Rosenberg (1978) model of organic enrichment. However, there are critical information gaps with respect to the etiology of bivalve aquaculture benthic effects. At the basic level, there is little information available on the production of biodeposits by bivalves in culture. Dose-response relationships for bivalve aquaculture, where "dose" is the flux of biodeposition to the bottom and the "response" is chemical, physical or biological in nature, are also lacking (McKindsey et al., 2006). Such empirical studies are needed to better predict benthic changes and to help guide managers in setting density limits to maintain a given benthic condition.

The aim of this study was to investigate i) the size-specific production and sedimentation dynamics of biodeposits produced by mussels (*Mytilus edulis*) in suspended aquaculture and ii) examine the effects of short-term mussel biodeposition on sandy benthic community characteristics using *in situ* mesocosms. Biodeposit production and sedimentation were evaluated in 2 sites. Benthic communities and related parameters within mesocosms were examined following exposure to 7 mussel biodeposition rates for 50 days that simulate conditions in Quebec mussel aquaculture sites in a single location.

Methods

Biodeposit production and sedimentation rates

Biodeposition by different mussel cohorts was evaluated *in situ* by placing a fixed number of mussels within cylindrical vexar cages fitted into the top of sediment traps made of PVC tubing (10.2 cm diameter, 76.2 cm height). The number of mussels used ensured that ca. 2/3 of the cage area was covered by a layer of mussels. Sediment traps containing dead mussels were used as controls to measure background sedimentation rates. Shell treatments were used because sedimentation rates may be altered by the mussel shells physically blocking a part of the trap area and modifying the hydrodynamics at the trap entrance. Traps were retrieved following 24 h periods and the contents filtered through pre-burned and pre-weighed glassfiber filters (Whatman GF/F, 0.7 μm). Filters were rinsed with ammonium formate, dried to constant weight, and weighed. Biodeposition was calculated as the amount of material collected in the sediment traps with mussels less the average sedimentation obtained in the corresponding shell controls, and expressed as biodeposit production per individual mussel.

Each treatment had three replicates in each experimental location on each trial date. Rates were evaluated on three trial dates in Great Entry Lagoon, Magdalen Islands (GE), in 2003 and on two trial dates in Cascapedia Bay, baie-des-Chaleurs (CAS), in 2005. The sediment traps were deployed on the bottom 800 m outside of the mussel farm in GE and hung on empty backlines in CAS. Experimental cages in GE each contained 6 mussels measuring 4.0 to 5.2 cm in length or 3 mussels measuring 6.7 to 6.9 cm for 0+ and 1+ mussels, respectively. Experimental cages in CAS each contained 6 mussels measuring 5.5 to 5.7 cm in length or 3 mussels measuring 6.6 to 6.7 cm for 1+ and 2+ mussels, respectively. These size ranges were selected based on preliminary field measurements of mussels on mussel lines at that time.

The sinking velocity of biodeposits was evaluated only in GE. Faecal pellets were collected for 5 size classes of mussels

(3, 4, 5, 6 and 7 cm shell length, 3 mussels trap^{-1}) using sediment traps as described above. The sinking speed of randomly chosen faecal pellets collected from the sediment traps was evaluated in a cylindrical glass sedimentation column (45 cm height, 10.5 cm diameter) filled with filtered (0.7 µm) seawater (21 ± 1°C, 28 psu) by measuring the time needed for faecal pellets to pass between 2 marks separated by 10 cm. The dimensions and sinking speed of at least 25 randomly chosen faecal pellets were measured for each mussel size class.

Local biodeposition rates were predicted based on the number and size of mussels on mussel lines in the study locations combined with measured biodeposit production and settlement velocities and local hydrodynamic regime (see Callier et al., 2006).

Benthocosms and benthic community analyses

Thirty five sediment cores (PVC pipes, 78.5 cm^2 cross-section area and 20 cm high, filled with benthic sediments to 17cm) were collected by SCUBA divers from a 5 m deep area with a sandy bottom in GE. Cores were fitted with PVC caps on both the tops and bottoms and transported to experimental racks – iron bars fitted with plastic caps secured at 40 cm intervals open end up to act as holders for the sediment cores - "benthocosms" (Fig. 1). Biodeposition was modified experimentally by placing 0, 1, 2, 3, 4, 5, or 6 mussels within cylindrical vexar cages fitted into the top of cores (5 replicates per mussel density), corresponding to 0 to 764 mussels m^{-2} (equivalent to the density of mussels found in Quebec aquaculture sites) or 0 to 16.8 g dw biodeposits m^{-2} d^{-1}.

The experiment was run for ca. 50 days (June 12 through August 4-6 2004), at which time benthocosms were collected and the macrofauna (> 500 µm) quantified. The period of 50 days was selected based on the turnover rate of one of the indicator species present in the general area, the opportunist polychaete *Capitella* sp. (37 to 50 days at 15

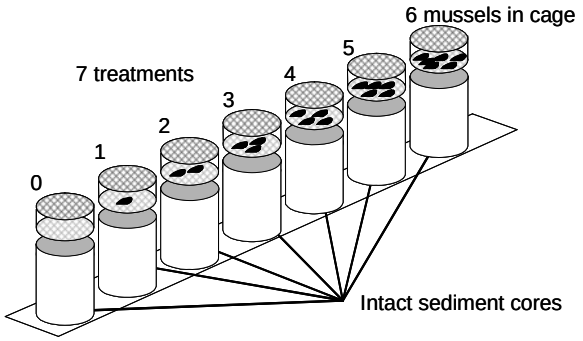

Fig. 1. Benthocosms (78.5 cm^2 sediment cores) exposed to 7 mussel densities (0, 1, 2, 3, 4, 5, 6 mussels. cage^{-1}). Five replicates per mussel density were placed randomly at 40 cm intervals along an iron support (diagram not to scale).

ºC, Grassle and Grassle, 1974). The experiment was done > 2 km from the mussel farm in GE and on the far side of a navigation channel and therefore not otherwise under the influence of mussel biodeposition.

Sites were characterised in terms of total abundance, total biomass and the number of species (species richness). Species were classified into ecological groups based on their sensitivity to organic enrichment to calculate a global index of community status (AMBI – see Borja et al., 2000) using AMBI version 4.0 (http://www.azti.es). The AMBI index was combined with richness and a diversity index (Shannon Wiener) to give a multivariate index (M-AMBI – see Muxika et al., 2007).

Statistical analysis

The relationships between: (i) mussel size and biodeposit production, (ii) mussel size and faecal pellet size, and (iii) faecal pellet size and sinking velocity were evaluated by linear regression. Variations in biodeposit production between dates were evaluated by ANCOVA, with mean mussel mass as the covariate on $\log_{10}$-transformed data. Macrofaunal benthic characteristics (species richness, abundance and biomass)

among the mussel densities were compared using analysis of variance (ANOVA). Nonparametric multivariate analyses of community structure (based on counts and biomass), including multi-dimensional scaling (MDS) were done using PRIMER version 5.2.9 (Clarke and Warwick, 1994) and DISTLM (McArdle and Anderson, 2001. Data were √-transformed for all multivariate analyses. Of 35 samples, 2 replicates were lost during the manipulation by divers (one each from the n = 1 and n = 4 mussel treatments). A further replicate (from the n = 5 mussel treatment) was considered as an extreme outlier (with a density of one species - *Tellina agilis* > 10 × greater than the next largest abundance for this species) and was not included in further analyses.

Results

Biodeposit production and sedimentation rates

Summarized results on the relationship between *M. edulis* size and biodeposit production are given in Tables 1 and 2. Both background and biodeposit-related sedimentation rates varied among sampling dates and locations (Table 1). Although larger mussels within a location produced a greater mass of biodeposits relative to that produced by smaller ones, biodeposit production per unit mussel biomass showed the opposite trend (data not shown). This relationship was further elucidated by size-based production and sedimentation evaluations, as outlined in Table 2. Sedimentation rates were best described by faecal pellet width, the two variables being positively correlated.

Benthocosms and benthic community analyses

Total abundance differed significantly among mussel density treatments such that abundance was greatest in control benthocosms and generally decreased thereafter, with the lowest abundance recorded in benthocosm with 3 mussels cage^{-1} (Fig. 2, Table 3). Control benthocosms had the greatest species richness and benthocosms with 3 and 4 mussels cage^{-1} had the smallest species

Table 1. Biodeposit production measured *in situ* for 2 mussel cohorts (0+ and 1+) in Great Entry Lagoon (GE) during 3 trial dates and for 2 mussel cohorts (1+ and 2+) in Cascapedia Bay (CAS) during 2 trial dates. Average mussel shell length (cm), minimum and maximum biodeposit production rates (mg mussel^{-1} d^{-1}) are given for each mussel cohort. Biodeposition was calculated as the amount of material collected in sediment traps with mussels less the average sedimentation obtained in the corresponding shell controls (see text for details). Each treatment had 3 replicates on each trial date.

Site	Trial date	Mussel size (cm)	Biodeposit production (mg mussel^{-1} d^{-1}) (range, mean, ± SE)
GE 0+	Aug 14-15	4.0 ± 1.1	24-32, 29.1 ± 4.8
	Aug 18-19	4.5 ± 0.3	25-75, 51.1 ± 25.2
	Aug 21-22	5.2 ± 0.3	13-21, 17.0 ± 5.7
GE 1+	Aug 14-15	6.9 ± 0.2	32-52, 44.4 ± 10.5
	Aug 18-19	6.7 ± 0.2	65-126, 86.0 ± 34.3
	Aug 21-22	6.7 ± 0.3	17-33, 24.2 ± 7.8
CAS 1+	July 6-7	5.7 ± 0.3	29-58
	July 9-10	5.5 ± 0.3	15-32
CAS 2+	July 6-7	6.7 ± 0.2	45-95
	July 9-10	6.6 ± 0.4	29-39

Table 2. Results of the linear regression analysis of: (i) biodeposit production DW as a function of mussel tissue DW on different sampling dates, and (ii) sinking velocity as a function of faecal pellet size. For all analyses: $y = ax + b$

	Dependent (y)	Independent (x)	a	b	r^2	p	n
(i)	Biodeposit production ($\log_{10}$, mg g^{-1} tissue d^{-1})	Mussel tissue DW ($\log_{10}$, g)					
		14 to 15 August	–0.691	1.625	0.762	0.005	8
		18 to 19 August	–0.809	1.832	0.714	0.001	11
		21 to 22 August	–1.060	1.316	0.656	0.001	7
(ii)	Sinking velocity (cm s^{-1})	Faecal pellet size (mm)					
		Width	0.589	0.328	0.426	0.000	235
		Length	0.037	0.761	0.128	0.000	235
		Area	0.029	0.783	0.193	0.000	235

richness (Fig. 2). The greatest biomass was recorded in benthocosms receiving biodeposits from 1 mussel $cage^{-1}$ (Fig. 2). Overall, abundance and species richness were negatively correlated with mussel density (Table 3).

The abundance and biomass of several dominant species were correlated with mussel density (see Fig. 3 for abundance data; for brevity, results using biomass data are not shown as they show the same general trends). The abundances of the polychaete *Pherusa plumosa* and the bivalve *T. agilis* were greatest in control benthocosms (i.e., no mussel biodeposition) and negatively correlated with mussel density (Fig. 3, Table 3). In contrast, the polychaete *Capitella* sp. was most abundant in benthocosms receiving biodeposition from 6 mussels $cage^{-1}$, although this trend was not statistically significant (Fig. 3).

Community structure. Community structure differed significantly among

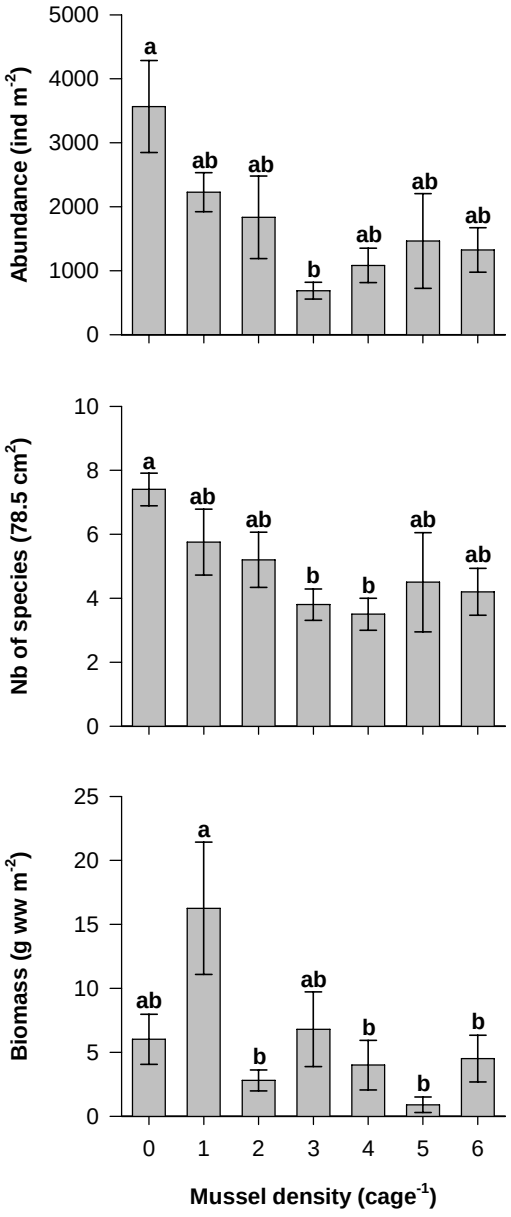

Fig. 2. Mean benthic macrofaunal abundance, species richness, and biomass (± SE, n = 4 to 5) measured in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels $cage^{-1}$). Different letters indicate significant differences between treatments. Data are standardized (m^{-2}), except for species richness (reported as number of species per benthocosm). →

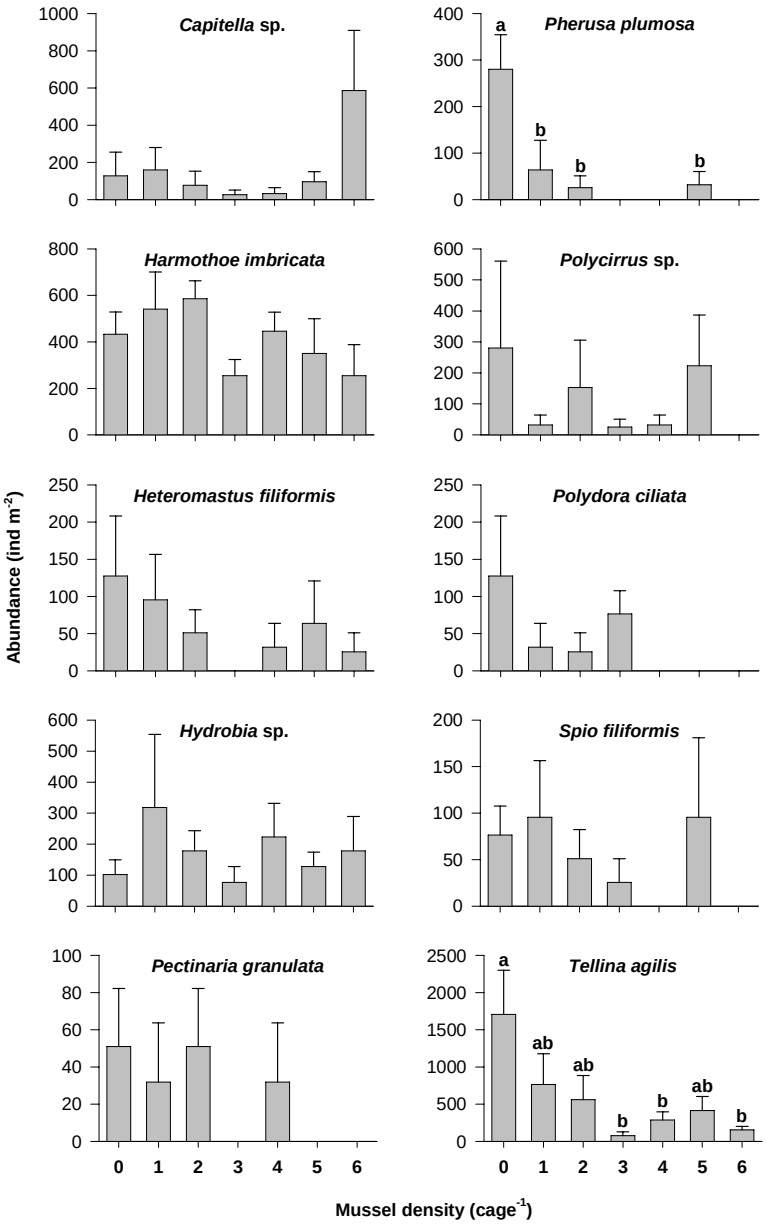

Fig. 3. Mean abundance (average ± SE, n = 4 to 5) of dominant species in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}). Different letters indicate significant differences between treatments.

treatments (Fig. 4, p = 0.036). That in control benthocosms (0 mussels) differed from those exposed to biodeposition from 3, 4 and 6 mussels and communities from benthocosms with 2 mussels differed from those with 6 mussels.

Ecological groups. Benthocosms receiving the greatest level of biodeposition had the greatest proportion of second-order opportunistic species (data not shown). Accordingly, M-AMBI was significantly negatively correlated to mussel density (Fig. 5) and the disturbance classification indicated a shift between a slightly disturbed to a moderately disturbed community structure at a density of 764 mussels m^{-2} (n = 6 mussels benthocosm^{-1}).

Table 3. Results of the significant relationships between mussel biodeposition rates in benthocosms and various parameters describing the communities within them, including abundance (N) and taxonomic richness (S), and the abundance of individual species.

Variable	r^2	p
N	0.250	0.004
S	0.277	0.002
Abundance		
Tellina agilis	0.268	0.002
Pherusa plumosa	0.322	0.001
Polydora ciliata	0.161	0.023
Pectinaria granulata	0.122	0.050

Discussion

The effect of organic enrichment on benthic marine communities has been well documented (Pearson and Rosenberg, 1978). However, organic enrichment related to bivalve farming does not always follow the general organic enrichment model described by Pearson and Rosenberg (1978) (e.g., Grant et al., 1995). Further, there is a lack of information on the dose-response relationship between bivalve biodeposition rates and benthic variables. The aim of this study was therefore to provide some useful information on the dose-response relationship between mussel biodeposition rates and macrofaunal communities.

Biodeposit production and sedimentation rates

Biodeposit production was shown to be a function of *M. edulis* size with smaller mussels producing more biodeposits per unit body mass than do large mussels. This has been explained by the higher clearance rates of younger mussels compared to older ones (Tsuchiya 1980).

Biodeposit production differed considerably between sampling dates, and this may be related to changes in food quantity and quality, as has been observed in previous studies (Tenore & Dunstan 1973). Although several studies have shown relationships between environmental conditions and mussel metabolism, a field study that measured daily seston availability and several environmental parameters showed that these factors explained only 28% of the variation in daily ingestion rates of mussels (Cranford & Hill 1999) and so this likely cannot explain the variations observed. But his does underline the importance of doing such experiments several times to better understand the natural variation in biodeposit production and, by extension, sedimentation rates.

Although increasing with mussel size, the average sinking velocity of 1.0 ± 0.3 cm s^{-1} for *M. edulis* faecal pellets measured in this study was about twice that observed by Chamberlain (2002) for 4.2 cm *M. edulis* individuals. Our results were within the 0.2 to 4.5 cm s^{-1} range observed for the mussel *Perna canaliculus* measuring 2.7 to 11.4 cm (Giles & Pilditch 2004). De Jong (1994) reported that faecal pellets of *P. canaliculus* settled at a rate of 1.2 ± 0.1 cm s^{-1}, although the size of the mussels studied was not given and Hartstein & Stevens (2005) reported that faecal pellets from 6 cm individuals of the same species settled at 3.0 ± 0.4 cm s^{-1}.

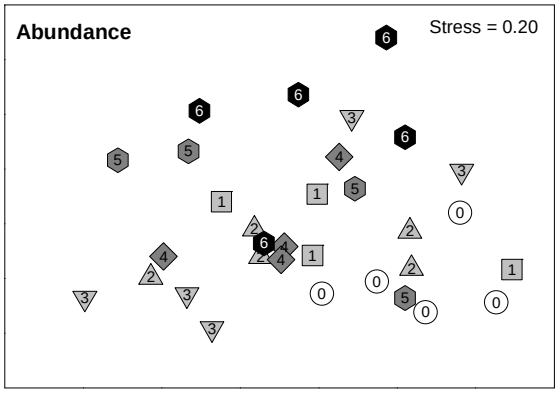

Fig. 4. MDS on abundance data of communities from benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels $cage^{-1}$).: 0 (○), 1 (□), 2 (△), 3 (▽), 4 (◆), 5 (⬢) and 6 (⬢) mussels $cage^{-1}$.

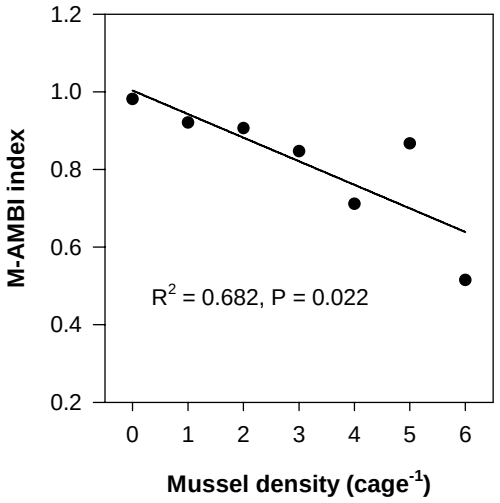

Fig. 5. Linear relationships between the biotic index (AMBI) and mussel density. Data from the 5 replicates at each level were pooled.

Variations in sinking velocity may be due in part to variations in food quality, which has been shown to influence faecal pellet density. For example, faecal pellets from mussels fed on diets with a high silt content sank more rapidly than those from mussels fed on mostly algal diets (Chamberlain 2002, Miller et al. 2002, Giles & Pilditch 2004).

Macrofaunal response

This part of the study was done to simulate biodeposition conditions in bivalve aquaculture farms in eastern Canada. Miron et al. (2005) have, for example, observed mussel densities ranging from 0.16 to 0.70 kg m^{-2} in Prince Edward Island and the mussel density in GE was ca 575 mussels per linear metre of longline (Callier et al., 2006). This range of densities is relatively low as compared to other countries. For example, mussel densities are ca. 24 kg m^{-2} in Sweden (Dahlbäck and Gunnarsson, 1981) and 175 kg m^{-2} in raft culture in South Africa (Stenton-Dozey et al., 1999). However, the different levels of deposition and associated organic loading that were created in experimental benthocosms in the present study were great enough to influence the biological and chemical environments within them.

Overall, abundance and species richness decreased with increasing biodeposition in accordance with the Pearson and Rosenberg (1978) general model of organic enrichment and as observed in other studies (e.g., Mattsson and Lindén, 1983; Chamberlain et al., 2001; Callier et al., 2007).

Only *P. plumosa* and *T. agilis* showed significant (negative) trends with mussel density. Both are classified as being sensitive to pollution. Although not statistically significant, *Capitella* sp. clearly responded to increased biodeposition. The present experiment was run over 50 days, which corresponds to the life span of *Capitella* sp. (37 to 50 days at 15 ºC, Grassle & Grassle 1974). That the abundance of this species was not increased substantially except for at the greatest biodeposition rate suggests that there may be a threshold or organic loading below which this species does not react.

Classifying species into ecological groups showed that opportunistic species dominated the benthocosms exposed to the greatest level of deposition. The related biotic index – M-AMBI – responded clearly to increased biodeposition rates and may therefore be a useful tool for assessing the effect of bivalve farming on the benthic environment, thus extending observations by Muxika et al. (2005) as to the generality utility of AMBI for detecting various sources of disturbance, including finfish aquaculture, to include the influence of bivalve aquaculture – even at the relatively low densities farmed in eastern Canada.

Conclusions

The use of cores probably limits the generalisation of the observed effects. Only *Capitella* sp. showed an increase in abundance with increased biodeposition and this perhaps only because its life history allowed it to increase its local (benthocosm-scale) abundance via self recruitment. Trends in abundances for other species were mostly decreases at greater biodeposition

levels. This may represent a lack of recruitment from within or outside of the benthocosms. However, relative comparisons between the treatments are valid as all treatments were similar in the way they were manipulated (excepting biodeposition levels). Another experimental design would be needed to allow for the recruitment to the sediments to be better represented within the study.

The results of this manipulative experiment are an important first step towards evaluating the environmental carrying capacity of sites for bivalve aquaculture. Further research is needed to extend the generality of the findings and to the range of biodeposition increase as well as to reduce potential experimental artefacts.

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References

Borja, À., Franco, J., Perez, V., 2000. A Marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Pollut. Bull. 40, 1100-1114.

Callier, M.D., Weise, A.M., McKindsey, C.W., Desrosiers, G., 2006. Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion. Mar. Ecol. Prog. Ser. 322, 129-141.

Callier, M.D., McKindsey, C.W., Desrosiers, G., 2007. Multi-scale spatial variations in benthic sediment geochemistry and macrofaunal communities under a suspended mussel culture. Mar. Ecol. Prog. Ser. 348: 103-115.

Campbell, D.E., Newell, C.R., 1998. MUSMOD©, a production model for bottom culture of the blue mussel, *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 219, 171-203.

Chamberlain, J., 2002. Modelling the environmental impacts of suspended mussel (*Mytilus edulis* L.) farming. PhD thesis, Napier University, Edinburgh, pp. 200.

Chamberlain, J., Fernandes, T.F., Read, P., Nickell, T.D., Davies, I.M., 2001. Impacts of biodeposits from suspended mussel (*Mytilus edulis* L.) culture on the surrounding surficial sediments. ICES J. Mar. Sci. 58, 411-416.

Clarke, K.R., Warwick, R.M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory. Plymouth. pp. 141.

Cranford, P.J., Hill, P.S., 1999. Seasonal variation in food utilization by the suspension-feeding bivalve molluscs *Mytilus edulis* and *Placopecten magellanicus*. Mar. Ecol. Prog. Ser. 190, 223-239.

Dahlbäck, B., Gunnarsson, L.Å.H., 1981. Sedimentation and sulfate reduction under a mussel culture. Mar. Biol. 63, 269-275.

Dame, R.F., 1996. Ecology of marine bivalves. An ecosystem approach. CRC Press, Boca Raton.

de Jong, R.J., 1994. The effects of mussel farming on the benthic environment, School of Biological Sciences. University of Aukland, Aukland, pp. 145.

Giles, H., Pilditch, C.A., 2004. Effects of diet on sinking rates and erosion thresholds of mussel *Perna canaliculus* biodeposits. Mar. Ecol. Prog. Ser. 282, 205-219.

Grant, J., Hatcher, A., Scott, D.B., Pocklington, P., Schafer, C.T., Winters,

G.V., 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries 18, 124-144.

Grassle, J.F., Grassle, J.P., 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. J. Mar. Res. 32, 253-284.

Hartstein, N.D., Stevens, C.L., 2005. Deposition beneath long-line mussel farms. Aquacult. Eng. 33, 192-213.

Mattsson, J., Lindén, O., 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. Sarsia 68, 97-102.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290-297.

McKindsey, C.W., Thetmeyer, H., Landry, T., Silvert, W., 2006. Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261, 451-462.

Miller, D.C., Norkko, A., Pilditch, C.A., 2002. Influence of diet on dispersal of horse mussel *Atrina zelandica* biodeposits. Mar. Ecol. Prog. Ser. 242, 153-167.

Miron, G., Landry, T., Archambault, P., Frenette, B., 2005. Effects of mussel culture husbandry practices on various benthic characteristics. Aquaculture 250, 138-154.

Muxika, I., Borja, Á., Bonne, W., 2005. The suitability of the marine biotic index (AMBI) to new impact sources along European coasts. Ecol. Indic. 5, 19-31.

Muxika, I., Borja, À., Bald, J., 2007. Using historical data, expert judgement and multivariate analysis in assessing reference conditions and benthic ecological status, according to the European Water Framework Directive. Mar. Pollut. Bull. 55, 16-25.

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Annu. Rev. 16, 229-311.

Stenton-Dozey, J.M.E., Jackson, L.F., Busby, A.J., 1999. Impact of mussel culture on macrobenthic community structure in Saldanha Bay, South Africa. Mar. Pollut. Bull. 39, 357-366.

Tenore, K.R., Dunstan, W.M., 1973. Comparison of feeding and biodeposition of three bivalves at different food levels Mar. Biol. 21, 190-195.

Tsuchiya, M, 1980. Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. J Exp Mar Biol Ecol 47:203-222