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CHAPITRE 1

INTRODUCTION GÉNÉRALE

1.1 CONTEXTE DE L'ÉTUDE

Depuis la fin des années 1980, la production mondiale de la pêche a atteint un maximum et reste stable (Figure 1.1). Les stocks de pêche s'épuisent, mais la consommation humaine de poissons ne cesse d'augmenter. Pour répondre à cette demande croissante, l'industrie aquacole se développe mondialement. Ainsi, la part de l'aquaculture dans la production totale de poissons, de mollusques et de crustacés est passée de 5 % en 1970 à 38 % en 2004 (http://www.fao.org/statistics/). La production annuelle aquacole a augmenté de 20 MT en 1992 à 60 MT en 2004, soit une augmentation de 7,1 % par an. L'aquaculture en milieu marin représente 51 % de la production totale. Les productions s'intensifient, s'étendent géographiquement et de nouvelles espèces sont cultivées.

Au Canada, l'aquaculture a produit 154 993 tonnes en 2005 dont 74 % de poissons (Figure 1.2). La production conchylicole représentait 38 283 tonnes en 2005 dont 60% de production mytilicole (22 842 tonnes).

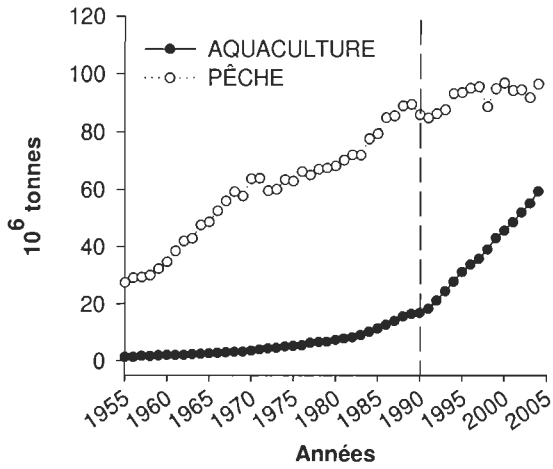

Figure 1.1 Production mondiale de poissons et mollusques en aquaculture comparée à la pêche par capture, donnée en millions de tonnes (http://www.fao.org/statistics/).

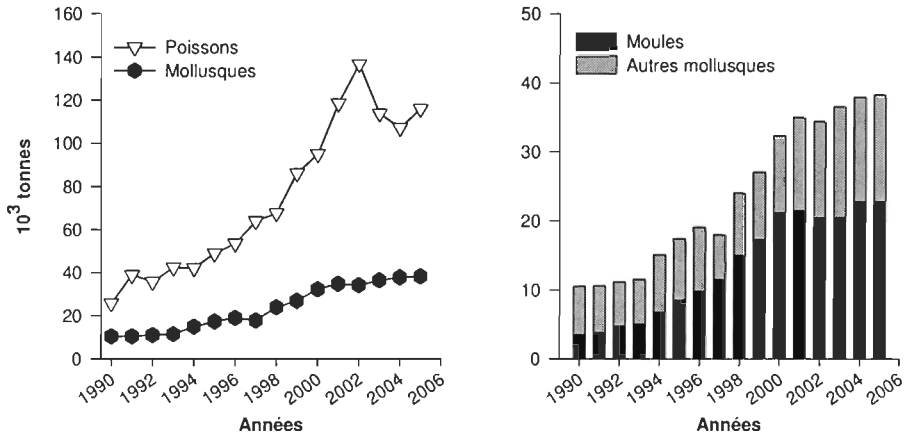

Figure 1.2 Évolution de la production totale aquacole depuis les années 90 au Canada (gauche) et de la production conchylicole (droite) (données obtenues en 2006 sur http://www.dfo-mpo.gc.ca/aquaculture/statistics/index_f.htm)

Comparée à la pisciculture, la conchyliculture est une industrie demandant un faible investissement financier, les bénéfices sont donc importants. Cette réalité économique a conduit à une expansion importante de la conchyliculture (Kaiser et al. 1998). Parmi les différents types de conchyliculture, la mytiliculture s'est développée très rapidement. Au Québec, la production conchylicole annuelle est passée de 76 tonnes en 1996 à 915 tonnes en 2005 (Figure 1.3) dont 82 % de moules (http://www.mapaq.gouv.qc.ca). Ces chiffres restent cependant faibles par rapport à d'autres régions du Canada comme l'Île du Prince Édouard où la production annuelle a atteint 18 911 tonnes en 2005 dont 85 % de moules (www.statcan.ca).

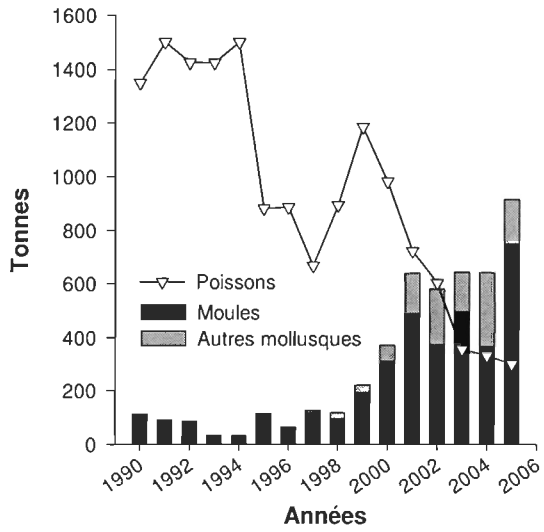

Figure 1.3 Production aquacole annuelle au Québec. La production piscicole a diminué au cours des 15 dernières années alors que la production mytilicole est en pleine expansion (données obtenues en 2006 sur http://www.mapaq.gouv.qc.ca).

1.2 INTERACTIONS CONCHYLICULTURE-ENVIRONNEMENT

De nombreuses études ont mis en évidence l'influence des activités aquacoles sur l'environnement (voir les revues de littérature par Black 2001, Hargrave 2005). Cependant, la majorité des études se sont intéressées aux effets environnementaux liés à la pisciculture en mer (Pearson & Black 2001, Pohle et al. 2001, Wildish et al. 2003), et en eau douce (Black 2001). Les effets environnementaux de la pisciculture sont reliés principalement : 1- à la sédimentation des fèces et de la nourriture excédentaire, qui peut induire une pollution organique importante sous les cages de poissons (Hall et al. 1990, Pohle et al. 2001, Stewart & Grant 2002) affectant les communautés benthiques (Findlay et al. 1995), 2- aux produits chimiques comme les pesticides, médicaments et agents antisalissures (Burridge 2003) et 3- aux interactions entre les poissons d'élevage et les espèces sauvages (transferts de maladies et interactions génétiques et écologiques) (Kapuscinski & Brister 2001).

La conchyliculture apparaît *a priori* moins dommageable pour l'environnement car elle ne nécessite pas d'ajout de nourriture, les bivalves se nourrissant du seston présent dans la colonne d'eau (Newell 2004). Cependant, de nombreuses interactions existent entre la conchyliculture et l'écosystème (Figure 1.4). Par l'activité de filtration, la conchyliculture a davantage d'influences sur le pelagos que l'aquaculture de poissons (Newell 2004, Cranford et al. 2006, McKindsey et al. 2006a). Et contrairement à la pisciculture, les cultures de bivalves sont souvent extensives, pouvant s'étendre sur des km^2. Les effets peuvent donc être plus diffus, plus étendus, et par conséquent plus difficiles à détecter.

La prochaine section présente une revue des connaissances sur les différentes interactions de la conchyliculture avec l'environnement pélagique et benthique. Les exemples d'études mentionnés concernent spécifiquement les cultures de bivalves.

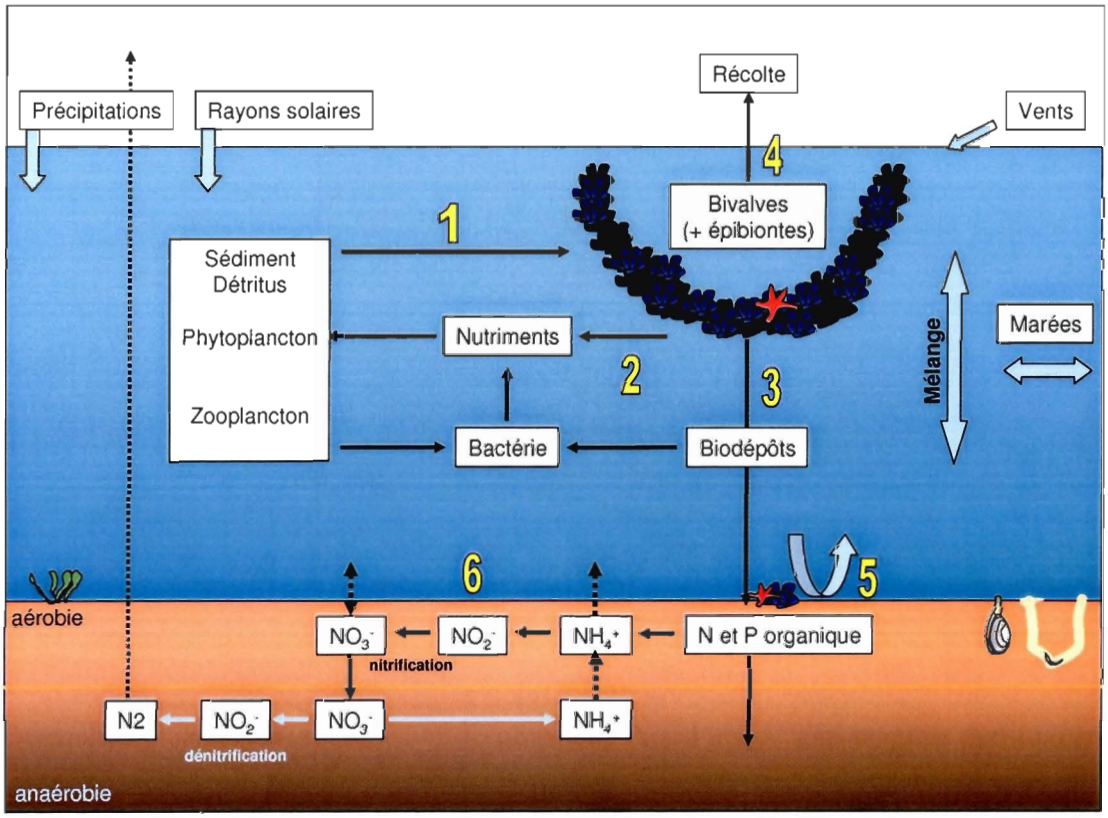

Figure 1.4 Schéma des principales interactions entre la conchyliculture et l'écosystème côtier. 1- Filtration du seston par les bivalves, 2- Excrétion sous forme dissoute (riche en ammonium), 3- Détournement de la matière organique (MO) par le processus de biodéposition 4- Retrait de la MO lors de la récolte, 5- Rôle des biodépôts sur le benthos, 6- Reminéralisation des biodépôts et flux à l'interface eau-sédiment (adapté de Newell 2004 et McKindsey et al. 2006a).

1.2.1 L'environnement pélagique

La filtration est un paramètre important dans la dynamique des composés particulaires (Mayzaud et al. 1992). Pour se nourrir, les bivalves filtrent la matière particulaire en suspension (MPS) ou seston, constituée principalement du phytoplancton, du zooplancton, de détritus et de particules inorganiques. La capacité de filtration des bivalves est limitée par la capacité de rétention des branchies (Cranford et al. 2006). Bien que ces valeurs varient selon l'espèce et la taille des individus, la capacité de rétention est de 100 % pour les particules >3 µm, et seulement de 50 % pour les particules <1 µm (Møhlenberg & Riisgård 1978). La limite supérieure de rétention est d'environ 0,5 à 6 mm (Karlsson et al. 2003). Ainsi, le nanoplancton (2-20 µm), le microplancton (20-200 µm) et le mesoplancton (200-1000 µm) sont efficacement filtrés par les bivalves, contrairement au picoplancton (0,2-2 µm) (Cranford et al. 2006). Karlsson et al. (2003) indiquent que des larges particules comme des détritus de plantes, des diatomées benthiques et des larves d'invertébrés peuvent être filtrées par les bivalves et constituent ainsi une source de nourriture pour les bivalves. Dans des systèmes où le temps de renouvellement des eaux est faible et/ou la densité de bivalves est élevée, des compétitions intra- et interspécifiques pour la nourriture entre les bivalves de culture et les espèces endémiques de bivalves ou encore le zooplancton sont possibles (Newell 2004).

Les bivalves peuvent à la fois : 1- diminuer la concentration en cellules planctoniques par le processus de filtration et 2- stimuler la production primaire par l'excrétion dissoute, et par la reminéralisation de la matière organique (MO) contenue dans les biodépôts (Prins

et al. 1998). La diminution de la turbidité par l'activité de filtration peut également permettre une meilleure pénétration de la lumière et ainsi favoriser la production primaire. Les deux premiers points sont détaillés ci-dessous.

1- L'ajout d'une grande densité de bivalves de cultures dans la colonne d'eau entraîne une diminution de la concentration de la MPS. Les effets peuvent être importants dans le cas où la prise des particules est plus rapide que leur remplacement par le renouvellement des eaux ou par la production primaire (Cranford et al. 2006). En France, par exemple, les cultures intenses d'huîtres ont induit un changement dans l'abondance et la qualité des particules en suspension dans le bassin de Marennes-Oléron (Héral et al. 1986). Sur l'Île-du-Prince-Édouard, dans 5 baies, la chlorophylle *a* est réduite de 45 à 88 % par les bivalves (Meeuwig et al. 1998). Il est cependant difficile d'évaluer précisément l'impact de la filtration des bivalves sur les flux de matière et d'énergie à l'échelle de l'écosystème. En effet, des connaissances sur les processus de stratification et de mélange de la colonne d'eau ou sur le renouvellement des eaux par les marées sont nécessaires.

2- De nombreuses études montrent que la conchyliculture peut affecter la dynamique des nutriments dans leur environnement. Le processus d'excrétion chez les bivalves se traduit par la production de composés dissous et particulaires (fèces et pseudofèces). L'azote absorbé par les bivalves est utilisé pour la croissance des tissus et le reste est excrété sous forme d'urine (70% constitué d'ammonium NH_4+, 0%-13% d'urée CON_2H_4 et 5-21% d'amino-N) (Bayne et al. 1976). La décomposition des biodépôts induit des flux de nitrates, phosphates et silicates à l'interface eau-sediment (Hatcher et al. 1994). La

croissance des microalgues peut être aussi stimulée par le mucus sécrété par les bivalves et rejeté dans leurs biodépôts (Cognie & Barille 1999). Ainsi, la conchyliculture, source de sels nutritifs, peut stimuler la croissance des microalgues dont les bivalves se nourrissent.

La conchyliculture peut également avoir un effet sur les ratio des nutriments avec des conséquences sur les compositions des communautés phytoplanctoniques. L'augmentation du rapport N:Si peut, par exemple, favoriser les cellules non-silicieuses (flagellés) au détriment des diatomées (Cloern 2001). D'autre part, les bivalves, en filtrant les cellules supérieures à 3 µm, favorisent la dominance du picoplancton et changent ainsi la composition spécifique du milieu (Newell 2004, Cranford et al. 2006). Ces changements peuvent avoir en retour des conséquences sur les cultures, le picoplancton étant moins nutritif pour les bivalves que le nanoplancton (Newell 2004).

La présence de culture des bivalves en suspension peut affecter la distribution de l'oxygène dissous. Les bivalves consomment de l'oxygène pour leur respiration. La faune et la flore associées à ces bivalves consomment ou produisent de l'oxygène. Les cultures de bivalves peuvent avoir un effet dramatique sur les teneurs en oxygène dissous, quand elles sont placées dans des milieux peu profonds avec de faibles courants. Des épisodes d'hypoxie ont été par exemple observés dans la lagune de Thau en France pendant l'été (Deslous-Paoli et al. 1998).

1.2.2 Le processus de biodéposition

Définition

Le terme de biodéposition est défini comme le phénomène de sédimentation de particules organiques ou inorganiques rejetées par des organismes filtreurs (Sornin 1984). Les particules pénétrant dans l'appareil digestif et rejetées par l'anus sont appelées fèces (Sornin 1984). Les particules filtrées mais non ingérées et agglomérées par du mucus sont rejetées sous forme de pseudofèces (Haven & Morales-Alamo 1966). L'ensemble des fèces et pseudofèces constitue les biodépôts (Figure 1.5). Le processus de biodéposition joue un rôle clef sur le couplage pelagos-benthos (Wotton & Malmqvist 2001).

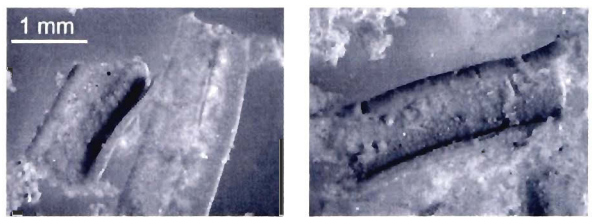

Figure 1.5 Photographies de fèces de moules *Mytilus edulis* (par Andréa Weise). La taille des fèces de *M. edulis* peut varier de 0,7 à 29,0 mm en longueur et de 0,3 à 1,8 mm en largeur (Callier et al. 2006).

Les fèces et pseudofèces, ayant une plus grande taille que les particules qui les composent, sédimentent plus rapidement vers le benthos (Wotton & Malmqvist 2001). Cette vitesse peut atteindre 4,5 cm s^{-1} pour les fèces de moule *Perna canaliculus* (Giles et

al. 2006). Haven et Morales-Alamo (1966) ont calculé que la vitesse de sédimentation de particules fines de 2 à 3 µm augmentait de 20 à 200 fois lorsqu'elles étaient agglomérées en fèces. Le processus de biodéposition a donc pour effet de détourner la matière en suspension des réseaux trophiques planctoniques vers les réseaux benthiques (Cloern 1982, Noren et al. 1999, Cranford et al. 2003).

Composition

Peu d'études ont évalué la composition des biodépôts de bivalves. Les rares études montrent que les biodépôts sont riches en carbone et azote organique avec des ratios de ces deux éléments variant entre 4,8 et 8,5 (Kautsky & Evans 1987, Loo & Rosenberg 1989, Ahn 1993, Miller et al. 2002), et des pourcentages de MO variant de 20 à 70 % (Cranford & Hill 1999). Ces valeurs indiquent que les biodépôts ont une forte valeur nutritive comparés au sédiment dont le ratio est généralement supérieur à 10 (Parson et al. 1977). La composition des biodépôts varie en fonction de la composition du seston. Plus le pourcentage de matière inorganique (MI) sera élevé dans la colonne d'eau, plus les bivalves excréteront des pseudofèces pauvres en MO (Miller et al. 2002). Lorsque les concentrations en MI sont élevées, les pseudofèces contiennent tout de même du carbone organique car du mucus est nécessaire pour agglomérer les particules inorganiques (Davies & Hawkins 1998). D'autre part, étant donné que les cultures de bivalves sont souvent placées dans des milieux à forte production primaire, les biodépôts ont généralement une forte valeur nutritive (Giles 2006).

La MO est composée de composés labiles et réfractaires. La partie labile contient des sucres simples et des protéines qui peuvent être rapidement minéralisées par les bactéries, cette partie est donc potentiellement disponible pour les niveaux trophiques supérieurs (Fichez 1991, Danovaro et al. 1993). Au contraire, la fraction réfractaire de la MO se dégrade lentement, elle est sujette à un enfouissement et n'est donc pas utilisable par les réseaux trophiques benthiques à court terme (Fabiano & Danovaro 1994). Les pelotes fécales sont colonisées par des micro-organismes dès leur excrétion. Composés majoritairement par de la MO labile, elles sont rapidement dégradées lorsqu'elles sédimentent sur le benthos. Par exemple, la demi-vie des biodépôts de *P. canaliculus* a été estimée à 4,3 jours (Giles & Pilditch 2006).

Bien qu'ayant un rôle important dans le couplage pelagos-benthos, la dynamique de biodéposition est encore peu étudiée (Cranford et al. 2003, Giles 2006). Peu de données sont disponibles sur la vitesse de sédimentation et le processus de resuspension des biodépôts qui sont essentiels dans l'évaluation du potentiel de dispersion des biodépôts (Giles & Pilditch 2004). Il est difficile d'estimer la vitesse de sédimentation en fonction d'équation, telle que la loi de Stokes, car la forme et composition des biodépôts varient en fonction de nombreux facteurs tels que la taille des individus et la composition du seston (Chamberlain 2002, Giles & Pilditch 2004) et ces équations sont valables pour des formes sphériques, cylindriques, coniques ou rectangulaires, ce qui n'est pas le cas des fèces et des pseudofèces (Taghon et al. 1984).

Les résultats disponibles sur la vitesse de sédimentation des biodépôts de moules ont été publiés récemment (Miller et al. 2002, Giles & Pilditch 2004, Hartstein & Stevens 2005). Ces études ont évalué l'effet des variations de la quantité et la qualité de nourriture sur la vitesse de sédimentation des biodépôts. Parmi ces études, seulement celle de Giles & Pilditch (2004) a évalué l'influence de la taille des bivalves sur la vitesse de sédimentation des biodépôts. Or, ce paramètre apparaît important étant donné que plusieurs cohortes de bivalves peuvent être cultivées en même temps. Giles & Pilditch (2004) ont montré que la vitesse de sédimentation augmentait avec la taille du bivalve. Cependant, les données existantes ne concernent que l'espèce *P. canaliculus* dont la taille commerciale peut atteindre 17 cm.

Il existe de nombreux modèles de capacité de production qui simulent la croissance des bivalves en fonction de la nourriture disponible (Gangnery et al. 2001). Par contre, les modèles de capacité de support environnementale prenant en compte le processus de biodéposition et ses effets sur le couplage pelagos-benthos sont rares et ne se développent que depuis très récemment (Grant et al. 2005, Hartstein & Stevens 2005, Giles 2006, McKindsey et al. 2006a, McKindsey et al. 2006b). Parmi ces modèles, seul celui de Giles (2006) et celui de Hartsein & Stevens (2005) utilisent des mesures de terrain pour valider ces derniers. Et dans tous les cas, l'effort d'échantillonnage est très faible et ne prend pas en compte les variations spatiales *in situ*.

Augmentation du taux de sédimentation

Le processus de biodéposition peut induire une augmentation du taux de sédimentation sous les élevages de bivalves. Les taux de sédimentation sous les sites conchylicoles peuvent être 30% à 450 % plus élevés que ceux sous les sites références (Hatcher et al. 1994, Stenton-Dozey et al. 1999, Danovaro et al. 2004, Hartstein & Rowden 2004). Une grande variation de taux de sédimentation est observée entre différents sites conchylicoles (Tableau 1.1). Ces différences sont principalement reliées :

1- aux caractéristiques d'élevage (ex. espèces, densité de production, âge, etc.).

2- aux taux de production de biodépôts, qui varient en fonction de la quantité et de la qualité de la nourriture (Tsuchiya 1980, Jaramillo et al. 1992, Navarro & Thompson 1997), de la température (Haven & Morales-Alamo 1966, Kautsky & Evans 1987), de la salinité (Widdows 1985) [une faible salinité peut par exemple diminuer le taux de filtration des moules (Navarro & Thompson 1997)] et du métabolisme des bivalves (Cranford & Hill 1999).

3- au potentiel de dispersion des biodépôts, qui dépend principalement de la vitesse des courants, de la vitesse de sédimentation et de la hauteur de la colonne d'eau.

Les résultats obtenus par différentes études sont résumés dans le Tableau 1.1. Une grande variation existe au niveau des surfaces des exploitations (0,2 à 200 ha), de la profondeur (3,5 à 33,5 m) ou encore des caractéristiques hydrodynamiques, avec des vitesses moyennes de courant variant de 2,6 à 24 cm s^{-1}. Tous ces paramètres influencent la

Tableau 1.1 Comparaison du taux de sédimentation à des sites conchylicoles et références: distance du site référence, espèces cultivées: les moules *Mytilus edulis* (Me), *Perna canaliculus* (Pc), *Mytilus trossulus* (Mt), *Mytilus galloprovinciallis* (Mg), *Mytilus planulatis* (Mp), et l'huître *Crassostreas gigas* (Cg); Production (Prod), profondeur (Prof), vitesse du courant moyen (VC), et vitesse du courant maximum (VC max).

Pays	Référence		Culture				Colonne d'eau		
	Distance	Taux	Espèces	Taux	Prod	Surface	Prof	VC	VCmax
	m	$g\ m^{-2}\ d^{-1}$		$g\ m^{-2}\ d^{-1}$	$t\ y^{-1}$	ha	m	$cm\ s^{-1}$	$cm\ s^{-1}$
[1]Suède	100	1,7 C	Me	2,8 C	100	0,3	10,5	3,0	nd
[2]Nouvelle Zélande	nd	nd	Pc	17,5% > R	nd	5	nd	2,6	11,8
[3]Canada	30	36	Me, Mt	89	nd	0,4	7	5,5	15
[4]Afrique du Sud	nd	1/3 culture	Mg	820 C + 123N	nd	80	11	nd	nd
[5]Canada	nd	≤40% culture	Cg	nd	nd	nd	nd	nd	nd
[6]Australie	100	*12	Cg, Mp	*12	73	6	8,3	3,8	18,5
[6]Australie	100	*10	Cg, Mp	14,5	220	13,8	9	3,4	10
[6]Australie	50	*7,2	Cg, Mp	7,2	108	5,6	10	nd	nd
[7]Italie	600	8,2	nd	10,8	nd	200	11	nd	nd
[8]Nouvelle Zélande	150	19	Pc	84	nd	1,8	33,5	3,2	7
[8]Nouvelle Zélande	150	20	Pc	77	nd	1,95	30	3,8	10,6
[8]Nouvelle Zélande	150	24	Pc	133	nd	1,15	11	10	24
[9]Canada	350	*30	Me	*58	nd	nd	4,5	nd	nd
[9]Canada	100	*44	Me	*45	nd	nd	3,5	nd	nd
[10]Nouvelle Zélande	1000	290	Pc	396	1680	45	13	nd	32,8
[11]Canada	100	42	Cv	50	nd	35	0,5	nd	nd
[+]Cette étude (0+ sous)	500	19	Me	20	180	200	6	5,5	18
[+]Cette étude (1+ sous)	500	19	Me	38	180	200	6	5,5	18

*estimé depuis une figure, nd = non disponible, (1- Dahlbäck & Gunnarsson 1981, 2- de Jong 1994, 3- Hatcher et al. 1994, 4- Stenton-Dozey et al. 1999, 5- Richardson & Newell 2002, 6- Crawford et al. 2003, 7- Danovaro et al. 2004, 8- Hartstein & Rowden 2004, 9- Grant et al. 2005, 10- Giles et al. 2006, 11- Mallet et al. 2006). [+] Moyenne juin-juillet

dispersion des biodépôts et induisent des variations dans les taux de sédimentation. D'autre part, la distance des sites références varie beaucoup entre les études, ce qui peut influencer la magnitude de variation entre le site conchylicole et le site référence. De plus, les informations sont souvent incomplètes et la comparaison entre les études est difficile.

1.2.3 Effets de la biodéposition sur l'environnement benthique

Un enrichissement organique peut apparaître sous des élevages de moules. Cet enrichissement est dû à l'augmentation de déposition de MO sous forme de fèces et pseudofèces (Hatcher et al. 1994), de la chute de moules, et de l'épifaune associée (Christensen et al. 2003). Ceci peut ainsi modifier les caractéristiques physico-chimiques du substrat (Sornin 1984, Hatcher et al. 1994, Mazouni et al. 1996, Smaal et al. 2001, Giles & Pilditch 2006). La biodéposition de MO a des conséquences sur le benthos à des échelles spatiales et temporelles variables (Dahlbäck & Gunnarsson 1981, Kaspar et al. 1985, Chamberlain et al. 2001).

Les effets liés à la biodéposition varient de «non significatifs» (Chamberlain et al. 2001, Crawford et al. 2003) à «très importants» (Mattsson & Lindén 1983, Hartstein & Rowden 2004). L'intensité des effets dépend de plusieurs facteurs, comme la qualité et la quantité de biodépôts, l'hydrodynamisme (Chamberlain et al. 2001, Newell 2004, Giles et al. 2006), la topographie, les caractéristiques physiques (ex. granulométrie) et chimiques du sédiment, et les communautés benthiques. D'autre part, les résultats obtenus et l'interprétation qui en découle dépendent des indicateurs et des méthodes employées

(Cranford et al. 2006). Certaines études évaluent l'influence des fermes conchylicoles en mesurant des caractéristiques chimiques du sédiment et d'autres études analysent les caractéristiques biologiques. Cependant ces indicateurs ont des temps de réponses différents. Ainsi, un enrichissement organique peut induire des changements de communautés benthiques avant même qu'une mesure chimique n'ait détecté une perturbation (Edgar et al. 2005).

La reminéralisation benthique de la MO induit une augmentation de la consommation en oxygène par une stimulation de l'activité microbienne et chimique (Valiela 1995). Les différentes réactions d'oxydoréduction dans les sédiments vont conduire à des flux de nutriments à l'interface eau-sédiment qui peuvent avoir des impacts importants sur l'ensemble du fonctionnement de l'écosystème. Par exemple, la régénération benthique des nutriments dans les milieux côtiers peut représenter 80% de l'apport des nutriments nécessaires (Jensen et al. 1990) pour la production primaire.

La diagenèse est l'ensemble des processus qui affectent la structure, la texture et la composition minéralogique des sédiments et les transforment progressivement en une roche dure et cohérente. La diagenèse précoce se produit immédiatement après le dépôt ou l'enfouissement des sédiments. Le moteur principal de la diagenèse précoce est le processus de dégradation de la MO (Valiela 1995). Ce processus implique une succession de réactions d'oxydoréduction dans la colonne sédimentaire qui s'établissent en fonction de la vitesse de minéralisation et qui dépendent de la qualité de la MO (Valiela 1995).

Les micro-organismes utilisent l'énergie libérée lors de ces réactions. La première réaction est celle qui libère le plus d'énergie. Lorsque l'oxydant est épuisé, un second est alors utilisé. Les molécules servent de donneur d'électrons et les composés minéraux d'accepteur d'électrons. Les composés accepteurs d'électrons sont dans l'ordre d'efficacité thermique : O_2, NO_3^-, MnO_2, FeO_2H, SO_4^{2-}, HCO_3^- (Figure 1.6).

- Dans la zone oxique, l'oxygène est utilisé pour dégrader la MO, les produits de cette réaction sont le nitrate NO_3^-et le phosphate PO_4^{3-}
- Dans la zone suboxique, quand l'oxygène devient insuffisant, les nitrates NO_3^- sont alors réduits en N_2 et NH_4^+. Le NH_4^+ libéré dans la phase dissoute peut migrer par diffusion vers la couche oxique et être réoxygéné en NO_3^-. Les oxydes de manganèse MnO_4^2 sont réduits en manganèse dissous Mn_2^+, libérés dans les eaux interstitielles. Les oxydes de fer (III) sont ensuite utilisés pour oxyder la MO et sont réduits en fer dissous (Fe^{2+})
- Dans la zone anoxique, les sulfates dissous servent d'oxydant pour minéraliser la MO. Quand les sulfates sont réduits, d'autres processus plus complexes et peu énergétiques (méthanogenèse) produisent du méthane et de l'acide acétique.

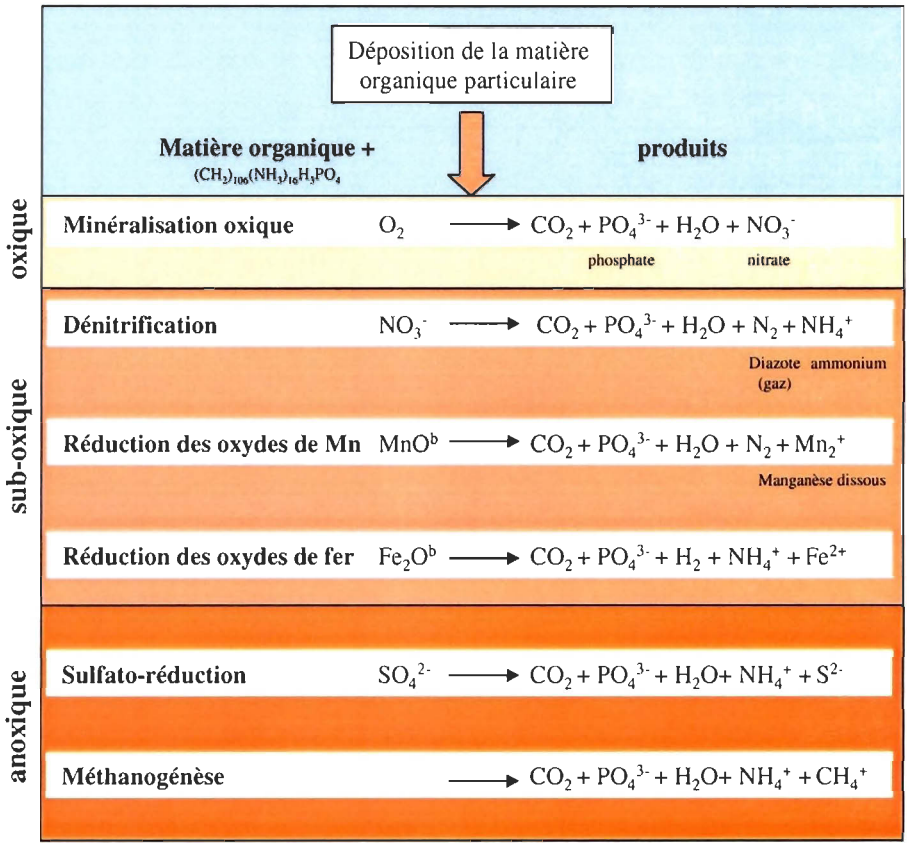

Figure 1.6 Processus de dégradation de la matière organique. Ce processus implique une succession de réactions d'oxydoréduction dans la colonne sédimentaire (adapté de Valiela 1995). Les équations des réactions ont été simplifiées.

En augmentant le flux de MO vers le benthos, la conchyliculture influence les flux de nutriments à l'interface eau-sédiment. Sous des conditions anoxiques, le processus de dénitrification est inhibé et l'azote est seulement régénéré en NH_4^+ (Newell et al. 2002). Hatcher et al. (1994) ont observé que l'augmentation de sédimentation sous des cultures de moules induisait une accumulation d'azote dans les sédiments, une diminution de la profondeur de la couche oxique et une augmentation des flux de NH_4^+ vers la colonne d'eau. D'autres études ont également observé une augmentation de la consommation d'oxygène (1,1 à 3 fois) (Mazouni et al. 1996, Stenton-Dozey et al. 2001, Christensen et al. 2003, Giles et al. 2006) et une augmentation des flux d'ammonium (jusqu'à 14 fois) sous les sites d'élevage (Kaspar et al. 1985, Christensen et al. 2003, Giles et al. 2006, Richard et al. 2007a).

L'oxygène pénètre par diffusion dans les premiers millimètres d'un substrat vaseux (Diaz & Rosenberg 1995). Les activités de bioturbation par les invertébrés benthiques permettent une distribution de l'oxygène plus en profondeur (Aller 1982, Michaud 2006). Cependant, lorsque la déposition de MO est trop importante, les communautés benthiques sont souvent dominées par des espèces à faible capacité de bioturbation (Heilskov & Holmer 2001). Le flux d'oxygène dans les couches inférieures du sédiment est d'autant plus diminué.

Quand les sédiments deviennent anoxiques, les sulphates sont réduits en sulphides, qui se combinent aux ions hydrogène dans le sédiment pour former le composé sulphide d'hydrogène (H_2S) :

$$(CH_2O)_{2n} + nSO^{2-}_4 \dashrightarrow 2nCO_2 + 2\,nH_2O + nS^{2-}$$

Dahlbäck & Gunnarsson (1981) montrent que la biodéposition des moules induit une réduction importante des sulfates sous les filières. Tenore et al. (1982) ont montré que la réduction des sulfates était 63% plus élevée sous les sites de mytiliculture par rapport aux sites contrôles. Les concentrations en H_2S sous les sites aquacoles peuvent atteindre des concentrations toxiques pour les organismes benthiques (Diaz & Rosenberg 1995). Donc, plusieurs programmes de monitorage sont basés sur l'évaluation de cet indice (voir revues dans Rosenthal et al. 2000).

La combinaison (i) d'un apport important en MO qui peut constituer une source de nourriture, (ii) de la diminution de la concentration en oxygène, et (iii) de l'augmentation des concentrations en sulphide dans les sédiments, peut induire des changements dans les communautés benthiques aux sites conchylicoles.

Effets de la biodéposition sur la macrofaune benthique

L'analyse de la structure des communautés benthiques est très utilisée dans l'évaluation d'impacts environnementaux (Pearson & Rosenberg 1978, Clarke & Warwick 1994). L'analyse de la macrofaune de substrat meuble est particulièrement utilisée pour la détection d'un enrichissement organique car les organismes qui composent ces communautés sont sessiles ou relativement sédentaires, leurs cycles biologiques sont assez longs (plusieurs mois à plusieurs années contrairement aux bactéries ou à la meiofaune) et les composantes du macrobenthos montrent différents niveaux de tolérance aux contraintes de l'environnement. De plus, les changements au niveau des communautés benthiques peuvent apparaître avant que des mesures chimiques aient pu détecter un effet (Edgar et al. 2005).

Une communauté benthique d'endofaune soumise à un enrichissement organique (Fig. 1.7) peut présenter (Pearson & Rosenberg 1978, Weston 1990):

1- Une diminution de la richesse spécifique.

2- Une augmentation du nombre total d'individus en réponse à l'augmentation de nombres d'espèces opportunistes.

3- Une réduction de la biomasse totale, bien qu'il puisse y avoir une augmentation de la biomasse des espèces opportunistes.

4- Un changement du poids individuel ou du poids moyen d'une espèce.

5- Une diminution de la profondeur de la portion de sédiment occupée par l'endofaune.

6- Une domination des déposivores au détriment des suspensivores.

7- Un changement dans la structure des communautés benthiques. Le long d'un gradient d'enrichissement organique, une succession continue de communautés est généralement observée. Pearson et Rosenberg (1978) ont décrit cette succession en quatre stades (Figure 1.7) : (Stade 3) Dans des conditions normales, les communautés stables sont généralement caractérisées par une forte diversité, une biomasse importante et une abondance modérée qui incluent des mollusques, échinodermes, crustacés et polychètes. (Stade 2) Dans les milieux modérément enrichis, la communauté dite «intermédiaire» est dominée par des Capitellidae, Spionidae et Cirratulidae ainsi que des petits bivalves Tellinidae (Stade 1) Un milieu très enrichi est généralement dominé par des espèces opportunistes, comme *Capitella* sp., qui peuvent devenir très abondantes. Ces polychètes tolèrent de faibles concentrations en oxygène et de fortes teneurs en sulphide, souvent associées à un flux de MO accru (Pearson & Black 2001). Les mollusques et les échinodermes, qui ne peuvent survivre dans un milieu fortement enrichi, sont absents. (Stade 0) Quand le flux de MO dépasse la capacité d'assimilation de la macrofaune, seules les bactéries parviennent à supporter les conditions.

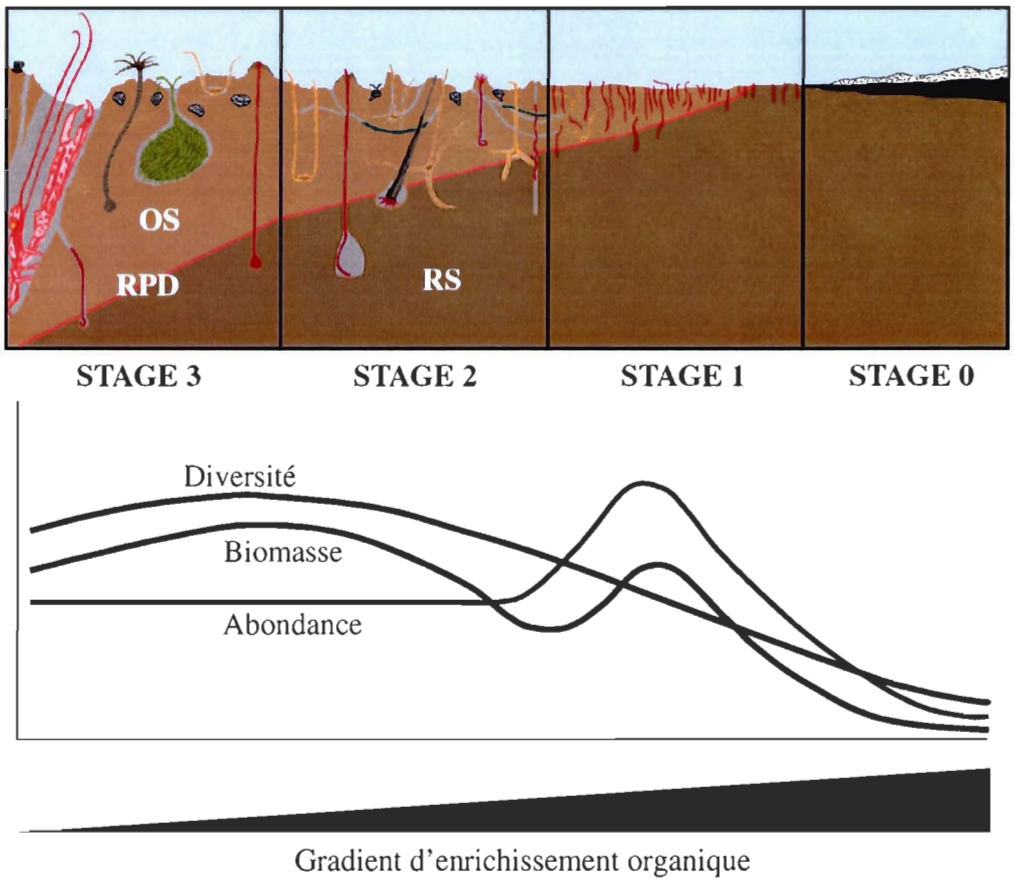

Figure 1.7 Succession des différentes communautés benthiques le long d'un gradient croissant de perturbation. Le graphe illustre le changement en diversité spécifique, abondance et biomasse le long de ce même gradient de perturbations (adapté de Pearson & Rosenberg 1978)

Observations aux sites conchylicoles

Une revue des études évaluant les effets de la conchyliculture sur la macrofaune benthique est présentée Table 1.2. Certaines études montrent que la biodéposition sous les sites conchylicoles peut entraîner une diminution du nombre d'espèces (Mattsson & Lindén 1983, Kaspar et al. 1985, Christensen et al. 2003), une diminution de la diversité (Mattsson & Lindén 1983, Kaspar et al. 1985, Stenton-Dozey et al. 1999, Chamberlain et al. 2001), et des différences de structure de communauté benthiques (Chamberlain et al. 2001, Hartstein & Rowden 2004). Mattson et Linden (1983) ont observé par exemple que les espèces dominantes *Nucula nitidosa, Echinocardium cordatum* et *Ophiura* spp. avaient été remplacées, environ un an après le début de l'exploitation conchylicole, par des polychètes opportunistes *C. capitata*, *Scolelepis fuliginosa* et *Microphthalmus sczelkowii,* ce qui suit le modèle général d'enrichissement organique. Christensen et al. (2003) ont également observé une dominance de petits déposivores de surface *D. incerta, C. capitata* et *Prionospio* spp. sous un site mytilicole. Ce changement a en retour un effet négatif sur le processus de pénétration de l'oxygène dans les sédiments étant donné que ces espèces ont une faible capacité de bioturbation.

Par contre, d'autres études ont observé des effets opposés, telles qu'une augmentation de la diversité et de la biomasse sous le site conchylicole (Grant et al. 1995, Giles et al. 2006). L'augmentation de biomasse est expliquée dans certains cas par la présence d'espèces carnivores attirées par les bivalves détachés des filières. Grant et al. (1995),

concluent de leur étude que les changements de communautés benthiques étaient davantage expliqués par la chute des moules que par l'augmentation du taux de sédimentation. La chute des bivalves d'élevage et de l'épifaune et flore associées sur le fond peut également constituer une source de nourriture pour la megafaune benthique. Ainsi, une plus grande abondance de prédateurs, tels que les crabes, étoiles de mer et homards a déjà été observée sous des sites conchylicoles (Mattsson & Lindén 1983). Des études sont en cours afin de tester si la conchyliculture induit une attraction de cette mégafaune ou si elle permet une augmentation de la production secondaire du milieu (D'Amours et Archambault 2005). Peu d'études ont évalué l'effet de la présence des bivalves d'élevage et des structures aquacoles sur la production secondaire. Ces structures peuvent agir comme des récifs artificiels et permettre la fixation d'épibiontes et d'endofaune vivant dans la matrice piégée entre les bivalves (McKindsey et al. 2006a).

Enfin, certaines études n'observent aucun effet significatif des sites conchylicoles sur l'environnement benthique (Crawford et al. 2003, Danovaro et al. 2004). Dans ces deux cas, les taux de sédimentation mesurés étaient faibles (moins de 15 g m^{-2} d^{-1}, voir Tableau 1.1). La production était faible et/ou les courants assez rapides pour permettre un bon renouvellement des eaux et une oxygénation du fond.

Parmi les études sur l'influence de la conchyliculture, de nombreuses présentent un plan expérimental qui ne permet pas une bonne interprétation des résultats. C'est le cas des études n'utilisant qu'un seul site sous la culture et un seul site référence. Une part de la variation observée entre les deux sites est expliquée par la variation naturelle et non pas par

les effets de la conchyliculture. D'autre part, aucune étude ne s'est intéressée aux variations spatiales à petite échelle à l'intérieur d'un site conchylicole, par exemple entre filières et sous filières. Or, cette variation apparaît importante si l'on veut modéliser l'influence de la biodéposition sur le benthos. Peu d'études ont évalué l'influence de l'âge des bivalves sur le taux de sédimentation et par conséquent sur le benthos. Or, le taux de biodéposition varie avec la taille des bivalves (Giles & Pilditch 2004). Une cohorte de bivalves de taille commerciale devrait donc induire un taux de sédimentation plus important qu'une cohorte de juvéniles et donc avoir une influence plus importante sur le benthos.

Il est encore difficile de prédire quelle densité maximale de bivalves peut être cultivée avant qu'il y ait des perturbations du milieu. Il est nécessaire de développer des modèles de capacité de support environnementale adaptés à la conchyliculture (McKindsey et al. 2006b). Ces modèles doivent, entre autres, prendre en compte le potentiel de dispersion des biodépôts dans le milieu et leurs effets subséquents sur le benthos.

Tableau 1.2 Exemples d'études sur l'influence des cultures conchylicoles sur les communautés benthiques (majoritairement macrofaune) (T = transect, ns = pas de différence significative entre les sites conchylicoles et sites références) H' (Shannon diversity index) (tableau adapté de Cranford et al. 2006).

Auteurs	**Distance max. Référence**	**Méthodes**	**Observations sur les sites d'aquaculture F comparées aux sites références R**
(Chamberlain et al. 2001) Ireland- 2 cultures	40-60 m	1T 3-4 stations	Augmentation de la dominance H': ns Structure de communautés: ns
			Dominance des déposivores Dominance des opportunistes. Diminution de la diversité H' Différence de structure de communautés
(Crawford et al. 2003) Tasmanie- 3 cultures	35-100 m	3 T 7-9 stations	ns
(Christensen et al. 2003) Nouvelle-Zélande	250 m	1T: 0, 5, 250 m, 1 site référence	Diminution du nombre d'espèces Diminution des espèces irrigatrices Augmentation des opportunistes
(da Costa & Nalesso 2006)	500 m	1T : 0, 50, 200 m 1 site référence	Nombre d'espèces : ns (mais 0m > Référence pendant 3 mois sur 6 mois) Diversité H': 0 m > Référence Abondance Référence > 0 m Équitabilité Pielou J': ns Différence de structure de communauté La majorité des polychètes étaient des prédateurs (*Goniada* sp., *Lumbrinereis*) carnivores, indifférent à un enrichissement organique, ou filtreurs (*O. fusiformis*) sensible à un enrichissement organique. Conclusion : pas d'impact négatif
(Danovaro et al. 2004) Méditerranée	600 m	3 sites références 3 sites moulières	Variations entre période > variations sites Abondance bactérienne augmente en automne Meiofaune: ns
(Giles et al. 2006) Nouvelle-Zélande	~1 km	2 sites sous et 50m	Abundance Culture > Référence Biomasse 50m > Culture > Référence Diversité H' : ns
(Grant et al. 1995) Canada	30 m	1 site référence 1 site moulière	Diminution de l'abondance Augmentation de la diversité H' Composition spécifique similaire (ns)
(Hartstein & Rowden 2004) Nouvelle-Zélande- 3 cultures	200 m	4 sites références 4 sites moulières	1&2 Dominance des polychètes opportunistes Disparition des ophiures *Amphiura spp.* Changement de structure de communauté

			3 Pas de différence de structure des communautés
(Kaspar et al. 1985) Nouvelle-Zélande	1 km	1 site référence 1 site moulière	Bomasse : ns Plus faible diversité Dominance des polychètes
(Mallet et al. 2006) Canada Seul le site dans la zone subtitale est considéré ici	100 m	2 sites (sous et entre les sacs) 2 sites références	ns
(Mattsson & Lindén 1983) Suède	50 m	1T 5 stations	Pic d'opportunistes *Capitella* en Avril Diversité H' diminue Les espèces dominantes *Nucula nitidosa, Echinocardium cordatum* et *Ophiura spp.* Remplacées par les opportunistes *Capitella capitata, Scolelepis fuliginosa* et *Microphthalmus sczelkowii*
(Miron et al. 2005) Canada, Ile du Prince Édouard		17 sites 2 sites références	Chaque site présentait une densité de moule différente. Toute la baie était caractérisée par une faible diversité Changements de communauté benthique en relation avec la densité de moule
(Mirto et al. 2000) Méditerranée	1 km	1 site référence 1 site moulière réplication	Diminution de l'abondance de la meiofaune Augmentation de l'activité bactérienne
(Stenton-Dozey et al. 1999) Afrique du Sud	750 m	3 T 3-4 stations par T + 9 sites moulières	Diminution de la richesse spécifique d Diminution de la diversité H' le long d'un transect seulement Dépositivores dominent tous les sites Carnivores co-dominant au site moulière, et suspensivores co-dominant aux sites références
(Yokoyama 2002) Japon	6 km	1 site référence 1 site moulière	Diminution de l'abondance de H' et d Communauté plus instable

1.3 OBJECTIFS DE LA THÈSE

Le processus de biodéposition est un élément clef des interactions entre la conchyliculture et l'environnement. Il est donc essentiel de pouvoir prédire quels sont les effets de différents taux de biodéposition sur l'environnement benthique. Des modèles sont en cours de développement (e.g., Chamberlain & Weise 2006) et permettront de prédire la capacité de l'environnement benthique à assimiler la biodéposition issu de la conchyliculture.

Les objectifs de cette thèse étaient:

1. De caractériser le processus de biodéposition et les variations de taux de sédimentation *in situ* à différentes échelles spatiales (filières, culture, lagune), en fonction de deux classes d'âge de bivalve *Mytilus edulis*.

2. D'évaluer l'influence du processus de biodéposition sur les caractéristiques chimiques et biologiques du sédiment à différentes échelles spatiales (filières, culture, lagune)

3. D'évaluer l'efficacité de différents indices utilisés pour détecter les effets de la mytiliculture sur l'environnement.

4. D'évaluer quelle densité de bivalves peut induire des changements significatifs sur le benthos.

1.4 HYPOTHÈSES DE RECHERCHE

Hypothèse 1 : Les taux de sédimentation:

- sont plus élevés sous le site mytilicole que sous des sites références.
- sont plus élevés sous les filières de moules qu'entre les filières.
- sont plus élevés sous des filières de moules âgées de un an et plus (cohorte de taille commerciale, 1+) que sous les filières des moules juvéniles (cohorte 0+)
- diminuent en fonction de la distance de la zone de mytiliculture.

Hypothèse 2 : La vitesse de sédimentation des biodépôts augmente en fonction de leur taille. La taille des biodépôts augmente en fonction de la taille des bivalves.

Hypothèse 3 : L'augmentation du taux de biodéposition induit une augmentation du % OM dans les sédiments, une diminution du potential redox, une augmentation des concentrations en sulphide, un changement de structure et une diminution de l'abondance, de la diversité et de la biomasse des communautés endobenthiques.

Hypothèse 4 : L'interprétation et les conclusions sur les effets de la conchyliculture sur le benthos dépendent des indicateurs utilisés.

Hypothèse 5 : L'augmentation de la densité de moules induit une augmentation du taux de biodéposition vers le benthos. L'augmentation du taux de biodéposition induit une diminution de l'abondance des espèces sensibles et une augmentation des espèces opportunistes.

1.5 STRUCTURE DE LA THÈSE

Le corps de cette thèse est divisé en 4 chapitres (2-5). Des approches complémentaires d'observations en laboratoire (chapitre 2), d'observations *in situ* (chapitre 2, 3, 4) et expérimentales *in situ* (chapitre 5) ont permis de répondre aux objectifs qui avaient été fixés en début de doctorat.

Chapitre 2: Le chapitre 2 examine la dynamique de biodéposition. Callier MD, Weise AM, McKindsey CW, Desrosiers G (2006) Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion. *Marine Ecology Progress Series* 322:129-141

Chapitre 3: Le chapitre 3 évalue l'effet de la biodéposition sur l'environnement benthique. Callier MD., McKindsey CW, Desrosiers G (2007) Multi-scale spatial variations in benthic sediment geochemistry and macrofaunal communities under a suspended mussel culture. *Marine Ecology Progress Series* 348:103-115

Chapitre 4 : Le chapitre 4 évalue la qualité des indicateurs couramment utilisés pour évaluer l'influence de la mytiliculture sur l'environnement benthique. Callier MD, McKindsey CW, Desrosiers G (sous presse) Evaluation of indicators used to detect mussel farm influence on the benthos: two case studies in the Magdalen Islands, Eastern Canada. *Aquaculture*

Chapitre 5 : Le chapitre 5 a pour objectif de déterminer quelle densité de moules conduit à des changements significatifs dans la structure de communautés benthiques. Callier MD, Richard M, McKindsey CW, Archambault P, Desrosiers G Responses of benthic macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: an *in situ* Benthocosm experiment. Article soumis à *Journal of Experimental Marine Biology and Ecology* en Juillet 2007. L'experience a été menée en collaboration avec Marion Richard (doctorante en 2006 à l'ISMER) qui a effectué les mesures des flux biogéochimiques.

1.6 SITE D'ÉTUDE : LA LAGUNE DE GRANDE-ENTRÉE

Le site principal de ces études est la lagune de Grande-Entrée (GEL) qui est située au nord-est des Îles-de-la-Madeleine dans le Golfe du St-Laurent (Québec) 47°37' N, 61°31'O (Figure 1.8). Depuis la fin des années 70, des études ont été effectuées aux Îles-de-la Madeleine pour déterminer, entre autres, les conséquences de la fermeture de la baie de Grosse-Île au nord de GEL (Bourget 1976, Bourget & Messier 1982), l'impact du dragage du chenal de navigation (données non publiées Munro 1984, Munro et al. 1997), et la capacité de production de la lagune pour la mytiliculture (Roy et al. 1991, Souchu & Mayzaud 1991, Souchu et al. 1991, Mayzaud et al. 1992) et plus récemment la capacité de support environnementale de la lagune (Callier et al. 2006, Trottet et al. 2007, Richard et al. 2007a). Des données physiques, biologiques et chimiques sur GEL sont disponibles dans la littérature.

1.6.1 Caractéristiques physiques

Une lagune est une étendue d'eau généralement peu profonde séparée de la mer par un cordon littoral. Ce plan d'eau est en liaison permanente avec la mer. La profondeur des lagunes étant faible, les forces à l'interface air-eau (température, précipitation et évaporation, vent) ont un rôle très important (Koutitonsky 2005) sur l'hydrodynamisme du milieu.

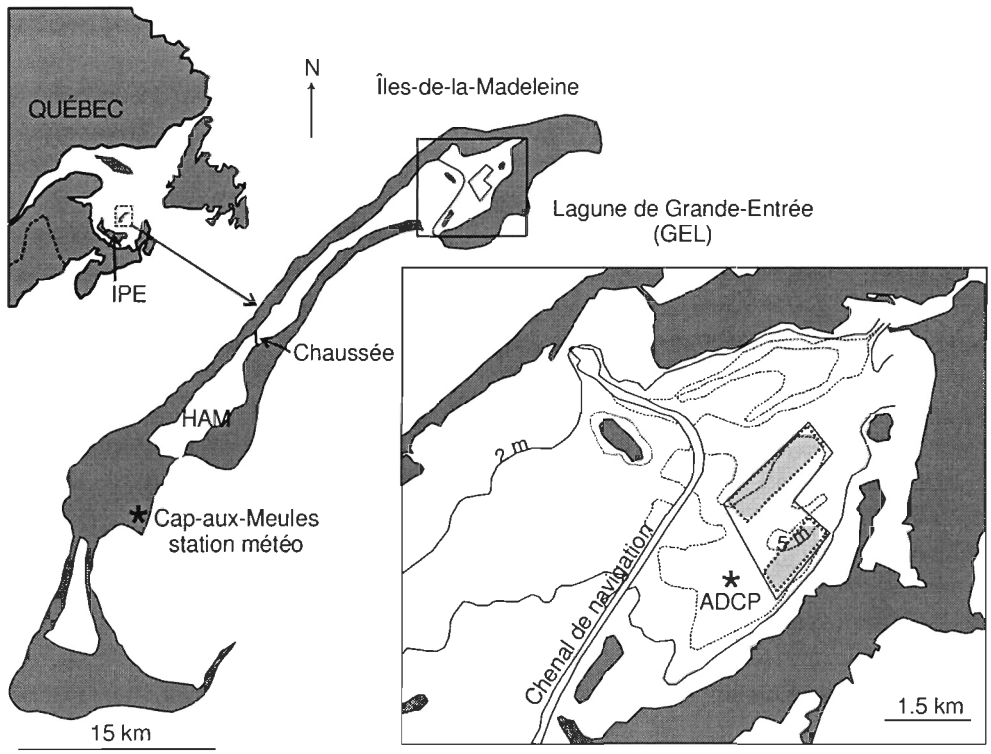

Figure 1.8 Localisation des Îles-de-la-Madeleine dans le Golfe du St. Laurent et de la lagune de Grande-Entrée. Le polygone indique le secteur mytilicole étudié.

Bathymetrie. La superficie de GEL est d'environ 58 km^2 (Mayzaud et al. 1992). GEL est caractérisée par deux zones distinctes séparées par un chenal de navigation : à l'ouest un bassin d'environ 1,5 à 3 m de profondeur, à l'est un bassin de 5 à 6 m de profondeur où se situe le secteur de mytiliculture (*M. edulis*) (Figure 1.8). Le chenal de navigation a été dragué au début des années 1980 afin de permettre la circulation des bateaux jusqu'à la mine de sels située au nord de la lagune. GEL est connectée à la lagune de Havre-aux-Maisons par un passage de 60 m de large et 7 m de profondeur sous la chaussée (voir Figure 1.8) (Koutitonsky 2005). Ce passage entre les deux lagunes étant étroit, des différences de phase entre GEL et Havre-aux Maisons induisent des courants de marées non négligeables dans certaines parties des lagunes (Koutitonsky et al. 2002).

La marée, les courants et les vents. Les Îles-de-la-Madeleine sont situées à proximité d'un point amphidromique, l'amplitude des marées est donc faible (0,58 m) (Bourget 1976). [Un point amphidromique est un point d'un système physique soumis à une force de marée où le marnage est voisin de zéro]. La lagune est caractérisée par des courants de marées de 0,5 à 1,0 m s^{-1} à l'ouest du chenal et par des courants de marées presque inexistants à l'est du chenal (0,01 m s^{-1}) (Koutitonsky et al. 2002).

Pendant l'année, les vents soufflent majoritairement du sud-ouest vers le nord-est (Figure 1.9). En 2003, 36 % du temps, les vents soufflent entre 7 et 11 m s^{-1} (25,2 – 39,6 km h^{-1}) et 1% du temps les vents atteignent plus de 17 m s^{-1} (61,2 km h^{-1}). Les vents prédominants durant l'été soufflent du sud-ouest vers le nord-est (Koutitonsky et al. 2002).

Les vents soufflant dans l'axe de la lagune vont créer des courants de dérive près des côtes, orientés dans la direction du vent dans les parties peu profondes (Figure 1.10). L'accumulation d'eau à l'extrémité de la lagune crée une élévation du niveau d'eau et un gradient de pression, qui induit un courant de fond, appelé courant de pente (Koutitonsky 2005). La direction du courant de pente est opposée à la direction du vent et plutôt près du fond, loin de la friction du vent de surface (Koutitonsky & Tita 2006) (Figure 1.10 et 1.11).

Les vents contribuent à l'homogénéisation de la colonne d'eau et aux échanges lagune-golfe (Souchu et al. 1991, Koutitonsky et al. 2002). Ils peuvent entraîner dans la lagune des courants d'une vitesse de 15 à 20 $cm.s^{-1}$ (V.G. Koutitonsky, comm. Pers). Callier et al. (cette thèse, 2006) ont mesuré des courants moyens pendant l'été 2003 de 5 $cm.s^{-1}$ avec des maxima à 18 cm s^{-1} lors des maxima de vents (Figure 1.9).

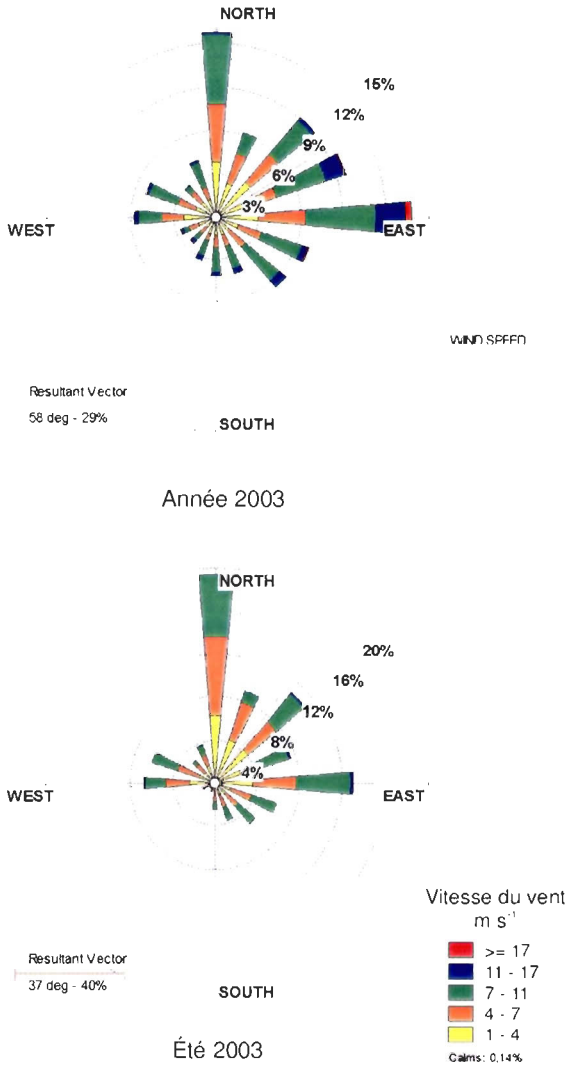

Figure 1.9 Vitesse et direction des vents pour l'année 2003 et pour l'été 2003. Les vents soufflent majoritairement du sud-ouest vers le nord-est à une vitesse moyenne de 6,4 m s^{-1} (soit à 23,1 km h^{-1}). Données météorologiques de Cap-aux-Meules analysées avec le logiciel WRplot (www.wenlakes.com).

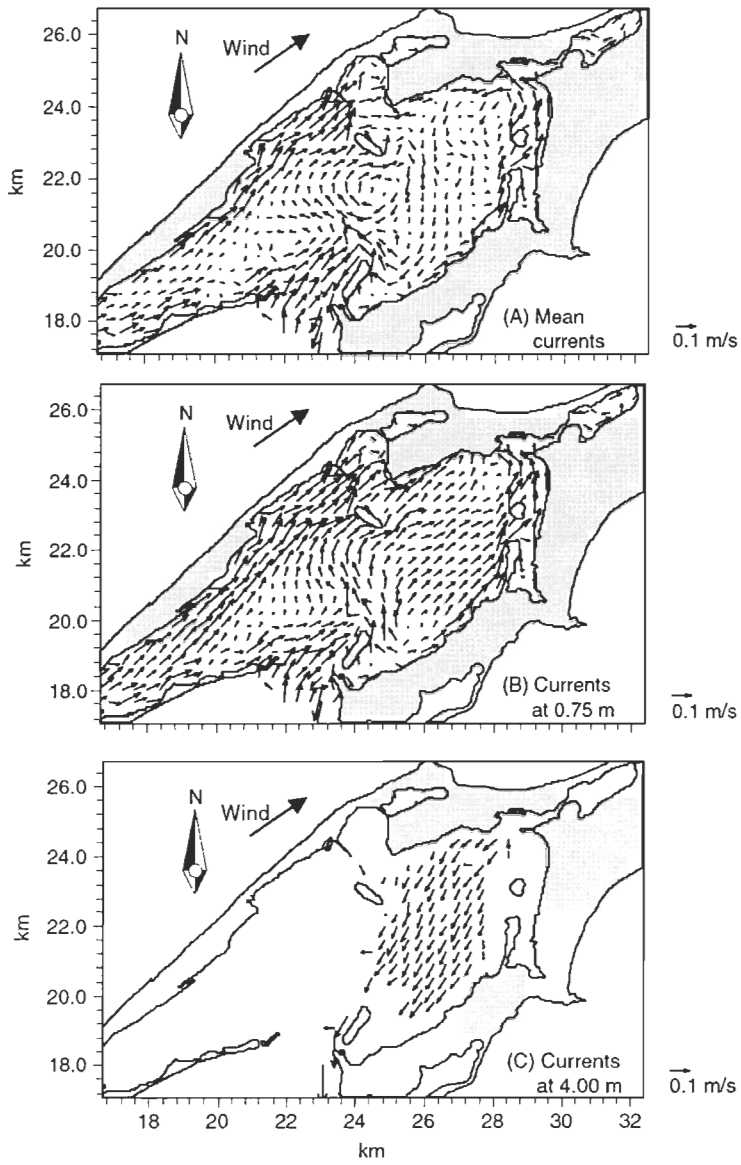

Figure 1.10 Simulation des courants moyens (A), des courants de surface (B) et des courants de fond (à 4 m) (C) sous les vents dominants du sud-ouest (exemple 12 Mai 1989) (d'après Koutitonsky 2005).

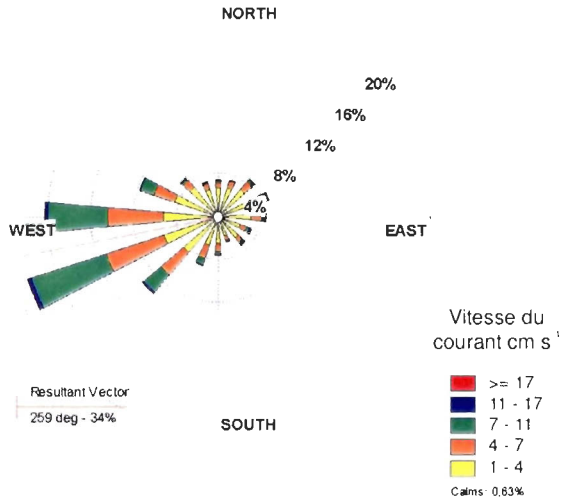

Figure 1.11 Vitesse et direction des courants de juin à octobre 2003 dans la lagune de Grande-Entrée à environ 4,5 m de profondeur (mesurées par ADCP. Figure 1.8).

Température et salinité. A cause de la faible profondeur de GEL, les vents entraînent une circulation verticale qui homogénéise la colonne d'eau. Les mesures de température et salinité effectuées à différentes profondeurs (1 et 4 m) sont semblables (Roy et al. 1991). De plus, le réchauffement des eaux est supérieur à celui des eaux du golfe en été. De juin à octobre, la température varie en général de 8 à 21° C (Figure 1.12) (Myrand 1991). En hiver, une couverture de glace s'installe. La température atteint -1,5 ° C en décembre (Bourget & Messier 1982). La salinité variait de 25 à 32 pendant l'été 1987 (Souchu et al. 1991) et de 30,3 à 31,1 en été 2003 (Figure 1.12). La faible diminution de salinité serait attribuée à l'arrivée progressive des crues printanières de l'estuaire du St-Laurent (Koutitonsky et al. 2002) par le biais du courant de Gaspé.

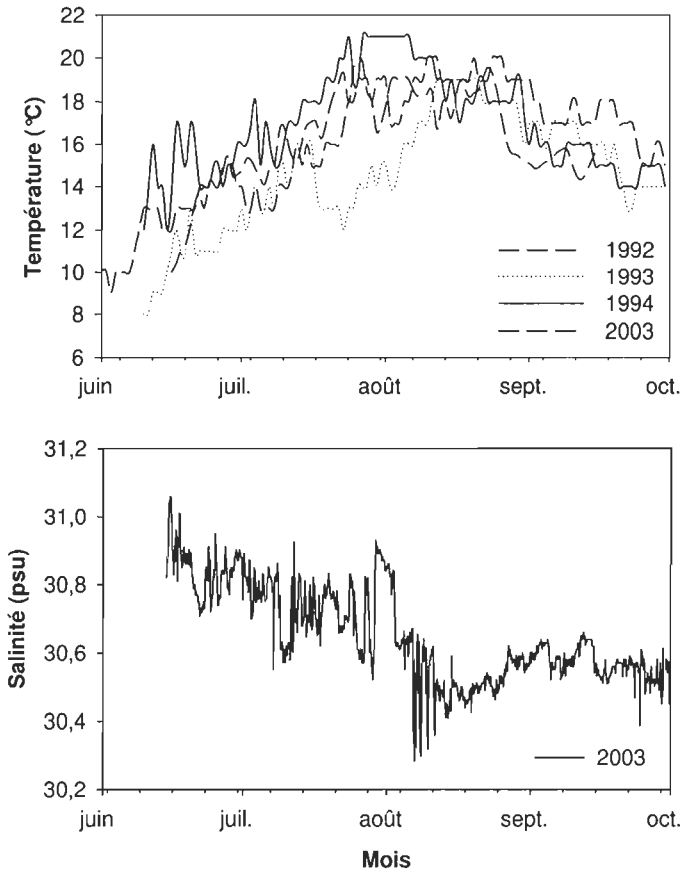

Figure 1.12 Température de l'eau de GEL en 1992, 1993, 1994 (Bruno Myrand, MAPAQ données non publiées) et 2003 (Bivalve Environmental Carrying Capacity Study, BECCS), et salinité pendant l'été 2003 (BECCS).

Temps de renouvellement des eaux. La lagune de Grande Entrée échange ses eaux avec celles du Golfe du St-Laurent par le canal de Grande-Entrée d'une largeur d'environ 275 m (Bourget 1976) et celles de la lagune de Havre-aux-Maisons (Figure 1.8). Des mesures ont permis de quantifier les échanges d'eaux golfe-lagune et de calculer le temps de renouvellement de l'eau de la lagune de Grande Entrée par l'eau du golfe (Koutitonsky & Tita 2006). « Le temps de renouvellement (TR) correspond au temps nécessaire pour que 62 % des eaux de la lagune initialement présentes soient renouvelées par des eaux en provenance de l'extérieur» (Koutitonsky & Tita 2006). Les eaux qui entrent dans la lagune se propagent dans le chenal de navigation et vers l'ouest à marée montante. Les eaux des zones plus profondes, à l'est du chenal où se situe la moulière, ne sont pas renouvelées rapidement par l'effet des marées. Ainsi le temps de renouvellement au site des moules a été évalué à environ 60 jours sous l'effet unique des marées et de 25 jours lorsque les vents sont considérés dans les calculs (voir Figure 1.13, Koutitonsky & Tita 2006).

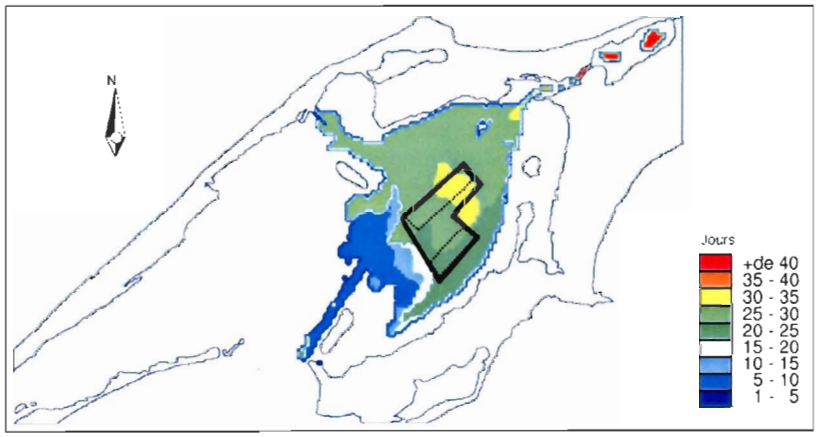

Figure 1.13 Temps de renouvellement des eaux de GEL à 4 m de profondeur sous l'action des marées et des vents (d'après Koutitonsky & Tita 2006).

1.6.2 Caractéristiques physico-chimiques et trophiques

Faibles concentrations en nutriments

En 1988, Souchu et al. (1991) avaient évalué la composition physico-chimique des eaux de la lagune de Grande-Entrée et avaient montré l'absence de stratification de la colonne d'eau et une bonne oxygénation du milieu, relié à l'hydrodynamisme du milieu (voir section précédente). Des concentrations très faibles en azote inorganique dissous (ammonium NH_4^+ + nitrates NO_3^- + nitrites NO_2^- < 0,1 µmol l^{-1}-N), des concentrations faibles en phosphates (PO_4^{3-} = 0,25 à 0,70 µmol l^{-1}) et silicates ($Si(OH)_4^-$ = 0,3 à 1,5 µmol l^{-1}) avaient été mesurées au cours de l'été. Cette caractéristique de la lagune a été confirmée par une étude récente (Trottet et al. 2007) qui indique des concentrations faibles en nitrates (0,3 µmol l^{-1} NO_3^-), en ammonium (0,2-0,8 µmol l^{-1}), en phosphates (0,3 µmol l^{-1}) et en silicates (1,1 µmol l^{-1}) dans la lagune pendant l'été 2003. L'absence de rivière aux Îles-de-la-Madeleine limite l'apport en nutriments dans les lagunes. De plus, aucun enrichissement significatif en sels nutritifs provenant du golfe (courant de Gaspé) ou de sources telluriques et anthropiques (lessivage des sols et rejets domestiques) n'a été observé (Souchu et al. 1991). Il n'y a pas de différence en concentrations de nutriments entre l'intérieur et l'extérieur de la lagune (Trottet et al. 2007). Les eaux du golfe ne seraient donc pas une source de nutriments pour la lagune. En fait, du printemps à l'automne, les pluies constituent la source principale de nitrates pour le système lagunaire des Îles-de-la-Madeleine (Souchu & Mayzaud 1991). Souchu et al. (1991) ont montré que le système

lagunaire de Grande-Entrée «présentait des caractéristiques oligotrophiques», considérant les faibles concentrations en nutriments.

Souchu et al. (1991) indiquent que les silicates et les phosphates ne sont cependant jamais épuisés dans la lagune. Les silicates ne sont ainsi pas limitants pour les espèces phytoplanctoniques à tests silicieux (comme les diatomées, chrysophycées, silicoflagellés) et les phosphates ne seraient pas limitants pour la production primaire. L'épuisement des nitrates observé en été est probablement relié à la consommation par les diatomées lors des efflorescences printanières. Le nitrate est alors renouvelé par les bactéries en automne. Les ressources en nutriments azotés sont particulièrement importantes dans le déclenchement de ces efflorescences dans les écosystèmes côtiers des zones tempérées (Legendre & Rassoulzadegan 1995). L'azote pourrait donc être un facteur limitant de la production primaire dans la lagune de Grande-Entrée.

Cependant « il n'y a pas d'évidence de déficience nutritive chez le phytoplancton» dans la lagune de Grande-Entrée (Roy et al. 1991). Il est possible que le phytoplancton utilise les formes organiques dissoutes de l'azote (Roy et al. 1991). Souchu et al. (1991) ont observé des concentrations élevées en azote et phosphore organique dissous (NOD = 7,2 à 29,1 µM-N, POD = 0,10 à 1,17 µM-P). La nature de la source azotée peut influencer le développement de certains groupes taxonomiques. Si le nitrate déclenche les efflorescences de diatomées (Malone et al. 1983), d'autres composés, comme l'ammonium, l'urée ou l'azote organique dissous peuvent favoriser le développement des flagellés (Glibert & Terlizzi 1999).

Chaîne trophique dominée par le réseau microbien

Petites cellules phytoplanctoniques et faible concentration en Chlorophylle a. L'étude d'Auclair (1977) effectuée avant l'implantation de la mytiliculture a fourni une base comparative pour l'étude de Roy et al. (1991) visant à définir le potentiel de production mytilicole de cet environnement et l'influence de la mytiliculture sur le milieu. Ces deux études décrivent l'environnement particulaire (taille et type de particules en suspension, concentration et composition du matériel particulaire et activité photosynthétiques des algues) de la lagune de Grande Entrée. En 1991, les descripteurs de biomasse (carbone particulaire, chlorophylle a (Chl *a*), concentration particulaire totale) indiquaient des valeurs généralement plus fortes au site moulière (Roy et al. 1991). Cependant lors de l'étude, la comparaison des sites moulières et témoins ne permettait pas de conclure un effet marqué de la moulière sur son environnement. Les valeurs de Chl *a* et d'activité photosynthétique de 1987 étaient comparables à celles récoltées avant l'installation de la mytiliculture (Auclair 1977).

La biomasse phytoplanctonique de la lagune de Grande-Entrée est dominée par des petites cellules : cellules nano- (2-20µm) et microplanctoniques (20-200 µm) (Roy et al. 1991). La majorité des cellules phytoplanctoniques (75%) sont < 20µm. En abondance, les flagellés autotrophes et les dinophycae dominent. Lors des efflorescences, les diatomées (Bacillariophycae) dominent. Les concentrations en chlorophylle *a*, indicateur de biomasse phytoplanctonique, variaient de 0,8-3,1 ug.l^{-1} pendant l'été 2003. 50 à 85% de la Chl *a* sont expliqués par des cellules de taille < 3µm. Les concentrations en Chl *a* sont faibles et

similaires aux concentrations dans le Golfe du St Laurent, excepté lors des efflorescences de diatomées (Trottet et al. 2007).

Dominance des hétérotrophes. Les communautés microplanctoniques (20-200 µm) de la lagune de Grande-Entrée sont dominées par les protistes hétérotrophes (majoritairement ciliés et flagellés hétérotrophes) en été et au début de l'automne (Trottet et al. 2007). Les hétérotrophes contribuent de façon significative à la chaîne alimentaire et au cycle des nutriments. Ils représentent probablement une source importante de nourriture pour les moules d'élevage (Trottet et al. 2007).

Production primaire. En 1977, Auclair suggérait que le milieu présentait un niveau de fertilisation suffisant pour permettre une productivité importante. Le taux de fixation de carbone, indicateur de la production primaire (25-250 mg C m^{-3} d^{-1}), augmente significativement au mois d'août (Roy et al. 1991, Trottet et al. 2007). En 1988, Roy et al (1991) indiquent que la productivité des eaux de la lagune présentait des valeurs moyennes normales pour une zone côtières (Parson et al. 1977). La production primaire est plus élevée dans la lagune que dans le Golfe. Les lagunes côtières sont connues pour être des habitats très productifs. À GEL, 15 à 65% de la production primaire sont expliqués par des cellules de taille < 3µm (Trottet et al. 2007).

Ainsi, GEL est caractérisée par de faibles concentrations en nutriments (Souchu et al. 1991), des petites cellules phytoplanctoniques (Roy et al. 1991), la domination des protistes hétérotrophes par rapport aux autotrophes (Trottet et al. 2007) et par une production

primaire importante (Roy et al. 1991, Trottet et al. 2007). Ces caractéristiques suggèrent la présence d'un réseau trophique microbien. Les nutriments proviendraient du recyclage de la MO par les bactéries présentes dans la colonne d'eau et à l'interface eau-sédiment (Figure 1.14 - Azam et al. 1983, Legendre & Rassoulzadegan 1995). Dans ce type de réseau, la biomasse bactérienne produite est consommée par le nanoplancton hétérotrophe (qui domine dans la lagune de Grande Entrée), qui est à son tour consommé par le microzooplancton avant d'atteindre les niveaux trophiques supérieurs (mesozooplancton-poisson) (Roy et al. 1991, Legendre & Rassoulzadegan 1995). Les éléments minéraux libérés de la MO peuvent ainsi connaître «une deuxième vie» et servir à la production primaire, dite de régénération.

Aucune donnée n'est disponible sur le type de bactéries présentes dans la lagune ainsi que sur le picoplancton (< 2 µm). Cependant la concentration bactérienne a été évaluée à $19.10^9 \pm 10.10^9$ cell.l^{-1} (Trottet et al. 2007).

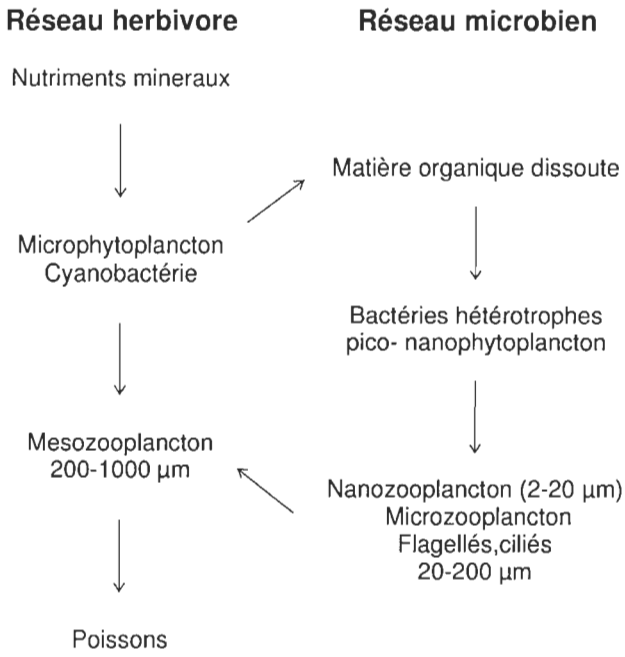

Figure 1.14 Réseau microbien comparé au réseau herbivore classique. La biomasse bactérienne produite est consommée par le nanoplancton hétérotrophe qui est consommé par le microzooplancton avant d'atteindre les chaînes trophiques traditionnelles (Mesozooplancton-poisson) (Roy et al. 1991, Legendre & Rassoulzadegan 1995). Les éléments minéraux libérés de la MO peuvent ainsi connaître «une deuxième vie» et servir à la production primaire, dite de régénération.

1.6.3 L'environnement benthique

Plusieurs modifications ont eu lieu dans la lagune de Grande-Entrée au cours des 30 dernières années. A la fin des années 1980, une mine de sel a été construite dans le nord de la lagune. Il y a eu également le dragage d'un chenal de navigation, et la création de deux îlots dans la lagune. Trois études principales ont été menées pour caractériser l'environnement benthique de GEL: en 1975 (Bourget 1976, Bourget & Messier 1982), en 1978 (Munro 1984, Munro et al. 1997, ces deux études ne sont pas publiées et seront référées ainsi dans la suite du texte) et en 1982 (Élouard et al. 1983). Seule l'étude de Munro et al (non publié) permet de distinguer différents types de sédiments et différents assemblages d'invertébrés selon la bathymétrie.

Granulométrie

GEL est alimentée par le transport éolien surtout sous l'effet des vents d'ouest (sable fin) et par les entrées de sédiments par les passes (sables moyens). Les zones soumises à l'action des marées se retrouveraient dominées par le sable moyen et les zones plus profondes, plus calmes, accumuleraient le sable très fin et la vase (Munro et al. 1997). Une circulation de Langmuir a été observée dans cette lagune (D. Booth, IML comm pers, dans Souchu et al. 1991), ces cellules de convection pourraient favoriser le mélange vertical et la resuspension de MO s'accumulant dans la zone des moulières. En 1978, des sables grossiers ont été observés dans la passe située entre GEL et HAM alors que la proportion de vase était importante dans la partie nord de GEL (34,3%) (Munro et al. 1997), les zones

profondes (5,2 m en moyenne) contenaient une proportion importante de limon et d'argile (19-55%). Élouard et al. (1982) caractérisaient également la zone à l'ouest du chenal comme un habitat sablo-vaseux contenant moins de MO et une richesse et une diversité plus élevées que dans la partie est. La granulométrie de GEL a été réévaluée en 2004 par QTC et par échantillonnage à plusieurs endroits de la lagune (Roy et al. en préparation). Cette étude montre que la proportion de vase et d'argile (particule < 63 µM) est le plus importante dans les zones situées 5-6,5m de profondeur (24 – 63%) (Figure 1.15).

Communautés benthiques

Il existe des variations entre les assemblages fauniques des lagunes des Îles-de-la Madeleine (Munro, non publié). Deux biocénoses ont été distinguées : la biocénose des sables fins sous eaux boréales dans les régions de faible profondeur et la biocénose des sables-vaseux sous eaux arctiques (Bellan 1978) dans les régions profondes des lagunes. Munro et al. (non publiée) observent des changements graduels à l'intérieur des deux biocénoses. Ils distinguent trois assemblages.

Les sites profonds (> 4m), caractérisés par des sédiments contenant souvent plus de 10% de vase et très peu de graviers ou sable grossier, sont dominés par des individus de très petites tailles, dont *Mya arenaria*. Dans la même région, Bourget et Messier en 1975 (Bourget 1976, Bourget & Messier 1982) et Élouard en 1982 (Élouard et al. 1983) ont observé les même espèces dominantes, soit *M. arenaria*, *Retusa canaliculata*, *Tellina agilis*, *Pectinaria (Cystena) granulata* et *Ensis directus* sur sable fin et vase. C'est à cet

endroit que la mytiliculture a été mise en place dans les années 80. Ce type d'assemblage a également été observé dans un estuaire de l'Île du Prince Édouard caractérisé par le présence de *T. agilis*, *E. directus*, *M. arenaria* et *P. granulata* (Hughes & Thomas 1971). *M. arenaria* est plutôt une espèce intertidale et sa présence dans les zones profondes pourrait s'expliquer par une période de recrutement d'individus juvéniles coïncidant avec la période d'échantillonnage (Munro et al., non publié).

Les sites peu profonds (< 4m) de la lagune de Grande-Entrée ressemblent à ceux de la lagune de Havre-aux-Maisons et de la lagune reliant GEL et HAM. Les fonds peu profonds, proches des zones intertidales, sont recouverts par des herbiers à zostères (*Zostera marina*) dont la biomasse est en moyenne de 760 g poids sec m^{-2} (De Sève et al. 1978). La faune est dominée par les nématodes, *Calliostoma occidentale*, *Gemma gemma*, *T. agilis* et *Corophium* sp. Le gastéropode *C. occidentale* est une espèce qui a besoin d'une température supérieure à 18°C pour la reproduction et pour la survie de ses larves. Cette espèce atteint la limite nord de sa distribution géographique dans le sud du Golfe (Dunbar et al. 1980).

Enfin, la faune de la lagune du Havre-aux-Basques (au sud des Îles) est différente. Cette lagune a été fermée en 1957 pour la construction d'une route. Elle est peu profonde et la salinité est plus basse et les températures estivales sont plus élevées que dans les autres lagunes. *Hydrobia minuta* et *Macoma balthica* dominent ce milieu.

Seule l'étude de Bourget et Messier (1982) évalue la biomasse des espèces d'invertébrés dans la lagune, et l'estime à 6,4 g poids sec m^{-2} pour 3398 ind m^{-2} en moyenne. La richesse, la densité et la biomasse des espèces sont faibles comparativement à celles des zones intertidales et subtidales échantillonnées ailleurs sur la côte est de l'Amérique du Nord. La productivité est plus faible qu'ailleurs en Nouvelle-Angleterre et à l'île du Prince Édouard (Bourget & Messier 1982). Burton et al. (1980) et Bourget (1976) caractérisent le milieu d'instable dont «la capacité de support est limitée».

Aucune donnée n'était disponible sur les communautés macrobenthiques depuis l'étude d'Élouard en 1983. Dans le Chapitre 2, les données obtenues en 2003 (cette thèse) sont comparées aux études précédentes afin d'évaluer l'influence de la mytiliculture sur les communautés benthiques.

Source de matière organique

La matière organiqueparticulaire (MOP) de la lagune peut-être aussi bien consituté de matériel détritique (décomposition d'organismes, biodépôts, particules sédimentaires, etc.) que de matériel vivant (phytoplancton, bactéries, microzooplancton, etc.) (Souchu et al. 1991).

Sédimentation et biodéposition. Aucune étude avant celles réalisées en 2003 et en 2004 n'a été menée pour estimer les flux de MOP vers le sédiment (voir cette thèse) et les flux d'ammonium et de phosphates à l'interface eau-sédiment (Richard et al. 2007a,b). Les résultats seront discutés dans le chapitre 2 et dans la discussion générale.

Herbier de zostères. Comme mentionné plus haut, les herbiers de zostères sont une source de MO pour la lagune. Les détritus de zostères, disséminés après la fonte des glaces, ont tendance à s'accumuler dans les parties les plus profondes de la lagune ou sur le littoral et constituent une source de débris qui est dégradé par les bactéries. Les zostères pourraient donc constituer une source importante de MOP pour le sédiment et de matière organique dissoute (MOD) pour la colonne d'eau.

Chute de moules. De nombreux problèmes ont été observés dès le début des élevages incluant la chute des rendements en chair des moules pendant l'été et des mortalités massives des moules de deux ans. De nombreuses études ont été conduites par Myrand et al. (Myrand 1991, Myrand et al. 2000) afin de comprendre ce phénomène. Ils ont montré que les moules étaient extrêmement faibles (contenu énergétique faible) à la fin de juillet, après la période de ponte et au moment du pic de température (> 20 °C). En septembre, ils enregistraient environ 65 % de perte. Léonard (2004) a évalué que la quantité de chute de moules et épibiontes pouvait atteindre 950 g m^{-1} de filières j^{-1} lors des fortes températures et pour des moules âgées de 2 ans (1+). Aucune mortalité n'avait été observée chez des moules du même stock placé en dehors de la lagune à 16 mètres de profondeur (Myrand et al. 2000).

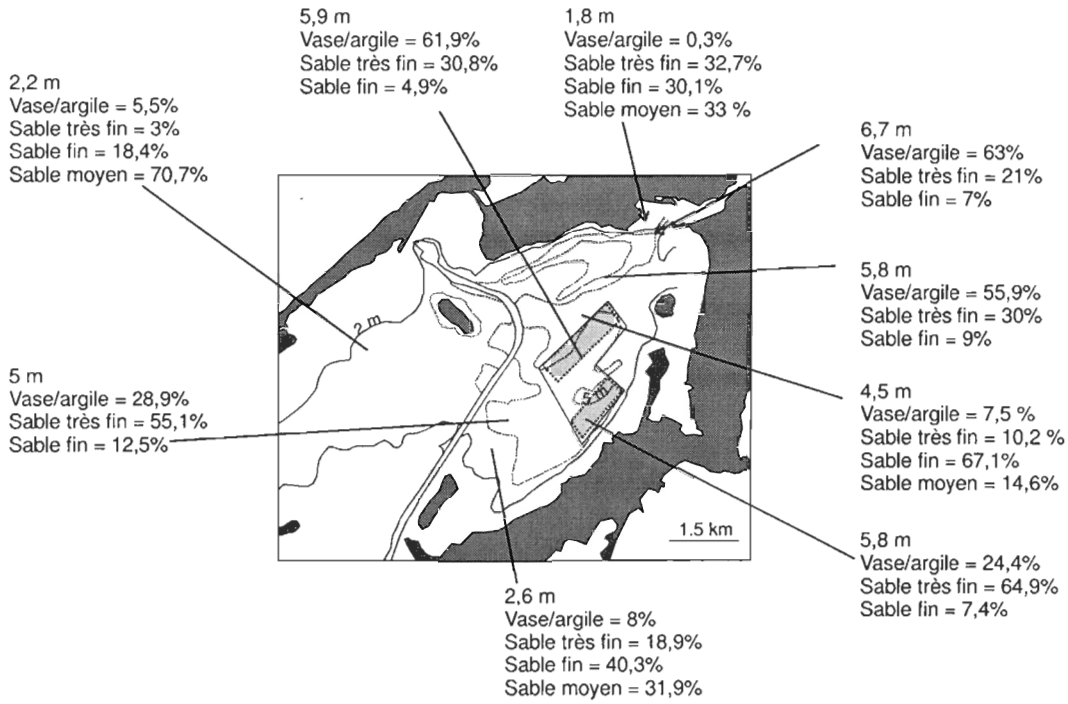

Figure 1.15 Valeur moyenne d'analyse granulométrique effectuée en 2004 par Roy, Simard et McKindsey. Vase + argile (<63µm), sable très fin (65-125µm), sable fin (125-250µm), sable moyen (250-500µm).

CHAPITRE 2

Sedimentation rates in a suspended mussel farm (Great-Entry Lagoon, Canada): biodeposit production and dispersion

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RÉSUMÉ: Des analyses expérimentales et des mesures *in situ* ont permis de caractériser la dynamique de biodéposition dans une culture de moules en suspension (*Mytilus edulis* L.) située dans la lagune de Grande-Entrée (Québec). Nous avons déterminé: (1) la quantité et la qualité des biodépôts produits par différentes classes d'âges de moules, (2) la relation entre la vitesse de sédimentation et la taille des fèces et (3) la variation de taux de sédimentation à différentes échelles spatiales et temporelles. Les moules de la cohorte 0+ produisaient en moyenne 63 % (32,4 mg masse sèche j^{-1} ind^{-1}) de la masse produite par les moules de la cohorte 1+ (51,5 mg masse sèche j^{-1} ind^{-1}). La quantité de biodépôts produite par unité de masse (poids sec de tissu) était, en revanche, plus élevée pour les moules 0+ que 1+. La vitesse de sédimentation des fèces était corrélée à leur largeur et variait de 0,27 à 1,81 cm s^{-1}, pour des moules mesurant 3 à 7 cm de long. Les taux de sédimentation étaient plus élevés sous la culture que sur les sites références, supportant l'hypothèse que la mytiliculture augmente les taux de sédimentation. Des variations temporelles et spatiales des taux de sédimentation ont été observées à petite échelle. Avant la récolte des bivalves 1+, les taux de sédimentation mesurés directement sous les filières de moules étaient deux fois plus élevés qu'entre les lignes (10 m plus loin), et que dans les autres zones (référence et 0+). L'évaluation des taux de sédimentation le long de transects autour de la zone de mytiliculture a confirmé la faible dispersion initiale des biodépôts, qui a été estimée entre 0 et 7,4 m (moules 1 +) et entre 7 et 24,4 m (moules 0+).

ABSTRACT: Experimental and field studies were done to characterise biodeposit dynamics in a suspended mussel *Mytilus edulis* L. farm in Great-Entry Lagoon, eastern Canada. We assessed: (1) the quantity and quality of biodeposits produced by different age classes of mussels, (2) the size-dependent sinking velocity of faeces and (3) the variation in sedimentation rates at different spatial and temporal scales. Individual 0+ mussels produced on average only 63% of the mass of biodeposits (32.4 mg dry wt d^{-1} ind^{-1}) that 1+ mussels did (51.5 mg dry wt d^{-1} ind^{-1}). In contrast, the amount of biodeposits produced per unit body weight (dry weight of soft tissue) was greater for 0+ than for 1+ mussels. Faecal pellet sinking velocity ranged from 0.27 to 1.81 cm s^{-1} for mussels ranging in size from 3 to 7 cm, and was best correlated with faecal pellet width. Sedimentation rates were greater within the farm than at reference sites, supporting the hypothesis that mussel farming increases sedimentation rates. Variations in sedimentation were also observed at small spatial scales and through time. Prior to the harvesting of 1+ mussels, sedimentation rates directly under the 1+ mussel lines were about twice those 10 m distant, between the lines, and in other zones (reference sites and sites in the lease with 0+ mussels). These observations and sedimentation patterns along transects leading away from the mussel farm suggest that biodeposits from the farm are not dispersed broadly. The estimated initial dispersal of faecal pellets ranges from 0–7.4 m (1+ mussels) to 7–24.4 m (0+ mussels).

2.1 INTRODUCTION

Aquaculture production of fish, shellfish and algae is increasing world wide, with greater volumes and varieties of species being produced. Thus, there are increasing concerns about the ecological implications of this industry, especially in coastal areas where the bulk of the production is located. To date, most research on aquaculture–environment interactions has focused on finfish (see reviews by Black 2001, Hargrave 2005). The influence of this type of culture is often considerable because of the great biomass that is often grown in small areas, the addition of external feed and the use of antibiotics. The accumulation of organic wastes under fish cages may induce local organic enrichment, potentially leading to increased oxygen uptake, ammonium release and changes in benthic community structure (Hargrave 2005). In contrast to finfish aquaculture, research on bivalve aquaculture–environment interactions is relatively scarce (see review by Kaiser et al. 1998). This may be partly due to the general perception that bivalve aquaculture has less dramatic environmental effects than does finfish aquaculture, as bivalves are grown at comparatively low biomass per unit area and feed is not added to the environment. However, bivalve farms are typically much more extensive than fish farms, at times covering many square kilometres. In Canada, the most important bivalve in production, in terms of biomass (22 857 t in 2004), is the mussel *Mytilus* spp. (http://www.dfo-mpo.gc.ca/communic/statistics/aqua/index_f.htm). In order to ensure the sustainable development of the mussel industry, a better understanding of the relationship between mussel production and its influence on the benthic environment is needed.

Bivalves produce faeces and pseudofaeces, hereafter collectively referred to as biodeposits, which are large compacted aggregates of particles (0.5 to 3 mm) that sink more rapidly than their constituent particles (Haven & Morales-Alamo 1966), thereby increasing sedimentation rates within bivalve culture sites (Dahlbäck & Gunnarsson 1981, Hatcher et al. 1994). Although some studies have not detected biodeposit-related responses at bivalve culture sites (Crawford et al. 2003, Danovaro et al. 2004), others have shown that the accumulation of biodeposits may lead to enhanced sulphate reduction (Dahlbäck & Gunnarsson 1981), enhanced ammonium release (Hatcher et al. 1994) and structural changes in the resident microbial (Mirto et al. 2000), meiofaunal (Mirto et al. 2000) and/or macrofaunal (Mattsson & Lindén 1983, Kaspar et al. 1985, Hartstein & Rowden 2004) communities.

Although biodeposition may play an important role in pelagic–benthic coupling, few studies have paid attention to the dynamics of biodeposition. Little is known about biodeposit quality (Navarro & Thompson 1997), biodeposit production rates (Kautsky & Evans 1987), or their potential for dispersion (Miller et al. 2002, Giles & Pilditch 2004, Hartstein & Stevens 2005). Further, empirical relationships between biodeposit size and sinking velocity are poorly estimated by simple sinking velocity equations, such as Stoke's law, as has been shown by Chamberlain (2002) and Giles & Pilditch (2004). A better understanding of the relationship between these factors is necessary in order to make accurate predictions of benthic loading and subsequent effects on the local environment (Henderson et al. 2001).

In the present study, we evaluated various parameters relating to the production and dispersal of biodeposits by cultured mussels in Great-Entry Lagoon, Magdalen Islands, eastern Canada. The work was done throughout the summer, when biodeposit production is likely to be maximal (Hatcher et al. 1994). Specifically, we assessed: (1) the quantity and quality of biodeposits produced by different age classes of mussels, (2) the size-dependent sinking velocity of faeces and (3) the variation in sedimentation rates at 3 spatial scales: among different zones within the lagoon (large scale), within the mussel culture site (small scale), as well as around the site (spatial extent). This work is part of a larger collaborative study to determine the benthic carrying capacity of sites for mussel farming.

2.2 MATERIALS AND METHODS

2.2.1 Study site

This study was done from June to September 2003, in Great-Entry Lagoon (GEL) in the Magdalen Islands, eastern Canada (47°37'N, 61°31'W) (Figure 2.1). The GEL has an approximate length of 25 km and a surface area of 58 km^2. The environmental conditions in GEL have been described in past studies (Auclair 1977, Mayzaud et al. 1992, Koutitonsky et al. 2002). GEL is characterised by an average tidal range of 0.58 m at its entrance and is covered by ice during the winter (Koutitonsky et al. 2002). Temperature increases from 8°C in June to an average maximum of 20°C during the third week of August and then decreases to 9°C by October (Myrand 1991). Seasonal salinity within the lagoon ranges

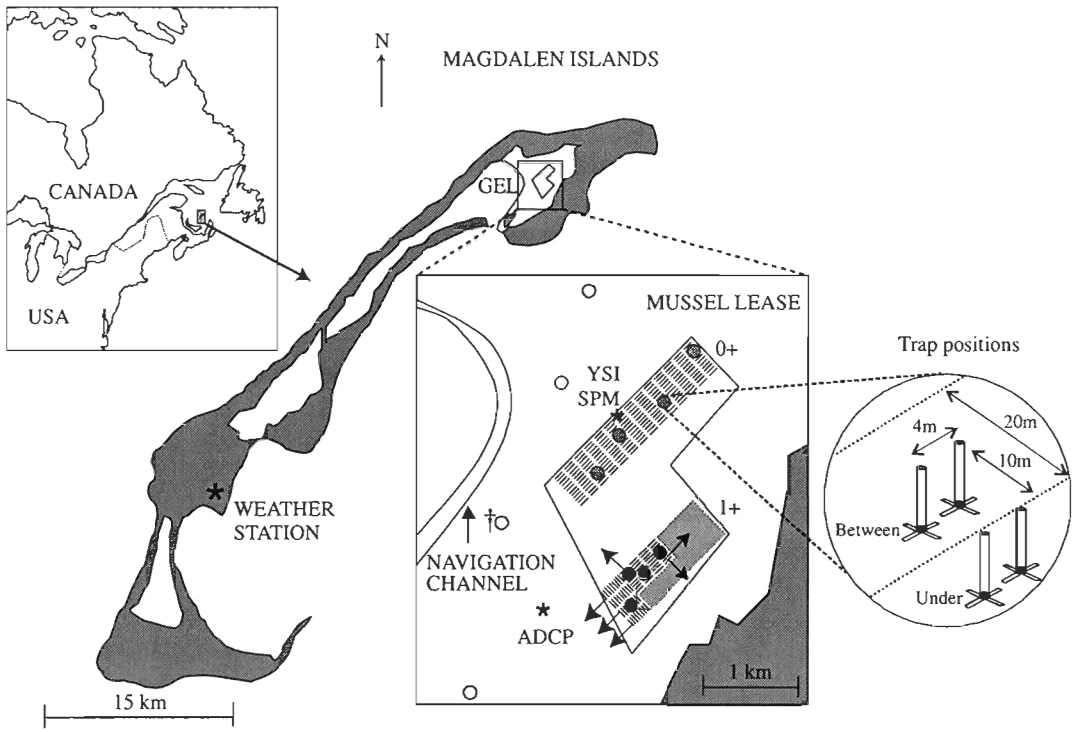

Figure 2.1 Location of the mussel farm (polygon) studied in Great-Entry Lagoon (GEL) in the Magdalen Islands, Canada. The farm is divided into 2 zones based on age classes: 0+ and 1+. Mussel lines are indicated by hatched rows and the area of harvested mussel lines (1+ zone) is light grey. Sampling sites (4 sites per zone) are indicated for: 0+ (◎), 1+ (●) and reference sites (○). The sites indicated on the map represent an example of the sampling design for 1 sampling date; positions differed on each of the 6 sampling dates. Black arrows represent transects, which were placed perpendicular (except for the NE direction) to the last mussel line on each side of the 1+ zone. Asterisks indicate the positions of the Yellow Springs Instruments multi-parameter probe, ADCP (acoustic Doppler current profiler), suspended particulate matter (SPM) and weather stations. The site for the biodeposit production experiments is indicated by a cross.

from 25 to 31.5‰ (Poirier & Myrand 1982). Mean currents in GEL are weak, with typical speeds of 5 cm s^{-1} and occasionally increasing to 10 cm s^{-1} during strong wind events, resulting in a well-mixed water column (Koutitonsky et al. 2002). An 8 m deep navigation channel separates the GEL into a shallow (1 to 3 m) sandy area to the west and a deeper (5 to 7 m) muddy basin to the east where the mussel farm is located (Figure 2.1). Mussels *Mytilus edulis* L. are cultured on longlines in a 2 yr grow-out cycle at a density of approximately 575 mussels m^{-1} of mussel line. Longlines are separated by 20 m. The farm currently produces 180 t yr^{-1} and has been in operation since the 1980s. The mussel culture site covers a 2.5 km^2 area and is divided into 2 zones, one with 0+ and the other with 1+ mussels, the latter are replaced by juveniles each fall following harvest. Mussels in the region spawn between May and August, and spat recruitment starts at the end of June and lasts about 3 mo. During this study, 0+ and 1+ mussels were ca. 11 to 14 and 23 to 26 mo old, respectively.

2.2.2 Environmental conditions

Wind direction and speed were obtained from the Environment Canada meteorological station located at Grindstone, ca. 35 km southwest of GEL (Figure 2.1). A 500 kHz SonTek acoustic Doppler current profiler was moored 500 m southwest of the mussel lease (Figure 2.1) between June and October 2003. The upward-facing instrument was mounted on a frame set on the seabed and measured current speed and direction in pulse-coherent mode in 20 equally spaced cells of 0.25 m thickness from 0.6 to 5.6 m above the bottom. Measurements were averaged over 2 min at 20 min intervals.

Temperature, salinity and chlorophyll *a* (chl *a*; fluorescence) were measured using a YSI-6600-EDS multi-parameter probe, moored within the mussel lease (Figure 2.1). Suspended particulate matter (SPM) concentration and quality (percent organic matter, %OM) were quantified within a collaborative study with Dr. Suzanne Roy (Université du Québec à Rimouski, Canada). Water samples were collected weekly at depths of 1 and 4 m at the YSI (Yellow Springs Instruments) station (Figure 2.1) and filtered through pre-burned and pre-weighed glassfibre filters (Whatman GF/F, 0.7 µm). Filters were then analysed as outlined in the 'Biodeposit production and quality' section.

2.2.3 Biodeposit production and quality

Biodeposition by the 0+ and 1+ mussel cohorts was measured *in situ* by placing a fixed number of mussels within cylindrical vexar cages fitted into the top of sediment traps for periods of 24 h. The sediment traps were constructed from PVC tubing (10.2 cm diameter, 76.2 cm height), with a funnel at the base leading to a 250 ml sampling bottle. The experimental design consisted of 5 treatments: 0+, 1+, $0+_{shell}$, $1+_{shell}$ and a control without mussels. Each treatment had 3 replicates on each trial date (14 to 15 August, 18 to 19 August, 21 to 22 August). Traps were deployed in an array 800 m from the mussel site at a depth of 7 m (Figure 2.1). Live mussels were used in the 0+ and 1+ treatments, while the $0+_{shell}$ and $1+_{shell}$ treatments consisted of only mussel shells. The number of mussels used ensured that about 2/3 of the cage area was covered by a layer of mussels. Thus, for the 0+ cohort, each cage contained 6 mussels measuring 3.0 to 4.5 cm in length and, for the 1+ cohort, each cage contained 3 mussels measuring 5.5 to 7.0 cm. These size ranges were

selected based on preliminary field measurements of mussels on mussel lines at that time. For the $0+_{shell}$ and $1+_{shell}$ treatments, mussels were boiled, the tissue removed and the valves glued together leaving an opening similar to a natural gape. The 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. A further control, without mussels, was also used to measure background sedimentation rates.

After 24 h, sediment traps were retrieved and the contents filtered through pre-burned and pre-weighed glassfibre filters (Whatman GF/F, 0.7 μm). Swimmers seen by the naked eye were rinsed to remove any particles adhering to them and then discarded. Filters were rinsed with ammonium formate, dried at 65°C for 72 h to constant weight and weighed. The %OM in the sedimented material was calculated as the weight loss of dried material combusted at 450°C for 5 h (Byers et al. 1978). Sub-samples of sedimented material from control traps without mussels and faecal pellets from traps with mussels were transferred with a Pasteur pipette to glassfibre filters (Whatman GF/F, 0.7 μm) for CHN (carbon, hydrogen and nitrogen) analysis on a Perkin-Elmer 2400 elemental analyzer.

Biodeposition was calculated as the amount of material collected in sediment traps with mussels minus the average sedimentation obtained in the corresponding shell controls. Biodeposition was then divided by the number of individuals in each trap to obtain an average biodeposit production per individual. Biodeposit production was also expressed in relation to mussel weight. Mussels were weighed to measure the fresh wet weight (WW), dried at 65°C and weighed to obtain tissue and total mussel dry weights (DW).

2.2.4 Biodeposit sinking velocities

The sinking velocity of faecal pellets was measured to estimate the dispersal of mussel biodeposits in GEL. Faecal pellets were collected for 5 size classes of mussels (3, 4, 5, 6 and 7 cm shell length) using sediment traps deployed for 24 h, as described in the previous section (3 mussels $trap^{-1}$). The sinking speed of individual faecal pellets was measured in a cylindrical glass sinking column (45 cm height, 10.5 cm diameter) filled with filtered (0.7 µm) seawater (21 ± 1°C, 28 psu) collected the same day. The contents of each sampling bottle were carefully transferred to a Petri dish. Individual faecal pellets were randomly chosen, measured (length and width) and transferred to the sinking column using a Pasteur pipette. Faeces were gently introduced just below the water surface, and the sinking velocities were measured by timing the decent between 2 marks, 10 cm apart, the first of which was 7 cm below the water surface. Preliminary tests showed that constant speed was attained and that a distance of 13 cm from the bottom of the sinking column was sufficient to avoid any influence from the bottom of the column on sinking velocity. The dimensions and sinking speed of at least 25 randomly chosen faecal pellets were measured for each mussel size class.

No pseudofaeces were observed in the samples. However, as the SPM concentration at which pseudofaeces are first produced is approximately 4.5 to 5 mg l^{-1} (Widdows et al. 1979), it is possible that pseudofaeces were produced in low quantities and were perhaps present but undetected in the flocculated sedimented matter. For consistency with other

studies, we use the term 'biodeposits' throughout the text, except when referring specifically to faecal pellets.

2.2.5 Sedimentation rates

Sedimentation rates were evaluated at 3 spatial scales: among zones within the lagoon (large scale), within the mussel farm (small scale) and around the farm (spatial extent). Sedimentation rates were evaluated using sediment traps, made from PVC tubing (50 cm height, 5 cm diameter) with clear PVC bases to allow for visual inspection. The 10:1 height:diameter ratio was chosen to limit the resuspension of particulate matter within the trap (Gust & Kozerski 2000). The traps fit into bases made of flat steel crosses, with a plastic pipe cap to allow for easy deployment and retrieval. Bases were installed on the bottom at least 24 h before deploying the sediment traps, to avoid contamination by resuspended matter. Sediment traps were deployed for 24 h, and no preservatives were used.

To evaluate large-scale effects, sediment traps were deployed at each of 4 sites within the 0+ and 1+ zones of the farm, as well as at 4 reference sites (R), located at least 500 m from the mussel farm (zone) on each sampling date. In all cases, sampling sites were randomly selected within each zone on each sampling date to ensure the independence of the data. Small-scale effects were evaluated by deploying pairs of sediment traps, separated by 4 m, directly under mussel lines with a further pair of traps 10 m NW of these, directly between mussel lines (position, Figure 2.1). Thus, SE and NW positions at reference sites

correspond to 'under' and 'between' positions in 0+ and 1+ zones. To evaluate if the patterns observed at the large scale were simply site-related differences and not related to aquaculture activities, we made use of a 'natural' experiment. Mussels in the 1+ zone were scheduled to be harvested in mid-August 2003; we divided our sampling effort to sampling before and after this time (Periods 1 and 2, respectively). Thus, sampling was done on 3 dates before and 3 dates after the scheduled 1+ harvest. It was predicted that sedimentation rates would change from 1+ > 0+ > R before the harvest to 0+ > 1+ = R after the harvest, thus showing the influence of aquaculture and discounting site effects. It was further predicted that $1+_{under} > 1+_{between}$ in Period 1 but that $1+_{under} = 1+_{between}$ in Period 2, following harvesting. However, some 1+ mussels were not harvested in August, but the planned sampling design was respected, and sediment traps were placed under lines without mussels, keeping in mind that 1+ mussels were still in this zone.

The spatial extent of biodeposition was evaluated using the sediment traps described above and set up along transects extending away from the mussel farm. Paired sediment traps, separated by 4 m, were positioned at distances of 0, 3, 6, 12, 15 and 30 m along transects placed perpendicular to the edge of the mussel farm and usually to the mussel lines themselves. To evaluate the spatial variation in along-transect sedimentation rates, we first measured sedimentation rates along 3 parallel transects separated by 100 m and all oriented in the direction of the dominant SW current on 2 to 3 August (Figure 2.1). To evaluate the dispersion of biodeposits around the farm, sedimentation rates along transects leading from each of the 4 sides of the 1+ zone were measured on 13 to 14 August (Figure 2.1). As differences were not observed among the 3 transects in the same direction (see

'Results'), transects were not replicated in the different directions. Following a 24 h deployment, sediment traps were retrieved and the contents analysed as outlined in the 'Biodeposit production and quality' section.

2.2.6 Statistical analyses

The relationship between: 1- mussel DW and WW, 2- mussel size and biodeposit production, 3- mussel size and faecal pellet size, and 4- faecal pellet size and sinking velocity were evaluated by linear regression using SYSTAT. Variations in biodeposit production between dates were evaluated by ANCOVA, with mean mussel mass as the covariate using SYSTAT on $\log_{10}$-transformed data. Variation in sedimentation rates was evaluated using ANOVA followed by Student–Newman–Keuls (SNK) multiple comparison tests (Underwood 1997). Data for sedimentation along transects in different directions was $\log_{10}$-transformed prior to analysis by ANOVA to satisfy the assumptions of the statistical model. Balanced ANOVA models were assessed using GMAV, unbalanced models, by using SYSTAT.

2.3 RESULTS

2.3.1 Environmental conditions

The temporal variations of temperature, chl *a*, and SPM concentration and quality are given in Figure 2.2. During the sampling period, temperature varied from 10°C in early June to a maximum of 20°C at the end of July. Salinity varied only slightly, ranging from

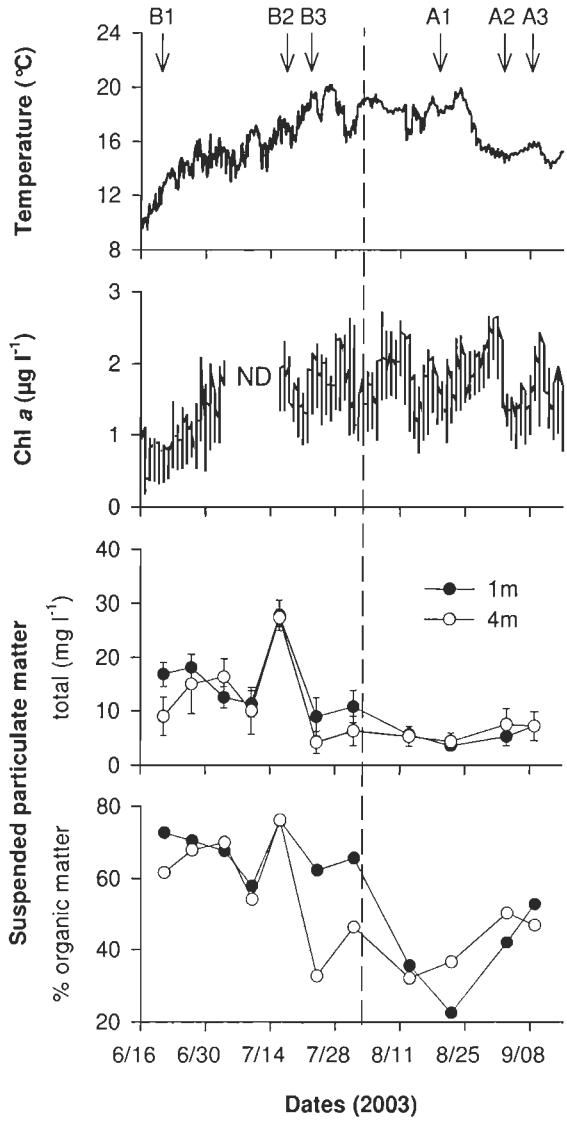

Figure 2.2 Time series of environmental data on temperature, chlorophyll *a* and suspended particulate matter (total and %organic matter), in 2003. (● and ○: samples that were collected at a depth of 1 and 4 m, respectively; B1, 2, 3 and A1, 2, 3: sampling dates before (B) and after (A) the 1+ mussel harvest (dashed line); ND: no data.

30.4 to 30.8‰ (data not shown). Chl *a* concentration increased from 0.2 µg l^{-1} at the beginning of the study and ranged between 1.0 and 2.7 µg l^{-1} from July to September. SPM concentrations ranged between 9.0 and 27.4 mg l^{-1} from mid-June to mid-July, thereafter decreasing to <10.8 mg l^{-1}. The %OM in SPM was generally high from mid-June to mid-July (54 to 76%) and <53% between mid-August and September.

2.3.2 Biodeposit production and quality

Detailed results on the relationship between *Mytilus edulis* size and biodeposit production are given in Table 2.1. For brevity, results are expressed in relation to tissue dry weight (see Table 2.2 a for conversions). Shell controls collected less sedimented material than did controls with no mussels (Table 2.1). We interpret this difference as being due to mussel shells in the $0+_{shell}$ and $1+_{shell}$ treatments having reduced the sedimentation rate by a proportion similar to the physical space they occupied and/or to the shells having altered the hydrodynamics at the trap entrance and thus its collection efficiency. These effects probably also occurred in the 0+ and 1+ treatments, and thus biodeposit production was estimated as the difference between the sedimented material recovered in the 0+ and 1+ treatments and that from the $0+_{shell}$ and $1+_{shell}$ treatments, respectively.

The natural background sedimentation rates varied between the 3 sampling dates (Table 2.1). On the last sampling date, about half the quantity of sedimented material was collected as compared to that on the first 2 dates. Biodeposit production was also temporally variable, but, on average, individual 0+ mussels produced 63% the mass of

biodeposits relative to that produced by 1+ mussels (32.4 vs. 51.5 mg DW d^{-1} $ind.^{-1}$, respectively; Table 2.1). In contrast, biodeposit production per unit mussel biomass was greater for 0+ than for 1+ mussels (72.7 vs. 34.7 mg d^{-1} g^{-1} tissue, respectively). There was a temporally variable but consistent negative linear relationship between mussel tissue DW and biodeposit production (mg DW g^{-1} tissue d^{-1}) (Figure 2.3, Table 2.3).

The %OM collected in the sedimented material was significantly greater in treatments containing live mussels than in controls and shell treatments on the first date (SNK test, data not shown). Between Dates 1 and 3, the %OM increased in the controls, but this trend was not apparent in the treatments with live mussels (Table 2.1). CHN analysis of the flocculated sedimented material and faecal pellets indicated that the percent organic carbon was slightly greater in faecal pellets than in naturally sedimented material: 2.4 ± 0.5 vs. 1.1 ± 0.2%, respectively (F = 13.40, p = 0.011). The percent organic nitrogen in faecal pellets and the SPM did not differ (F = 3.857, p = 0.097) and ranged between 0.2 and 0.4%. The average carbon to nitrogen ratio of faecal pellets (7.4) was greater than that of naturally sedimented material (6.1) (F = 8.137, p = 0.029).

Table 2.1 *Mytilus edulis*. Biodeposit production measured in situ for 2 mussel cohorts (0+ and 1+) and 3 control treatments (cage without mussels [control], cages with $0+_{shell}$ and with $1+_{shell}$) in Great-Entry Lagoon during 3 sampling periods. Mean mussel length, tissue weight (DW), mass of sedimented material and percent organic matter (% OM ± SE) are given. 0+ treatments: 6 mussels $cage^{-1}$ (n = 3); 1+ treatments: 3 mussels $cage^{-1}$ (n = 3).

Date/Treatment	Mean mussel length cm	Mean tissue weight (g)	Sedimented material (mg d^{-1})	%OM	Biodeposit production rate	
					(mg $ind.^{-1}$ d^{-1})	(mg g^{-1} tissue d^{-1})
14 to 15 August						
Control	–	–	124.6 ± 38.9	12.7 ± 0.5	–	–
$0+_{shell}$	–	–	67.2 ± 23.8	13.7 ± 0.4	–	–
$1+_{shell}$	–	–	71.8 ± 23.3	12.5 ± 3.6	–	–
0+	4.0 ± 1.1	0.4 ± 0.3	241.4 ± 28.5	20.4 ± 0.4	29.1 ± 4.8	80.4 ± 13.7
1+	6.9 ± 0.2	1.4 ± 0.7	204.9 ± 31.6	21.7 ± 1.6	44.4 ± 10.5	31.1 ± 8.1
18 to 19 August						
Control	–	–	105.7 ± 30.3	14.8 ± 0.8	–	–
$0+_{shell}$	–	–	54.0 ± 13.9	17.8 ± 1.8	–	–
$1+_{shell}$	–	–	42.7 ± 14.5	17.8 ± 1.9	–	–
0+	4.5 ± 0.3	0.5 ± 0.1	360.6 ± 151.0	21.0 ± 0.7	51.1 ± 25.2	114.0 ± 65.2
1+	6.7 ± 0.2	1.6 ± 0.3	300.7 ± 103.0	21.9 ± 1.0	86.0 ± 34.3	54.7 ± 16.9
21 to 22 August						
Control	–	–	63.5 ± 33.1	19.8 ± 3.8	–	–
$0+_{shell}$	–	–	39.1 ± 27.2	23.7 ± 6.3	–	–
$1+_{shell}$	–	–	21.6 ± 20.1	28.4 ± 11.3	–	–
0+	5.2 ± 0.3	0.7 ± 0.4	140.9 ± 34.2	23.4 ± 2.0	17.0 ± 5.7	23.6 ± 8.5
1+	6.7 ± 0.3	1.4 ± 0.5	104.8 ± 23.5	24.7 ± 1.4	24.2 ± 7.8	18.3 ± 8.3

Table 2.2 *Mytilus edulis*. Results of the linear regression analysis of: (a) mussel dry weight (DW) as a function of mussel wet weight (WW), (b) biodeposit production DW as a function of mussel tissue DW on different sampling dates, (c) faecal pellet size as a function of mussel length for 3 to 6 cm mussels, and (d) 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
(a)	Mussel DW (including shell, g)	Mussel WW (including shell, g)	0.391	0.820	0.965	0.001	27
	Mussel tissue DW (g)	Mussel DW (including shell, g)	0.137	0.255	0.918	0.001	27
(b)	Biodeposit production	Mussel tissue DW (log_{10}, g)					
	(log_{10}, mg g^{-1} tissue d^{-1})	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
(c)	Faecal pellet size (mm)						
	Width	Mussel length cm	0.222	0.022	0.539	0.000	178
	Length	Mussel length cm	1.141	–1.523	0.162	0.000	178
	Area	Mussel length cm	2.152	–5.477	0.232	0.000	178
(d)	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

2.3.3 Biodeposit characteristics and sinking velocity

Faecal pellets could be seen by the naked eye and were easily differentiated from the flocculated sedimented matter. The faecal pellets were shaped as long half cylinders cut lengthwise, had a grainy texture and were light to dark brown in colour. Mussels produced faecal pellets of varying sizes, ranging from 0.7 to 29.0 mm in length and from 0.3 to 1.8 mm in width. Of the 3 measures of faecal pellet size evaluated, mussel size best predicted pellet width (Table 2.2c). Overall, larger mussels produced larger faeces. However, 7 cm mussels were an exception to this trend (see Table 2.4) and were thus not included in the correlation between mussel size and faecal pellet size given in Table 2.2c. Variation in sinking velocity was best explained by faecal pellet width, although surface area and length also explained significant but lesser proportions of the variance in sinking velocity (Table 2.2d). The relationship between sinking velocity and faecal pellet width is given in Figure 2.4. Minimum and maximum sinking velocities were 0.27 and 1.81 cm s^{-1}, respectively (Table 2.4). Long faecal pellets, folded in half, had the greatest sinking velocity.

2.3.4 Field measures of sedimentation rates

The variation in sedimentation rates and the quality of the sedimented material (%OM) throughout the sampling period at large and small spatial scales is given in Figure 2.5. On the whole, the results support the hypothesis that sedimentation rates are greatest within the culture area with 1+ mussels (significant position × zone × period interaction;

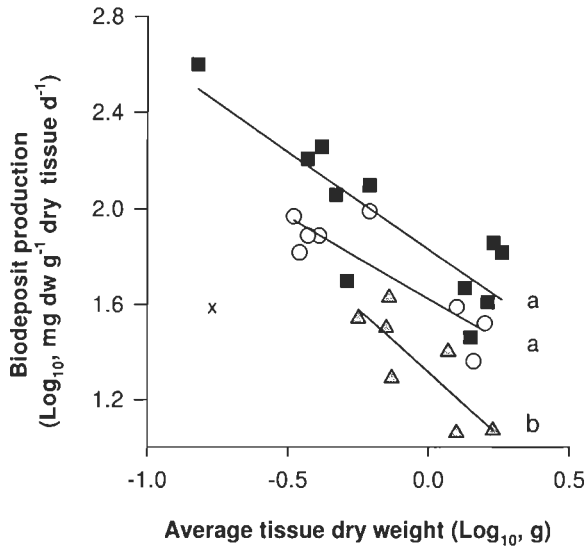

Figure 2.3 *Mytilus edulis*. Relationship between biodeposit production and dry weight of mussels on 3 sampling dates: 14 to 15 August (○), 18 to 19 August (■) and 21 to 22 August (△). The 'x' symbol represents an outlier from the 14 to 15 August data. Solid lines represent linear regressions fitted to the $\log_{10}$-transformed data. Regression statistics are given in Table 2.2b. Daily biodeposit production denoted by different letters are significantly different (pairwise comparison, $p < 0.01$). ANCOVA analysis is given in Table 2.3.

Table 2.3 *Mytilus edulis*. ANCOVA examining the influence of sampling date and mussel size (dry weight of soft tissues) on the production of biodeposits. All data were log_{10}-transformed prior to analysis: (a) analysis to test the assumption of equal slopes (i.e. the interaction effect) and (b) analysis to test for main effects with the variance associated with the interaction effect pooled with the residual error.

Source of variation	df	MS	*F*	p
(a)				
Date	2	0.521	19.85	**0.000**
Mass	1	0.825	31.41	**0.000**
Date × mass	2	0.010	0.37	0.693
Error	20	0.026		
(b)				
Date	2	0.547	22.09	**0.000**
Mass	1	1.295	52.23	**0.000**
Error	22	0.025		

Table 2.4 *Mytilus edulis*. Summary of mussel characteristics (average mussel shell length and average mussel tissue weight), mean faecal pellet width (mean ± SD) and associated sinking velocities of faecal pellets produced by mussels of different size classes. Several long and folded faecal pellets (denoted by asterisks) were produced by mussels in the 6 cm size class. Parentheses: number of faecal pellets measured in each size class.

Mussel size class (shell length, cm)	Mean tissue weight (DW, g)	Mean faecal pellet width (mm)	Sinking velocity ($cm\ s^{-1}$)		
			Minimum	Maximum	Mean
3.1 ± 0.1	0.16 ± 0.04	0.62 ± 0.20 (56)	0.27	0.99	0.63 ± 0.17
4.1 ± 0.2	0.37 ± 0.06	0.99 ± 0.24 (67)	0.45	1.67	0.92 ± 0.24
4.9 ± 0.1	0.61 ± 0.07	1.19 ± 0.04 (25)	0.73	1.45	1.04 ± 0.17
6.3 ± 0.1	1.40 ± 0.33	1.16 ± 0.10 (21)	0.73	1.56	1.09 ± 0.21
		1.52 ± 0.19 (9)*	1.17	1.62	1.35 ± 0.16*
7.0 ± 0.1	1.53 ± 0.38	0.91 ± 0.25 (57)	0.50	1.81	0.86 ± 0.25

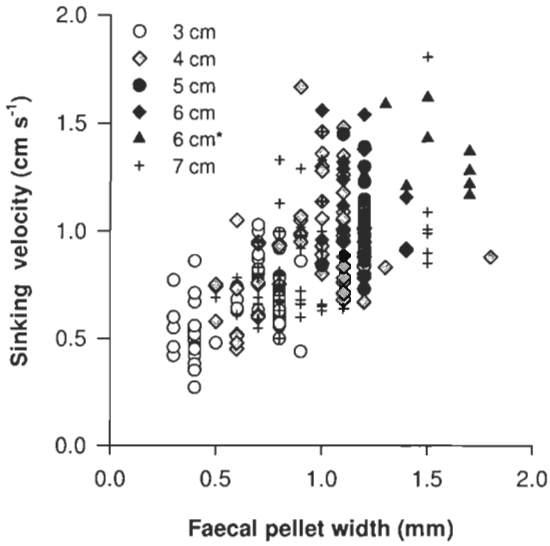

Figure 2.4 *Mytilus edulis*. Relationship between the sinking velocity (cm s^{-1}) and faecal pellet width (mm) produced by 5 mussel size classes (6 cm*: faecal pellets from the 6 cm mussel size class that were observed to fold in half while settling). Regression statistics are given in Table 2.2d.

Table 2.5). During the first period, sedimentation rates directly under the mussel lines in the 1+ zone were almost twice those observed in other zones and positions (Figure 2.5a). In contrast, sedimentation rates for $1+_{under}$ and $1+_{between}$ did not differ after harvesting. An overall increase in sedimentation rates was observed at all positions and in all zones throughout the sampling period. The increase in sedimentation rates was, however, most pronounced in the 0+ zone (sedimentation rates during Period 2 were 3.5 times greater than those in Period 1). Moreover, differences between positions ($0+_{between}$ vs. $0+_{under}$) were significant only in the 0+ zone during Period 2.

The %OM of sedimented material varied among zones between the 2 periods (Figure 2.5b) such that it was typically greatest in the 0+ and 1+ zones during Period 1, but did not differ among sites in Period 2. The %OM of sedimented material tended to decrease in Period 2, although this effect was not statistically significant (Table 2.5).

2.3.5 Dispersion

The 3 parallel transects deployed perpendicular to the last SW mussel line indicated that along-transect sedimentation rates did not differ significantly among transects (Table 2.6a). This shows that a single transect is representative of sedimentation patterns for a given direction. The single transects placed in each of 4 different directions (3 of which were used in the statistical analyses) around the mussel farm showed that the dispersion of biodeposits was fairly localised. Regardless of transect direction, sedimentation decreased

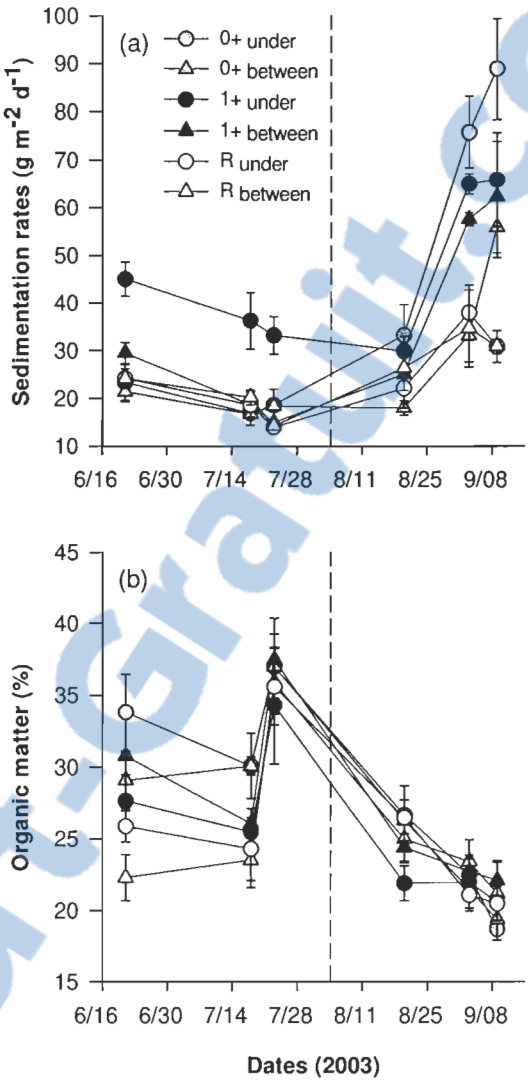

Figure 2.5 *Mytilus edulis*. (a) Sedimentation rates (mean ± SE, n = 4 for each value) and (b) %OM of the sedimented material at 1+, 0+ and reference (R) sites, in 2003. Data are given for positions 'under' and 'between' mussel lines, corresponding to the SE and NW positions for reference sites, respectively. The dashed vertical line separates samples from prior to and after the harvesting of the 1+ mussels.

Table 2.5 *Mytilus edulis*. ANOVA results for sedimentation rates and %OM observed within and outside a mussel farm in Great-Entry Lagoon in the summer 2003. Fixed factors were zone (Z), period (Pe) and position (Po). Random factors were site (S) and date (D). See 'Materials and methods' for details. Statistically significant values are indicated in bold.

Source of variation	df	Sedimentation rates			%OM		
		MS	*F*	p	MS	*F*	p
Z	2	25 705.38	5.90	**0.027**	124.59	2.87	0.115
Pe	1	143 033.64	4.89	0.091	4354.90	5.67	0.076
D (Pe)	4	29 225.78	23.81	**0.000**	768.26	21.16	**0.000**
Z × Pe	2	10 772.33	2.47	0.146	172.82	3.98	0.063
Z × D (Pe)	8	4 360.46	3.55	**0.002**	43.38	1.19	0.320
S (Z × D [Pe])	54	1 227.50	4.90	**0.000**	36.32	3.37	**0.000**
Po	1	23 912.96	23.13	**0.009**	2.80	0.20	0.675
Po × Pe	1	2 812.63	2.72	0.174	11.97	0.87	0.403
Po × D (Pe)	4	1 034.05	2.14	0.088	13.72	1.01	0.409
Po × Z	2	7 139.84	16.78	**0.001**	55.58	4.70	**0.045**
Po × Z × Pe	2	11 756.31	27.62	**0.000**	11.51	0.97	0.418
Po × Z × D (Pe)	8	425.60	0.88	0.539	11.82	0.87	0.545
Po × S (Z × D [Pe])	54	483.36	1.93	**0.001**	13.54	1.26	0.144
Error	144	250.33			10.77		

rapidly along the transects leading away from the mussel farm and became indistinguishable from background levels by about 3 m in the NW direction, 6 m in the SE direction and 12 m in the SW direction (Figure 2.6a, Table 2.6b).The dominant water current direction during the sampling period was towards the SW (Figure 2.6b), and this likely explains the pattern of sedimentation at this time. The NE transect, which unlike all other transects continued in the same orientation as the mussel line, was not included in the statistical analyses.

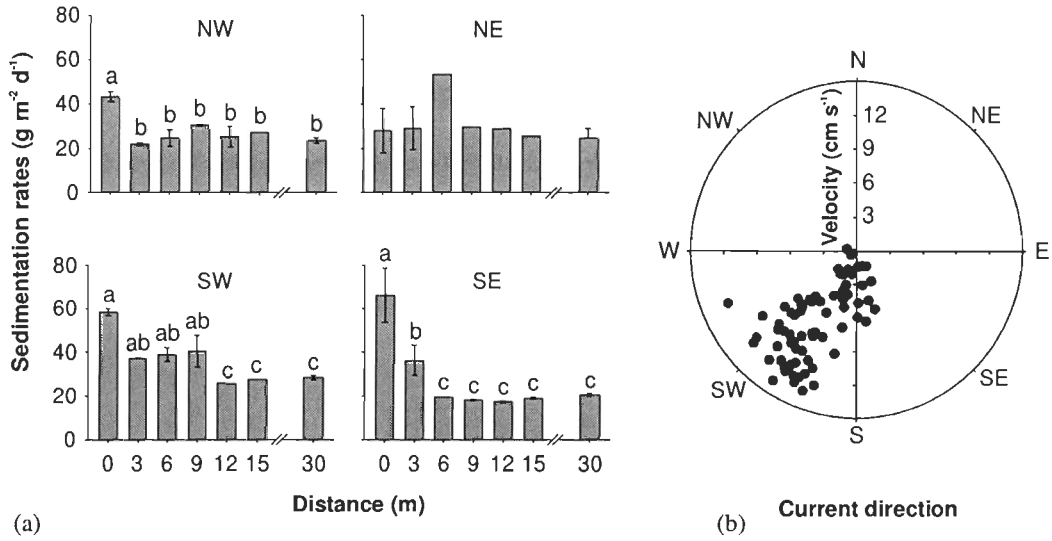

Figure 2.6 *Mytilus edulis*. (a) Sedimentation rates (mean ± SE, g m^{-2} d^{-1}) recorded on 13 to 14 August along 3 transects, placed perpendicular to mussel lines and orientated towards the SE, SW, or NW. Results of the corresponding ANOVA are given in Table 2.6b. The NE transect ran along the same orientation as the mussel line and was therefore not included in the statistical analyses. Differences in sedimentation among distances within a direction are indicated by different letters. (b) Current direction and velocity (cm s^{-1}) 1 m above the bottom during the 24h sampling period. Black dots represent averaged measures recorded over 2 minutes at 20 minute intervals.

Table 2.6 ANOVA examining along-transect variation in sedimentation rates among transects placed perpendicular to mussel lines: (a) 3 transects oriented in the SW direction and (b) single transects oriented in a SE, SW, or NW direction. The NE transect was not included in the analysis, since it was not perpendicular to the mussel lines. Data were $\log_{10}$-transformed to obtain homoscedasticity. Statistically significant values are highlighted in bold.

Source of variation	df	MS	*F*	p
(a) Same direction				
Transect	2	44.881	2.42	0.113
Distance	6	84.792	4.57	**0.004**
Transect × Distance	12	14.802	0.80	0.649
Error	21	18.555		
(b) 3 directions				
Direction	2	0.089	13.27	**0.000**
Distance	6	0.103	15.32	**0.000**
Direction × Distance	12	0.018	2.63	**0.025**
Error	21	0.007		

2.4 DISCUSSION

2.4.1 Biodeposit production

This study showed that biodeposit production was a function of *Mytilus edulis* size. The 2 mussel cohorts differed in terms of their biodeposit production, with 1+ mussels producing, on average, 1.6 times more biodeposits than the 0+ mussels. In contrast, the amount of biodeposits produced per unit body weight was greater for smaller mussels than for larger ones. Similar patterns have been reported for *M. edulis* by (Tsuchiya 1980) and for other suspension-feeding bivalves, including the oyster *Crassostrea virginica* (Haven & Morales-Alamo 1966) and the lamellibranch *Laternula elliptica* (Ahn 1993). This has been explained by the higher clearance rates of younger mussels compared to older ones (Tsuchiya 1980). Physiological rates are an allometric function of body size and thus decline with the relative body surface area available for oxygen diffusion, which decreases with respect to body size as the organism grows (Hawkins & Bayne 1992).

Biodeposit production differed 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, Navarro & Thompson 1997). The quantity of naturally sedimented matter on the first 2 sampling dates was almost twice that on the third date. This could suggest a difference in seston concentration on these dates. Although seston concentration data were not available for these specific dates to support this hypothesis, there was a general decrease in SPM concentration between 13 and 22 August from 5.6 ± 1 to 3.6 ± 0.5 mg l^{-1}

(1 m depth), which may explain the observed variations in biodeposit production. Some studies have shown a positive relationship between biodeposit production and temperature (Tsuchiya 1980, Kautsky & Evans 1987), and/or salinity (Widdows 1985). However, variation in temperature and salinity were probably not responsible for the observed differences in biodeposit production, as both were relatively stable throughout the sampling period. 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). Further, excretion has been shown to vary greatly over small periods of time (8 h) without any apparent relationship with exogenous influences (Hawkins & Bayne 1992). It is thus difficult to identify which factors best explain the observed temporal variation in biodeposit production in this study.

2.4.2 Faecal pellet sinking velocity

As noted by Giles & Pilditch (2004), sinking velocity was best correlated with faecal pellet width. Thus, measures of pellet width are more important for understanding sinking velocity than are other measures of pellet size. Faecal pellet width is related to mussel morphology, whereas pellet length is more a function of current speed (Giles & Pilditch 2004). Thus, mussel size may be used to predict sinking velocities under varying current regimes, allowing for valid estimates of dispersal in the field. In the present study, faecal

pellet width was a function of mussel size for mussels in the size range of 3 to 6 cm. However, for unexplained reasons, 7 cm mussels produced smaller faecal pellets.

The average sinking velocity of 1.0 ± 0.3 cm s^{-1} for *Mytilus 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}. Miller et al. (2002) found sinking velocities for *Atrina zelandica* faecal pellets, ranging from 1.1 to 3.0 cm s^{-1}, but these were from considerably larger individuals (18.5 to 26 cm) than those used in the present study. Variations in sinking velocity are likely due in part to variations in faeces composition. Food quality 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).

2.4.3 Field measurements of sedimentation rates

This study noted significant variations in sedimentation rates at all spatial and temporal scales considered. In general, sedimentation rates were greater within the farm than at reference sites, supporting the hypothesis that mussel farming increases

sedimentation rates of SPM (Kautsky & Evans 1987). Our results are in accordance with other studies, which have shown that suspended mussel culture can increase sedimentation by a factor of 1.3 to 5.5 (Hatcher et al. 1994, Stenton-Dozey et al. 1999, Danovaro et al. 2004, Hartstein & Rowden 2004).

As predicted, sedimentation rates were initially greatest directly under the mussel lines in the zone with 1+ mussels. Further, after these were harvested, sedimentation was greatest in the $0+_{under}$ position, and no differences were observed between $1+_{under}$ and $1+_{between}$ positions. These observations support the hypothesis that the enhanced sedimentation in the 1+ zone was due to the presence of mussels and not due to some other intrinsic feature of the zone. However, during the second period, sedimentation rates in the 1+ zone were still greater than those at reference sites. A combination of easily resuspendable faecal material (Walker et al. 2005) that had accumulated in the 1+ zone and an overall increase of wind strength during August and September may have resulted in sediment resuspension being greater at this time. Moreover, because not all of the 1+ mussel lines had been harvested by the second period, the presence of mussels and the handling of longlines by the mussel grower may have increased overall turbidity in the water column and thus sedimentation rates in the 1+ zone.

That higher sedimentation rates were observed within the 1+ zone than within the 0+ zone prior to harvesting may be explained by the greater biodeposit production (per individual) of 1+ mussels relative to 0+ mussels. Biodeposition from epibiota (such as polychaetes, starfish and hydrozoans), which were more abundant on 1+ than 0+ lines

(authors' pers. obs.), may also have contributed to this observation. The increased sedimentation rates observed at the end of August and in September may have resulted from several factors. First, the increase in sedimentation rates, which was more pronounced within the 0+ zone than within the other zones, was probably partly due to the rapid growth of the 0+ mussels, from 2.5 cm in June to >4.5 cm in September (A. Trottet pers. comm.), which would lead to a greater overall production of biodeposits. Second, differences in food quantity and quality may have increased biodeposition rates. Although increased SPM concentrations were not observed in relation to the increase in sedimentation rates, the particulate organic matter decreased from Period 1 (ranging from 5.4 to 20.8 mg l^{-1}) to Period 2 (<3.8 mg l^{-1}). It is possible that mussels increased their filtration rates to compensate for the lower food quality (Bayne et al. 1993) and thus increased their biodeposit production. However, no data on seston composition were available to confirm a relationship between food quality and sedimentation rates.

In addition to large-scale variations, we observed that sedimentation rates were generally greater under than between mussel lines, providing further evidence that mussel biodeposit production increases sedimentation locally. That this effect became more pronounced through the summer for 0+ mussels may be explained by a number of factors. As the 0+ mussels grew, they became heavier, and the lines sank closer to the bottom due to insufficient flotation (authors' pers. obs.). Therefore, biodeposits had less time to sink and thus be dispersed before they were collected by the sediment traps. Further, as the mussels grew, their faeces would tend to get larger and thus have a greater sinking velocity,

again enhancing sedimentation under the lines. The presence of more easily resuspended sediments in the mussel lease (Walker et al. 2005) may have increased this effect.

The sedimentation rates measured along the 4 transects around the 1+ zone also show that biodeposit dispersion is limited to about 12 m around the mussel farm. That the sedimentation rates measured between lines and at reference sites did not differ throughout the sampling period further supports the idea that biodeposition is localised. Most studies that have evaluated biodeposit dispersion based on biodeposit settling velocity, water depth and current velocity (Chamberlain 2002, Giles & Pilditch 2004, Hartstein & Stevens 2005) have suggested that dispersion is limited to within about 50 m of the farm site.

2.4.4 Estimated dispersion of mussel biodeposits

A small variation in biodeposit sinking velocity, current velocity, or water column depth may have a significant impact on the extent of biodeposit dispersion (Giles & Pilditch 2004). The potential dispersion of mussel biodeposits in GEL differed greatly between the 2 mussel cohorts. The average summer current speed in GEL was 5.5 cm s^{-1}. Given the average sinking velocity of 0.79 cm s^{-1} for 0+ mussel faecal pellets and the distance between the 0+ mussel lines and the bottom (1 to 3.5 m), the initial deposition may be estimated to be between 7 and 24.4 m. In contrast, faecal pellets from the 1+ mussels sank at an average velocity of 0.97 cm s^{-1}, the distance below 1+ mussel lines was between 0 and 1.3 m and, thus, the initial deposition is estimated to be between 0 and 7.4 m. However, during strong wind events, the current velocity can reach 18 cm s^{-1} and the

estimated dispersion of biodeposits may be up to 79.7 and 24.1 m for faecal pellets from the 0+ and 1+ mussels, respectively.

Both the field studies reported here and the simple dispersal estimates suggest that initial deposition of biodeposits is localised to the vicinity of mussel lines. It is obvious that the choice of a site for mussel farming will determine the dispersal potential for the biodeposits produced there. In the Gulf of St. Lawrence region, mussel farms are usually established in relatively shallow coastal areas (e.g. 3-5 m, Grant et al. 2005) as compared to other areas (e.g. 8-42 m in New Zealand, Hartstein & Stevens 2005) and characterised by low current velocities. All things being equal, the accumulation of biodeposits will be higher in these types of farms than in ones established in areas with deep waters and strong currents (Hartstein & Stevens 2005).

2.4.5 Ecological implications

Given the observed low initial dispersal of biodeposits and that the labile component of mussel biodeposits is degraded very quickly (Fabiano et al. 1994), the potential effects on benthic communities would also be expected to be quite localised. We estimated that during the first half of the summer the flux of OM under the 1+ mussel lines was twice that at reference sites. Several studies have shown that an increase in biodeposition associated with bivalve aquaculture may lead to changes in benthic sediment geochemistry and communities (Dahlbäck & Gunnarsson 1981, Mattsson & Lindén 1983). This also appears to be the case for GEL, as the sediment below mussel lines was organically enriched

compared to that at reference sites, and benthic communities were dominated by opportunistic species (Callier et al. 2004).

Results from the present study are part of a larger programme to determine the benthic carrying capacity of mussel aquaculture sites. The spatial extent of aquaculture-related biodeposition and the benthic response to varying levels of biodeposition will be modelled by adapting the DEPOMOD model (Cromey et al. 2002), originally developed for marine cage fish farming, to bivalve aquaculture.

CHAPITRE 3

Multi-scale spatial variations in benthic sediment geochemistry and macrofaunal communities under a suspended mussel culture

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RÉSUMÉ: Les effets chimiques et biologiques de la biodéposition issue de la mytiliculture, ont été évalués à plusieurs échelles spatiales pendant l'été 2003 dans la lagune de Grande-Entrée, à l'est du Canada. Des échantillons de sédiments ont été prélevés sur plusieurs sites (à l'échelle de 100 m), dans trois zones (à l'échelle du km, cohortes de moules 0+, 1+ et référence-R). À petite échelle (10 m, position), les échantillons prélevés directement sous les filières de moules ont été comparés à ceux prélevés entre les filières de moules. En général, le potentiel redox diminuait et les concentrations en sulphide augmentaient avec la profondeur du sédiment mais ne différaient pas entre les zones (R, 0+ et 1+) et les positions (sous et entre filières). Des différences de structures de communautés de macrofaune ont été observées entre les zones et entre les positions $1+_{sous}$ et $1+_{entre}$. La communauté benthique sur les sites $1+_{sous}$ était dominée par des espèces opportunistes (*Capitella capitata*) et présentait la plus faible diversité et la plus faible biomasse. Les sites 0+ étaient caractérisés par le nombre d'espèces et la biomasse les plus élevés, indiquant que certaines espèces ont bénéficié d'un flux modéré de matière organique provenant des moules 0+. Des données historiques indiquent que la zone profonde de la lagune de Grande-Entrée, où est située la culture, est un environnement naturellement enrichi. La mytiliculture contribue probablement à l'enrichissement organique local. La comparaison des communautés benthiques de cette étude à des données historiques similaires de trois périodes [avant la mytiliculture, au début de l'activité mytilicole et après la récolte des moules 1+] a montré que la communauté de macrofaune différait considérablement de celles des autres dates, à cause de la plus forte abondance de déposivores en 2003. Les différences de structure de communautés benthiques entre les trois périodes n'étaient, cependant, pas plus importantes que les différences entre les années de chaque période.

ABSTRACT: The chemical and biological effects of biodeposition from a mussel culture were evaluated at multiple spatial scales during the summer of 2003 in Great-Entry Lagoon, eastern Canada. Sediment samples were collected from multiple sites (100 m scale) in each of 3 zones (Reference-R, 0+ and 1+ mussel cohort zones, km-scale). At a small scale (10 m, position), samples taken directly below mussel lines were compared to others taken from between the mussel lines. In general, redox potential decreased and sulphide concentration increased with sediment depth but did not differ among zones or positions. A clear difference in macrofaunal community structure was observed between zones (R, 0+ and 1+) as well as between $1+_{under}$ and $1+_{between}$ positions. The benthic community at $1+_{under}$ positions was dominated by an opportunistic species (*Capitella capitata*) and had the lowest diversity and biomass. 0+ sites were characterised by the greatest number of species and biomass, suggesting that some species have benefited from a moderate organic loading from the 0+ mussels. Historical data indicated that the deeper part of the lagoon was a naturally enriched environment. The mussel farm probably contributes to local organic enrichment. Comparison of benthic communities from the present study to similar historical data from 3 periods (before mussel farming, at the start of farming activities and after the 1+ mussel harvesting) showed that community structure differed largely because of the greater abundance of deposit feeders in 2003. However, differences in benthic community structure among these 3 periods were no greater than differences observed between years within periods.

3.1 INTRODUCTION

Aquaculture production is increasing worldwide and concerns about its influence on the environment are increasing (see review by Hargrave 2005). Suspension-feeding bivalves produce biodeposits (faeces and pseudofaeces) that have greater sinking velocities than their constituent particles (Haven & Morales-Alamo 1966). Consequently, bivalve biodeposition may increase sedimentation rates under culture sites (by a factor 1.3 to 5.5, see Hatcher et al. 1994, Callier et al. 2006, Giles et al. 2006). The accumulation of biodeposits under suspended bivalve culture may lead to local organic enrichment and potentially increased oxygen uptake and ammonium release (Hatcher et al. 1994), sulphate reduction (Dahlbäck & Gunnarsson 1981) and changes in benthic community structure (Mattsson & Lindén 1983, Kaspar et al. 1985).

According to the general model of organic enrichment outlined by Pearson & Rosenberg (1978), macrobenthic communities subject to increased organic loading will exhibit decreased species richness, increased abundance because of the dominance of opportunistic species, a decrease of total biomass, and shifts in the dominance of trophic groups (Weston 1990). For example, subsurface deposit feeders are expected to become increasingly dominant with increasing organic enrichment (Pearson & Rosenberg 1978). However, studies on the influence of suspended bivalve culture on the benthic environment do not show consistent effects. While some studies have observed a lower total number of individuals, a lower species richness (Mattsson & Lindén 1983, Kaspar et al. 1985, Chamberlain et al. 2001), and a dominance of opportunistic species at mussel farms

compared to reference sites (Chamberlain et al. 2001- site 2), others have not detected significant differences (Chamberlain et al. 2001- site 1, Miron et al. 2005). In some cases, "non classical eutrophication responses", such as greater Shannon diversity index measures and biomass have been observed at mussel farm sites (e.g., Grant et al. 1995) due to the presence of scavengers attracted by mussel drop-off. Differing effects may be explained in part by site (hydrodynamics, topography, background enrichment, sediment type) and culture (bivalve density, culture depth, mussel size) differences. Together, these factors may influence biodeposit production and dispersion (Giles & Pilditch 2004, Callier et al. 2006) and therefore their potential impact on the benthic environment.

In this study, we evaluated the influence of suspended mussel (*Mytilus edulis* L.) culture on the chemical and biological benthic environment of Great-Entry Lagoon - GEL, eastern Canada. At this site, Callier et al. (2006) observed that sedimentation rates under mussel lines with 1 year-old (1+) mussels were twice those 10 m distant, between the lines, and in other zones (reference sites and sites with 0+ mussels). It was predicted that the benthic condition in GEL will vary in relation to observed differences in organic sedimentation. Although several studies have examined the influence of bivalve culture on benthic environments, few have evaluated smaller-scale variations in benthic characteristics within a culture site (1) under long lines vs. between long lines, (2) in areas with juvenile bivalves (i.e., at the beginning of the growth cycle) vs. bivalves of commercial size. Such variation should be taken into account when evaluating the influence of bivalve culture on the benthic environment and when determining the environmental carrying capacity of sites for bivalve aquaculture.

The objective of this study was therefore to determine the influence of the mussel farm in GEL on the benthic environment at several spatial scales: 10 m scale (under and between mussel lines) and 1 km scale (between zones with 0+ and 1+ mussels and a reference zone). Multiple sites (100 m scale) were sampled within each zone to ensure the generality of the findings in GEL. We assessed effects in terms of both chemical (redox potential, sulphide concentration and percent organic matter - % OM) and biological (diversity, abundance, biomass, and community and trophic group structure) characteristics. The chemical indicators examined were chosen because these have been described as the most sensitive physicochemical indicators of organic enrichment (Hargrave et al. 1997). Further, we compared the benthic community data from the current study with similar historical data in the study area to evaluate the long-term temporal changes in benthic community structure to better understand the importance of bivalve culture in influencing benthic communities.

3.2 MATERIAL AND METHODS

3.2.1 Study site

The mussel farm studied is located in GEL in the Magdalen Islands, eastern Canada (N 47° 37', W 61° 31') (Figure 3.1). Detailed environmental conditions in the lagoon are provided in Callier et al. (2006). The farm covers a total surface area of ca. 2.5 km^2, has

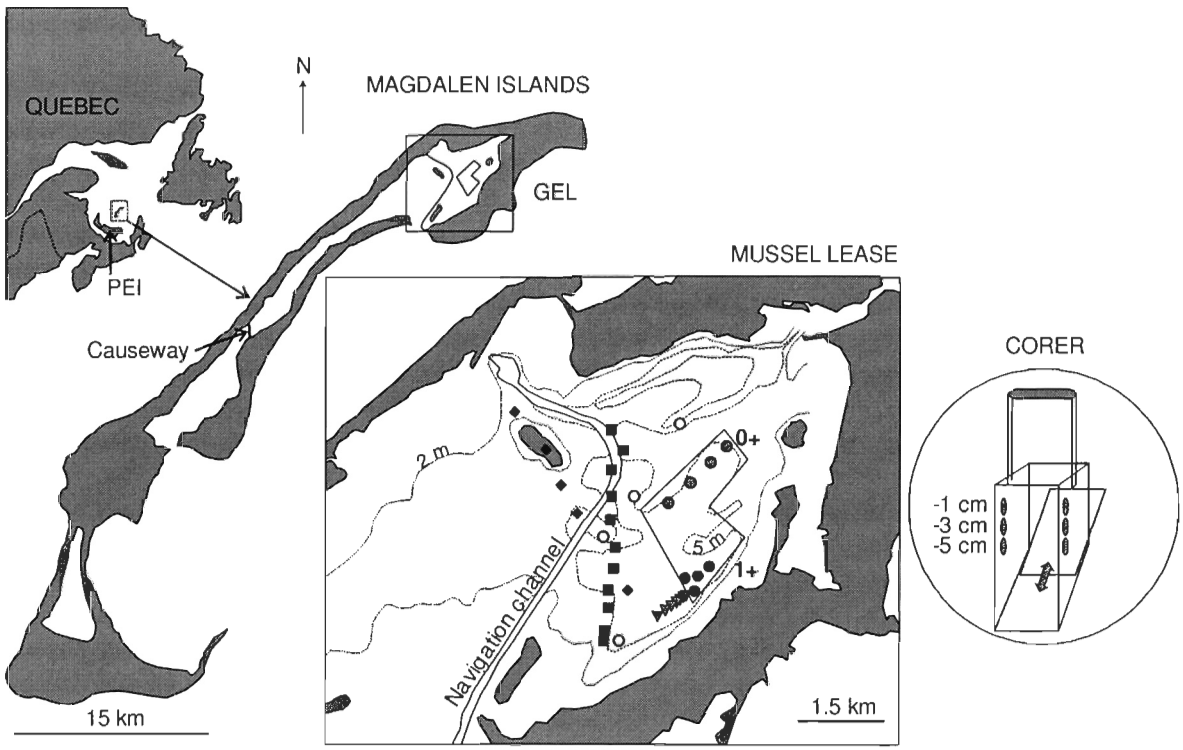

Figure 3.1 Location of the mussel lease (polygon) studied in Great-Entry Lagoon (GEL) in the Magdalen Islands, Canada. The lease is divided into two zones based on the age classes of mussels within them: 0+ and 1+. Sampling sites in the present study (4 sites per zone) are indicated by round symbols: 0+ (○), 1+ (●) and reference sites (○). At each site, 3 core replicates were taken both under and between the mussel lines. At reference sites, 'under' and 'between' positions correspond to SE and NW and positions, respectively. Sampling sites from historical studies are indicated by (◆) 1975; (■) 1978; (▼) 2004. Sampling sites in 1982 were situated within the mussel lease but their exact positions are unknown.

been in operation for about 23 yr and produces about 180 tonnes of mussels annually. The 1+ mussels attain market size (5 to 6 cm) and are harvested and replaced by juveniles each fall. Thus the farm is divided into two zones which are stocked with either 0+ or 1+ mussel cohorts, the age classes in a zone alternating between years. Each zone contains ca. 200, 91 m longlines separated by 20 m. Water depth in the sampling area ranged from 5 to 7 m. During the sampling period, average surface temperature and salinity were, respectively, 18 °C and 31 ppt. The average water current velocity (at 4 m depth) during the summer of 2003 was 5 cm s^{-1} with a maximum of 18 cm s^{-1} (Callier et al. 2006).

3.2.2 Sampling design

The study was done in summer (August 2003), when biodeposit production is likely to be maximal (Hatcher et al. 1994). Variations in sediment characteristics and benthic communities were evaluated at 3 spatial scales. At the largest scale (km, Zone), samples were collected in each of 2 farm zones (0+ and 1+) and in a reference zone (R). These zones were separated by at least 500 m (Figure 3.1). In order to account for natural variation in benthic characteristics, samples were taken in each of 4 randomly chosen sites within each zone (100 m-scale, Site). During the sampling period, we observed that one of the 4 reference sites (the most northern site) was situated in a depositional zone for detritic seagrass (*Zostera marina*) and macroalgae. We thus decided to remove this site from subsequent analyses.

To evaluate the small-scale influence of the mussel farm, samples were taken directly under mussel lines (e.g., $0+_{under}$) and at positions 10 m NW of these, between the mussel lines (e.g., $0+_{between}$) (10 m-scale, Position). The same sampling design was used at both mussel and reference sites to allow for comparisons of small-scale spatial patterns in different zones. Thus, 'under' and 'between' positions in 0+ and 1+ zones correspond to SE and NW positions at reference sites, respectively (i.e., R_{under} and $R_{between}$ positions) . At each position, 3 replicates were sampled using a wedge corer (Figure 3.1) with a vertical array of pre-drilled holes in the sides of the corer to take sediment sub-samples at -1, -3 and -5 cm sediment depths (Depth) to determine chemical sediment characteristics. Samples were taken by scuba-divers to ensure that the cores were returned to the surface as undisturbed as possible.

3.2.3 Sedimentation rates

Callier et al. (2006) evaluated sedimentation rates in GEL in June through September 2003. In sum, they observed greater sedimentation in the $1+_{under}$ position than in all other positions (which did not differ) in June. This trend changed as 0+ mussels grew and 1+ mussels were harvested to a situation where sedimentation was greatest in $0+_{under}$ positions later in August and September.

3.2.4 Sediment geochemical characteristics

Redox potentials (Eh, mV, 2 replicates $depth^{-1}$ $core^{-1}$) were measured in the field, directly from the sediment core, using a combined reference and platinum redox electrode. The redox probe was calibrated using Zobell's solution. Eh was expressed as millivolts at ambient temperature relative to a normal hydrogen electrode (Eh_{NHE}). A cut-off, 5 ml plastic syringe was pushed through holes at each depth to obtain sediment sub-samples. Sediment sulphide concentration (µM, 2 replicates $depth^{-1}$ $core^{-1}$) was determined using an Orion® silver/silver sulphide electrode with a combined calomel electrode as reference. A sulphide anti-oxidant buffer solution was added to each sediment sub-sample. The analysis was done in the field and when storage was required for a short period of time (<3h), samples were placed on ice in the dark. Details of the methodology used are provided in Wildish et al. (1999). The percent organic matter (% OM) from the sediments was calculated as the weight loss of dried material combusted at 450 °C for 5 h (Byers et al. 1978).

3.2.5 Macrofaunal community analysis.

The corer sampled an area of 263 cm^2 to a depth of ca. 15 cm. Samples were gently sieved through a 500 µm mesh. The material retained on the sieve was preserved in a 5% formaldehyde-saline solution. Infaunal specimens were stored in 70 % ethanol after sorting. Identifications were done to the lowest taxonomic level possible, usually to species. Sites were characterised in terms of total abundance, total biomass and diversity (number of species per site - S, Shannon Wiener diversity index - H', and equitability - J'). The biomass of each species was measured as blotted wet weight. All individuals of a species in a core

were grouped for biomass measurements. Animals were removed from tubes prior to biomass determination but the biomass of molluscs includes their shell weight (Weston 1990).

3.2.6 Statistical analysis

Variations in redox potential, sulphide, % OM and univariate indices of the benthic communities were evaluated using ANOVA followed by Tukey multiple comparison tests with SYSTAT. Data were transformed when necessary to satisfy the assumptions of the statistical model (see Results for details). Nonparametric multivariate analyses of community structure, including multi-dimensional scaling (MDS), and SIMPER analyses (to determine the contribution of each species to the total similarity among samples within a given zone) were performed using PRIMER. Analyses were done using individual cores as replicates. Variation in benthic community structure was evaluated using DISTLM (a distance-based nonparametric multivariate analogue of ANOVA) (Anderson & Ter Braak 2003). Multivariate pair-wise comparisons were done using ANOSIM. Data were $\sqrt{}$-transformed for all multivariate analyses. Species were classified into trophic groups according to the classification available in the literature (e.g., Word 1990).

3.2.7 Inter-annual comparison

The community structure based on abundance data observed in the present study was compared to similar data from before the farm was established (1975- Bourget 1976,

Bourget & Messier 1982 - 625 cm^2 grab sieved on a 500 µm screen; 1978- Munro unpublished data – 560 cm^2 grab sieved on a 500 µm screen), at the start of farming activities (1982- Élouard et al. 1983- 625 and 1000 cm^2 sieved on a 1 mm screen), and after the mussels in the 1+ zone were harvested (2004 - Callier et al. sous presse, 78.5 cm^2 core sieved on a 500 µm screen). In all but one case (Élouard et al. 1983), the raw georeferenced data was available and provided by the appropriate authors (see Figure 3.1). In the case of Élouard et al. (1983), only means of a total of 8 samples from the general area within the present culture site on each of 3 sampling dates (June, August and October) were available from the publication. In all other cases, sampling was done in August. Because of taxonomic inconsistencies among the different data sets, the combined data set was reduced such that each taxa was at the same level of taxonomic resolution. Thus, although most taxa were identified to the species-level, some were grouped at higher taxonomic levels (e.g., Capitellidae). For 2003 and 2004, replicate samples within a position were pooled to obtain surface sampling areas that were similar to those sampled in 1975 and 1978 (i.e., 3, 263 cm^2 replicates for 2003 and 5, 78.5 cm^2 replicates for 2004). All data were then transformed to ind m^{-2} prior to analysis. Because of inconsistencies among data sets, trends are compared graphically (MDS) and with respect to trophic groupings.

3.3 RESULTS

3.3.1 Sediment geochemical characteristics

Sediment redox potentials, sulphide concentrations and % OM did not differ among zones (0+, 1+ and R) and positions (under vs between) but all measurements varied significantly with depth (Table 3.1). The greatest sulphide concentrations and the lowest redox potentials were recorded at -3 and -5 cm (Figure 3.2). % OM decreased significantly with increasing sediment depth (Table 3.1, Figure 3.2). A uniform black colour was observed throughout all sediment cores.

3.3.2 Benthic community

Abundance and biomass. The mean abundance of organisms was 1177 ind m^{-2}, ranging from 280 to 2560 ind m^{-2}. Although a visual inspection of the data (Figure 3.3) suggests that abundance was greatest in the 0+ zone, this effect was not statistically significant (Table 3.2). Biomass differed significantly among zones (Table 3.2) such that the greatest biomass was observed in the 0+ zone and the lowest in the 1+ zone. However, part of this pattern was driven by the presence of 6 large individuals (*Ensis directus*, *Nereis virens*, *Glycera dibranchiata* and *Yoldia limatula* with body mass ranging from 100 to 10^4 mg ww) within separate replicates. As the sampling protocol was not designed to sample this size class of organism (see review by Andrew & Mapstone 1987), these organisms were removed from the data set and the analysis rerun (see biomass* in Table 3.2). The new analysis supported the original results (Figure 3.3).

Table 3.1 ANOVA results for sulphide concentration (μM), Redox potential (Eh_{NHE}, mV) and percentage organique matter (log OM) measured within and outside a mussel farm in Great-Entry Lagoon in the summer 2003. Fixed factors were Zone (Z), Position (PO) and Depth (DE). Random factor was Site (SI). See text for details. Statistically significant values are indicated in bold.

		Sulphide (μM)			**Redox potential (mV)**				**log OM**		
Sources of variations	df	MS	F	P	MS	F	P	df	MS	F	P
Z	2	3152809	1.419	0.304	8951	0.496	0.629	2	0.123	0.815	0.476
SI (Z)	7	2222241	5.386	**0.000**	18064	12.594	**0.000**	8	0.151	13.860	**0.000**
PO	1	870843	0.632	0.453	1088	0.232	0.645	1	0.003	0.500	0.500
DE	2	4575458	16.100	**0.000**	23324	21.072	**0.000**	2	0.064	4.267	**0.033**
Z × PO	2	4081792	2.960	0.117	8370	1.783	0.237	2	0.002	0.333	0.726
Z × DE	4	637374	2.243	0.117	1665	1.504	0.254	4	0.028	1.867	0.166
PO × SI (Z)	7	1378945	3.342	**0.002**	4693	3.272	**0.003**	8	0.006	0.534	0.827
DE × SI (Z)	14	284185	0.689	0.783	1107	0.772	0.699	16	0.015	1.352	0.195
PO × DE	2	184717	0.782	0.477	3485	1.886	0.188	2	0.025	1.667	0.220
Z × PO × DE	4	140119	0.593	0.673	1363	0.738	0.582	4	0.018	1.200	0.349
DE × PO × SI (Z)	14	236309	0.573	0.884	1848	1.288	0.219	16	0.015	1.404	0.168
Error	176	412599			1434			65	0.011		

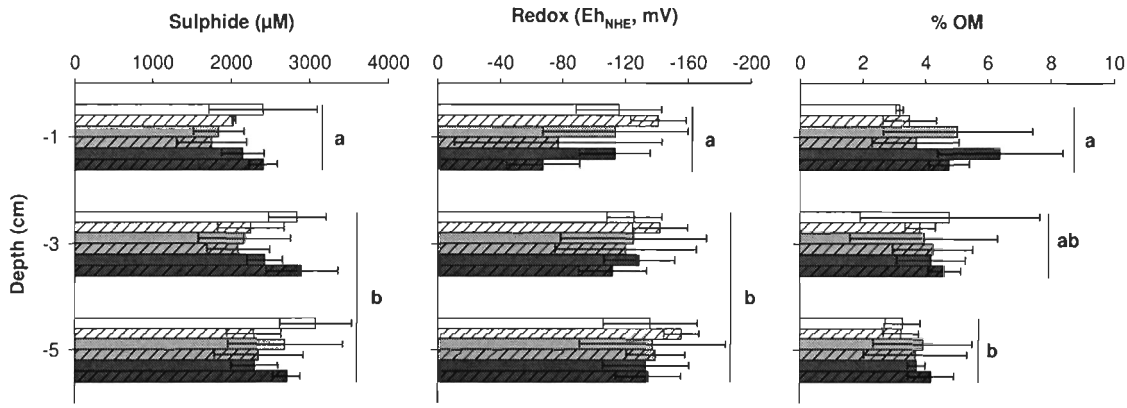

Figure 3.2 Sediment depth-specific sulphide concentration (µM), redox potential (Eh_{NHE}, mV) and percentage organic matter (% OM) (average ± SD, n = 3 to 4). Zones = R (white), 0+ (light grey) and 1+ (dark grey) zones. Positions = under the line – solid colours, and between the lines – hatched. Results from the corresponding ANOVAs are given in Table 3.1.

Diversity. A total of 45 species was observed. The number of species observed was a function of the interaction between Zone and Position (Table 3.2) such that the greatest number of species was recorded in the 0+ zone and the lowest in the 1+ zone, with a trend for greater and lesser richness directly under lines in the 0+ and 1+ zones, respectively (Figure 3.3). Both H' and J' differed significantly among zones (Table 3.2) such that H' was greatest in the 0+ zone and least in the 1+ zone and J' was least in the 1+ zone (Figure 3.3).

Community structure. Analysis of community structure based on abundance and biomass data showed the same pattern. Samples from R, 0+, 1+between and 1+under sites formed clusters that were distinct (Figure 3.4) and significantly different (Tables 3.3, 3.4) from one another. DISTLM analysis showed that, other than variation among replicates, differences among zones explained the greatest proportion of the variation in community structure (Table 3.3).

The average abundance and biomass of the dominant species, as well as their contribution to the similarity among replicates within zones and positions are given in Table 3.5. In the reference zone, *Pectinaria granulata*, juvenile *Macoma calcarea* and *Polydora ciliata* were the most abundant species and *Heteromastus filiformis* and *P. ciliata* accounted for the greatest biomass. In the 0+ zone, juvenile *M. calcarea*, *Hydrobia minuta* and *P. granulata* were the most abundant species. The greatest biomass was represented by *P. granulata* and *Nassarius trivittatus* at $0+_{between}$ positions, whereas juvenile *Nereis* sp. and *Nephtys caeca* accounted for most of the biomass at $0+_{under}$ positions. At $1+_{between}$ positions,

juvenile *M. calcarea* and *Capitella capitata* were the most abundant species and represented the greatest biomass. The dominance of these two species switched in the $1+_{under}$ positions, where *C. capitata* represented 59 % of the total biomass.

Trophic structure. Of the species observed, 18 were deposit feeders, 8 were suspension feeders (e.g. *Spio filicornis*, *Polycirrus* sp. *Mya arenaria*, *E. directus*, *Dyastylis polita*), and 8 were carnivores (e.g. *Retusa canaliculata*, *N. caeca*, *Harmothoe imbricata*). All communities were dominated by deposit feeders (Table 3.6) which accounted for more than 70% of the total number of individuals in each zone. Suspension feeders accounted for ca 10 % of the abundance at reference and 0+ sites.

Inter-annual comparison. MDS analysis showed that benthic community structure differed among years (Figure 3.5). However, samples taken from some years before (1975), at the start of (1982) and after > 20 years of mussel culture (2004) in the lagoon were relatively similar and different from those from 1978 and 2003. In fact, comparing samples from these 3 years shows that differences in benthic community structure among these 3 periods are no greater than differences observed between years within periods [i.e., before (1975 and 1978) and after (2003 and 2004) the start of mussel culture]. The similarity among samples from 1975, 1982, and 2004 is largely explained by the dominance of the carnivorous gastropod *R. canaliculata* and the extent to which its presence contributes to the within-year similarity among replicates (30-50%) (Table 3.7). The deposit feeder *Tellina agilis* was also common in each of those 3 years. In 1975 and 1982, the benthic community was characterised by a *Retusa-Tellina-Spisula* association and in 2004 by a

Retusa-Nassarius-Hydrobia association (Table 3.7). The 1978 community differed from those in 1975 and 1982 because of the high abundance of *M. arenaria* (33696 ind m^{-2}). Other than *M. arenaria*, the 1978 benthic community was also characterised by a *Retusa-Tellina-Polydora* association. The 2003 community was dissimilar to the others largely because of the absence of the suspension feeder *S. solidissima/polynyma* (also absent in 2004) and the dominance of deposit feeders (81% of all organisms, see Table 3.7).

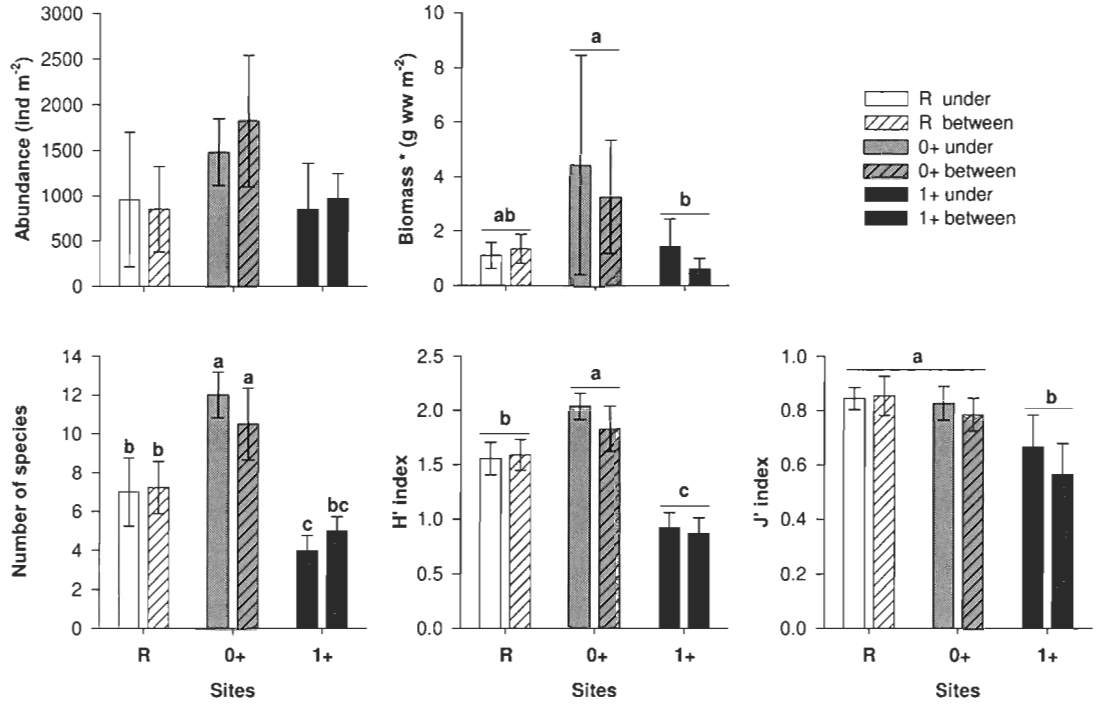

Figure 3.3 Macrofaunal characteristics from 3 zones and 2 positions (average ± SD, n = 3 to 4). Note that Abundance and Biomass* are expressed as a function of m^{-2} and that Biomass* includes only those organisms < 100 mg ww (see text for details). Results from the corresponding ANOVAs are given in Table 3.2. Significant differences among groups as identified by pair-wise contrasts are indicated by different letters.

Table 3.2 ANOVA results for macrofauna characteristics (Abundance, Biomass, Biomass* - without rare individuals weighing > 100 mg, Number of Species core^{-1}, Shannon-Wiener diversity H' and equitability J' indices) observed at GEL during the summer 2003. Fixed factors were Zone (0+, 1+, R) and Position (under and between the mussel lines). Site was a Random factor (4 sites in 0+ and 1+ and 3 sites in R). Abundance and biomass data were (log x +1) transformed to satisfy the assumptions of the statistical model.

		Log Abundance			**Log Biomass**			**Log Biomass***		
Sources of variations	df	MS	F	P	MS	F	P	MS	F	P
Z	2	0.727	3.847	0.068	1.194	5.686	**0.029**	0.672	9.205	**0.008**
SI (Z)	8	0.189	3.259	**0.005**	0.210	0.955	0.483	0.073	0.890	0.533
PO	1	0.092	1.278	0.291	0.473	2.867	0.129	0.008	0.108	0.751
Z ×PO	2	0.008	0.111	0.896	0.134	0.812	0.477	0.032	0.432	0.663
PO × SI (Z)	8	0.072	1.241	0.299	0.165	0.750	0.648	0.074	0.902	0.523
Error	43	0.058			0.220			0.082		

		Number of Species S			**Shannon H'**			**Equitability J'**		
Sources of variations	df	MS	F	P	MS	F	P	MS	F	P
Z	2	277.243	35.412	**0.000**	6.617	79.723	**0.001**	0.336	18.667	**0.000**
SI (Z)	8	7.829	1.260	0.289	0.083	0.449	0.885	0.018	0.783	0.620
PO	1	0.194	0.092	0.770	0.086	1.564	0.246	0.031	1.240	0.298
Z × PO	2	9.643	4.559	**0.048**	0.075	1.364	0.309	0.016	0.640	0.552
PO × SI (Z)	8	2.115	0.340	0.945	0.055	0.297	0.963	0.025	1.087	0.390
Error	43	6.213			0.185			0.023		

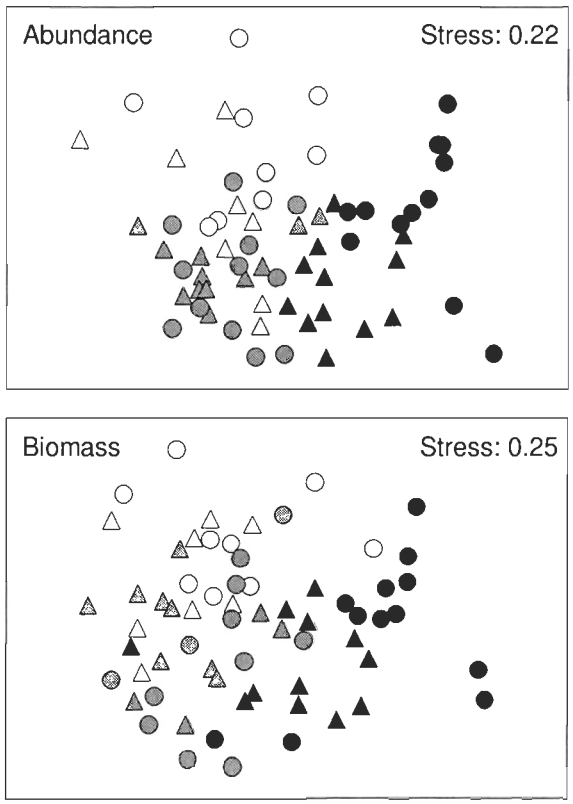

Figure 3.4 Non-metric multi-dimensional scaling illustrating variation in community structure (√-transformed) among R (white), 0+ (grey) and 1+ (black) zones in both between (triangle) and under (circle) mussel line positions. Results from the corresponding DISTLM analysis are given in Table 3.3 and pair-wise comparisons (ANOSIM) in Table 3.4.

Table 3.3 DISTLM (Distance-based multivariate analysis) results for the benthic community structure sampled in GEL in summer 2003. Fixed factors were Zone (0+, 1+, R) and Position (under and between the mussel lines). Site was a Random factor. VE % indicates the percentage of variation explained by each factor. Analyses based on both total abundance and total biomass data of each species are given. All data were √-transformed prior to analysis.

Source of variations	df	MS	Abundance Pseudo-F	P (perm)	VE%
Z	2	18212.42	6.056	0.000	25.2
SI (Z)	8	3007.39	2.137	0.000	16.6
PO	1	8050.30	6.713	0.000	5.6
Z × PO	2	4248.26	3.543	0.000	5.8
SI (Z) × PO	8	1199.21	0.852	0.823	6.6
Residual	54	1407.58			

Source of variations	df	MS	Biomass Pseudo-F	P (perm)	VE%
Z	2	19216.78	5.054	0.000	18.1
SI (Z)	8	3802.46	1.513	0.001	14.3
PO	1	8281.34	3.871	0.000	3.9
Z × PO	2	4519.29	2.113	0.005	4.3
SI (Z) × PO	8	2139.14	0.851	0.889	8.0
Residual	54	2512.92			

Table 3.4 Results of pair-wise comparisons of community structure between zone and position using ANOSIM. Upper right half of table compares abundance data whereas lower half compares biomass data. See text for heading definitions. Statistically significant values are indicated in bold.

	R_{under}	$R_{between}$	$0+_{under}$	$0+_{between}$	$1+_{under}$	$1+_{between}$
R_{under}	-	0.444	**0.009**	**0.027**	**0.001**	**0.001**
$R_{between}$	0.191	-	**0.001**	**0.001**	**0.001**	**0.001**
$0+_{under}$	**0.036**	**0.001**	-	0.131	**0.001**	**0.001**
$0+_{between}$	**0.006**	**0.001**	0.491	-	**0.001**	**0.001**
$1+_{under}$	**0.001**	**0.001**	**0.001**	**0.001**	-	**0.001**
$1+_{between}$	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	-

Table 3.5 Mean abundance (N – ind m^{-2}) and biomass (B – g m^{-2}) of dominant species in R, 0+ and 1+ zones in both between and under positions. Results of SIMPER analyses identifying species that contribute most to the similarity among replicates within zones and positions are also given (%). Data were √-transformed. "juv" indicates juvenile specimens. AS = average similarity. ns = species abundance or biomass does not contribute significantly to the similarity among replicates.

Species	**N**	**%**	**B**	**%**	**Species**	**N**	**%**	**B**	**%**
R $_{between}$	AS = 42.7		AS = 39.8		**R $_{under}$**	AS = 37.2		AS = 27.1	
Pectinaria granulata	228	17	130	11	*Pectinaria granulata*	292	21	ns	ns
Macoma calcarea (juv)	203	21	58	10	*Polydora ciliata*	156	24	205	23
Polydora ciliata	97	27	134	27	*Macoma calcarea* (juv)	110	20	22	11
Heteromastus filiformis	89	20	489	41	*Heteromastus filiformis*	97	12	549	45
Mya arenaria (juv)	59	3	ns	ns	*Capitella capitata*	46	11	124	10
Nereis sp. (juv)	ns	ns	23	3					
0+$_{between}$	AS = 50.7		AS = 29.8		**0+$_{under}$**	AS = 44.8		AS = 26.3	
Macoma calcarea (juv)	463	27	190	19	*Macoma calcarea* (juv)	459	26	351	20
Hydrobia minuta	371	11	117	7	*Pectinaria granulata*	171	15	102	14
Pectinaria granulata	260	18	941	22	*Hydrobia minuta*	155	5	46	5
Heteromastus filiformis	158	12	247	11	*Mya arenaria* (juv)	89	11	18	8
Mya arenaria (juv)	98	4	ns	ns	*Hydrobia* sp.	70	5	48	5
Polydora ciliata	89	7	127	10	*Nereis* sp. (juv)	67	4	1475	8
Tellina sp. (juv)	54	5	12	3	*Polydora ciliata*	54	6	98	9
Retusa canaliculata	51	4	ns	ns	*Ensis* sp. (juv)	41	7	13	5
Nassarius trivittatus	ns	ns	717	5	*Heteromastus filiformis*	38	4	77	4
Nereis sp. (juv)	ns	ns	89	4	*Harmothoe imbricata*	35	4	ns	ns
Scoloplos armiger	ns	ns	113	3	*Nephtys caeca*	ns	ns	618	5
					Ampharete sp.	ns	ns	54	3
1+$_{between}$	AS = 52.7		AS = 35.2		**1+$_{under}$**	AS = 47.6		AS = 31.2	
Macoma calcarea (juv)	732	76	78	57	*Capitella capitata*	548	47	781	59
Capitella capitata	44	5	35	11	*Macoma calcarea* (juv)	200	46	23	30
Polydora ciliata	38	6	ns	ns					
Hydrobia sp.	ns	ns	36	12					
Retusa canaliculata	ns	ns	81	8					

Table 3.6 Composition of trophic groups (% ± SD) at the R, 0+ and 1+ zones in both between and under positions.

	$R_{between}$	R_{under}	$0+_{between}$	$0+_{under}$	$1+_{between}$	$1+_{under}$
Abundance (%)						
Deposit feeders	79 ± 11	75 ± 2	82 ± 8	71 ± 8	84 ± 5	85 ± 4
Carnivores	7 ± 6	1 ± 2	4 ± 2	7 ± 2	5 ± 4	4 ± 1
Suspension feeders	9 ± 7	10 ± 10	10 ± 5	12 ± 4	6 ± 1	6 ± 3
Herbivores	1 ± 1	2 ± 3	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Omnivores	2 ± 2	3 ± 2	1 ± 1	4 ± 3	1 ± 0	1 ± 1
Non determined	2 ± 4	10 ± 8	3 ± 3	6 ± 8	3 ± 1	3 ± 1

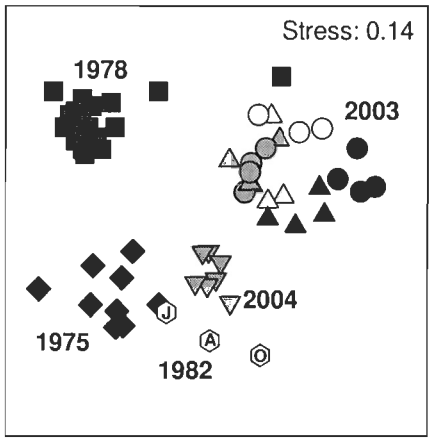

Figure 3.5 Non-metric multi-dimensional scaling illustrating variation in historical community structure in GEL. Sample dates include the period prior to the dredging of a navigation channel and the start of mussel farming (1975, 1978), after the dredging and at the beginning of farming (1982), and following > 20 yrs of mussel aquaculture (2003 – the current study, and 2004). Different years are indicated by different symbols (see also Figure 3.1) except for 2003, the symbols for which are as indicated for Figure 3.4. The letters in the symbols for 1982 indicate the sample date (J-June, A-August, and O-October).

Table 3.7 Results of SIMPER analysis (√-transformed data) to show major differences in community structure among sample years. Average abundances (N, ind m^{-2}) and the % contribution of the major taxa to within-year similarities (%) are shown. Data compared are from 1975 (Bourget 1976, Bourget & Messier 1982), 1978 (Munro et al. unpublished data), 1982 (Élouard et al. 1983), 2003 (the present study) and 2004 (Callier at al. sous presse).

	1975		1978		1982		2003		2004	
	N	%	N	%	N	%	N	%	N	%
Carnivores										
Retusa canaliculata	924	(49)	1296	(10)	260	(30)	21		827	(50)
Suspension feeders										
Spisula (solidissima/polynyma)	105	(12)	123		2361	(27)				
Ensis directus	5		1123		1		25	(6)	4	
Mya arenaria			33696	(58)			55	(3)		
Omnivores										
Nephtys sp.	46	(17)	33		14	(12)	4		29	
Nereis sp.			3		4		22	(3)		
Deposit feeders										
Tellina agilis	167	(8)	1897	(11)	164	(10)	19	(3)	49	(4)
Pectinaria granulata	110	(5)	153	(4)			151	(10)	5	
Nassarius trivittatus	18		9		14	(11)	11	(2)	147	(21)
Polydora sp.			1188	(10)	1		64	(9)	29	
Capitellidae			85		6	(3)	202	(23)	76	(10)
Hydrobia minuta			14		2		106	(4)	79	(8)
Macoma sp.			33				355	(30)	22	

3.4 DISCUSSION

We examined the influence of a 23-year-old mussel farm on the sediment and infaunal benthic community at multiple spatial scales. As a concomitant study (Callier et al. 2006) observed a greater flux of organic matter to the bottom in some zones and positions relative to others, we predicted to observe corresponding chemical and biological signatures.

3.4.1 Sediment geochemical characteristics

The flux of organic matter to the bottom in June-July ranged from 5 to 11 g OM m^{-2} d^{-1} at reference and $1+_{under}$ positions, respectively (Callier et al. 2006). This flux represents approximately 1 to 3 g C m^{-2} d^{-1} based on 30% carbon in organic matter (Holmer et al. 2005). Sedimentation rates of 1 to 5 g C m^{-2} d^{-1} may result in hypoxic sediments and increases in sulphate reduction around bivalve aquaculture sites (Dahlbäck & Gunnarsson 1981). Thus it was predicted that increased organic loading resulting from the presence of mussel lines would increase the organic content of the sediments and consequently lead to a localized reducing environment characterized by negative redox potentials and increased sulphide concentrations in the sediments. However, none of the sediment characteristics varied significantly among zones or positions.

It was predicted that the greatest % OM would be observed in $1+_{under}$ sediments, where the greatest sedimentation rates were recorded (Callier et al. 2006). Although the average % OM at the -1 cm depth tended to be greatest at $1+_{under}$ sites (see Figure 3.2), this

was not statistically significant. The analysis of the labile component of the OM in the 0-0.5 cm of the sediment surface, where the biodeposits accumulate, would have probably been a more appropriate method to detect difference between zones (Nickell et al. 2003). White mats, likely the sulphur bacteria *Beggiatoa* spp., were observed directly under the 1+ mussel lines (authors' pers. obs.), as they have been in mussel culture sites elsewhere (Grant et al. 1995). The presence of *Beggiatoa* indicates that reducing conditions have reached the sediment-water interface at those sites (Holmer et al. 2005)

Sediment sulphide concentrations increased with depth at all sites and were typically >2000 μM, indicating hypoxic benthic conditions (Wildish et al. 1999). Redox potentials decreased slightly with depth, as is expected in muddy and silty habitats (Diaz & Rosenberg 1995). However, both parameters did not differ among zones. Sediment redox potential and sulphide levels can be used to detect the effects of high organic loading under fish cages (Hargrave et al. 1997, Anderson et al. 2005), but were probably not sensitive enough to detect the effect of mussel biodeposition. Other recent studies on bivalve aquaculture have reached the same conclusion (Anderson et al. 2005, Miron et al. 2005). Anderson et al. (2005) suggested that in depositional environments where the content of organic matter is naturally high, biodeposition from cultured bivalves does not significantly affect these parameters.

Relatively small increases in sedimentation, as measured in GEL by Callier et al. (2006), may have been obscured by background processes. Giles et al. (2006) suggested that rapid mineralization of mussel biodeposits in mussel farms may lead to a decoupling of

sedimentation and sediment characteristics. Detritus from other sources within culture sites, such as plankton, seagrass or biodeposits from species associated with the cultured species (Stenton-Dozey et al. 2001), may further obscure the influence of mussel biodeposition. For example, Giles (2006) has estimated that only 14 % of the increased biodeposition within a mussel culture site in New Zealand was due to mussel faeces biodeposition.

3.4.2 Benthic community

Subtle changes in environmental conditions may be reflected in altered biomass or species composition of macrofaunal communities before they are detectable in sediment chemical properties (Weston 1990, Edgar et al. 2005). This was observed in the current study using both univariate or multivariate indices such that the observed differences were likely due to differences in deposition rates among zones and positions.

Although not statistically significant, the abundance of benthic fauna tended to be greatest in the 0+ zone. Biomass was greatest in 0+ sites, largely due to the presence of *N. caeca*, *N. trivittatus*, *P. granulata*, and juvenile *Nereis* spp. that probably benefit from the moderate organic loading. Various responses have been observed in term of biomass at mussel farms. Kaspar et al. (1985) did not detect a pattern with respect to biomass but other studies have observed either lower (Stenton-Dozey et al. 1999) or greater (de Jong 1994, Grant et al. 1995) biomass under mussel farms, the latter being due at times to the presence of scavengers attracted by mussel fall off.

All measures of diversity evaluated (S, H', J') were reduced in the 1+ zone and S and H' were greatest in the 0+ zone. Other studies have reported decreases in S and H' (Mattsson & Lindén 1983, Kaspar et al. 1985, Stenton-Dozey et al. 1999, Chamberlain et al. 2001) of benthic macrofaunal communities under mussel cultures. Low H' in the 1+ zone resulted from the low number of species present. The dominance of the *C. capitata* at $1+_{under}$ positions and of juvenile *M. calcarea* at $1+_{between}$ positions further contributed to the low H' and accounted for the low J' values in the 1+ zone.

In the present study, the analysis of trophic structure was not useful for detecting differences between mussel farm and reference zones as the communities in all zones were dominated by deposit feeders, indicating a generally enriched environment. This is likely related to the high level of organic sedimentation in the lagoon (1 to 3 g C m^{-2} d^{-1}). Benthic communities in organically enriched areas are typically dominated by deposit feeders (Pearson & Rosenberg 1978) while suspension feeders often dominate less organically rich environments as organic debris may have a smothering impact preventing them from thriving (Kaspar et al. 1985). The results obtained from studies on trophic structure in mussel farms are inconsistent. Mattsson and Lindén (1983) observed higher abundances of deposit feeders at mussel culture sites compared to reference sites. In contrast, others have observed a dominance of predators and carnivores under mussel farms (de Jong 1994, Grant et al. 1995, Stenton-Dozey et al. 1999) that profit from mussel drop-off. Thus, care should be taken in using deposit-feeders as indicators of organic enrichment at bivalve farms. This is particularly true in coastal areas where many such farms are located and have naturally organically enriched sediments (Miron et al. 2005).

Although effects were not detected with trophic structure analysis, species-level effects were apparent in this study at both large and small spatial scales. *M. calcarea* was, overall, dominant in all sites in 2003. However, the initial spatfall and distribution of *Macoma* sp. has been shown to be largely a function of hydrodynamic processes (Armonies & Hellwig-Armonies 1992). The juveniles then undergo a secondary dispersal into low intertidal and infralittoral areas. Their importance in signalling organic inputs is, therefore, doubtful and they are not discussed further.

Reference and 0+ zones were dominated by *P. ciliata*, *P. granulata*, and *H. filiformis* with *H. minuta* also being dominant in the 0+ zone. Some species, such as *H. minuta*, may have benefited from the moderate organic loading in the 0+ zone. This was apparent by their great abundance there and near absence in other zones. Other abundant species, such as *P. granulata* and *P. ciliata*, are generally abundant in both the 0+ and reference zones and may reflect a general enrichment of the lagoon as they are characteristic of an intermediate stage of organic enrichment (Pearson & Rosenberg 1978). Communities differed at small spatial scales but only within the 1+ zone. $1+_{between}$ positions were dominated by *P. cilata* and *C. capitata* while, at $1+_{under}$ positions, *P. ciliata* was absent and *C. capitata* increased in abundance by more than a factor of 12. This suggests a shift from an intermediately enriched environment between mussel lines to a greatly enriched stage directly under the $1+_{under}$ lines, only 10 m distant. Such a switch between *P. ciliata* and *C. capitata* has been described in the past (Pearson & Rosenberg 1978) with *P. ciliata* living at the edge of an enriched area dominated by *C. capitata*. *C. capitata* is a non-specialized

surface deposit feeder and has some resistance to sulphide toxicity and hypoxia (Diaz & Rosenberg 1995).

A number of biological interactions may also explain the absence of other species at 1+ sites. The mussels may have had indirect effects on infaunal community structure by feeding on the larvae of infauna (Woodin 1976) and generally decreasing food resources (Peterson & Black 1987). In contrast, Commito & Boncavage (1989) have shown that mussels do not affect the abundance of infaunal species that do not disperse as planktonic larvae. *Capitella* sp. produces broods of 30 to 400 eggs which develop into lecithotrophic larvae that are competent to settle almost immediately after being released by female worms (Linton & Taghon 2000), possibly partly explaining the abundance of this species in $1+_{under}$ positions. Predation by large invertebrates attracted by the presence of fallen mussels (de Jong 1994, Grant et al. 1995) may also have an influence on the infauna. For example, lobsters were observed feeding on razor clams, *Ensis directus*, in the culture site during this study.

As benthic effects as described above may be limited to the areas directly below the mussel lines, remote methods (i.e., ship-deployed) are likely less efficient for detecting such localised effects. Studies using direct sampling methods (i.e., scuba divers) have often observed accumulations of scavengers attracted by mussel fall-off (e.g., de Jong 1994, Grant et al. 1995) that have not been observed using remote methods. This may have an impact on our perception of the role of bivalve culture on the benthic environment and make comparisons between studies difficult.

3.4.3 Historical data

The present study showed localised effects of mussel culture. The comparison between $1+_{under}$ and $1+_{between}$ positions that were only 10 m apart showed that near-field benthic effects were likely due to the biodeposition of the mussels and not other intrinsic features within the zone. However, all zones showed some indications of organic enrichment and it is difficult to determine if the benthic communities at the 0+ and reference zones were under a diffuse and broader influence of the mussel farm or if the mussel farm had no influence on those zones. Indeed, there are a number of factors that may explain such general organic enrichment in GEL. The lagoon is a very complex system as various modifications have occurred within it over the past half century. A causeway that separates GEL from the lagoon to the south (see Figure 3.1) was constructed in 1947. A navigation channel was dredged in the 1980's for a port constructed in GEL. Islands were also constructed with the material dredged during this activity (e.g., the island next to the opening of the channel in Figure 3.1). Commercial mussel farming was initiated in the early 1980's. Traditional ecological knowledge also suggests that *Z. marina* beds have expanded considerably in recent years. Separating the importance of these different factors, which may modify currents and/or sedimentation rates and thus benthic community structure, is difficult.

To address this question, the benthic communities observed in the present study were compared to others done before the mussel farm was established (1975, 1978), at the start of farming activities (1982), and after the 1+ mussels were harvested (2004). Although the

comparison was difficult because of differences in site locations (see Figure 3.1) and sampling methods, some observations could be made. Benthic communities differed among years but 1975, 1982, and 2004 were similar. *R. canaliculata* and *T. agilis* were very abundant in all years except 2003. This *Retusa-Tellina* association has been previously observed in neighbouring Prince Edward Island (see PEI, Figure 3.1) by Hughes and Thomas (1971). They also mentioned the presence of a *Yoldia-Tellina* association with *R. canaliculata* and *P. granulata* for deeper sites. Miron et al (2005) also reported that the gastropods *Retusa obtusa* and *N. trivittatus* and the bivalves *T. agilis* and *Y. limatula* were the dominant species at mussel farm sites in PEI (Figure 3.1).

The 2003 community was dissimilar to the others largely as a function of the absence of the suspension feeder *S. solidissima*, the lesser abundance of the carnivore *R. canaliculata* and the greater abundance of Capitellidae and *Macoma* sp. Weisberg et al. (1997) indicated that *Spisula* sp., *Retusa* sp. and *Macoma* sp. are pollution-sensitive taxa, while Capitellidae is a pollution-tolerant family. As discussed above, the great abundance of *M. calcarea* in 2003 was probably due to their recruitment to the deeper part of the lagoon as *M. calcarea* is a typical intertidal species (Bourget 1976). The absence of *S. solidissima/polynyma,* a large active suspension feeding bivalve, is possibly explained by greater organic input related to mussel farming. One year after the mussel harvest (2004), *C. capitata* was almost absent, indicating that the organic enrichment decreased rapidly. However, the presence of the deposit feeders *N. trivittatus*, *H. filiformis* and *H. minuta* in 2004 indicates that the sediment was still organically rich.

Bourget (1976) and Bourget & Messier (1982) suggested that the low benthic diversity and biomass in the middle of GEL was characteristic of an "unstable community". They also compared the biomass of the benthos in GEL to other regions and found that it was considerably lower than that observed elsewhere (e.g. PEI). In 1978, Munro et al. (unpublished data) observed lower macrofaunal diversity and abundance in the deeper part as compared to other parts of the lagoon. They also found that the sites > 4 m deep were characterized by a greater proportion of mud than other parts of the lagoons. Water currents are reduced in the deeper parts of the lagoon and water turnover in the area where the mussel farm is located, is ca. 25 days or 40 days (Koutitonsky & Tita 2006). This relatively low flushing rate likely contributes to the general hypoxic conditions of the sediment, especially when winds are weak and water temperatures high, as observed in August. Degradation of seagrass and algae detritus during the ice-covered winter months may further contribute to the general hypoxia of the deeper parts of the lagoon.

Irrespective of the source of variation among infaunal communities and sampling periods (before, at the start of and following > 20 yr of mussel farming), several observations may be made. First, macrobenthic community samples taken from each of these three periods are, at times, quite similar. Second, differences in community structure between years within periods are at least as large as differences among community structures among periods. Together, this suggests that any impacts associated with aquaculture, at decadal temporal scales, will be hidden by natural temporal variation in benthic macrofaunal community structure. The data from the current study showing a preponderance of deposit feeders in 2003, especially in the $1+_{under}$ position, suggest that

mussel aquaculture does have local enrichment effects. However, any such effects seem to disappear within one year as the structure of benthic communities from 2004 is very similar to that before and at the start of the mussel farming.

CHAPITRE 4

Evaluation of indicators used to detect mussel farm influence on the benthos: two case studies in the Magdalen Islands, Eastern Canada

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RÉSUMÉ : L'objectif de cette étude était d'évaluer différents indices utilisés pour détecter l'effet de la mytiliculture sur l'environnement. Les caractéristiques du sédiment [taille de particules, image du profil sédimentaire (SPI), pourcentage de matière organique (% MO)] et des communautés benthiques (abondance, biomasse, nombre d'espèces, l'indice de richesse spécifique Margalef, de diversité Shannon Weiner, d'équitabilité Pielou, la masse individuelle, le groupe trophique, l'indice biotique -AMBI et la structure de communauté) ont été évaluées dans deux sites mytilicoles à Grande-Entrée (GE) et Havre-aux-Maisons (HAM) aux Îles-de-la-Madeleine (Québec, Canada). Les stations d'échantillonnage étaient positionnées directement sous la filière la plus externe de la culture, à 3, 6, 9, 15, 30 m et sur un site contrôle (300-500 m) le long d'un transect placé dans la direction du courant dominant. Deux patrons différents ont été observés à GE et HAM. À GE, les caractéristiques du sédiment et des communautés benthiques ne variaient pas entre les stations. Les communautés de macrofaune étaient caractérisées par une faible diversité, abondance et biomasse. Au contraire, à HAM, le % MO diminuait et la diversité et l'abondance de la macrofaune augmentaient avec la distance. La biomasse, faible sous la filière, était plus élevée entre 3 et 30 m et redevenait faible à 300 m. Ceci était expliqué par la présence du polychète *Pectinaria granulata*, qui semble avoir bénéficié d'un flux modéré de matière organique. La biomasse moyenne individuelle des déposivores et opportunistes de second ordre *P. granulata* et *Heteromastus filiformis* diminuait avec la distance, alors qu'elle augmentait pour le suspensivore *Ensis directus* et le déposivore *Tellina agilis,* deux espèces sensibles à la pollution. À HAM, les effets de la mytiliculture étaient localisés autour de la culture, alors qu'à GE, le patron était plus difficile à interpréter. La culture avait soit peu d'influence sur l'environnement, soit un effet plus diffus et plus étendu. L'étude montre que le choix *a priori* des stations d'échantillonnage et des indicateurs avait une grande influence sur l'interprétation. L'analyse de la structure de communautés et celle du profil sédimentaire ont permis la détection des effets à la fois proches et éloignés de la mytiliculture, contrairement aux autres indices.

ABSTRACT: The aim of this study was to identify appropriate indicators to determine the influence of mussel aquaculture on the benthic environment. Both sediment [particle size, sediment profile imaging (SPI), % OM] and benthic community (abundance, biomass, number of species, Margalef's species richness, Shannon-Weiner diversity, Pielou's eveness, individual body mass, trophic group, a biotic index – AMBI, and community structure) characteristics were evaluated at two mussel farms in Great-Entry (GE) and Havre-aux-Maisons (HAM) lagoons in the Magdalen Islands (Quebec, Canada). Sampling stations were positioned directly beneath the outer-most mussel lines (0 m) and at distances of 3, 6, 9, 15, 30 m and at a control site (at either 300 or 500 m) along a transect leading from each farm. Contrasting patterns were observed. At GE, sediment characteristics and benthic communities did not vary among stations and were characterised by low diversity, abundance and biomass. At HAM, % OM decreased and macrofaunal diversity and abundance increased with increasing distance from the farm. Biomass was low under the mussel line, increased between 3 and 30 m and was low again at 300 m. This was explained by the abundance of the polychaete *Pectinaria granulata,* which seems to have benefited from a moderate organic loading associated with the mussel farm. The mean individual biomass of the second order opportunistic deposit feeders *P. granulata* and *Heteromastus filiformis* decreased with distance from the farm, whereas that of the pollution-sensitive suspension feeder *Ensis directus* and deposit feeder *Tellina agilis* increased with increasing distance from the farm. At HAM, the effects of mussel farming were restricted to the vicinity of the farm, while at GE the pattern was less clear. The GE mussel farm had either little effect on the local environment or else larger-scale but diffuse effects. The study showed that the *a priori* choice of the sampling stations and indicators may influence the interpretation of the results. Community structure and SPI were the most efficient indices for detecting both small- and broader-scale influences of suspended mussel farming.

4.1 INTRODUCTION

The introduction of a large density of bivalves in suspended culture may induce important changes in the coastal ecosystem. The potential impacts of bivalve farming include 1) a depletion of phytoplankton, zooplankton and seston in the water column resulting from the great filtration capacity of bivalves (Dame 1996), and 2) an increase of the natural sedimentation rates from biodeposition (Haven & Morales-Alamo 1966, Hatcher et al. 1994, Danovaro et al. 2004, Callier et al. 2006). The accumulation of biodeposits on the bottom under culture sites may induce organic enrichment and change sediment geochemistry and benthic community characteristics (Mattsson & Lindén 1983, Chamberlain et al. 2001, Christensen et al. 2003, Hartstein & Rowden 2004, Callier et al. 2007). According to a general model (Pearson & Rosenberg 1978, Weston 1990), increased organic loading causes macrobenthic communities to exhibit: 1) a decrease in species richness and an increase in the total number of individuals because of high densities of a few opportunistic species, 2) a general reduction in biomass – although biomass may be greater due to dense assemblages of opportunistic species, 3) a general or species-specific decrease in body size, 4) a shallowing of the portion of the sediment column occupied by infauna, and 5) a shift in the relative dominance of trophic groups.

Results from previous studies on the influence of bivalve farming have not always followed the general model of organic enrichment. Its influence on the environment depends on various factors, including site (hydrodynamics, topography, enrichment background, etc.) and culture characteristics (density of production, species cultured,

associated species, etc.). Various culture-related factors may influence the benthic environment in a number of ways. Bivalves and epifauna falling from the structure may also increase organic input as well as creating micro-habitats for the development of hard-bottom epibenthic communities. Farmed bivalves may constitute a food source for larger organisms, such as sea stars. The aquaculture structure themselves may act as an artificial reef such that considerable epibenthic communities may develop on the culture structures, potentially increasing local secondary productivity (McKindsey et al. 2006b).

However, detecting the influence of bivalve farming on benthic habitats is complex as bivalve farms generally result in only moderate increases in organic enrichment and are typically extensive, at times covering many square kilometres (e.g., Danovaro et al. 2004). Moreover, the experimental design used to detect the influence of bivalve culture on the benthos has differed greatly between studies (Cranford et al. 2006) and may also influence the observed results. For example, some studies have compared a single bivalve aquaculture site to a single reference station. However, two sites may differ naturally without any anthropogenic impacts. The distance between culture and control stations has also varied such that distances range between 30 m (Grant et al. 1995) and 1 km (Mirto et al. 2000). Other studies have examined benthic characteristics along transects leading away from sites (e.g., Chamberlain et al. 2001). Cranford et al. (2006) highlighted the need to identify appropriate indicators to detect the influence of bivalve culture on the benthic environment and to evaluate them in multiple sites to show their general applicability. Empirical studies are needed to determine the most appropriate indicators for detecting both

local- and broad-scale effects related to bivalve aquaculture. This will permit to identify general patterns and develop predictive models.

The objective of this study was thus to evaluate the efficiency of quantitative and qualitative indices to detect the extent of the influence of bivalve farms on the benthic environment. The study also compares sampling designs (transect vs distant control sites) to contrast interpretations. The physicochemical indices considered are the percentage organic matter, sediment particle grain size and Sediment Profile Imaging (SPI). Redox potentials and total sulphides were not evaluated in the current study. Although these parameters are effective for monitoring the influence of fish cage aquaculture (Hargrave et al. 1997), they were shown to be not sensitive to detect the effect of mussel biodeposition in a previous study done in Great-Entry Lagoon – one of the study locations, a year before the present study (Callier et al. 2007). Other studies (Anderson et al. 2005, Miron et al. 2005, Mallet et al. 2006) have also suggested that biodeposition from cultured bivalves in depositional environments, where the content of organic matter is naturally high, does not significantly affect these parameters. SPI analysis was evaluated as it has been useful for detecting the influence of finfish farms on the benthic environment (Karakassis et al. 2002), but has yet to be evaluated in the case of bivalve farming. The biological indices evaluated were abundance, total biomass, number of species – S, and the three most widely used measures of diversity (Costello et al. 2004): Margalef's species richness – d, Shannon Wiener diversity – H', and Pielou's eveness – J'. These indices have often been used in studies on bivalve aquaculture impact (Mattsson & Lindén 1983, Grant et al. 1995, Stenton-Dozey et al. 1999, Chamberlain et al. 2001, Yokoyama 2002, Crawford et al. 2003,

Miron et al. 2005, Callier et al. 2007). Species-specific individual body mass was also evaluated. Species were classified into trophic groupings based on the literature and the tolerance of the communities to organic loading evaluated synthetically using a biotic index – AMBI (Borja et al. 2000). Community structure was also evaluated using multivariate methods. This work was replicated in two mussel farms in the Magdalen Islands, eastern Canada, to evaluate the generality of observed patterns.

4.2 MATERIALS AND METHODS

4.2.1 Study sites

The two studied mussel farms, Great-Entry (GE) and Havre-aux-Maisons (HAM), are located in separate lagoons in the Magdalen Islands, eastern Canada (Figure 4.1). Both farms have been in operation since the 1980s. The lagoons are characterized by an average tidal range of 0.58 m and are covered by ice during winter (Koutitonsky et al. 2002). Water temperature increases from 8 °C in June to an average maximum of 20 °C during the third week of August and then decreases to 9 °C by October (Myrand 1991). Seasonal salinity within the lagoon ranges from 25 to 31.5 ‰ (Poirier & Myrand 1982). In both farms, mussels are cultivated on suspended long-lines over a 2 year grow-out cycle, until the mussels reach a commercial size of 5 to 6 cm.

Mean currents in GE are weak, with typical speeds of 5 cm s^{-1} and occasionally increasing to 10 cm s^{-1} during strong wind events, resulting in a well-mixed water column (Koutitonsky et al. 2002). Current speed during the summer of 2003 averaged 5 cm s^{-1} with

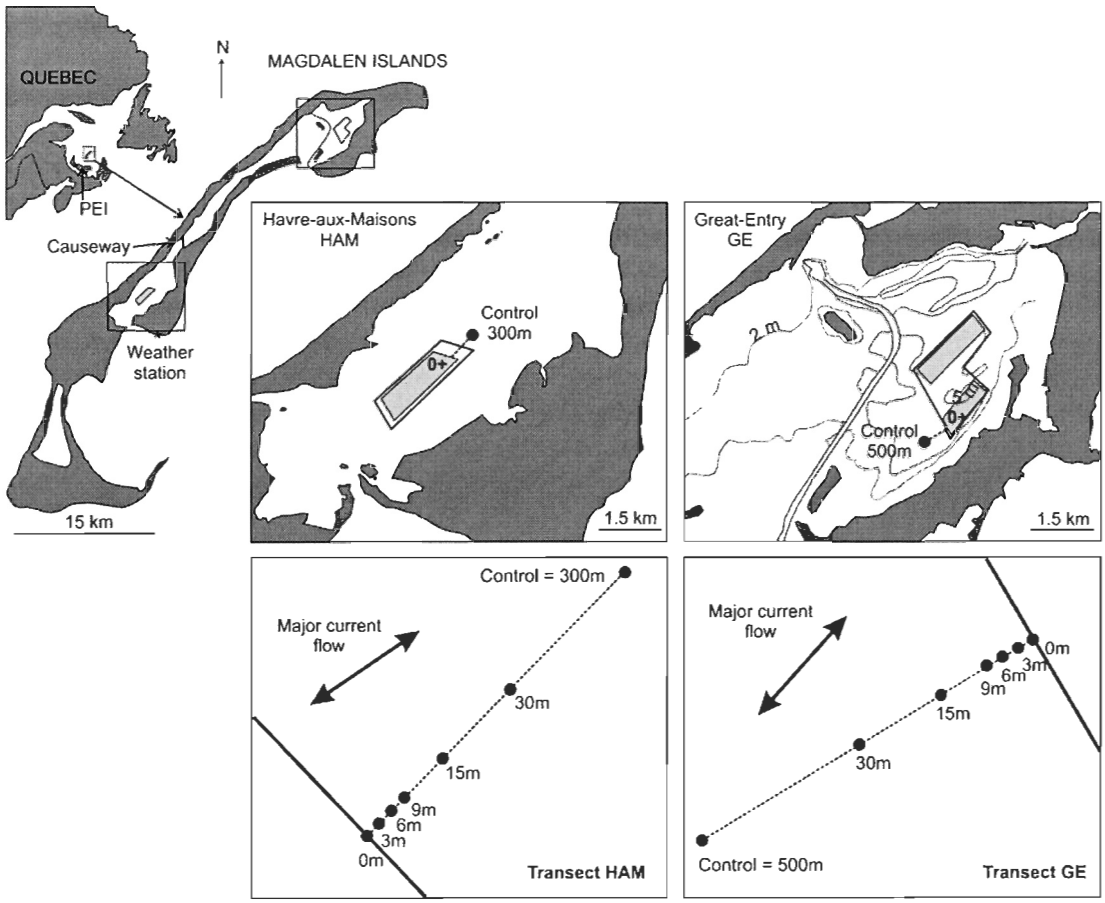

Figure 4.1 Location of the mussel leases studied in 2004 and the two transects in Great-Entry and Havre-aux-Maisons lagoons situated in the Magdalen Islands, Quebec, Canada.

a maximum of 18 cm s^{-1} (Callier et al. 2006). Water depth in the sampling area ranges from 5 to 7 m. The lease covers a total surface area of ca. 2.5 km^2 and produces about 180 tonnes of mussels annually. GE is divided into two zones, one with 0+ and the other with 1+ mussels (Figure 4.1). Each zone contains 200, 91 m longlines separated by 20 meters.

The HAM mussel lease is 1.25 km^2 with an annual production of 160 tonnes (Richard et al. 2007b). In summer 2004, current speed was on average 4.7 cm s^{-1} (Weise, personal communication). The lease is also divided in two cohorts (0+ and 1+ mussels) with 200, 76 m mussel lines, separated by ca. 12 m (Huet, personal communication). Water depth in the sampling area is about 6 m. In 2004, mussel cultures were located in the north-west portion of the lagoon. Giant scallops (*Placopecten magellanicus*) have been cultivated on suspended longlines in the south-east part of the lagoon since the end of the 1990s.

4.2.2 Sampling stations

In both sites, sediment samples were collected in early August 2004 at 7 stations located along a transect leading from the outer-most mussel lines (Figure 4.1, T.HAM and T. GE) of the 0+ mussel cohort zone and in the direction of the main water current direction. We examined the 0+ mussel lines because the 1+ mussels had already been harvested at the time of the study. Thus samples were taken at 0, 3, 6, 9, 15, 30 m and at a control station situated at 300 m in HAM and 500 m in GE. Although it was planned to sample control sites at 500 m in both lagoons, the HAM control site was placed at 300 m to maintain a similar water depth. Samples were taken at small intervals because a prior study

(Callier et al. 2006) showed that the initial dispersion of biodeposits from mussel lines in GE is low in the summer (< 12 m with a current velocity of 5 cm s-1).

4.2.3 Sediment characteristics

Three sediment core samples of the 0-2 cm surface layer were taken at each station with a cut-off 10 ml syringe. The percent organic matter (% OM) in the sediment was calculated as the weight loss of dried material combusted at 450 °C for 5 h.

A 3 cm diameter cut-off syringe was used to collect sediments for particle size analysis. Three samples (5 cm depth) were taken at each station and frozen for subsequent analysis. Particle size was evaluated using wet sediments with a laser diffraction particle size analyzer (LS 13 320).

Sediment profile imaging was used to assess sediment conditions, such as the depth of the apparent redox potential discontinuity (aRPD), the presence of faecal pellets, and the degree of bioturbation. The aRPD is the mean depth of the reworked oxidized layer defined by the colour shift from brown/yellow to grey/black. The term "apparent" is used in describing this parameter because no actual measurement is made of the redox potential. It is assumed that given the complexities of iron and sulphate reduction-oxidation chemistry the brown/yellow sediment color tones indicate sediments that are in an oxidative geochemistry state, or at least are not intensely reducing (Nilsson & Rosenberg 2006). At each station, a single sediment core was sampled using a transparent plexiglass wedge corer, as described by Wildish et al. (2003). After collection by scuba-divers, the cores

were returned to the surface ensuring that they were kept upright. The camera was set up about 1–2 m away from the sediment core in natural but diffused light. Care was taken to ensure that the plane of the camera was close to right angles to the sediment profile. Detailed methods are given in Wildish et al. (2003). The sediment profile images were analysed using Image-Pro Express 4.0.

4.2.4 Macrofaunal community analysis

Five replicate samples were collected at each sampling station using 10 cm diameter cores to a depth of 15 cm. Sediments were gently sieved through a 0.5 mm mesh and the material retained preserved in a buffered 5% formaldehyde-saline solution. Infaunal specimens were stored in 70 % ethanol after sorting. Identification was made to the highest taxonomic resolution possible, usually to species. Samples were characterised in terms of total abundance, total biomass and the average number of species per distance – S, as well as H', J' and d, which were calculated using PRIMER (Clarke & Warwick 1994). Biomass was measured as wet weight after blotting with absorbent paper for 10 s. All individuals of a species in a given core were grouped for biomass measurements. Animals were removed from tubes prior to biomass determination, but biomass of molluscs includes the weight of calcified structures (Weston 1990). Species were classified into trophic groups according to the classification available in the literature (Fauchald & Jumars 1979, Word 1990).

The Marine Biotic Index, AMBI, proposed by Borja et al. (2000), was used to establish the ecological quality of the macrofaunal community in GEL and HAM. The

benthic species are classified into five ecological groups, based on the sensitivity/tolerance of fauna to pollution. The ecological groups correspond to: I – sensitive to pollution, II – indifferent to pollution, III – tolerant to organic matter, IV – second-order opportunists, V – first-order opportunists (for details, see Borja et al. 2000, Borja et al. 2003). The distribution of these ecological groups provides a biotic index with 5 levels of classification. Note that *Pectinaria granulata* was assigned to group IV, based on the classification for *Pectinaria koreni* and some species were assigned based on the classification of their genera (e.g., *Bittium* sp. for *Bittium alternatum*).

4.2.5 Statistical analysis

Variations in % OM and univariate indices of the benthic communities were evaluated using ANOVA followed by Tukey multiple comparison tests with SYSTAT. Data were transformed when necessary to satisfy the assumptions of statistical models (see Results for details). Nonparametric multivariate analyses of community structure (ANOSIM) and multi-dimensional scaling (MDS), were performed using PRIMER (Clarke & Warwick 1994). The level of similarity and the contribution of each species to the total similarity among samples were determined using SIMPER. Analyses of community structure were done using √-transformed abundance data. One replicate was missing in each transect (at 3 m and 300 m in GE and HAM, respectively).

4.3 RESULTS

4.3.1 Sediment characteristics

At GE, sediment % OM varied between 3.6 to 4.6 % but did not differ significantly between stations ($F_{6,14}$ = 1.342, P = 0.303, Figure 4.2). In contrast, sediment % OM at HAM decreased significantly with increasing distance from the farm, with a maximum of 6.8 % directly under the mussel line to a minimum of 2.5 % at the control site ($F_{6,14}$ = 10.562, P < 0.001, Figure 4.2).

All GE sediments were classified as muddy sand except at 6 m, which was classified as sandy mud (Figure 4.2). The highest proportion of sand in the sediments was observed at the control site, 500 m distant from the mussel farm. All HAM sediments were classified as muddy sand and the proportion of sand increased to a maximum of 87.1 % at 300 m (Figure 4.2).

Sediment profile images at GE were similar along the transect, except for those at 500 m (Figure 4.3). In general, no oxic layer was observed at the surface of the sediments in GE. A black surficial layer, which extended to a depth of 8 to 10 cm, consisted of decomposing faecal pellets and seagrass detritus. Patchy brown sediments within this layer were probably undegraded fecal pellets. The black color is likely related to the presence of sulphide as Callier et al. (2007) measured average sulphide concentrations of 2000 µM at 1 cm depth in sediments under mussel lines in GE. At 500 m, void marks were present and may represent infaunal burrows, indicating a potential reworking of the sediment (Figure

4.3). Below the black sediment, there was a layer of grey mud. This type of sediment was the only one observed at the 500 m distance. At HAM, sediment profile images differed between distances (Figure 4.3). There was a 3 cm yellow/brown surficial layer overlying a black layer directly under the mussel line, which increased to a depth of 7-9 cm at intermediate distances (from 3 m to 30 m) (Figure 4.3). The limit between the light brown and the black sediment likely corresponds to the apparent aRPD. We interpret this layer as being the top oxygenated layer that has been reworked by infauna (see discussion). At 300 m, the sediment column appears to be well mixed and no sulphide layer was observed. The presence of empty mussel shells (Figure 4.3) on the sediment surface of the 0 m stations was observed at both GE and HAM, thus indicating mussel drop off from the mussel lines.

4.3.2 Macrofaunal characteristics

Abundance, biomass, richness and diversity indices

None of the biological indices evaluated (abundance, biomass, S, d, H' or J') differed among distances in GE (Table 4.1, Figures 4.4, 4.5), although, as a group, the stations distant from the mussel farm (at 15, 30 and 300 m) had a greater mean abundance than the group of stations close to it (from 0 to 9 m; $F_{1,32}$ =5.74, P = 0.023; Figure 4.4). In contrast, all indices differed significantly among distances in HAM (Table 4.1, Figures. 4.4, 4.5) and, with the exception of d and J', were generally greater than the equivalent measures in GE. In HAM, abundance ranged from 1273 ± 386 to 6471 ± 215 individuals m^{-2} and was lowest directly underneath the mussel lines (Figure 4.4). *P. granulata* was dominant in

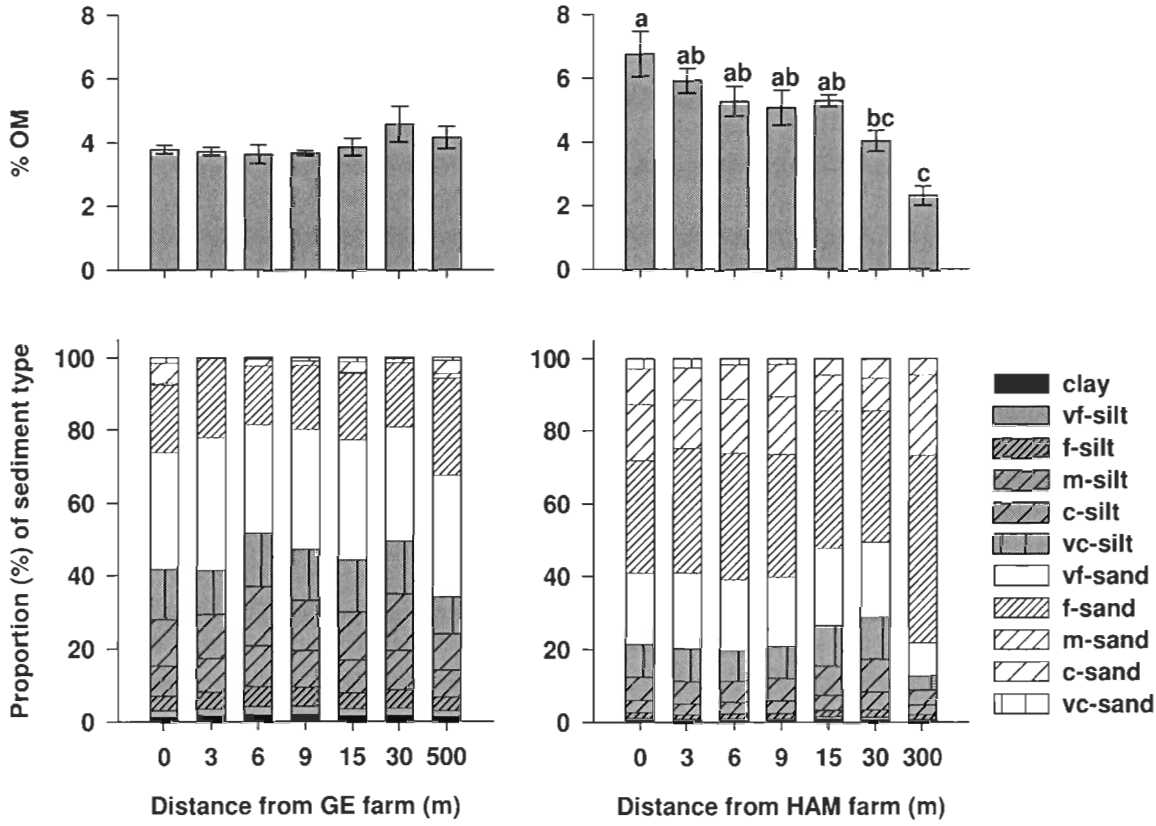

Figure 4.2 Sediment characteristics: % organic matter (% OM, mean ± SE) and proportion of clay, silt and sand in sediments at GE and HAM mussel farms. Upper white-scale represents the sand fractions and lower grey-scale represents the silt fractions, the clay fraction is at the very bottom of the histograms (black). Silt and sand are further separated into very fine (vf), fine (f), medium (m), coarse (c), and very coarse (vc) fractions. Different letters indicate significant differences between treatments.

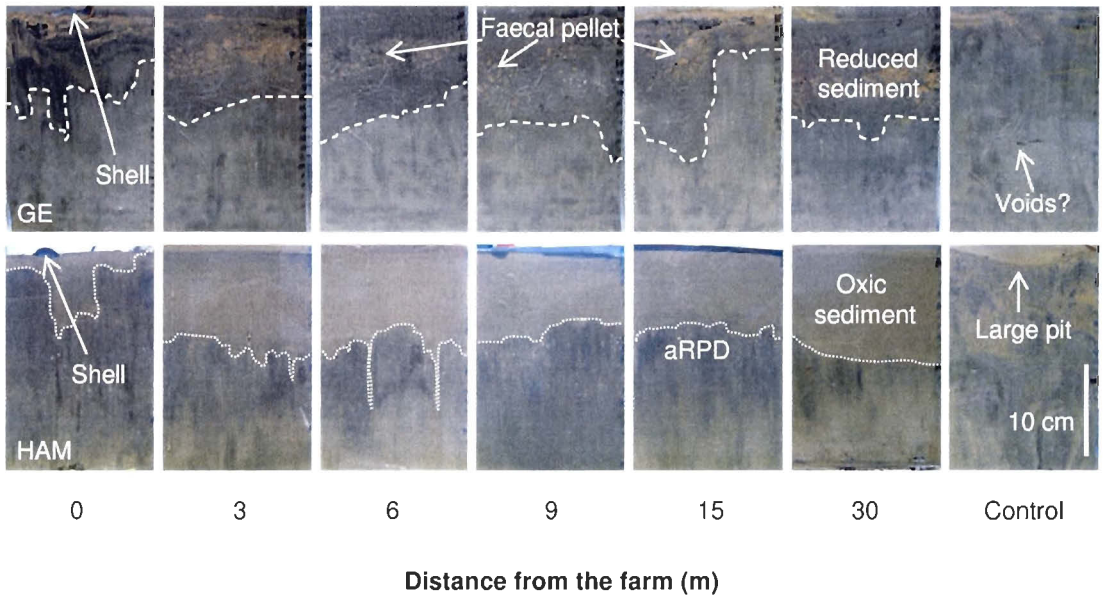

Figure 4.3 Sediment profile images of representative sediment cores taken at 0, 3, 6, 9, 15, 30 m and control sites (500 and 300 m) from GE and HAM mussel farms. Penetration depth was approximately 25 cm in all cores. In GE, the line indicates the separation between the black layer (consisted of decomposing faecal pellets and seagrass detritus) and the grey mud. At HAM the line corresponds to the apparent redox potential (aRPD).

terms of abundance (Table 4.2), such that total abundance ranged from 892 ± 288 (0 m) to 4013 ± 1006 individuals m^{-2} (300 m) when the abundance of *P. granulata* is not included. Similarly, biomass was lowest under the mussel line, was significantly greater between 3 and 30 m, and then decreased again at 300 m (Figures 4.4). Again, most of these differences were due to the presence of *P. granulata* such that biomass varied between 46.1 ± 5.1 to 450.8 ± 60.9 g ww m^{-2} but only between 16.2 ± 7.2 to 138 ± 61 g ww m^{-2} when the biomass of this species is not included. The mean number of species $core^{-1}$ ranged from 4.2 ± 0.8 to 9.7 ± 1.1 and increased with increasing distance from the mussel line (Figure 4.4). H' and Margalef's d were greatest at 300 m whereas J' was greatest at both 0 and 300 m (Figure 4.5), again due to the great abundance of *P. granulata* at intermediate distances and the low number of species directly below the mussel line.

Individual body weight

The hypothesis that the mean size of individuals of a given species increases with increasing organic matter was evaluated using the species present at 5 or more of the 7 transect distances in either lagoon. *Retusa canaliculata* and *Nassarius trivittatus* showed no obvious trend in body size with increasing % OM (Figure 4.6). Body size of *Heteromastus filiformis* and *P. granulata* increased with increasing % OM (Figure 4.6). In contrast, *Tellina agilis* and *Ensis directus* body size decreased with increasing % OM (Figure 4.6). These trends were obvious in HAM but not in GE where % OM did not vary significantly among stations, there were fewer individuals and those that were present were typically smaller than those in HAM.

Table 4.1 ANOVA results for macrofauna characteristics along transects at GE and HAM mussel farms: total abundance, total biomass, Number of species, Margalef's richness d, Shannon diversity H' and Pielou's evenness indices J'.

		GE				HAM			
		df	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
Total abundance	Distance	6	927853	1.343	0.273	6	14536300	13.277	0.000
	Error	27	690905			27	1094808		
Total biomass	Distance	6	1.997	1.205	0.334	6	121919.04	11.585	0.000
	Error	27	1.657			27	10524		
Number of species	Distance	6	0.370	0.142	0.989	6	12.072	4.660	0.002
	Error	27	2.607			27	2.591		
Richness d	Distance	6	0.217	1.099	0.393	6	0.750	4.884	0.002
	Error	23	0.197			27	0.153		
Diversity H'	Distance	6	0.149	1.227	0.329	6	0.334	5.529	0.001
	Error	23	0.122			27	0.060		
Evenness J'	Distance	6	0.048	1.843	0.135	6	0.043	8.830	0.000
	Error	23	0.026			27	0.005		

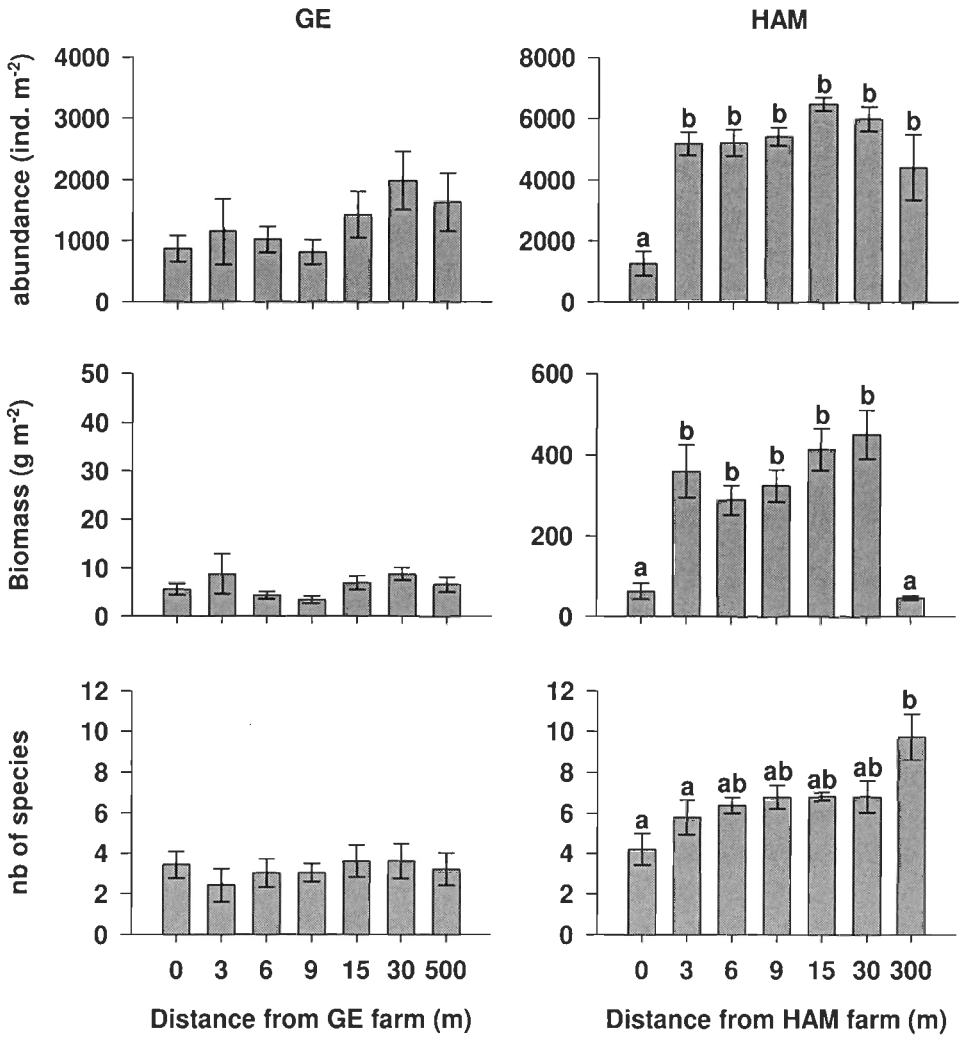

Figure 4.4 Macrofaunal characteristics (mean ± SE, n = 4 to 5, see text for details) along two transects leading from mussel farms. Abundance and biomass are expressed as number of individuals m^{-2} and total biomass ww m^{-2}, respectively. Note the scale differences for the Y axes for abundance and biomass between the two lagoons. Different letters indicate significant differences between treatments.

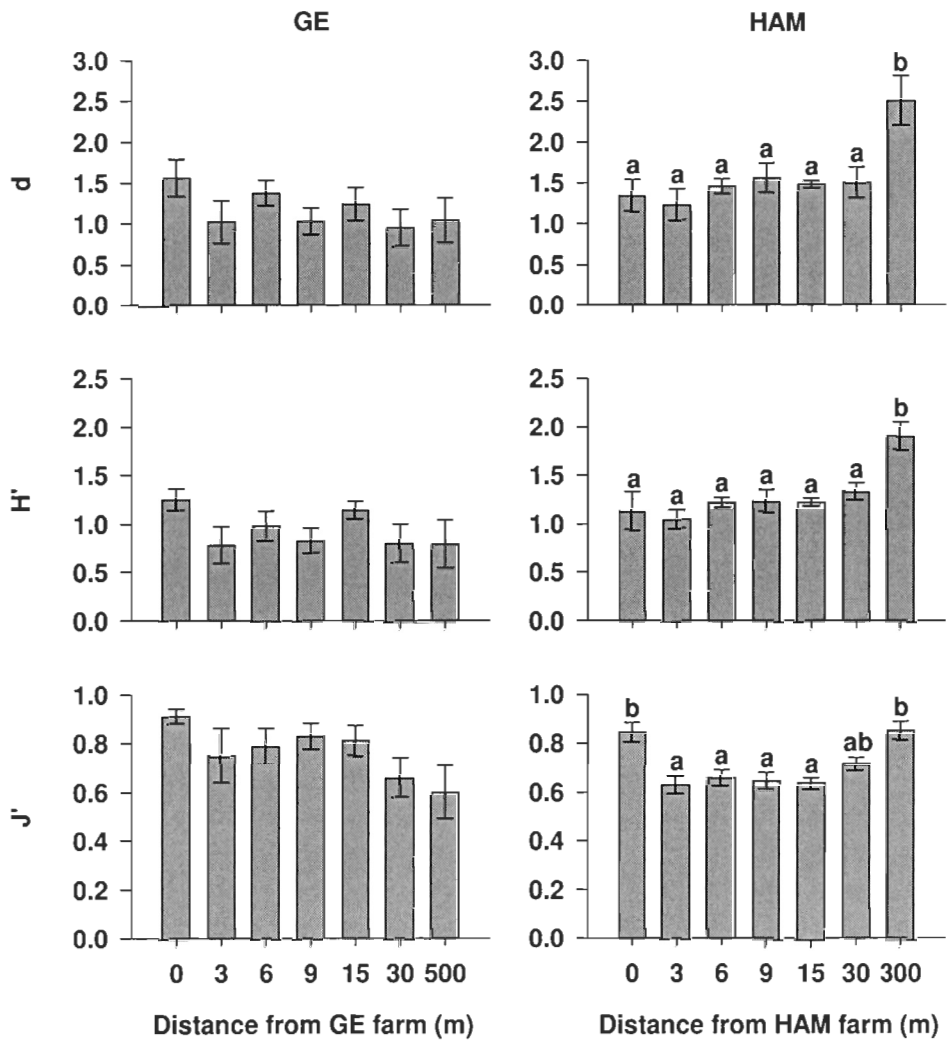

Figure 4.5 Macrofaunal characteristics (mean ± SE, n = 4 to 5, see text for details) along two transects leading from mussel farms. Margalef's species richness (d), Shannon Wiener diversity (H') and Pielou's eveness (J') indices (mean ± SE, n = 4 to 5). Different letters indicate significant differences between treatments.

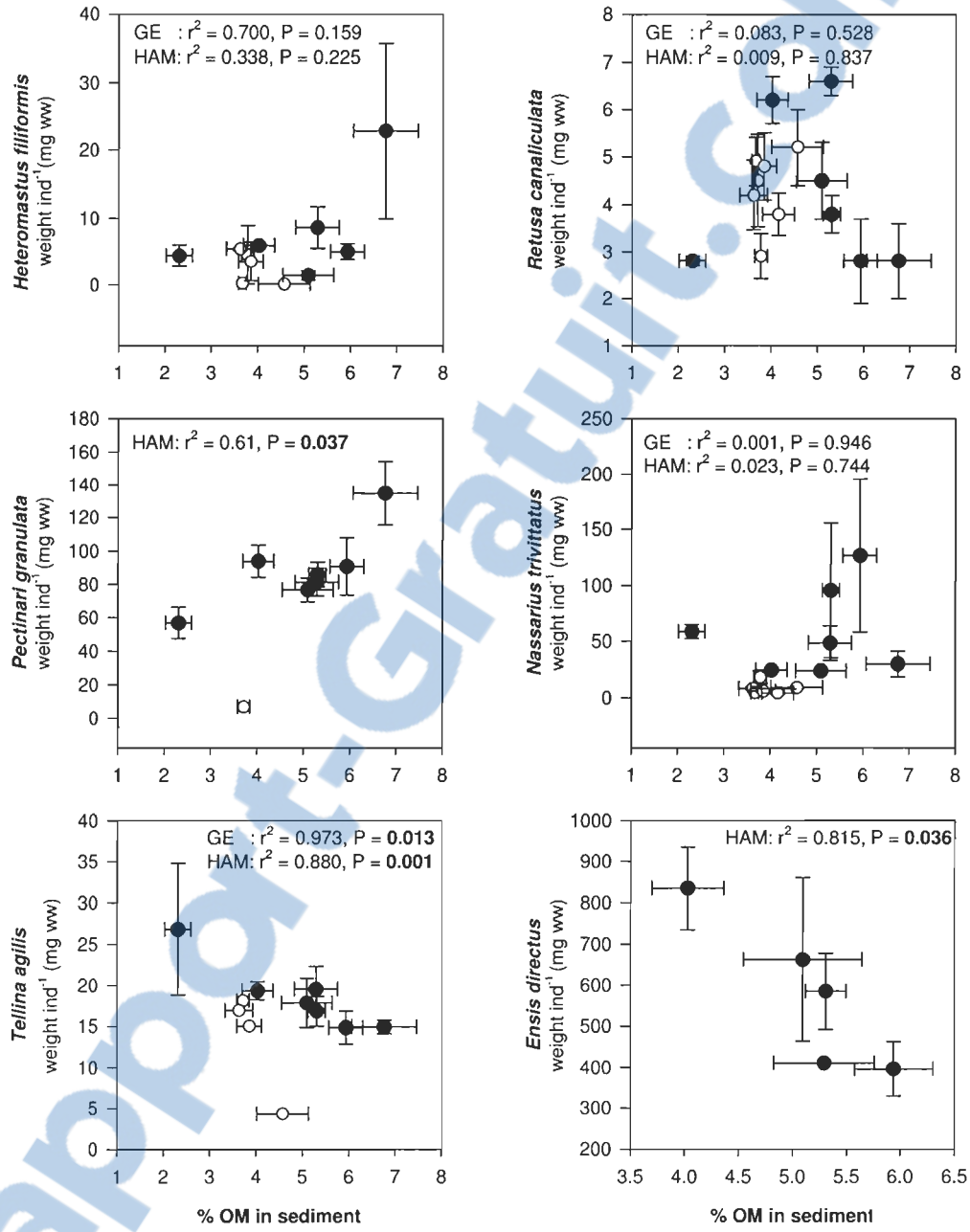

Figure 4.6 Average individual body weight (mean ± SE, mg ww) in relation with % OM in the sediments (mean ± SE) at different stations at mussel farms in GE (white) and HAM (black).

Trophic structure

Carnivores were usually dominant in GE, largely explained by the presence of *R. canaliculata* (Tables 4.2, 4.3). However, at 0 m, deposit feeders were the most abundant trophic group. Surface deposit feeders were dominant at HAM, except at the control distance where carnivores were the most abundant trophic group. This pattern is mainly driven by the high abundance of the deposit feeders *P. granulata* and *T. agilis* and the carnivore *R. canaliculata* (Tables 4.2, 4.3).

AMBI

On a range from 0 (no disturbance) to 6 (heavily disturbed), infaunal sediment communities from GE and HAM are classified as being slightly to moderately disturbed (Table 4.4). The greatest AMBI values in GE were observed directly under the mussel line (0 m), but this trend was not significant ($F_{6,27}$ = 1.325, P = 0.280). The corresponding values in HAM were typically greater, again due to the great abundance of *P. granulata*, which is classified as a second-order opportunist (see methods), at intermediate distances. Accordingly, the greatest AMBI values in HAM were at intermediate distances (3 to 15 m) and differed from the control station (300 m) which had the lowest AMBI values ($F_{6,27}$ = 4.474, P = 0.003; Table 4.4). This indicates that the control station is characterized by communities that are characteristic of relatively less disturbed conditions. There were intermediate AMBI values directly under the mussel line (i.e., 0 m did not differ significantly from those at intermediate or control distances).

Table 4.2 Mean abundance (N - # m^{-2}) of dominant species at six distances from two mussel farms and results of SIMPER analyses (√-transformed data) identifying species that contribute most to the similarity among replicates (%). AS=Average similarity of community structure between replicates at each distance.

Distance from GE farm	N	%	Distance from HAM farm	N	%
0	AS=35.8		**0**	AS=33.2	
Hydrobia minuta	153	32.2	*Pectinaria granulata*	357	62.9
Retusa canaliculata	306	26.7	*Tellina agilis*	178	14.7
Nassarius trivittatus	153	16.1	*Nassarius trivittatus*	102	13.1
Nephtys caeca	102	14.2			
Heteromastus filiformis	102	10.9			
3	AS=45.7		**3**	AS=74.8	
Retusa canaliculata	1051	65.8	*Pectinaria granulata*	3338	52.8
Nassarius trivittatus	159	21.7	*Retusa canaliculata*	790	21.1
Hydrobia minuta	96	12.5	*Tellina agilis*	611	18.2
6	AS=46.3		**6**	AS=71.2	
Retusa canaliculata	739	87.5	*Pectinaria granulata*	2981	47.3
Nassarius trivittatus	51	5.0	*Retusa canaliculata*	1070	22.8
			Tellina agilis	637	20.6
9	AS=44.5		**9**	AS=70.7	
Retusa canaliculata	484	81.0	*Pectinaria granulata*	3287	47.0
Nassarius trivittatus	76	8.3	*Retusa canaliculata*	866	24.0
Polydora ciliata	127	5.8	*Tellina agilis*	662	19.0
15	AS=38.8		**15**	AS=76.4	
Retusa canaliculata	713	51.4	*Pectinaria granulata*	3949	46.7
Nassarius trivittatus	229	26.3	*Retusa canaliculata*	1121	23.2
Tellina agilis	76	18.7	*Tellina agilis*	611	16.3
			Spisula sp.	306	7.9
30	AS=61.3		**30**	AS=69.9	
Retusa canaliculata	1248	65.4	*Pectinaria granulata*	3287	45.2
Nassarius trivittatus	229	28.2	*Tellina agilis*	994	24.5
			Retusa canaliculata	739	19.3
			Spisula sp.	178	3.3
500	AS=52.6		**300**	AS=65.5	
Retusa canaliculata	1248	81.1	*Retusa canaliculata*	1561	25.1
Nassarius trivittatus	127	8.7	*Pyramidella* sp.	701	19.5
Hydrobia minuta	102	7.7	*Tellina agilis*	350	14.9
			Pectinaria granulata	414	14.7
			Heteromastus filiformis	191	10.0
			Spisula sp.	287	6.2

Table 4.3 Percentage of trophic groups at the different distances (m) from the GE and HAM mussel farms (based on abundance data).

GE	0	3	6	9	15	30	500
Carnivores	43	73	73	63	54	63	77
Deposit feeders DS	57	27	25	37	41	32	19
Suspensivores SUS	0	0	3	0	0	0	0
DS, SUS	0	0	0	0	2	0	0
Non determined	0	0	0	0	4	5	5

HAM	0	3	6	9	15	30	300
Carnivores	29	17	21	18	19	18	53
Deposit feeders DS	67	80	74	78	74	76	38
Suspensivores SUS	2	2	2	3	6	5	8
DS, SUS	2	0	1	0	0	0	0
Non determined	0	0	2	0	1	0	1

Table 4.4 Marine Biotic Index (AMBI coefficients and the Biotic Index – BI) calculated to establish the ecological quality of the soft-bottom community in GE and HAM (see text for details). Different superscript letters indicate significant differences between treatments.

Stations	I(%)	II(%)	III(%)	IV(%)	V(%)	AMBI mean	AMBI sd	BI	Disturbance Clasification
GE									
0	3	65	21	12	0	2.48	1.19	2	Slightly disturbed
3	5	86	7	2	0	1.84	0.47	2	Slightly disturbed
6	5	80	0	13	3	1.86	0.43	2	Slightly disturbed
9	3	75	3	19	0	1.83	0.68	2	Slightly disturbed
15	11	71	13	6	0	1.35	0.82	2	Slightly disturbed
30	10	80	0	10	1	1.62	0.27	2	Slightly disturbed
500	0	89	8	2	2	1.74	0.24	2	Slightly disturbed
HAM									
0	23	31	6	40	0	2.53 ^{ab}	1.21	2	Slightly disturbed
3	14	17	1	68	0	3.36 ^{b}	0.29	3	Moderately disturbed
6	15	24	2	59	0	3.09 ^{b}	0.28	2	Slightly disturbed
9	16	18	2	63	0	3.18 ^{b}	0.25	2	Slightly disturbed
15	18	19	1	61	0	3.09 ^{b}	0.19	2	Slightly disturbed
30	28	14	1	58	0	2.81 ^{b}	0.28	2	Slightly disturbed
300	31	38	7	23	0	1.79 ^{a}	0.28	2	Slightly disturbed

Community structure

Community structure did not differ among distances in GE (Figure 4.7, Table 4.5) although (uncorrected) *a priori* comparisons showed that communities at 0 m differed from those from 6 m through 30 m. In contrast, three clear groupings were apparent in HAM such that communities at 0 and 300 m differed from each other and those at the 5 intermediate (3-30 m) distances, which tended to be more similar at a given distance and among distances (Table 4.2) although a very tight grouping of samples from 15 m caused these communities to differ significantly from those from most other distances (Figure 4.7, Table 4.5). Overall, % similarity in community structure among replicate cores was lowest directly under the mussel lines in both sites and increased with distance (Table 4.2), indicating greater small-scale variation in community structure under the lines and a more homogeneous structure further from the farms. Overall, the % similarity among replicate cores was lower in GE than in HAM (Table 4.2).

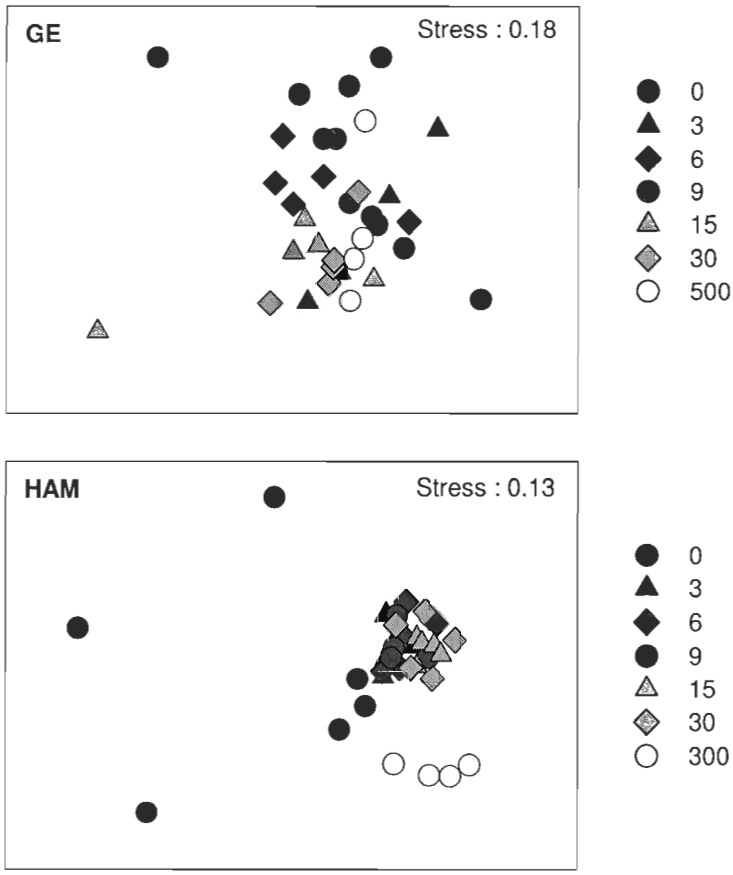

Figure 4.7 MDS plots (data were √-transformed) of community structure at six distances (m) along transects leading away from 2 mussel farms (GE and HAM).

Table 4.5 Results of pair-wise comparisons of community structure between distances (m) from GE and HAM mussel farms using ANOSIM. Statistically significant values are indicated in bold. GE: Global R = 0.070, P = 0.089; HAM: R = 0.409, P = 0.001.

	0	3	6	9	15	30
GE						
3	0.508					
6	**0.040**	0.278				
9	0.389	0.500	0.714			
15	0.198	0.421	0.492	0.230		
30	**0.008**	0.222	0.175	0.079	0.262	
500	0.103	0.706	0.556	0.524	0.183	0.548
HAM						
3	**0.008**					
6	**0.008**	0.881				
9	**0.008**	0.841	0.452			
15	**0.008**	**0.040**	**0.048**	**0.040**		
30	**0.008**	0.262	0.627	0.143	0.452	
300	**0.048**	**0.008**	**0.008**	**0.008**	**0.008**	**0.008**

4.4 DISCUSSION

The basis for examining the influence of suspended bivalve aquaculture on the benthic environment is a sampling design capable of unambiguously detecting an influence if it exists. Information about robust sampling designs may be found in numerous texts (Underwood 1997, Downes et al. 2002) and will not be discussed further here. In this study, we combined two common sampling approaches, namely transect sampling leading away from culture areas over fairly small (< 100 m) spatial scales (e.g., Chamberlain et al. 2001) as well as the use of control sites outside of the sphere of influence of suspended bivalve aquaculture areas (REF). Sampling was not replicated at multiple sites within the farms studied as previous work in GE (Callier et al. 2007) showed little between-site variation within the mussel lease and the effects were mostly limited to sediments directly under mussel lines. Thus, we concentrate on showing how different, commonly used, sampling strategies and the choice of multiple physicochemical and biological indices may affect the interpretation of the influence of suspended mussel aquaculture on the benthic environment.

4.4.1 GE and HAM: contrasting patterns

Considerable differences were observed between the two lagoons studied such that there was little evidence of the influence of suspended mussel aquaculture in GE whereas very clear patterns were observed in HAM. All of the positions studied in GE seem to be characterized by moderate organic loading whereas organic loading in HAM seems to be

greater and much more localized. The GE site is more open than HAM and thus bottom currents during wind events may be greater and thus more effectively homogenize the benthic environment in GE. Weaker currents in HAM may allow for stronger gradients to develop. Alternately, the greater density of mussel lines in HAM may also partially account for the stronger gradients observed there.

It is unclear if the mussel culture in GE had little effect on the benthos or if it has influenced the whole lagoon. Callier et al. (2007) evaluated historical data on benthic communities in GE from periods from before, at the start of, and after several years of farming and could not identify clear changes in benthic community structure related to aquaculture activities. The area where the mussel farm is located is a naturally enriched environment (Bourget & Messier 1982). Thus, it is difficult to suggest that the generally enriched condition of GE is related to the influence of suspended mussel culture. The greater background enrichment may also make it difficult to detect an incremental increase in organic loading, although Callier et al. (2007) had done so in GE the year prior to the current study. Regardless the cause, the striking differences between the two lagoons shows the importance of site-related effects in the manifestation of suspended bivalve aquaculture effects.

4.4.2 Indices

As mentioned above, redox potentials and total sulphides were not evaluated in the current study as they were shown to be ineffective in a previous study done a year earlier in

GE (Callier et al. 2007). These measures were also shown to be incapable of detecting the effect of oyster farms in Tasmania by Crawford et al. (2003). These same authors highlighted issues with respect to the reliability of the methods being used to measure redox values. Further, many suspended bivalve farms are in low energy protected coastal zones and thus are commonly organically enriched areas to start with. This is in contrast with fish cage aquaculture sites which are typically in higher energy areas and for which the measures of redox potentials and sulphide levels have been shown to be effective for monitoring (Hargrave et al. 1997). Thus, the use of these measures for monitoring for suspended bivalve culture seems difficult.

The present study showed that % OM, sediment size class differentiation, and SPI were useful for detecting effects when patterns were strong, as in HAM. In contrast, only the latter two methods performed well when patterns were weak. All stations in GE had similar % OM. However, a slightly lower proportion of silts in sediments was observed at the 500 m control distance. SPI showed that the black-reduced sediment layer observed directly underneath the mussel lines and at intermediate distances in GE was not present at the control distance. The enrichment in GE may result from sources of organic matter other than those related to mussel farming. The accumulation seagrass (*Zostera*)-related products, which are quite stable forms of carbon (Holmer et al. 2005), may contribute to the general organic enrichment of the lagoon (Callier et al. 2007) and have masked the influence of aquaculture when evaluating sediment % OM. In HAM, a decline in % OM was observed with increasing distances from the mussel lines, an observation that is consistent with the concept of decreasing biodeposition with increasing distance from the mussel culture. The

determination of sediment size class distributions was able to detect broad-scale effects of the culture as the proportion of clay and silts was least at the distant control sites. Near- and broad-scale effects were apparent using SPI in HAM as there was an increase in oxygenated layer depth by the 3 m distance, relative to the sediments directly under the mussel lines. This deeper oxygenated layer was present at all intermediate distances. In contrast, there was no evidence of an anoxic layer at the 300 m control site, indicating a well-mixed sediment column. SPI was useful as it provided information on sediment reworking. Although the % OM in HAM was greater than in GE (from 0 to 30 m), the oxygenated layer was deeper in HAM. Some macrofaunal species may have reworked the sediment, allowing oxygenated water to enter deeper into the sediments and organic matter to be degraded. In particular, *Pectinaria* sp. was much more abundant in HAM than in GE. *Pectinaria* sp. (= *Lagis*) is a subsurface deposit feeder and a major bioturbator (Rhoads 1974, Swift 1993) as it is able to bury detrital material to a depth of 8 cm, promoting downward movement of surficial material (Word 1990).

The univariate biological indices examined failed to detect significant mussel culture-related effects on the bottom of GE, although abundance tended to be greater beyond 15 m. In HAM, abundance and the number of species increased with increasing distance from the farm. However, the greatest biomass was observed at intermediate distances (3 to 30 m) from the farm. Biomass directly under the mussel line and at the 300 m control site was less than 20 % of that observed at intermediate distances. This reponse is mainly attributable to the great density of *Pectinaria* sp. which seems to have benefited from the moderate organic loading at intermediate distances, as suggested by the individual body mass

analysis (see below). This shows the importance of sampling stations at multiple distances and evaluating various indices to determine the extent of a farm's influence. If samples were taken at only 0 and 300 m, it could be concluded that the mussel farm had no influence on biomass. In contrast, if samples had not been taken at 300 m and only the transect over 30 m was sampled, then it could have been concluded that there was only an effect of reduced biomass at 0 m. Both H' and Margalef's d indices only showed broad-scale effects of the culture, such that the control distance differed from the other distances. In contrast, evenness showed a different pattern such that J' directly under the mussel lines differed from that at intermediate distances but not from that at 300 m. The evaluation of diversity indices alone could lead to misinterpretation as conclusions vary with experimental design, as shown by the evaluation of J'. Such measures have often been used to assess the effect of bivalve farming on the benthic environment (particularly H', e.g., Mattsson & Lindén 1983, Grant et al. 1995, Stenton-Dozey et al. 1999, Chamberlain et al. 2001, Yokoyama 2002, Crawford et al. 2003, Miron et al. 2005, Callier et al. 2007), although various authors have pointed out the many short-comings of diversity indices (Gray 2000). Despite attempting to correct for sample size, diversity indices are much influenced by sampling effort (Magurran 2004). Further, communities with different species compositions may have equivalent "diversity." It is therefore necessary to analyse complementary aspects of the benthic communities to prevent misinterpretation.

Intra-specific measures of animal size (body mass) were in some cases positively correlated with increasing organic enrichment (*P. granulata*) while others were negatively correlated with increasing organic enrichment (*T. agilis, E. directus*). Weston (1990) has

also shown such varying relationships for different species. This shows the importance of evaluating both inter- and intra-specific effects on biomass. Decreased oxygen in sediments may favour smaller sized individuals because of their greater body surface area:volume ratio favours oxygen uptake via diffusion (Weston 1990). However, this study shows that some species have larger body sizes with increasing organic enrichment. Oxygen depletion or related factors do not always have a negative influence on body size (Weston 1990). For some species, increased organic matter increases food supply. *P. granulata* appears to be well adapted to profit from increased organic matter in the sediments, feeding at a depth to ca. 10 cm while keeping its tail at the water-sediment interface, allowing contact with the oxygenated water (Word 1990). However, given that its abundance was smaller directly under the mussel line might also indicate that there is a threshold, above which, increased organic oxygen deposition has a negative effect on this species. The relationships between individual body size and organic enrichment is complex and depends on the quantity and quality of the organic matter (Weston 1990). Although a positive relationship between organic enrichment and the body size of deposit feeders may be predicted *a priori*, this was not always the case in this study as the body size of the deposit feeder *T. agilis* showed a negative relationship with organic enrichment. However, *T. agilis* has been classified as an organic–sensitive species (Borja et al. 2000), thus explaining why its body size decreased with increasing sediment % OM. Intra-specific changes in body size with organic enrichment have been little explored (Weston 1990) and thus do not constitute a simple or robust index for detecting the effects of bivalve aquaculture.

Overall, surface deposit feeders, mostly *P. granulata*, and *T. agilis*, were dominant in HAM, but carnivores, particularly *R. canaliculata*, were dominant in GE. In both mussel farms, the lowest percentage of deposit feeders were observed at control sites, probably indicating the lowest biodeposition rates in those positions. Deposit feeders were likely present because of biodeposition from mussels in suspended culture whereas carnivores may have been attracted by the presence of epibenthic species (mussels, other bivalves, polychaetes, etc.) that dropped off from the mussel lines. However, care should be taken when interpreting trophic groups. Several factors make this analysis difficult for detecting the influence of aquaculture. The trophic roles of some species are unknown or, at times, inconsistent (Weston 1990). Some species are also able to occupy different trophic levels (omnivors) (Fauchald & Jumars 1979, Word 1990). Observations at aquaculture sites do not always follow the general pattern of organic enrichment described by Pearson and Rosenberg (1978) that predicts the abundance of deposit feeders to increase with increasing biodeposition. For example, the fall-off of bivalves being cultured may also attract carnivores and scavengers (de Jong 1994, Grant et al. 1995), making the analysis of trophic groups difficult. However, most such organisms are not classified as infauna and may not be well represented by sampling with sediment cores as was done in this and most other similar studies on the influence of suspended aquaculture on the bottom. Further, observed patterns may also be driven by one or a small number of species (Weston 1990).

AMBI is based on the known ecology of the different organism in the sampled community. As for the other biological indices evaluated AMBI detected no significant differences among GE positions, although the position directly under the mussel line (0 m)

had the greatest AMBI values (i.e. greater disturbance). In contrast, in HAM, differences between intermediate sites and the control site were detected by AMBI. The intermediate positions were considered as the most disturbed, which was explained by the presence of *P. granulata* from the ecological group IV, representing more than 50% of the total abundance. Although not significant, lower AMBI values were recorded at 0 m as compared to sites at intermediate distances. This may be because although the great organic loading at this position decreased the abundance of *P. granulata*, the abundance of the even more organic-tolerant polychaete, *Capitella capitata*, which was very abundant under mussel lines in GE in 2003, was uncommon in 2004. This position presented the lowest total abundance, the lowest number of species as well as the greatest variability between replicates, the group IV ranging from 20% to 80% of the community at this position. The control site was considered to be the least disturbed sites, which was consistent with other indices (number of species, d, H').

Community structure did not differ among distances in GE whereas three different community types were observed in HAM (sites under the mussel line, at intermediate distances, and the control site). Thus the analysis of benthic community structure appears able to detect both near- and broad-scale effects of mussel aquaculture on the benthos. As was the case for AMBI, community structure directly under the mussel line was most variable relative to that at other distances in both GE and HAM. The low similarity among replicates at 0 m probably indicates that those stations were particularly disturbed as Warwick and Clarke (1993) have shown increased multivariate variability among replicate samples from disturbed treatments for a variety of community types (macrobenthos,

meiobenthos, coral, reef-fish). In the present study, biodeposition rates under mussel lines may have been heterogeneous and induced variable benthic responses.

4.4.3 Comparisons and recommendations

The present study is not the only one to compare several indices of benthic condition with respect to suspended bivalve culture, including multivariate analysis of benthic community structure. For example, Crawford et al. (2003) compared several physicochemical and biological indices for three suspended oyster farms in Tasmania and found that only multivariate analysis of community structure (ANOSIM) detected spatial patterns related to the placement of culture sites. Chamberlain et al. (2001) similarly compared various physicochemical and biological indices along transects leading from two suspended mussel farms in Ireland. The physicochemical indices evaluated detected patterns in only one of the two sites, as was also true for Shannon-Wiener diversity. In contrast, multivariate methods (MDS) detected patterns or trends in both sites. Christensen et al. (2003) compared benthic consumption of oxygen and nutrient fluxes as well as benthic communities with multivariate methods (MDS) and found clear differences between a site outside of a New Zealand mussel farm versus 2 sites within the farm. However, clear differences between the sites within the farm (directly under versus between mussel lines) were not evident even though they were visually obvious on the bottom in the field (Christensen et al. 2003). Da Costa and Nalesso (2006) compared sediment % OM and granulometric composition, several univariate biological measures (abundance, richness, Shannon-Wiener diversity, Pielou's eveness), and multivariate

community structure in and around a mussel farm in Brazil and found that most indices (except for sediment % OM, species richness and Pielou's evenness) detected differences among stations related to the presence of the mussel culture site.

In the present study, univariate indices did not consistently detect near- and broad-scale influences as sites directly under the mussel lines usually presented similar values at intermediate distances or at the control distance in HAM. Univariate indices should be interpreted with care as when considered by themselves may lead to misinterpretation (e.g., as for J' and biomass). Moreover, profound changes in community composition could occur without any alteration in the overall number of species (Keough & Quinn 1991). Among all the indices assessed, only SPI and multivariate analysis of community structure detected both near- and broader-scale influences. Our results support the conclusion of Nilsson and Rosenberg (2006) that SPI can be used to characterize organic enrichment gradients. SPI has been used to monitor the impact of fish farming on the benthos (e.g., Karakassis et al. 2002, Wildish et al. 2003). Karakassis et al. (2002) have shown a very good correlation between data obtained through SPI analysis and macrofaunal analysis. Because SPI monitoring is relatively low cost and provides information quickly, this method may be useful in rapid assessment. However, the use of SPI is mainly restricted to muddy and silty substrates and complementary measures are necessary to better interpret the observed patterns. However, as this and a number of indices found very localized effects (i.e., directly under the mussel lines relative to other distances), this suggests that sampling to detect such differences must be done directly by scuba divers. The precision of remote methods such as grabs may not be sufficient to detect such localized effects. As has

been reported previously, the use of multivariate statistics is a powerful method to detect changes in benthic assemblages (Clarke 1993, Gray 2000) and may be appropriate to detect the influence of mussel aquaculture on the benthic environment. However, information on community differences may be difficult to interpret in terms of specifying the level of disturbance (Warwick & Clarke 1991). The complementary analysis of the species sensitivity/tolerance and the determination of a biotic index, such as AMBI or other indices of biotic integrity (IBIs) (Borja et al. in press) will help to interpret the observed changes. The combination of complementary indices to create a multivariate indices such as M-AMBI (combining AMBI, number of species and Shannon H', see Borja et al. in press) might be useful to prevent misinterpretations. The usefulness of AMBI and other IBIs may be limited to the geographical areas for which species tolerance lists have been compiled (e.g., Weisberg et al. 1997, Borja et al. 2000) and the creation of more complete lists of the ecological aspects of benthic species is necessary to benefit fully from these indices.

CHAPITRE 5

Responses of benthic macrofauna and biogeochemical fluxes to various levels of mussel biodeposition: an in situ «benthocosm» experiment

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RÉSUMÉ: Une expérience a été menée *in situ* pour déterminer l'influence de différents taux de biodéposition de moules sur la structure d'une communauté benthique de sable et sur les flux biogéochimiques. Des communautés benthiques naturelles, placées dans des carottes de sédiment (benthocosmes), ont été exposées *in situ* pendant 50 jours à 7 niveaux de biodéposition de moules (équivalent à 0, 127, 255, 382, 510, 637 et 764 moules m^{-2}). Bien que le taux de biodéposition était positivement corrélé avec la densité de moules, le pourcentage de matière organique dans les sédiments ne l'était pas. Malgré la grande variabilité entre les réplicats, une réponse de la communauté macrobenthique a été observée. L'abondance totale et la richesse spécifique ont diminué avec l'augmentation de biodéposition. L'abondance et la biomasse de l'espèce opportuniste *Capitella* sp. ont augmenté dans les benthocosmes exposés à la plus forte densité de moules, tandis que l' abondance d'espèces sensibles comme le bivalve *Tellina agilis* et le polychète *Pherusa plumosa* a diminué avec l'augmentation de la densité de moules. En raison d'une forte variabilité intra-traitement, les flux biogéochimiques (consommation d'oxygène, flux d'ammonium, de phosphate et de nitrite) à l'exception de flux de silicates, ne variaient pas entre les traitements. Cette étude apporte des informations utiles sur les relations «dose-réponse» (biodéposition – communautés benthiques et flux biogéochimiques) qui aideront à déterminer la limite de production de moules et assurer que la capacité de support environnementale ne soit pas dépassée.

ABSTRACT: An *in situ* manipulative experiment was done to determine the influence of differing levels of mussel biodeposition on the structure of sandy benthic communities and biogeochemical fluxes. Natural benthic communities within sediment cores (benthocosms) were exposed *in situ* during 50 days to 7 different levels of mussel biodeposition (to the equivalent of 0, 127, 255, 382, 510, 637 and 764 mussels m^{-2}). Although biodeposition rates increased linearly with mussel density, sediment % organic matter was not correlated to mussel density. Despite the high variability between replicate samples, macrofaunal community showed trends in relation to increased biodeposition. Total abundance and species richness decreased with increasing biodeposition. Important increases in the abundance and biomass of opportunistic species (*Capitella* sp.) were observed in the benthocosms exposed to the greatest biodeposition. Sensitive bivalve (*Tellina agilis*) and polychaete (*Pherusa plumosa*) species tended to decrease in abundance and biomass with increasing mussel density. Benthic organisms may have contributed to the recycling of organic biodeposits. Because of high intra-treatment variability, oxygen consumption, ammonium, phosphate and nitrite fluxes did not vary significantly between treatments. Only the flux of silicate was positively correlated to biodeposition. This study presents some useful information on the dose-response relationship (biodeposition – benthic communities and biogeochemical fluxes) to help set mussel production density limits to ensure that the environmental carrying capacity of sites are not surpassed.

5.1 INTRODUCTION

Bivalve aquaculture production is growing worldwide and concerns about its impact on the environment are increasing. The environmental influences of bivalve aquaculture are mainly related to the filtration of the plankton and seston (Héral et al. 1986, Dame 1996) and the production of organically-rich faeces and pseudofaeces by the bivalves that may accumulate on the bottom (Hatcher et al. 1994, Danovaro et al. 2004, Hartstein & Rowden 2004, Callier et al. 2006). Numerous models have been developed to determine production carrying capacity (i.e., maximizing production, based mostly on food limitation for bivalves) (e.g., Campbell & Newell 1998, Gangnery et al. 2001). However, less effort has been directed at modelling the effect of bivalve biodeposition on the benthos and benthic-pelagic coupling (McKindsey et al. 2006b). Thus, there is 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. 2006b). There is also a need to better understand benthic-pelagic coupling (of oxygen and nutrients) related to bivalve aquaculture, especially in shallow areas where this effect may be considerable relative to background levels (Richard et al. 2007a), to better refine production capacity models.

The extent and intensity of benthic effects depend on many factors, including the age and size of culture, the species being cultivated, bivalve density, local hydrodynamic conditions and topography (Black 2001). Chamberlain and Weise (2006) combined these factors into three broad categories: 1- the quantity and quality of material exiting a farm, 2-

the dispersion of material exiting a farm, and 3- the fate of waste material post-deposition. These factors vary considerably between sites and thus general conclusions about the influence of bivalve culture on the benthic environment are difficult to establish. Results from previous studies on the influence of bivalve aquaculture on the benthos have ranged from "not significant" (Chamberlain et al. 2001, Crawford et al. 2003) to "very important" (Mattsson & Lindén 1983, Hartstein & Rowden 2004). Predictive models, such as DEPOMOD – which was initially used for finfish aquaculture (Cromey et al. 2002), are currently being adapted to predict: 1- the production and dispersion of biodeposits from cultured bivalves (Chamberlain & Weise 2006) and 2- the benthic responses to different levels of biodeposition.

The decomposition of bivalve biodeposits that may accumulate under bivalve culture may increase sediment oxygen uptake (Mazouni et al. 1996, Stenton-Dozey et al. 2001, Christensen et al. 2003, Giles et al. 2006, Richard et al. 2007a,b). This may lead to sediment anoxia and the accumulation of free sulphide (Dahlbäck & Gunnarsson 1981) which can affect the abundance, biomass and diversity of benthic communities (Mattsson & Lindén 1983, Diaz & Rosenberg 1995, Stenton-Dozey et al. 2001, Hartstein & Rowden 2004, Callier et al. 2007). High mineralisation rates of bivalve biodeposits and changes in benthic community bioturbation can accelerate nutrient turnover at the sediment-water interface (Kaspar et al. 1985, Baudinet et al. 1990, Christensen et al. 2003, Giles et al. 2006, Richard et al. 2007a,b) with concomitant consequences for the pelagic environment. Indeed, benthic nutrient regeneration can provide up to 80 % of the nutrients required for primary production in coastal ecosystems (Jensen et al. 1990, Giles 2006). An increase of

benthic ammonium, phosphate and silicate release has already been observed under bivalve farms compared to reference sites (Lerat et al. 1990, Hatcher et al. 1994, Christensen et al. 2003, Richard et al. 2007a), which may affect the abundance, biomass and the specific composition of phytoplankton communities (Baudinet et al. 1990, Newell 2004).

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 lacking (McKindsey et al. 2006b). Some experimental studies have evaluated the benthic response to a single deposition of a large quantity of organic matter simulating, for example, a phytoplankton bloom (Gee et al. 1985, Webb 1996). A recent study evaluated the effect of a single addition of mussel (*Perna canaliculus*) biodeposits on sediment oxygen demand and nutrient fluxes to evaluate biodeposit decay rates (Giles & Pilditch 2006). However, no study has evaluated the effect of continuous and varying levels of biodeposition to simulate conditions in bivalve culture. 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 experiment was to investigate the effects of short-term mussel biodeposition on sandy benthic community characteristics and biogeochemical fluxes using *in situ* mesocosms. This experiment was done in summer 2004 in the Magdalen Islands (Quebec, eastern Canada). 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. Specifically, this study assessed

the influence of biodepostion rates on: 1) sediment % organic matter, 2) macrofaunal abundance, species richness and biomass, 3) benthic macrofaunal community structure, 4) the relative proportion of ecological groups - ranging from organic-sensitive species to opportunists, 5) a related biotic index – M-AMBI, and 6) sediment oxygen demand and nutrient fluxes at the sediment-water interface.

5.2 MATERIALS AND METHODS

5.2.1 Benthocosms and biodeposition rates

Thirty five sediment cores (PVC pipes, 78.5 cm^2 cross-section area and 20 cm high) were collected from a 5 m deep area with a sandy bottom in Great-Entry Lagoon in the Magdalen Islands (N 47° 37', W 61° 31'), in Eastern Canada. All cores were collected by SCUBA divers who pressed the pipe lengths into the bottom sediments to a depth of 17 cm. The cores were removed from the bottom by digging out beside them and then sealing them from the bottom with a PVC cap so as to not disturb the sediments and associated organisms within them. Each core was then capped from above temporarily for transport to experimental racks. The racks were iron bars fitted with plastic caps that were secured to the bars at 40 cm intervals, open end up to act as holders for the sediment cores, hereafter referred to as "benthocosms" (Figure 5.1). Biodeposition was modified experimentally by placing randomly 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} (Figure 5.1). A previous study done in the same area (Callier et al. unpublished data)

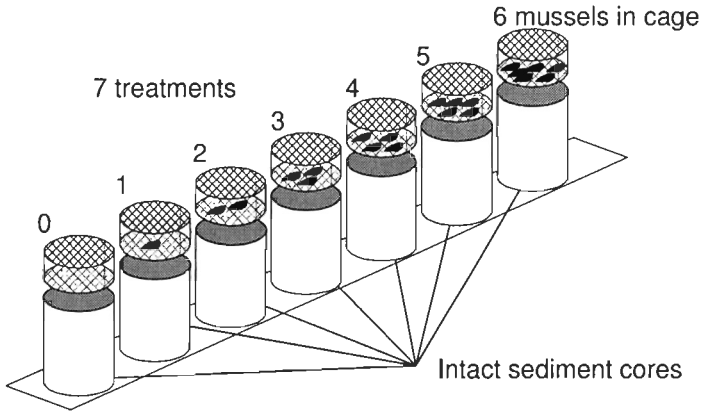

Figure 5.1 Benthocosms (sediment core of 78.5 cm^2) exposed to 7 mussel densities (0, 1, 2, 3, 4, 5, 6 mussels. $cage^{-1}$). Five replicates per mussel density were placed randomly at 40 cm intervals along an iron support (diagram not to scale).

showed that biodeposition rates are significantly correlated to mussel density such that biodeposit production for the size of mussels used (ca. 2.75 g wet weight) averages ca. 22 mg day^{-1} $mussel^{-1}$ (see Table 5.1, for equivalences). The experiment was run for ca. 50 days (between June 12 and August 4-6 2004), after which time all benthocosms were collected and the macrofauna (> 500 µm) quantified, following measuring the various fluxes of interest. The period of 50 days was set based on the turnover of one of the indicator species present in the general area (Callier et al. 2007, the opportunist polychaete *Capitella* sp. (37 to 50 days at 15 °C, Grassle & Grassle 1974). The area where the experiment was done is situated in the western part of Great-Entry Lagoon, more than 2 km from the mussel farm, on the other side of a navigation channel and was therefore not under the influence of mussel biodeposition.

5.2.2 Sediment organic matter content

A single sediment sample was collected from each core using a cut-off 5 ml disposable syringe to determine the % organic matter in the top 2 cm of sediments. Additional core samples (n = 3) of the natural surrounding sediment were taken in the area before (T0) and after (T50) the experiment. Samples were frozen (-20°C) before being dried at 60°C for 48 to 72 hours to attain a constant weight, weighed, burned for 4h at 450°C, and reweighed to calculate sediment ash-free dry weights (AFDW) (Byers et al. 1978). All weights were measured to the nearest 10^{-5} g with an AG285 Mettler Toledo balance. Sediment organic matter content is expressed as % loss of total sediment weight following combustion.

Table 5.1 Equivalence between mussel density per cage, mussel density per m^{-2} and biodeposition rates. Mussels used were approximately 2.75 g wet weight.

Mussel density	**Mussel m^{-2}**	**Biodeposition rates** (g dw biodeposit m^{-2} d^{-1})
0	0	0.00
1	127	2.80
2	255	5.61
3	382	8.41
4	510	11.21
5	637	14.01
6	764	16.82

5.2.3 Macrofaunal community analysis

The contents of the benthocosms were sieved through a 500 μm mesh and the material retained on the sieve preserved in a 5% formaldehyde-saline solution. Macrofaunal specimens were stored in 70 % ethanol after sorting. Identifications were done to the lowest taxonomic level possible, usually to species. The biomass of each species was measured as blotted wet weight. All individuals of a species in a sample were grouped for biomass measurements. Animals were removed from tubes prior to evaluating biomass. The biomass of molluscs includes the weight of their shells (Weston 1990). 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: I, very sensitive to organic enrichment, II; indifferent to organic enrichment; III, tolerant to excess organic enrichment; IV, second-order opportunistic species; V, first-order opportunistic species (Borja et al. 2000, Borja et al. 2003). Note that *Pectinaria granulata* was assigned to group IV, based on the classification for *Pectinaria koreni* and two species were assigned based on the classification of their respective genera *(Bittium alternatum* and *Nereis grayi)*. The organisms thus classified were used to calculate a global index of community status (AMBI – see Borja et al. 2000) using the software 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 called (M-AMBI - see Muxika et al. 2007).

5.2.4 Biogeochemical fluxes

At the end of the experiment, but prior to sampling the benthocosms, dark hermetic benthic chambers were installed on the top of each benthocosm (Figure 5.2) by scuba divers to evaluate nutrient fluxes and benthic respiration. To obtain the fluxes for the 35 cores, the manipulation was run over three consecutive days (ca. 2 cores analysed per hour). The benthic chamber system used is a smaller version of one used in previous studies to monitor oxygen and biogeochemical fluxes (Boucher & Clavier 1990, Richard et al. 2007a). The system is composed of a small benthic chamber (10 cm diameter × 20 cm high), a submersible pump with a variator, a YSI 6600 probe, and three hoses (Figure 5.2). The mean volume (± SE) of the whole system was 2.99 ± 0.01 L. The benthic chambers were deployed for one hour. The YSI probe recorded oxygen concentration (mg L^{-1} ± 0.01), temperature (°C ± 0.01) and salinity (± 0.01) in the system at 1-min intervals. Biogeochemical parameters were evaluated by collecting three water samples using 60-ml syringes via access ports at both the beginning and end of the hour. Ten millilitres per syringe were immediately sampled in the field to measure ammonium concentration using the OPA method (Holmes et al. 1999) with an Aquafluor handheld Turner Designs fluorometer. The remainders of the water samples were stored in three cryovials and frozen (-80°C) after filtering through 0.2 µm cellulose acetate Target syringe filters. Analyses for dissolved nitrate, nitrite, phosphate and silicate were done using a PAA II Brann + Luebbe auto-analyzer following Tréguer and Le Corre (1975). Biogeochemical fluxes were determined either from the slopes of the linear regressions between oxygen concentration and incubation time (values expressed as mg O_2 L^{-1} h^{-1}) or from changes in nutrient

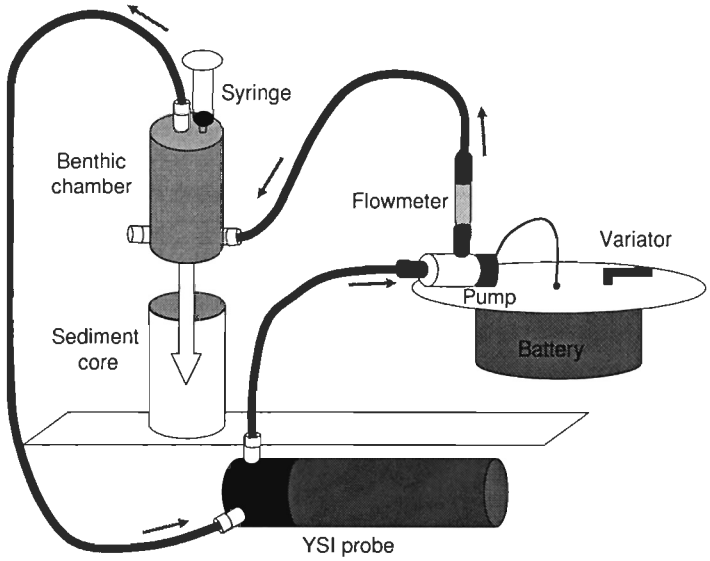

Figure 5.2 System to measure nutrient fluxes and oxygen consumption composed of the benthocosm, a benthic chamber, YSI probe, a submersible-pump powered by a waterproof battery, and three hoses. Grey arrows indicate water circulation in the system. The white arrow indicates the sealing of the system.

concentrations over the incubation time (µmol nutrients L^{-1} h^{-1}), multiplied by system volume (values expressed as mg or µmol h^{-1}). Fluxes were standardized and are expressed as mg O_2 or µmol of nutrients m^{-2} h^{-1}.

5.2.5 Statistical analysis

Organic matter content, macrofaunal benthic characteristics (species richness, abundance and biomass) and biogeochemical fluxes among the mussel densities were compared using analysis of variance (ANOVA). Data were log-transformed when necessary to satisfy the assumptions of ANOVA and indicated in corresponding tables. Some replicates for some biogeochemical parameters (from 1 to 4 of 35) were excluded as their Cook's D influences were greater than 4/n (n = total number of replicates, Cook & Weisberg 1982). Tukey pair-wise multiple comparison tests adapted for unbalanced designs were used to identify the differences when there was a significant ($p < 0.05$) effect of mussel density. Linear regression of organic matter and biogeochemical fluxes vs. mussel density and organic matter content was tested using SYSTAT version 10.2. 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 & Warwick 1994) and DISTLM (a distance-based nonparametric multivariate analogue of ANOVA) (McArdle & Anderson 2001, Anderson 2004). 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* more than 10 × greater than the next largest abundance for this species) and was not include in further analyses.

5.3 RESULTS

5.3.1 Sediment organic matter content

Sediment organic matter content (% OM ± SE) in the natural surrounding sediment was similar at the beginning of the experiment (T0 = 3.1 ± 0.2 %) and at the end of the experiment (T50 = 2.9 ± 0.2 %). Sediment % OM in benthocosms differed significantly between mussel densities (Figure 5.3, $F_{8,33} = 4.287$, $P = 0.001$). After 50 days, % OM ranged from 3.1 ± 0.3 % to 5.5 ± 0.8 % but was not correlated with mussel density ($r^2 = 0.090$, $P = 0.095$) because of the low % OM recorded in the 3 and 5 mussel density benthocosms (Figure 5.3).

5.3.2 Macrofauna

Total abundance, total biomass and species richness. Abundance differed significantly among mussel density treatments (Table 5.2a). The greatest mean abundance (3567 ind m^{-2}) was recorded in control benthocosms and generally decreased thereafter, with the lowest abundance recorded in benthocosm with 3 mussels $cage^{-1}$ (Figure 5.4).

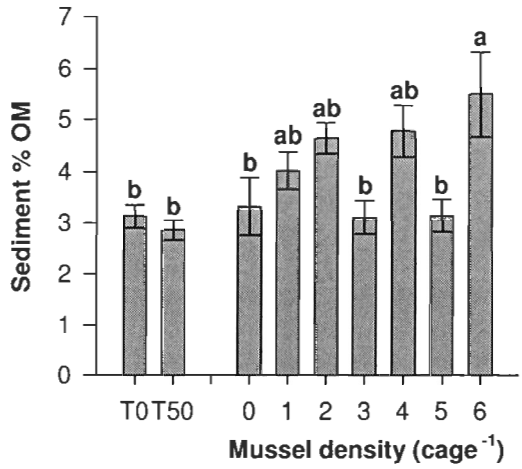

Figure 5.3 Mean organic matter contents (± SE, n = 5) measured in the top 2 cm of sediments exposed to biodeposition by 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}) for 50 days. Different letters indicate significant differences between treatments. T0 and T50 indicate % OM from surrounding natural sediments at the start and end of the experiment.

Control benthocosms had the greatest species richness and benthocosms with 3 and 4 mussels cage^{-1} had the smallest species richness. The greatest total biomass was recorded in benthocosms receiving biodeposits from 1 mussel cage^{-1}. Overall, total abundance and species richness were negatively correlated with mussel density (Table 5.2b).

Species abundance and biomass. The abundance and biomass of several dominant species were correlated with mussel density (Figures 5.5, 5.6, Table 5.2). The polychaete *Pherusa plumosa* and the bivalve *Tellina agilis* are classified as being sensitive to organic enrichment and had the greatest abundance and biomass in control benthocosms (i.e., mussel biodeposition). The abundance and biomass of these two species as well as the biomass of *P. granulata* were negatively correlated with mussel density (Table 5.2b). In contrast, the greatest abundance and biomass of the polychaete *Capitella* sp. appeared to be in benthocosms receiving biodeposition from 6 mussels cage^{-1}. However, this trend was not significant.

Community structure. Community structure based on both abundance and biomass data differed significantly among treatments (Figure 5.7, Table 5.3). MDS and pair-wise comparisons showed significant differences in benthic community structure based on abundances between control benthocosms (0 mussels) and those exposed to biodeposition from 3, 4 and 6 mussels and a significant difference between communities from benthocosms with 2 and 6 mussels. Community structure based on biomass differed between control benthocosms and those with 3 and 6 mussels and between those receiving biodeposition from 3 and 5 mussels.

Table 5.2 (a) ANOVA testing the effect of biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}) on total abundance (N), species richness (S) and biomass (B) and (b) results of the significant relationships between N, S and individual species abundances and biomass with mussel density.

(a)

	df	F	P
N	6 25	3.630	**0.010**
S	6 25	2.672	**0.038**
B	6 25	3.611	**0.010**

(b)

	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
Biomass		
Tellina agilis	0.136	0.038
Pherusa plumosa	0.212	0.008
Pectinaria granulata	0.137	0.037

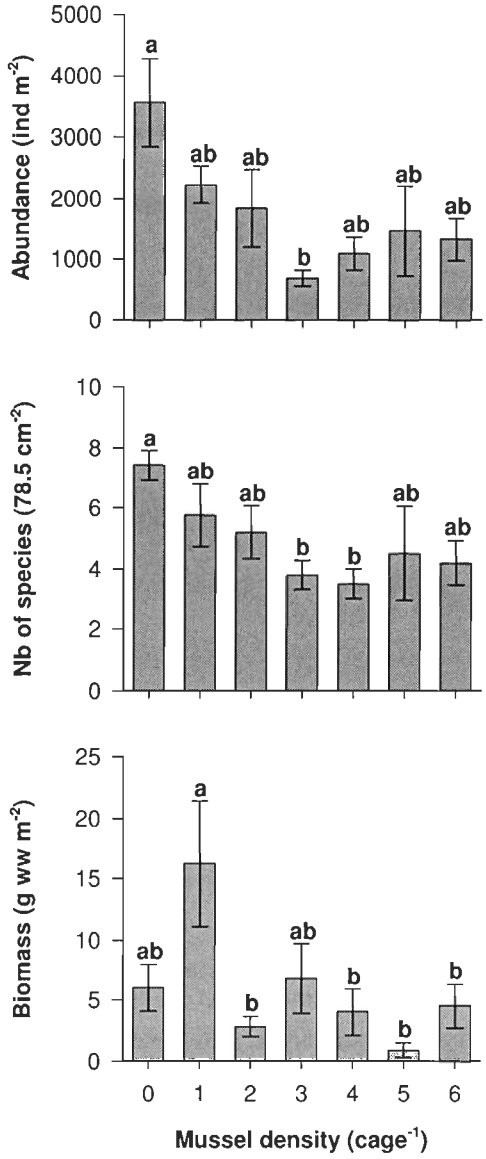

Figure 5.4 Mean benthic macrofaunal abundance, species richness, and biomass (± SE, n = 4 to 5) measured in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels $cage^{-1}$). Different letters indicate significant differences between treatments. Data are standardized (m^{-2}), except for species richness (reported as number of species per benthocosm).

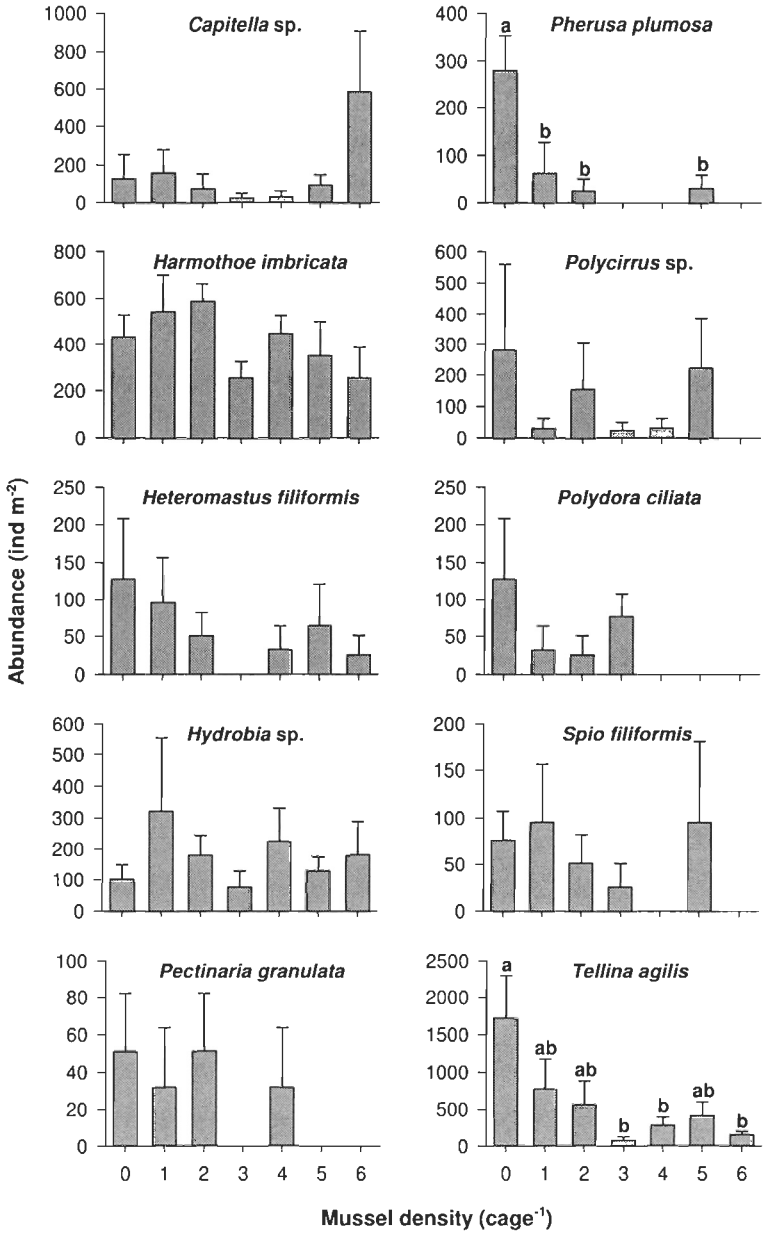

Figure 5.5 Mean abundance (average ± SE, n = 4 to 5) of dominant species in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}). Different letters indicate significant differences between treatments.

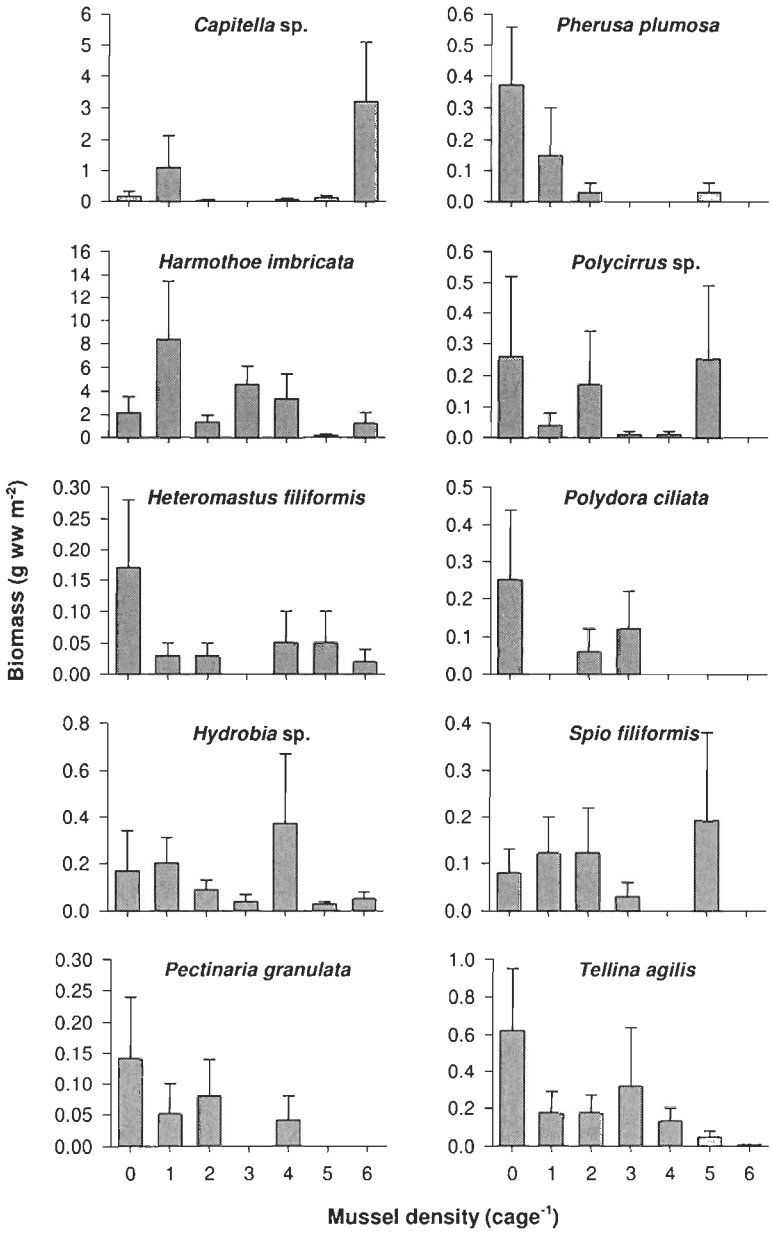

Figure 5.6 Mean biomass (average ± SE, n = 4 to 5) of selected species measured in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}). Different letters indicate significant differences between treatments.

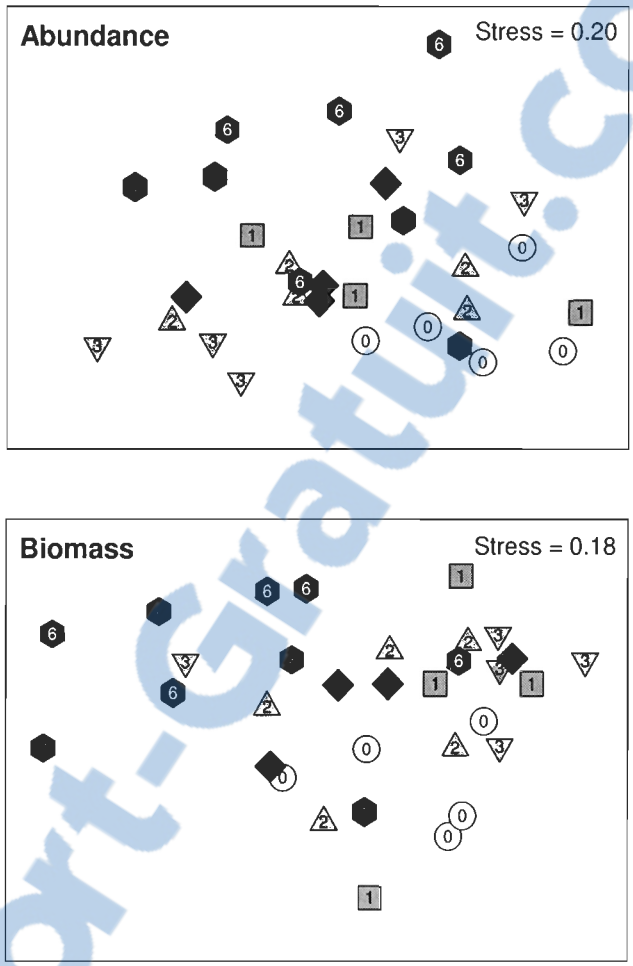

Figure 5.7 MDS on abundance and biomass data of communities from benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels cage^{-1}).: 0 (○), 1 (□), 2 (△), 3 (▽), 4 (◆), 5 (●) and 6 (⬢) mussels cage^{-1}.

Table 5.3 Results of pair-wise comparisons (DISTLM) of community structure between benthocosms subjected to various levels of biodeposition (0, 1, 2, 3, 4, 5, 6 mussels $cage^{-1}$). Upper right half of table compares biomass data whereas lower half compares abundance data. Statistically significant values are indicated in bold. Global DISTLM result was significant for abundance ($F_{6,25} = 1.529$, $P = 0.036$) and biomass ($F_{6,25} = 1.467$, $P = 0.033$).

	0	**1**	**2**	**3**	**4**	**5**	**6**
0		0.584	0.460	**0.039**	0.234	0.061	**0.027**
1	0.587		0.576	0.482	1.000	0.169	0.175
2	0.115	0.967		0.282	1.000	0.330	0.085
3	**0.008**	0.312	0.253		0.564	**0.040**	0.082
4	**0.017**	0.827	0.977	0.349		0.274	0.166
5	0.064	0.943	0.749	0.261	0.971		0.698
6	**0.008**	0.200	**0.043**	0.808	0.131	0.651	

Ecological groups. Benthocosms receiving the greatest level of biodeposition had the greatest proportion of second-order opportunistic species (group V, see Table 5.4) based on abundance and biomass data (Figure 5.8, Table 5.5). 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). The biotic index, M-AMBI, was significantly negatively correlated to mussel density (Figure 5.9).

5.3.3 Biogeochemical fluxes

Sediment oxygen consumption varied between 133.9 and 192.7 mg O_2 m^{-2} h^{-1}, ammonium (NH_4) fluxes ranged from 230.1 and 608.9 µmol m^{-2} h^{-1}, phosphate (PO_4) fluxes varied between 4.5 and 40.2 µmol m^{-2} h^{-1}, and nitrite (NO_2) fluxes varied between 0.97 and 4.40 µmol m^{-2} h^{-1} (Figure 5.10). None of these parameters varied among treatments (Table 5.6; Figure 5.10), potentially because of great within-treatment variability. In contrast, nitrate (NO_3) and silicate ($SiOH_4$) fluxes varied significantly among treatments (Table 5.6; Figure 5. 10). Nitrate fluxes ranged from -10.9 and 7.52 µmol m^{-2} h^{-1} and were least in benthocosms receiving biodeposits from 4 mussels. Silicate Si $(OH)_4$ fluxes ranged from 220.7 µmol m^{-2} h^{-1} (control benthocosms) to 918.5 µmol m^{-2} h^{-1} (mussel density = 6). Biogeochemical fluxes were not correlated with mussel density or organic matter content, except for silicate fluxes which were positively correlated with mussel density (Figure 5.10, Table 5.7). Phosphate fluxes were negatively correlated with macrofaunal biomass and abundance. O_2 consumption was negatively correlated with macrofaunal abundance (Table 5.7).

Table 5.4 Classification of the species into ecological groups: I, very sensitive to organic enrichment; II, indifferent to organic enrichment; III, tolerant to excessive organic enrichment; IV, second order opportunistic species; V, first order opportunistic species (Borja et al. 2000, 2003).

	Ecological group
Pherusa plumosa	I
Tellina agilis	I
Bittium alternatum	I
Aricidea jeffreysi	I
Harmothoe imbricata	II
Mya truncata	II
Nassarius trivittatus	II
Nephtys caeca	II
Pholoe minuta	II
Corophium sp.	III
Hydrobia sp.	III
Nereis grayi	III
Spio filicornis	III
Ophryotrocha sp.	IV
Heteromastus filiformis	IV
Cirratulidae	IV
Pectinaria granulata	IV
Polycirrus medusa	IV
Polydora ciliata	IV
Capitella sp.	V

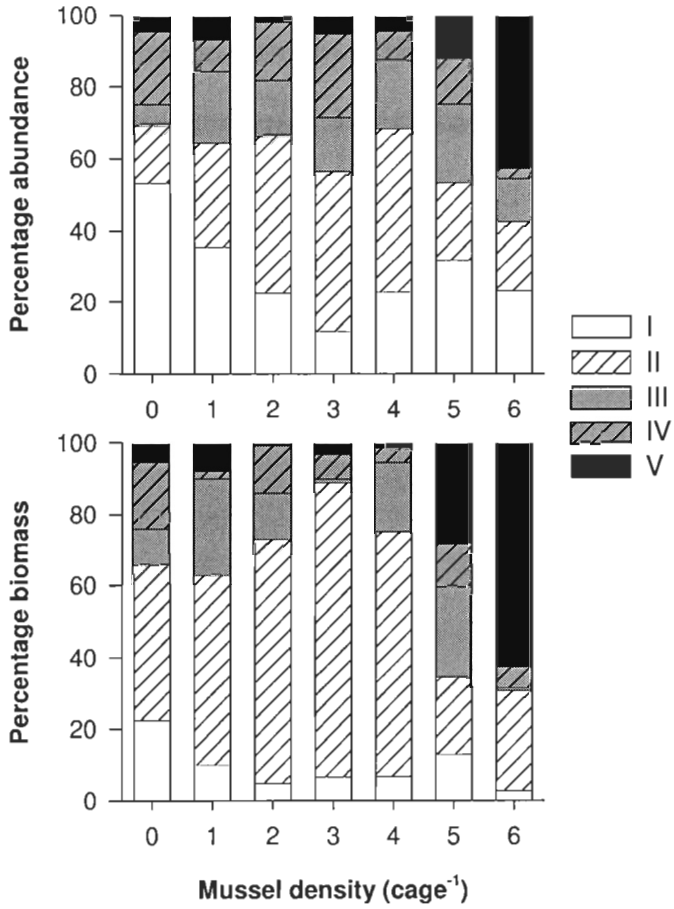

Figure 5.8 Proportion (%) of the abundance and biomass represented by different ecological groups (I-V, after Borja et al. 2000 classification) in benthocosms exposed to biodeposition from 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels benthocosm^{-1}). I, very sensitive to organic enrichment; II, indifferent to organic enrichment; III, tolerant to excessive organic enrichment; IV, second order opportunistic species; V, first order opportunistic species.

Table 5.5 Summary of ANOVAs testing the effect of biodeposition from different densities of mussels (MD) on the abundance and biomass of each ecological group. Significant effects are highlighted in bold.

	Abundance		**Biomass**	
Ecol. Group	$F_{6,25}$	**P**	$F_{6,25}$	**P**
I	1.615	0.185	0.854	0.542
II	2.016	0.101	2.012	0.102
III	0.655	0.686	0.909	0.504
IV	0.304	0.136	0.927	0.493
V	0.406	**0.012**	4.402	**0.004**

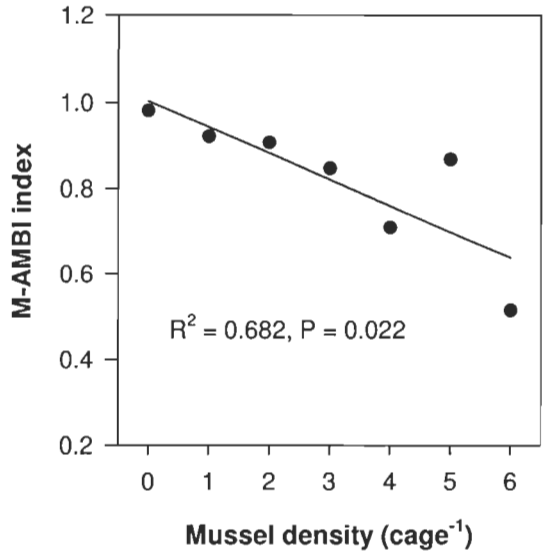

Figure 5.9 Linear relationships between the biotic index (AMBI) and mussel density. Data from the 5 replicates at each level were pooled.

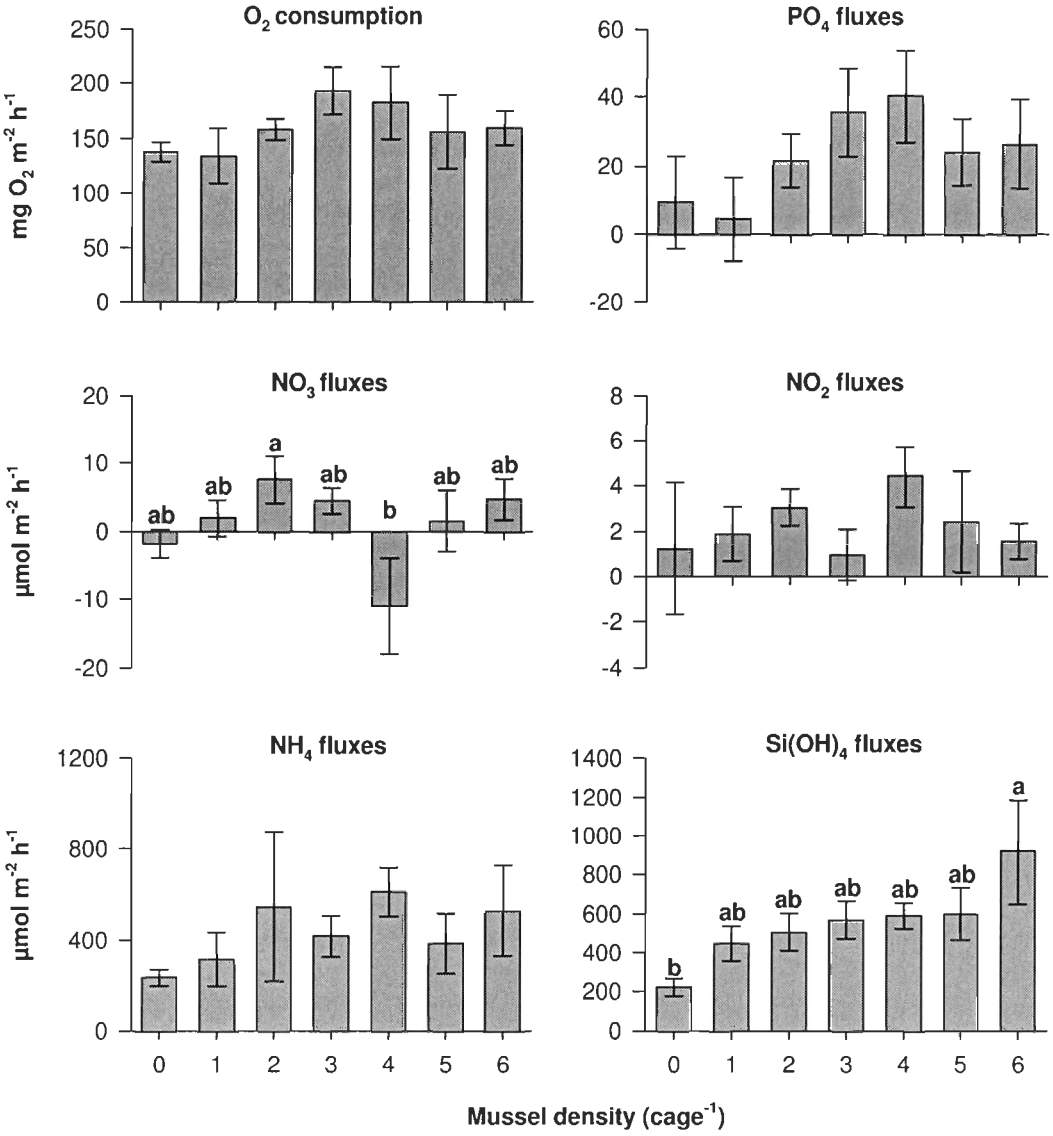

Figure 5.10 Mean oxygen consumption and nutrient fluxes (phosphate – PO_4, nitrate – NO_3, nitrite – NO_2, ammonium– NH_4, and silicate – Si $(OH)_4$) (± SE) measured at the water-sediment interface of benthocosms exposed to biodeposition by 7 densities of mussels (0, 1, 2, 3, 4, 5, 6 mussels $cage^{-1}$). Different letters indicate significant differences between treatments.

Table 5.6 Summary of one-way ANOVAs testing the effect of mussel density (MD) on benthic fluxes (oxygen: O_2, silicate: $Si(OH)_4$, ammonium: NH_4, phosphate: PO_4, nitrate: NO_3, nitrite: NO_2).

Variables	df		F	P
	MD	error		
O_2	6	25	0.981	0.459
NO_2	6	23	0.476	0.818
PO_4	6	23	1.124	0.380
NO_3	6	25	3.493	**0.013**
$Si(OH)_4$	6	26	2.501	**0.048**
NH_4	6	24	0.490	0.810

Table 5.7 Linear regression of benthic fluxes (oxygen: O_2, silicates: $Si(OH)_4$, ammonium: NH_4, phosphates: PO_4, nitrates: NO_3, nitrites: NO_2) vs. mussel density, % OM, macrofaunal biomass and abundance. Significant ($P < 0.05$) relationships are highlighted in bold.

	Mussel density		Sediment %OM		Macrofaunal biomass		Macrofaunal abundance	
	r^2	p	r^2	p	r^2	p	r^2	p
O_2	0.049	0.224	0.034	0.331	0.088	0.111	0.242	**0.006**
$Si(OH)_4$	0.314	**0.001**	0.077	0.131	0.030	0.355	0.119	0.057
PO_4	0.092	0.103	0.011	0.592	0.164	**0.033**	0.207	**0.015**
NH_4	0.041	0.278	0.033	0.348	0.013	0.550	0.008	0.643
NO_3	0.001	0.906	0.007	0.664	0.020	0.466	0.055	0.222
NO_2	0.004	0.761	0.000	0.942	0.054	0.242	0.001	0.906

5.4 DISCUSSION

The effect of organic enrichment on benthic marine communities has been well documented (Pearson & 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 and biogeochemical fluxes. The experiment was done to simulate real 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 the Great-Entry lagoon in Quebec 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 & 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.

5.4.1 Biodeposition rates vs sediment organic enrichment

Although sediment cores were subject to increased biodeposition rates with increasing mussel density (Callier, unpublished data), no clear relationship was observed between mussel density and sediment organic matter. An increase of organic matter content was generally observed with increasing mussel density, but two densities (3 mussels and 5 mussels $cage^{-1}$) did not show greater organic content than was observed at the beginning of the experiment. It is possible that the benthic organisms in benthocosms may have contributed to the change of vertical distribution of this organic matter in sediments via bioturbation and recycling of the organic fraction of biodeposits via metabolic activities (Aller 1977, Michaud et al. 2005). Despite this lack of a linear relationship, low OM content was observed in sandy cores at the beginning of the experiment and in control cores whereas the highest OM content was observed in the treatment subjected to the greatest biodeposition rates. At the greatest biodeposition rates, mussel faeces and pseudofaeces accumulated in the sediment and lead to organic enrichment as observed by several authors under shellfish farms (e.g., Stenton-Dozey et al. 2001, Hartstein & Rowden 2004). The greatest level observed in the present study (OM = 5.5 %) was equivalent to levels observed under one year old mussel lines (Callier et al. 2007), thus showing the efficacy of the treatments to mimic local depositional conditions. These levels of organic matter are lower than those observed in sediments under other shellfish cultures (24 %: Dahlbäck & Gunnarsson 1981, 22%: Mattsson & Lindén 1983, 15-20%: Deslous-Paoli et al. 1998, 12-13%: Christensen et al. 2003) and thus the results must be taken in context of this fact.

5.4.2 Macrofaunal response

Overall, abundance and species richness decreased with increasing biodeposition in accordance with the general model of organic enrichment outlined by Pearson and Rosenberg (1978). Decreased species richness and abundance in suspended mussel farms have been observed in other studies (e.g., Mattsson & Lindén 1983, Kaspar et al. 1985, Chamberlain et al. 2001, Christensen et al. 2003, Callier et al. 2007).

The great variation between cores is likely due in part to the natural variation among cores at the beginning of the experiment. In fact, the observed similarity among benthocosms within biodeposition treatments was similar to the similarity among benthic cores taken from the general area (Callier, unpublished data). Of all the species considered individually, only *P. plumosa* and *T. agilis* showed significant trends with mussel density. Both the abundance and biomass of *P. plumosa* and the biomass of *T. agilis* decreased with increasing biodeposition. Both of these species have been classified as being sensitive to pollution (Borja et al. 2000). In a study done in the mussel farming in GEL (Callier et al. 2007), *P. plumosa* was only observed in the zone with first-year mussels and then only at very low abundances (13 ind m^{-2}). Historically, *T. agilis* was one of the dominant species in the eastern part of the lagoon (Bourget & Messier 1982, Élouard et al. 1983) but has only been observed at low abundances within aquaculture sites there (Callier et al. 2007). The body size of *T. agilis* has been shown to decrease with increasing % OM (Callier et al. in press), thus confirming that this species does not thrive in organically enriched environments. The decrease of *Heteromastus filiformis* abundance and biomass may be

explained by its preference for muddy sediments that have a relatively low concentration of organic materials (volatile solids = 1.5 %, in Word 1990, p 255).

Although not statistically significant, *Capitella* sp. clearly responded to increased biodeposition. An increase in abundance and individual biomass of *Capitella* sp. in response to organic loading had already been shown in a previous mesocosm experiment (e.g., Webb 1996). Population explosions of *Capitella* sp. due to organic enrichment resulted from earlier reproduction and increased body size and fecundity (Grassle & Grassle 1974, Bridges et al. 1994). The dominance of *Capitella* sp. in organically enriched areas may be explained by its resistance to hypoxia and high sulphide concentration (Cuomo 1985, Diaz & Rosenberg 1995) and by its ability to use diverse forms of organic matter for growth (Tsutsumi et al. 1990). In the present study, the abundance of *Capitella* sp. increased to 586 ind m^{-2} at a density of 764 mussels m^{-2} (16.8 g biodeposits m^{-2} d^{-1}, the greatest depositional treatment). Callier et al. (2007) observed that the abundance of *C. capitata* reached a density of 548 ind m^{-2} under mussel lines in GEL, where the average biodeposition was estimated at 19 g m^{-2} d^{-1} (Callier et al. 2006). Thus, there appears to be a relationship between biodeposition rates and the abundance of *Capitella* sp. This observation further confirms *Capitella* sp. to be a good indicator of bivalve farm-related disturbance (Mattsson & Lindén 1983, Tsutsumi 1990, Weston 1990, Christensen et al. 2003). The present experiment was run over 50 days, which corresponds to the life span of *Capitella* sp. (37 to 50 days at 15 °C, Grassle & Grassle 1974). Because benthocosms were kept under near-natural conditions *in situ*, recruitment to the cores was possible. Moreover, larvae may settle immediately after being released (Linton & Taghon 2000). At the highest

mussel density, we observed both large (46.7 mg ww body weight) and very small individuals (<1 mg ww body weight), which were likely new recruits that hatched during the experiment. Of interest is the fact that the abundance of *C. capitata* was not increased substantially except for at the greatest biodeposition rate. Similarly, the abundance of the species has also been shown to be increased substantially only directly under mussel lines with second year mussels in GEL (Callier et al. 2007), its abundance was not substantially increased below first year mussel lines or between mussel lines. This 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. This is largely explained by the low abundance of *Tellina* (group I = sensitive to pollution) and the great abundance of *Capitella* sp. (group 5 = opportunistic of first order). A shift between slightly disturbed to moderately disturbed conditions occurred at a density corresponding to 764 mussels m^{-2}. 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. This extends the 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. Other sensitive species that are present in GEL and that have been shown to be correlated with organic enrichment, such as *P. granulata* (see Callier et al. 2007) have different life histories and thus could not be expected to respond as quickly to the increased biodeposition as *Capitella* sp.

5.4.3 Biogeochemical fluxes

An increase in organic matter loading to the bottom is known to increase sediment oxygen demand and nutrient fluxes (Dahlbäck & Gunnarsson 1981, Heilskov & Holmer 2001). Sediment oxygen consumption (Mazouni et al. 1996, Christensen et al. 2003) and ammonium, phosphate and silicate fluxes (Baudinet et al. 1990, Grenz et al. 1990, Christensen et al. 2003) were expected to increase with increasing biodeposition. However, except for silicate, significant differences in biogeochemical fluxes were not observed among mussel densities, although several trends were observed.

Sediment oxygen demand in benthocosms was great (133-193 mg O_2 m^{-2}-h^{-1}) and, although not significant, tended to be greater in benthocoms with mussels as compared to control benthocosms (1.1 to 1.4 × greater, except for benthocosms with one mussel). In a laboratory experiment, Giles and Pilditch (2006) showed that sediment oxygen demand increased by ca 1.5 × immediately after the addition of 331 g dw m^{-2} of mussel biodeposits. Greater sediment oxygen demand (1.2 to 3 ×) has also been observed, *in situ*, under mussel farms relative to reference sites (Mazouni et al. 1996, Christensen et al. 2003, Richard et al. 2007a). The levels measured in this study are similar to those observed in the mussel farm in GE in July-August 2003 (133 mg O_2 m^{-2} h^{-1}, Richard et al. 2007a) and greater than in other mussel farms in Canada (48 mg m^{-2} h^{-1}, Hatcher et al. 1994). The study did not show a correlation between sediment oxygen demand and increased mussel density. Oxygen consumption is not considered as a sensitive indicator of the impact of mussel culture on the benthic system since it is affected by many factors (Grant et al. 1995, Stenton-Dozey et

al. 2001). In contrast, oxygen consumption was negatively correlated with macrofaunal abundance. Oxygen demand observed in the most enriched benthocosms could be more a function of microbial-mediated oxidation of organic matter and reduced inorganic metabolites (Nickell et al. 2003) than by macrofaunal respiration, as expected in the control and lowest enriched benthocosms.

Ammonium and phosphate fluxes were generally greater (1.4 to 2.7 × and 2.3 to 4.3 ×, respectively) in the presence of mussels than in control benthocosms (except for PO_4 in the benthocosms with 1 mussel). These fluxes from sediments may be explained by the mineralisation of mussel biodeposits, which are rich in nitrogen and phosphorus (Kautsky & Evans 1987). An increase in sediment ammonium and phosphate release is generally observed *in situ* under mussel farms (Hatcher et al. 1994, Christensen et al. 2003, Richard et al. 2007a,b) and has also been observed in laboratory conditions following the addition of mussel biodeposits to sediments (Giles & Pilditch 2006). Although ammonium and phosphates fluxes tended to vary among mussel densities, the differences were not significant. This may be explained by the high within-treatment variability and may be related to the use of benthic chambers with small surface areas, which may amplify the effect of micro-scale spatial heterogeneity of benthic fauna (Balzer et al. 1983) relative to that observed in ones with large surface areas (Glud & Blackburn 2002). Ammonium fluxes could result from denitrification processes in enriched benthocosms, illustrated by large nitrate uptakes observed in some of the enriched benthocosms (e.g., NH_4, Figure 5. 10). Sediment phosphate release may also result from bacterial decomposition of biodeposits in the more enriched benthocosms. For this process to occur, sediments must be

anaerobic so that the phosphate remains mobile and does not combine with iron (Dame et al. 1991). This may explain why phosphate fluxes were negatively correlated with macrofaunal biomass and abundance as bioturbation by macrofauna is known to increase oxygen concentration in deeper sediments (Aller 1977).

Silicate fluxes increased with increasing mussel density in the present study (2 to 4.2 × greater than in control benthocosms). Silicate fluxes are likely a function of the dissolution of biogenic silica trapped in mussel biodeposits accumulated at the water–sediment interface (Lerat et al. 1990). Indeed, mussel faeces contain frustules and small chains of diatoms (Navarro & Thompson 1997), which have tests of biogenic silica (Balzer et al. 1983). In contrast to the mineralization of organic nitrogen and phosphorus, which is largely driven by bacterial and faunal metabolism, silicate is mainly regenerated thought dissolution processes that are related to physical processes (temperature, salinity, pH) (Lerat et al. 1990). Therefore, micro-spatial heterogeneity of benthic fauna probably had less of an influence on silicate than on ammonium and phosphate fluxes. The greatest silicate fluxes (~ 920 μmol m^{-2} h^{-1}) observed in benthocosms exposed to the greatest biodeposition rate were similar to the average silicate fluxes (~ 700 μmol m^{-2} h^{-1}) observed under 2-yr-old suspended mussel lines in August 2003 in GEL (Richard et al. 2007a). These silicate fluxes were 10 × greater under the mussel lines than in nearby control sites (Richard et al. 2007a).

5.4.4 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 decreases of macrofaunal biomass and abundance, the disappearance of sensitive species and the appearance of opportunistic species illustrate a shift to an organically-enriched environment with increasing mussel density. In the most enriched benthocosms, biodeposition was perhaps greater than the carrying capacity of the local (benthocosm) benthic assemblage. Anaerobic processes, which promote ammonification and sulphate reduction (Holmer et al. 2005) probably occurred in benthocosms and may explain the less complex benthic communities (Pearson & Rosenberg 1978, Diaz & Rosenberg 1995). Benthic fluxes integrate all these benthic process changes and are modified in turn by the decrease of species and functional diversity (Aller 1977, Michaud et al. 2005). Supplementary manipulative experiments would be necessary to illustrate the shift of

benthic metabolism to anticipate the response of biogeochemical fluxes to various level of biodeposition.

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.

CHAPITRE 6

CONCLUSIONS GÉNÉRALES ET PERSPECTIVES

L'objectif de cette thèse était de comprendre et quantifier les variations spatio-temporelles de l'influence de la mytiliculture (*Mytilus edulis*) sur l'environnement benthique. Ces informations sont nécessaires afin de développer une industrie conchylicole durable.

Malgré les nombreuses études sur l'influence de la conchyliculture, et particulièrement sur les effets de la mytiliculture sur le benthos, les mécanismes restent peu connus par rapport aux échelles spatiales et temporelles impliquées. Il est donc nécessaire de déterminer les relations dose-réponse (flux de biodéposition – réponse du benthos) et d'évaluer la capacité de différents indices à détecter l'effet de la mytiliculture sur l'environnement. Les études menées dans le cadre de ce doctorat ont permis de:

- Déterminer la production de biodépôts de différentes classes d'âges de moules afin d'évaluer le taux de biodéposition dans les différentes zones de la culture (zone des moules juvéniles 0+ / zone des moules de taille commerciale 1+)
- Mesurer la vitesse de sédimentation de pelotes fécales produites par des moules de différentes tailles afin d'estimer la dispersion des biodépôts dans les différentes zones de la culture (0+, 1+), en tenant compte du courant et de la hauteur des filières.
- Évaluer les variations de taux de sédimentation à différentes échelles spatiales (sous filières/entre filières; sous culture/ zone référence), et entre les différentes cohortes de moules présentes dans la culture (0+/1+), en répliquant les mesures dans le temps.
- Évaluer l'influence du processus de biodéposition sur les caractéristiques chimiques et biologiques du sédiment aux mêmes échelles spatiales (filières, culture,

lagune) afin d'évaluer la relation entre les taux de sédimentation et la réponse de l'environnement benthique.

- Comparer les mesures physico-chimiques et biologiques du sédiment à des données historiques afin de séparer les effets naturels des effets reliés à la mytiliculture.
- Déterminer la capacité de nombreux indices à détecter les effets de la mytiliculture à différentes échelles spatiales. Comparer l'influence de deux sites mytilicoles.
- Évaluer la réponse d'une communauté benthique et des flux biogéochimiques à différents taux de biodéposition, en faisant varier la densité de moules (relation dose-réponse).

Ainsi, des observations *in situ* combinées à une approche expérimentale ont permis de tester les hypothèses émises au début de ce doctorat. Les principaux résultats obtenus, l'originalité et les perspectives d'étude sont abordés dans ce chapitre.

6.1 PROCESSUS DE BIODÉPOSITION

Dans les études précédentes, les mesures des taux de sédimentation présentent souvent des problèmes méthodologiques dûs à un manque de réalisme (ex., mesures de biodéposition effectuées en laboratoire, bivalves nourris avec des cultures monospécifiques de phytoplancton) et à un manque de réplication (ex., taux estimés à partir de pièges placés sur un seul site de culture et un seul site référence) (Chapitre 1).

Lors de ce doctorat, une expérience menée *in situ* (Chapitre 2) a permis de montrer que la production de biodépôts variait en fonction de la taille des individus (*Mytilus edulis*). Les moules de la cohorte 1+ (taille commerciale, environ 6 cm) produisaient 1,6 fois plus de biodépôts que les moules de la cohorte 0+ (3 cm). La vitesse de sédimentation des fèces était corrélée à leur largeur. Étant donné que la largeur des fèces dépend de la taille des moules, cette dernière variable pourrait donc être utilisée pour prédire la dispersion des biodépôts.

La vitesse moyenne de sédimentation des fèces de *Mytilius edulis* (3-7 cm) était de $1,0 \pm 0,3$ cm s^{-1}. En considérant la vitesse du courant moyen en été (5,5 cm s^{-1}), la hauteur des filières (0 - 4 m) et la vitesse de sédimentation des fèces des moules 0+ (0,79 cm s^{-1}) et des moules 1+ (0,97 cm s^{-1}), la dispersion initiale des biodépôts a été estimée entre 7 et 24,4 m (0+) et entre 0 et 7,4 m (1+). Cependant lors des pics de vents, la vitesse des courants pouvant atteindre 18 cm s^{-1} en été, les biodépôts pourraient être dispersés jusqu'à 24,1 m (1+) et 79,7 m (0+).

Afin de vérifier nos estimations de dispersion, les taux de sédimentation ont été mesurés *in situ*. L'originalité de l'étude (Chapitre 2) est d'avoir pris en compte les variations spatiales à petite (10 m – sous vs. entre filière), moyenne (100 m – sites) et grande échelle (1 km, culture vs site référence), ainsi que les variations liées aux différences de taux de biodéposition par les cohortes de bivalves présentes dans la culture (0+ et 1+) et d'avoir répliqué ces mesures dans le temps. Dans cette étude, 48 pièges ont été déployés à chaque date d'échantillonnage (3 zones, 4 sites par zone, 2 positions par site).

Les mesures des taux sédimentation ont montré des différences significatives entre les sites. En général, les taux de sédimentation étaient plus élevés sous la culture que sur les sites références supportant l'hypothèse selon laquelle la mytiliculture augmente les taux naturels de sédimentation. Les taux de sédimentation étaient plus élevés dans la zone 1+ que dans la zone 0+, probablement à cause de la différence de taux de production de biodépôts entre les deux cohortes et à cause de la différence de dispersion des biodépôts. Les taux de sédimentation directement sous les filières étaient plus élevés qu'entre les filières (les filières étaient séparées de 20 m à Grande-Entrée), confirmant la faible dispersion des biodépôts dans la zone 1+. Des mesures de taux de sédimentation, le long de quatre transects autour de la culture, ont montré une bonne relation entre la direction du courant et la dispersion des biodépôts et ont confirmé la faible dispersion des biodépôts autour de la culture.

Les taux de sédimentation mesurés pourraient être expliqués à la fois par les taux de biodéposition de moules mais également par la biodéposition de la faune associée aux filières (ex, épibiontes, crabes) et par le processus de resuspension. Il est probable que les taux de sédimentation ont été surestimés. Étant donnée la faible profondeur de la lagune (5 m), les vents ont pu remettre en suspension les sédiments et ainsi augmenter le taux de sédimentation mesuré. Cependant, nos conclusions restent valides puisque les mesures ont été effectuées de façon simultanée dans chaque site.

L'étude a été effectuée en été lorsque les taux de biodéposition sont les plus élevés (Hatcher et al. 1994). Il serait intéressant d'effectuer des mesures de taux de sédimentation

pendant les autres saisons. En automne, les vents sont plus importants aux Îles-de-la-Madeleine et par conséquent, les taux de resuspension et de dispersion des biodépôts devraient augmenter dans la lagune. Par contre, en hiver, la lagune étant sous couvert de glace, on peut supposer que la biodéposition est plus localisée. En hiver, les teneurs en matière en suspension sont probablement plus faibles qu'en été, ce qui devrait diminuer les taux de production de biodépôts.

6.2 EFFETS DE LA BIODÉPOSTION SUR LE BENTHOS

Parmi les études sur l'influence de la conchyliculture, de nombreuses présentent un plan expérimental qui ne permet pas une bonne interprétation des résultats. C'est le cas des études n'utilisant qu'un seul site sous la culture et un seul site référence (Chapitre 1). Une part de la variation observée entre les deux sites peut être expliquée par la variation spatiale naturelle et non pas par les effets de la conchyliculture. D'autre part, très peu d'études se sont intéressées aux variations spatiales à petite échelle à l'intérieur d'un site conchylicole, par exemple entre filières et sous filières. Or, cette variation apparaît importante si l'on veut modéliser l'influence de la biodéposition sur le benthos. Peu d'études ont évalué l'influence de l'âge des bivalves sur le taux de sédimentation et par conséquent sur le benthos. Or, le taux de biodéposition varie avec la taille des bivalves (Chapitre 2).

Dans cette étude (Chapitre 3), les caractéristiques physico-chimiques et biologiques du benthos ont été évaluées aux mêmes échelles spatiales que celles utilisées pour évaluer les taux de sédimentation. Ceci a permis d'examiner la variation spatiale des communautés

macro-benthiques en relation avec les différents taux de sédimentation dans la lagune. Des variations dans la structure de communautés ont été observées à petite échelle, ce qui n'avait jamais été étudié auparavant. Cette étude a permis de déterminer les effets dans une période critique, quand les taux de biodéposition sont maximaux.

L'hypothèse selon laquelle les pourcentages de matière organique (MO) et les concentrations en sulphide augmenteraient, et les potentiels redox diminueraient en fonction du taux de sédimentation, n'a pas été vérifiée. Aucune différence significative n'a été observée entre les sites. Cette thèse confirme les observations d'études récentes montrant que les sulphides et le potentiel redox ne sont pas des paramètres assez sensibles pour détecter l'influence de l'aquaculture de bivalves sur l'environnement, lorsque le flux de MO est relativement faible. Ceci est particulièrement vrai dans les lagunes et baies qui sont déjà sous l'influence d'une charge organique naturelle importante (ex. déposition de plancton, algues en décomposition), comme c'est probablement le cas pour la lagune de Grande-Entrée.

Il aurait été intéressant de mesurer le pourcentage de carbone et d'azote organique et déterminer le ratio C/N au niveau du sédiment de surface (0-0,5 cm). L'azote étant dégradé plus rapidement que le carbone, de faibles ratios indiquent une MO labile tandis que des ratios élevés indiquent de la MO réfractaire (Nickell et al. 2003). Un ratio POC:PON entre 4 et 8 correspond par exemple à du phytoplancton ou des pelotes fécales facilement dégradables ayant une forte valeur nutritionnelle, tandis qu'un ratio plus élevé (>10) est caractéristique des détritus, du sédiment ou autre matière minéralisée à faible valeur

nutritive (Kautsky & Evans 1987). Plusieurs études sur la dispersion de la MO provenant de cages de poissons ont utilisé la méthode des isotopes stables (Sarà et al. 2006) afin de mieux comprendre l'origine et le devenir de la matière organique (Hobson 1999).

Contrairement aux indices chimiques, les communautés benthiques variaient significativement entre les sites. L'augmentation des taux de sédimentation a induit une réduction de la diversité des communautés benthiques et une augmentation des espèces opportunistes sous les filières 1+ dans la lagune de Grande-Entrée. Ainsi, les espèces normalement dominantes dans la lagune (ex: *Tellina agilis* et *Retusa obtusa*) ont été remplacées par des espèces opportunistes: *Capitella capitata* sous les filières 1+, et *Polydora ciliata* entre les filières 1+. La biomasse macrobenthique était plus élevée sous les filières 0+. Les communautés sous ces filières étaient soumises à un taux modéré de biodéposition (Chapitre 2). Certaines espèces comme *Hydrobia ulvae* ont probablement profité de ce flux modéré de MO.

La comparaison des résultats de cette étude à des données historiques (1975, 1978, 1982, avant la mytiliculture) a permis d'interpréter les résultats sur une grande échelle temporelle (30 ans). Les résultats remettent en cause les conclusions de certaines études qui attribuent certains effets à l'aquaculture, sans prendre en compte les conditions naturelles du milieu. Les communautés présentes au début de la mytiliculture (1982) étaient très similaires aux communautés échantillonnées en 2004. La comparaison des données de 2003-2004 dans la zone 1+ a montré que la communauté benthique tendait vers son état

initial et ceci moins d'un an après le retrait des moules (diminution de *C. capitata* et augmentation de l'abondance des espèces *Retusa canaliculta* et *T. agilis*).

Les résultats ont montré un effet localisé de la mytiliculture dans la lagune de Grande Entrée. La condition hypoxique du sédiment observée dans la lagune (concentration en sulphide de 2000 µM en moyenne) serait cependant plus attribuable aux conditions hydrodynamiques du milieu (ex. faible temps de renouvellement des eaux dans cette partie de la lagune, chenal de navigation, voir Chapitre 1, Site d'étude). La faible diversité de la faune benthique avait déjà été observée dans la partie relativement profonde de la lagune, avant la mise en place de la mytiliculture. La capacité de support de l'environnement benthique de la lagune de Grande-Entrée est probablement naturellement faible. La présence des cultures mytilicoles, même à des faibles densités, induit donc un enrichissement organique sous les filières, avec la colonisation du sédiment par des espèces opportunistes. Les résultats montrent que les effets de la mytiliculture peuvent être limités aux zones situées immédiatement sous les filières. Certaines méthodes d'échantillonnage (depuis un bateau par exemple) peuvent donc être inefficaces pour détecter de tels impacts.

6.3 INDICES

Le choix des variables analysées peut avoir une grande influence sur l'interprétation des effets de la mytiliculture sur l'environnement (Chapitre 3, 4, 5). L'étude d'observation à Grande-Entrée (Chapitre 3) et l'expérience en mésocosme (Chapitre 5) ont montré que les communautés benthiques étaient des indices plus sensibles que les indices biogéochimiques

(concentrations en sulphide, potentiel redox ou encore la consommation en oxygène du sédiment). L'étude effectuée à Grande-Entrée et Havres-aux-Maisons en 2004 (Chapitre 4) illustre le fait que les conclusions d'une étude dépendent de l'indice choisi. Les indices univariés, en particulier, doivent être interprétés avec précaution. Seuls, ils peuvent conduire à une mauvaise interprétation (exemple de la biomasse, Chapitre 4). Les indices biologiques multivariés, comme la structure de communautés benthiques, semblent être les indices les plus sensibles permettant de détecter des effets proches (3 m) et éloignés de la culture (300 m).

L'analyse du profil sédimentaire (SPI), donne une indication sur le niveau de bioturbation du sédiment et semble être un outil rapide et efficace pour détecter l'étendue des effets de la mytiliculture (Chapitre 4). L'analyse SPI a conduit aux mêmes conclusions que l'analyse des communautés benthiques. D'autres études devront être cependant menées pour confirmer l'efficacité de cette méthode dans le cas de la conchyliculture.

Bien que l'analyse de structure des communautés soit très sensible aux effets de la mytiliculture, la différence de structure ne donne pas d'information sur les changements et leurs conséquences sur le milieu. Si deux structures diffèrent, il est nécessaire d'évaluer en quoi elles sont différentes. L'utilisation d'un indice biotique (AMBI, Chapitre 4) calculé à partir du pourcentage de chaque groupe écologique (variant de sensible à tolérant à la MO, Borja et al. 2000) permet d'interpréter les changements.

6.4 RELATION DOSE-RÉPONSE

Pour prédire l'effet d'un site mytilicole sur l'environnement, des études empiriques comme celles menées lors de cette thèse sont nécessaires (Chapitre 2 et 3). Il est également important d'effectuer des expériences afin de déterminer précisément la relation dose-reponse (flux de biodéposition-flux biogéochimique et changements d'espèces benthiques). Ce type d'étude permet de définir la densité de moules qui peut être produite avant perturbation inacceptable du milieu.

L'étude en mésocosme (Chapitre 5) a montré que l'abondance et le nombre d'espèces étaient corrélés à la densité de moules. Le patron suivait le modèle général d'enrichissement organique de Pearson et Rosenberg (1978). Une diminution de l'abondance de deux espèces sensibles (*Pherusa plumosa* et *T. agilis)* en fonction de l'augmentation de la densité de moules a été observée dans cette étude. Une augmentation importante de l'abondance de *Capitella* sp (586 individus $m^{-2)}$ a été observée à partir d'une densité de 764 moules m^{-2} (ou 16,8 g biodépôts m^{-2} d^{-1}). Ces valeurs étaient proches de celles observées *in situ* sous les filières de moules de Grande-Entrée (Chapitre 2). Cette étude confirme donc que cette espèce permet de détecter les effets de différentes densités de moules sur l'environnement benthique. La classification des espèces en fonction du groupe écologique a permis de calculer un indice biotique (AMBI). Cet indice biotique était corrélé à la densité de moules. Un tel indice semble être un outil utile pour prédire les effets de la mytiliculture sur l'environnement benthique.

La demande en oxygène, les flux d'ammonium et de phosphate n'étaient pas corrélés à l'augmentation de densité de moules. Ces indices sont difficiles à interpréter car ils ne dépendent pas que du flux de MO mais également d'autres facteurs (ex. activité de bioturbation des organismes benthiques). Cette étude montre la complexité de la réponse des flux biogéochimiques aux variations de quantité de biodéposition. Dans cette expérience les carottes de sédiment étaient intactes, la diversité spécifique et l'abondance pouvaient donc différer sensiblement entre les replicats. De futures experiences devraient contrôler la diversité fonctionnelle des organismes benthiques pour déterminer la relation entre les taux de biodéposition et les flux biogéochimiques. La méthode pourrait être celle employée par Michaud et al. (2005, 2006): c'est-à-dire étudier les effets des groupes fonctionnnels en sympatrie et allopatrie sur les flux biogéochimiques en contrôlant le biovolume des espèces et en faisant varier les taux de biodéposition.

6.5 PERSPECTIVES DE RECHERCHES

Le développement de modèles de prédiction est nécessaire pour anticiper les effets de la conchyliculture sur un environnement donné. Les résultats de cette thèse vont contribuer à la paramétrisation et au développement d'un modèle de prédiction sur la dispersion des biodépôts et leurs effets sur l'environnement benthique (Weise et al. en préparation). Ce modèle va permettre: 1- la prédiction du taux de production des biodépôts et leur dispersion en fonction de différentes variables (ex., hydrodynamisme du milieu, densité de production) et 2- la prédiction des effets de la biodéposition de bivalves sur les communautés benthiques.

Cette thèse apporte des connaissances sur les variations spatio-temporelles des taux de sédimentation sous des cultures conchylicoles à différentes échelles et sur les effets de ces variations sur la qualité physico-chimique du sédiment et sur les communautés endobenthiques. L'étude du processus de resuspension, de la vitesse de dégradation des biodépôts, du processus de bioturbation ou encore de l'utilisation de la MO par le réseau trophique, apparaît comme une prochaine étape pour approfondir nos connaissances sur les interactions entre la conchyliculture et l'écosystème.

L'activité de bioturbation des organismes benthiques modifie les échanges de MO dans les sédiments et les voies de minéralisation à l'interface eau/sédiment (Aller 1977). L'étude effectuée à Havre-aux-Maisons (Chapitre IV) a montré qu'il existait une relation entre la présence de l'espèce bioturbatrice, *Pectinaria granulata,* et la profondeur de la couche oxique. Ainsi, bien que le pourcentage de MO ait été important, la présence de cette espèce, par son action de bioirrigation, a probablement permis un transport de l'oxygène dans les couches plus profondes du sédiment. L'hypothèse est que le processus de bioturbation augmente la capacité d'assimilation du benthos au flux de biodéposition. De futures études pourraient tester cette hypothèse en mesurant par exemple les caractéristiques du sédiment (ex, hauteur de la couche oxique, diversité spécifique, flux de nutriments) avant et après l'ajout d'espèces bioturbatrices (ex, *Nereis virens*) sous des cultures.

Il serait également important de considérer les effets «positifs» de la conchyliculture sur l'écosystème. Les cultures de bivalves peuvent en effet constituter une source de

nourriture et d'habitat pour d'autres espèces (McKindsey et al. 2006a). Deux études (D'Amours et Archambault 2005, Robichaud 2007) menées en parallèle aux Îles-de-la-Madeleine, ont observé une augmentation de l'abondance de la mégafaune (ex., crabes, étoiles, homards, plies) sous les filières de moules par rapport à des sites références. Ces études montrent que les filières agissent comme des récifs artificiels en apportant notamment un substrat sur lequel les épibiontes peuvent se fixer (ex. *Styela clava* fixée sur les coquilles). Il reste à déterminer si cette augmentation d'abondance est la conséquence d'une attraction de ces organismes ou si les cultures de bivalves augmentent significativement la production secondaire du milieu.

Plusieurs hypothèses peuvent être testées: (1) Les fèces et pseudofèces constituent une source de nourriture pour les déposivores, qui sont à leur tour consommés par les prédateurs (ex, poissons, homard), (2) Les bivalves, fixés sur les filières ou tombés sur le sédiment constituent également une source de nourriture pour la mégafaune. Afin de tester ces hypothèses et comprendre l'influence de la conchyliculture sur le fonctionnement des réseaux trophiques, les rapports de concentration des différents isotopes stables pourraient être analysés. En effet, les isotopes stables sont utilisés pour évaluer les positions des organismes dans la chaîne alimentaire et permettent de quantifier les relations entre les différents groupes trophiques. La mesure de la signature isotopique d'un organisme du réseau et de ces sources potentielles de nourriture (ex. phyto- et zooplancton, biodépôts, débris de zostères, bivalves etc) permettrait d'estimer la part de ces différentes sources dans son alimentation.

Dans une étude sur l'effet d'une ferme ostréicole sur la structure trophique du réseau alimentaire (Dubois 2007), l'analyse des isotopes stables a ainsi permis de calculer la position trophique des organismes dans le réseau. L'étude indique que sous les tables d'huîtres, le microphytobenthos et les détritus de macroalgue semblent constituer la source principale de nourriture des suspensivores, alors que de fortes valeurs δ15N chez les déposivores de surface et de sub-surface indiquent que la MO sédimentée (après dégradation par les bactéries) constituent la source de nourriture principale de ces derniers.

L'étude des interactions entre conchyliculture et environnement, en privilégiant l'approche écosystémique, permettra de déterminer la capacité de support environnementale de la conchyliculture.

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