

UNIVERSITÉ DU QUÉBEC

**INFLUENCE DE LA MYTILICULTURE ET DE L'ASCIDIE ENVAHISSANTE
STYELA CLAVA SUR LES COMMUNAUTÉS DE MACROINVERTÉBRÉS
BENTHIQUES À L'ÎLE-DU-PRINCE-ÉDOUARD**

MÉMOIRE

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RÉSUMÉ

L'influence de la conchyliculture en suspension sur les macroinvertébrés benthiques dans le sédiment est bien connue en ce qui concerne certains paramètres classiques décrivant la structure de ces communautés (ex. abondance, diversité), mais l'influence de cette activité sur la productivité secondaire des macroinvertébrés benthiques reste méconnue. Pourtant, ce paramètre s'avère très utile pour la compréhension des flux d'énergie dans les écosystèmes et pour la gestion des ressources halieutiques. De plus, les organismes qui vivent en association avec les bivalves en culture, et les ascidies envahissantes qui y sont souvent associés, ont généralement été exclus en ce qui a trait aux effets environnementaux de la culture de bivalves. L'objectif de cette étude était donc de déterminer l'influence de la mytiliculture et de l'ascidie envahissante *Styela clava* sur l'ensemble des macroinvertébrés « benthiques » dans les sites mytilicoles. À cette fin, les macroinvertébrés associés au sédiment ainsi que ceux associés aux moules cultivées en suspension ont été échantillonnés à l'intérieur et à l'extérieur de sites mytilicoles dans 8 baies à l'Île-du-Prince-Édouard : 3 envahies par *S. clava* et 5 où *S. clava* était absent.

L'abondance, la biomasse, la productivité secondaire ainsi que la diversité et structure des assemblages de macroinvertébrés benthiques ont été comparées à l'intérieur et à l'extérieur des sites mytilicoles. Les communautés associées au sédiment étaient significativement moins abondantes dans les sites mytilicoles, et une diminution non-significative de leur biomasse et de leur productivité a aussi été observée. En utilisant ces mêmes paramètres, les communautés de macroinvertébrés sur les boudins de moules de sites envahies par *S. clava* ont été comparées à celles des sites où *S. clava* était absent. L'abondance des communautés de macroinvertébrés associés aux boudins de moules étaient plus élevés dans les baies envahies par *S. clava* et ces communautés étaient caractérisées par une structure différente. En combinant l'abondance, la biomasse et la productivité des communautés de macroinvertébrés dans le sédiment et sur les boudins de moules, un patron inverse à celui décrit pour les macroinvertébrés dans le sédiment a été observée : l'abondance, la biomasse et la productivité secondaire des macroinvertébrés étaient plus élevées à l'intérieur des sites mytilicoles. Contrairement aux résultats prédits, la présence de *S. clava* n'a pas augmenté l'effet de la mytiliculture sur la productivité secondaire totale (fond et boudins combinés). Ces résultats indiquent que les macroinvertébrés associées aux moules en suspension ont compensé les effets négatifs observés sur le fond et démontrent donc qu'il serait utile de considérer ces organismes dans l'étude et la gestion des effets environnementaux des activités conchylicoles.

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INTRODUCTION GÉNÉRALE

La conchyliculture est une industrie croissante à travers le monde et les contributions de cette industrie à la sécurité alimentaire et aux économies locales et rurales peuvent être importantes (Naylor *et al.* 2000, Shumway *et al.* 2003, Alain 2005). Généralement, les effets écologiques de la conchyliculture sont considérés moins importants que ceux de la pisciculture, notamment, car aucune nourriture additionnelle n'est ajoutée dans l'environnement pour nourrir les bivalves (Shumway *et al.* 2003). Néanmoins, la culture de bivalves est souvent extensive et peut exercer une grande influence sur les organismes pélagiques et benthiques ainsi que sur le fonctionnement des écosystèmes (Cranford *et al.* 2003). La conchyliculture, comme les autres activités aquacoles, représente donc une préoccupation environnementale, d'autant plus que les habitats côtiers où se déroule cette activité sont déjà modifiés par les activités humaines de plusieurs façons (Simenstad *et al.* 2000). Afin de répondre à ces préoccupations, une meilleure compréhension des effets de la culture de bivalves est nécessaire (Department of Fisheries and Oceans Canada 2006). Un aspect particulièrement méconnu est le rôle des bivalves comme substrats et vecteurs pour les espèces envahissantes, ainsi que leurs influences sur la structure des communautés benthiques (McKindsey *et al.* 2007). La présente étude traite de l'influence de la mytiliculture et de l'ascidie envahissante *Styela clava* sur les macroinvertébrés dites « benthiques » à l'Île-du-Prince-Édouard (ÎPÉ).

L'industrie mytilicole est en croissance à l'ÎPÉ depuis les années 1980 (Smith 2006) et en 2004 le total des débarquements à l'ÎPÉ était de 15,6 millions de kg (communication personnelle, Division des statistiques, Pêches et Océans Canada,

Région du Golfe). La culture de moules est l'industrie aquicole la plus développée à l'ÎPÉ et elle contribue de façon importante à la production totale de bivalves au Canada. À l'échelle nationale, les industries mytilicoles et conchyliques dans les autres provinces de l'Atlantique (Terre-Neuve-et Labrador, Nouvelle-Écosse, Nouveau-Brunswick), au Québec et en Colombie-Britannique continuent aussi à se développer (Department of Fisheries and Oceans Canada 2007).

Structure du mémoire

Ce mémoire est composé de 3 sections. La première section commence par une brève introduction suivie d'une revue de nos connaissances actuelles de l'influence de 1) la mytiliculture et 2) les ascidies sur les communautés de macroinvertébrés benthiques, et, étant donné l'importance des notions de la productivité secondaire pour ce travail, 3) une présentation de cette mesure et de son estimation. Cette revue est suivie d'une discussion des facteurs qui influencent la structure des communautés de moules. Dans la section suivante, je présente une expérience visant à évaluer les objectifs du mémoire et une interprétation des résultats obtenus. Dans la dernière section je présente une conclusion générale des travaux réalisés et une discussion de leur importance en lien avec l'état des connaissances actuel de l'influence de la conchyliculture sur l'environnement.

L'effet de la mytiliculture sur les macroinvertébrés

Au Canada, la plupart des moules (ainsi que les huîtres et les pétoncles dans certains endroits) sont cultivées en suspension dans la colonne d'eau où ils se nourrissent de phytoplancton, zooplancton, et de détritus. Les moules en culture représentent un lien entre les réseaux trophiques pélagiques et benthiques. Ils excrètent une portion des particules qu'ils filtrent dans la colonne d'eau sous forme de fécès et pseudofécès, riches en matière organique, qui sédimentent rapidement au fond (Callier *et al.* 2006). En conséquence, des taux de sédimentation significativement plus élevés ont été observés sous les structures mytilicoles par rapport aux sites témoins (Dahlbäck & Gunnarsson 1981, Callier *et al.* 2006). La décomposition des biodépôts sur le sédiment dans les sites mytilicoles peut entraîner des changements géochimiques tels que l'ammonification et la réduction des sulfates (Dahlbäck & Gunnarsson 1981, Richard *et al.* 2007). Plusieurs auteurs ont étudié l'effet de la biodéposition sur les communautés macrobenthiques en décrivant l'abondance, la biomasse, la diversité et la structure des communautés benthiques dans les sites mytilicoles, par rapport à des sites témoins (voir revue dans Cranford *et al.* 2003). Parmi ces études, certaines ont démontré des diminutions de l'abondance (Mattsson & Lindén 1983, da Costa & Nalesso 2006), de la biomasse (Stenton-Dozey *et al.* 1999), et de la diversité des communautés macrobenthiques (Mattsson & Lindén 1983) ainsi que des augmentations d'espèces opportunistes (Mattsson & Lindén 1983, Callier *et al.* 2007) sous les moules en culture. Cependant, la mytiliculture semble avoir peu d'effet à certains sites (Chamberlain *et al.* 2001, Miron *et al.* 2005) ou même des effets positifs sur certains

paramètres étudiés (Grant *et al.* 1995, Callier *et al.* 2007, Richard *et al.* 2007). Par exemple, Grant *et al.* (1995) ont observé une augmentation de la biomasse des macroinvertébrés benthiques dans un site mytilicole, qu'ils ont expliqué par l'apport de nourriture provenant de la chute de moules et de la matière organique des boudins de moules.

En plus des effets susmentionnés sur l'environnement benthique, l'effet des bivalves en culture est aussi lié à la structure biogénique qu'ils créent en tant qu'espèces « ingénieurs », qui modifient, maintiennent ou créent des habitats (Jones *et al.* 1994). Plus particulièrement, les coquilles de bivalves peuvent fournir une structure biogénique complexe sur laquelle les macroinvertébrés peuvent se fixer, et qui offre une protection contre la prédation et les conditions environnementales défavorables (Gutiérrez *et al.* 2003). De plus, ces macroinvertébrés (comme ceux vivant sous les moules en culture) peuvent consommer les moules ou les biodépôts qu'ils produisent (Tenore & Dunstan 1973, Tenore & Gonzalez 1975). Les bancs de moules naturels peuvent supporter une communauté macrobenthique productive de forte biomasse et diversité (Nixon 1971, Tsuchiya & Nishihira 1985) et les moules envahissantes en eau douce semblent également créer un habitat pour les macroinvertébrés. À la suite d'invasions de bivalves dreissenidés en eau douce, on a observé une augmentation de la densité et de la diversité de macroinvertébrés (Strayer *et al.* 1999, Ward & Ricciardi 2007). Par contre, Johannsson *et al.* (2000) ont observé que l'invasion de *Dreissena* spp. dans le lac Erie n'a pas affecté la biomasse des autres macroinvertébrés présents.

De façon semblable, les bivalves en culture peuvent aussi offrir un bon habitat pour les macroinvertébrés (Shumway *et al.* 2003). Il a été suggéré que les structures utilisées pour la culture de bivalves peuvent agir comme des récifs artificiels et favoriser le développement de communautés de macroinvertébrés (Tenore & Gonzalez 1975, Shumway *et al.* 2003) et de poissons et grands macroinvertébrés, tel que le crabe et le homard (McKindsey *et al.* 2006, D'Amours *et al.* en révision). En effet, de nombreux macroinvertébrés vivent directement sur les bivalves suspendus en culture (Arakawa 1990, Khalaman 2001, LeBlanc *et al.* 2003a, O'Beirn *et al.* 2004, Murray *et al.* 2007). Aussi, des études ont démontré que les structures employées pour la culture d'huîtres et de myes sur le fond offrent un meilleur habitat pour les macroinvertébrés et les poissons que les fonds sablonneux (Dealteris *et al.* 2004, Ferraro & Cole 2007, Powers *et al.* 2007). Ces habitats pourraient même être utilisés de façon équivalente aux herbiers de zostère (Dealteris *et al.* 2004, Ferraro & Cole 2007).

Contrairement aux effets souvent perçus de façon négative qui sont associés aux communautés macrobenthiques sous les moules en culture, ces études démontrent un effet positif de la conchyliculture sur les macroinvertébrés qui vivent en association avec les bivalves. Ces macroinvertébrés occupent la même fonction que les macroinvertébrés benthiques dans le sédiment et il est donc logique de les considérer avec les macroinvertébrés benthiques dans le sédiment pour dresser un portrait réaliste quant à l'effet de la conchyliculture. Ainsi, pour la présente étude, une influence globale neutre ou positive de l'influence de la mytiliculture est prédite lorsque l'ensemble des macroinvertébrés dans les sites mytilicoles est considéré : ceux qui

vivent sur les moules ainsi que ceux qui vivent dans le sédiment sous les structures mytilicoles.

L'effet des ascidies sur les macroinvertébrés

Des espèces exotiques envahissantes, notamment les ascidies, font souvent partie des communautés de macroinvertébrés qui vivent en association avec les bivalves en culture (Getchis 2005). Elles peuvent être introduites dans les sites conchylicoles de façon directe avec le transfert des stocks de bivalves, ou bien par d'autres vecteurs comme le transport maritime (Lambert 2007). Il est probable que la culture de bivalves facilite l'établissement des ascidies envahissantes (Locke *et al.* 2007, McKindsey *et al.* 2007) et celles-ci sont particulièrement nombreuses dans les sites mytilicoles à l'ÎPÉ, où au moins quatre espèces ont été introduites depuis 1998. *Styela clava* a été observé pour la première fois en 1998 et son arrivée a été suivi de *Botryllus schlosseri* en 2001, *Botrylloides violaceus* en 2002, et *Ciona intestinalis* en 2004 (Prince Edward Island Department of Fisheries and Aquaculture 2008).

Entre autres, l'ascidie plissée *S. clava* entraîne des conséquences économiques importantes, car la culture ainsi que la transformation des moules demande plus d'effort en sa présence (Department of Fisheries and Oceans Canada 2008). Cependant, la croissance et le rendement en chair des moules ne semblent pas être affectés par la présence de *S. clava* (Thompson & MacNair 2004). Colautti *et al.* (2006) ont estimé, à l'aide d'un modèle empirique, que les coûts associées à *S. clava* pourraient s'élever à plus de 88 000 000\$ pour l'industrie conchylicole au Canada.

Les ascidies peuvent également créer des habitats pour les macroinvertébrés. Paine et Suchanek (1983) ont souligné plusieurs similarités écologiques de l'ascidie *Pyura praeputialis* et la moule *Mytilus californianus* dans les milieux intertidaux (e.g. taille, refuge de la prédation par la taille, formation de matrices complexes, compétitivité supérieure) et ils ont aussi noté que ces deux espèces vivent en association avec des communautés macrobenthiques complexes. Plus récemment, certaines espèces envahissantes tels que les ascidies solitaires ont aussi été décrites comme des espèces « ingénieurs », qui peuvent augmenter l'abondance et la diversité des organismes indigènes, possiblement en augmentant la complexité ou l'hétérogénéité de l'habitat (Crooks 2002, Rodriguez 2006). En Afrique du Sud, Fielding *et al.* (1994) ont observé une grande densité, biomasse et richesse d'espèces macrobenthiques dans des bancs intertidaux et subtidaux de l'ascidie *Pyura stolonifera*. Les auteurs ont suggéré que la récolte de ces ascidies peut entraîner une perte de la productivité secondaire de la communauté macrobenthique, car la période de rétablissement de *P. stolonifera* est longue. De plus, Monteiro *et al.* (2002) ont démontré que la structure des communautés macrobenthiques varie selon la configuration de l'habitat créé par *P. stolonifera* en Australie. Castilla *et al.* (2004) ont observé une augmentation de la diversité de macroinvertébrés associée aux bancs de *Pyura praeputialis* au Chili.

En comparaison à ces ascidies, l'effet de *S. clava* sur les macroinvertébrés est moins bien connu. À l'ÎPÉ, l'ascidie envahissante *S. clava* peut atteindre une taille de 14 cm et peut se fixer sur des boudins de moules et sur d'autres substrats en très hautes densités (Thompson & MacNair 2004). L'ascidie *S. clava* peut donc créer une structure

complexe et peut servir de substrat pour la fixation de certaines espèces macrobenthiques (Whitlatch *et al.* 1995, Dijkstra *et al.* 2007, Locke *et al.* 2007). Il est possible que la structure produite par la présence de cette espèce sur les moules en culture puisse faciliter l'établissement et le maintien des populations de macroinvertébrés benthiques. Il est donc prévu que l'influence de la mytiliculture sur les macroinvertébrés sera augmentée par la présence de *S. clava* sur les boudins.

Estimation de la productivité secondaire

L'influence de la conchyliculture sur la productivité des communautés benthiques est moins bien connue que l'influence de cette activité sur d'autres paramètres tels que la diversité et l'abondance des organismes benthiques. Cependant, la productivité des communautés benthiques est d'une grande importance pour la compréhension des effets environnementaux et la gestion de cette industrie. La production secondaire est mesurée de l'incorporation de la matière organique par les organismes hétérotrophiques par unité de surface et de temps (Cusson & Bourget 2005) et ce paramètre est souvent exprimé par un flux d'énergie, par exemple $\text{KJ m}^{-2} \text{année}^{-1}$ (Benke 1993). La production secondaire intègre plusieurs caractéristiques biologiques qui décrivent le succès d'une population : la densité, la biomasse, le taux de croissance, la reproduction, la survie et la période de développement (Benke 1993). Elle indique donc l'importance fonctionnelle d'une population au sein d'une communauté ou d'un écosystème (Odum 1968, Benke 1993). De plus, des modifications des flux d'énergie des populations ou des communautés peuvent affecter le fonctionnement de l'écosystème (Benke 1993). En ce qui a trait à la gestion des pêches au Canada, la

Politique de gestion de l'habitat du poisson vise à protéger la capacité de production de l'habitat du poisson (Department of Fisheries and Oceans Canada 1986).

Les méthodes classiques employées pour estimer la production secondaire demandent un effort considérable (Crisp 1984) et il est particulièrement difficile de mesurer la production totale d'une communauté à l'aide de ces méthodes. Plusieurs auteurs ont donc élaboré des modèles empiriques pour faciliter l'estimation de la productivité secondaire des macroinvertébrés (Edgar 1990, Tumbiolo & Downing 1994, Brey 2001, Cusson & Bourget 2005). Les modèles sont basés sur la relation entre la productivité et la biomasse ainsi que d'autres caractéristiques des populations (ex. taxon, habitat) et des paramètres environnementaux. L'erreur associée aux estimations de productivité réalisées à l'aide de modèles empiriques peut être considérable pour une seule population (Benke 1993, Brey 2001). Cependant, cette erreur diminue beaucoup lorsque la productivité d'une communauté entière est estimée (Brey 2001), car l'erreur est distribuée de façon aléatoire. Ces modèles sont donc très utiles pour faire des comparaisons de la productivité macrobenthique totale au sein de différents habitats et écosystèmes (ex. Taylor 1998, Bologna & Heck Jr 2002, Nilsen *et al.* 2006). Les termes *productivité secondaire* et *production secondaire* sont souvent employés comme synonymes. Cependant, le terme *productivité secondaire* est utilisé ici puisqu'il décrit des estimations de production potentielle pour des conditions spécifiées (Davis 1963 cité par, Crisp 1984).

Objectifs du mémoire

L'objectif de ce projet de maîtrise était de déterminer l'influence de la mytiliculture et de l'espèce envahissante *S. clava* sur les communautés macrobenthiques qui vivent en association avec les moules cultivées en suspension, ainsi que celles associées au sédiment sous-jacent. Plus spécifiquement, pour tester l'hypothèse que la culture de moules en suspension influence les communautés macrobenthiques qui vivent dans le sédiment, l'abondance, la biomasse, la productivité secondaire ainsi que la diversité et la structure des assemblages macrobenthiques ont été comparées à l'intérieur et à l'extérieur des sites mytilicoles. De plus, l'hypothèse suivante a été testée : une influence globale neutre ou positive sur l'ensemble des macroinvertébrés sera observée lorsque la communauté de macroinvertébrés qui vit en association avec les moules en culture est incluse dans le calcul de paramètres benthiques. Cette hypothèse a été testée en combinant les données des échantillons prélevés dans le sédiment avec les données des échantillons de boudins de moules. De plus, des sites envahies par l'ascidie envahissante *S. clava* ont été échantillonnées pour tester l'hypothèse que la présence de cette espèce augmentera davantage l'effet de la mytiliculture sur les macroinvertébrés dans les sites mytilicoles (dans le sédiment et sur les boudins). L'influence de la mytiliculture sur les macroinvertébrés a été observée dans 8 baies de l'ÎPE : 3 baies avec *S. clava* et 5 baies sans cette espèce.

CHAPITRE 1

**INFLUENCE OF SUSPENDED MUSSEL AQUACULTURE AND AN
ASSOCIATED INVASIVE ASCIDIAN ON MACROINVERTEBRATE
COMMUNITIES**

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1.1 Abstract

The influence of mussel aquaculture on classic descriptors of benthic community structure (e.g. abundance, diversity) is well known, but the influence of this activity on benthic productivity has not been studied, despite its importance for understanding ecosystem dynamics and for fisheries management. As well, the macroinvertebrates living in association with bivalves in culture have generally been excluded from studies on the environmental effects of bivalve aquaculture. As suspended bivalve aquaculture creates new macroinvertebrate habitat in the water column, this study tests the hypothesis that mussel aquaculture increases overall macroinvertebrate productivity when both sediment and mussel sock invertebrates are considered. Further, the presence of the invasive ascidian *Styela clava* was expected to increase this effect, by adding additional structure to mussel socks.

Macroinvertebrates in the sediment and on mussel socks were thus sampled in 8 bays on Prince Edward Island, eastern Canada: 3 invaded by *S. clava* and 5 where *S. clava* was absent. The abundance, biomass, and productivity as well as the diversity and structure of assemblages of sediment macroinvertebrates were compared inside and outside mussel leases. Sediment macroinvertebrates in areas inside leases were significantly less abundant and showed a trend towards decreased biomass and productivity. Using these same parameters, mussel sock invertebrate communities were compared in bays with and without *S. clava*, showing greater abundance in bays with *S. clava*. When sediment and mussel sock macroinvertebrates were combined to determine overall macroinvertebrate abundance, biomass and productivity inside mussel

leases, these measures were greater inside mussel leases than in areas outside. The presence of *S. clava* did not change this trend. Macroinvertebrates on suspended mussels may offset negative impacts commonly observed with respect to macroinvertebrates in the underlying sediments, and should be included in any attempts to understand and manage bivalve aquaculture from a holistic point of view.

1.2 Introduction

Multiple anthropogenic stressors in coastal aquatic ecosystems are of increasing concern for the general public, habitat managers and ecologists alike. Along with direct habitat loss, aquaculture and invasive species are among those with the greatest perceived impacts (Simenstad *et al.* 2000, Costa-Pierce & Bridger 2002, Kappel 2005). Bivalve aquaculture is expanding in many countries worldwide, including Canada, and Prince Edward Island's suspended long-line mussel industry is a major contributor to Canada's total production of bivalves.

This industry may influence the benthic environment, as bivalve feces and pseudofeces may accumulate on sediments below suspended bivalve aquaculture structures (Dahlbäck & Gunnarsson 1981). Increased organic loading under suspended mussels may induce changes to sediment chemistry such as increased ammonification and sulphate reduction (Dahlbäck & Gunnarsson 1981, Richard *et al.* 2007). In particular, the influence of this practice on the abundance, biomass and diversity of macrobenthic communities under culture sites has been studied in coastal waters around the world. This work has shown that suspended bivalve culture may negatively influence the abundance, biomass (Stenton-Dozey *et al.* 1999), diversity and structure (Mattsson & Lindén 1983, Chamberlain *et al.* 2001, Callier *et al.* 2007) of macrobenthic communities. However, other studies have shown no change or positive influences on benthic macroinvertebrate abundance (Richard *et al.* 2007, Callier *et al.* 2007), biomass and diversity (Grant *et al.* 1995), as well as little change in structure of macrobenthic

assemblages (Chamberlain *et al.* 2001, Miron *et al.* 2005). In comparison, little effort has focused on the influence of suspended bivalve culture on the secondary productivity of these communities. This basic measurement of benthic community functioning describes energy flow through benthic macroinvertebrate communities, which provide an important link from primary producers to higher trophic levels and for the recycling of sedimented organic matter (Crisp 1984, Tumbiolo & Downing 1994). Moreover, invertebrate and fish productivity form the basis for fisheries management in some jurisdictions, including Canada (Department of Fisheries and Oceans Canada 1986, Minns 1997).

Furthermore, little work has concentrated on the influence of the structure created by bivalves suspended in the water column on benthic communities. In general, bivalves create important biogenic structure, and have been described as ecosystem engineers. In this way, bivalves growing in suspension may create favourable habitats for macroinvertebrates, as they can provide refuges from predation and adverse environmental conditions (Gutiérrez *et al.* 2003). Bivalve communities can also provide a direct source of food for other macroinvertebrates, as well as biodeposits that may be consumed by detrital organisms (Tenore & Dunstan 1973, Tenore *et al.* 1985). Indeed, both natural and cultivated mussel populations have been shown to support important macroinvertebrate communities. For example, high macroinvertebrate biomass and diversity has been observed in intertidal mussel beds (Nixon 1971, Tsuchiya & Nishihira 1985). However, following the invasion of Lake Erie by *Dreissena* spp., Johannsson *et al.* (2000) observed no change in biomass of

macroinvertebrates (excluding *Dreissena* spp.). Work has also shown that abundant macrobenthic communities live in association with cultured bivalves, especially mussels suspended in the water column (Tenore & Gonzalez 1975, LeBlanc *et al.* 2003a, Murray *et al.* 2007), as well as with both on- and off-bottom oyster cultures (Dealteris *et al.* 2004, O'Beirn *et al.* 2004, Ferraro & Cole 2007). As such, structures used for bivalve aquaculture appear to provide high-quality habitat for macroinvertebrates and are increasingly recognised as artificial reefs that may benefit macroinvertebrates as well as megafauna and fish (Tenore & Gonzalez 1975, Shumway *et al.* 2003, McKindsey *et al.* 2006, Powers *et al.* 2007, D'Amours *et al.* in revision).

As the macroinvertebrate communities associated with suspended bivalves are functionally part of the benthic environment, we suggest that consideration of both sediment macroinvertebrates and mussel sock macroinvertebrates may be a more realistic way to evaluate the effect of bivalve aquaculture on benthic communities. As outlined above, many studies of the impact of suspended bivalve culture on benthic infaunal communities have shown either negative or neutral effects on commonly measured benthic parameters. We predict that the inclusion of the fraction of the benthic macroinvertebrate community associated with suspended bivalves in culture in the calculation of macrobenthic community parameters will change such relationships to show either neutral or positive influences of suspended bivalve culture on macrobenthic community parameters.

Exotic ascidians are currently infesting suspended bivalve culture operations around the world (Lambert 2007). Historically, bivalve aquaculture has been a major vector for the spread of invasive species and has also suffered great losses due to the presence of these organisms (Getchis 2005, McKindsey *et al.* 2007). This is also true in Prince Edward Island (PEI), eastern Canada, where four exotic ascidians have appeared over the past decade including the clubbed tunicate, *Styela clava*. This ascidian has invaded multiple mussel culture sites since it was first identified in 1998 (Thompson & MacNair 2004). The structure provided by solitary ascidians in natural beds and in aquaculture sites, like the biogenic structure provided by cultured mussels, may also enhance the abundance and diversity of macroinvertebrates, possibly by increasing habitat complexity or heterogeneity (Paine & Suchanek 1983, Crooks 2002, Rodriguez 2006). For example, great abundance, biomass and diversity of macroinvertebrates has been reported from subtidal and intertidal beds of the solitary ascidian *Pyura stolonifera* in South Africa (Fielding *et al.* 1994) and from intertidal beds in Australia (Monteiro *et al.* 2002). In the context of suspended bivalve culture, Khalaman (2001) showed that in Russia, when large abundances of the ascidian *Styela rustica* were present on mussels, associated macroinvertebrate communities had greater average species richness than macroinvertebrate communities associated with mussels with fewer *S. rustica*.

In comparison to these ascidians, the habitat value of *S. clava* is less well known, but macroinvertebrates have been observed on surfaces colonised by *S. clava* (Whitlatch *et al.* 1995, Thompson & MacNair 2004, Dijkstra *et al.* 2007). Macroinvertebrates may thus be facilitated by the presence of *S. clava*, as these solitary ascidians grow up to 14

cm long (Thompson & MacNair 2004) and create a complex structure. Therefore, we also predict that the presence of solitary ascidians will create additional biogenic structure on bivalves in suspended culture, and thus further increase the positive influence of suspended bivalve culture on macrobenthic community parameters, relative to macrobenthic communities living on mussel socks where this additional structure is absent.

The broad aim of this study was to determine the effect of suspended mussel aquaculture and the invasive ascidian *S. clava* on benthic macroinvertebrate communities, including both those inhabiting the underlying sediments and those living in association with the cultured bivalves. Specifically, to test the hypothesis that suspended mussel culture has an influence on benthic infaunal communities, we compared the abundance, biomass, diversity and secondary productivity of infauna from sediments within mussel aquaculture sites to infauna from sediments of nearby control sites. We also test the hypothesis that the inclusion of the macroinvertebrate community living in association with cultured mussels in the calculation of benthic community parameters (i.e. combining data from sediment infauna and mussel line fouling communities) will show that suspended bivalve culture has a positive influence on macrobenthic community parameters. This hypothesis is further extended by including sites fouled by the invasive ascidian *S. clava* to test the hypothesis that the presence of *S. clava* will further strengthen this promotion of benthic macroinvertebrate community parameters in aquaculture sites, relative to aquaculture sites not infested by this ascidian. These hypotheses were evaluated using an observational experiment by

sampling a series of eight embayments with suspended mussel culture, including some infested with *S. clava*, in Prince Edward Island.

1.3 Materials and methods

1.3.1 Study site

This study was done in 8 bays used for mussel aquaculture on Prince Edward Island (PEI), eastern Canada (Figure 1). They were selected for the availability of control sites of similar depth and oceanographic conditions to culture sites (see below). On PEI, mussels are grown-out on traditional subsurface dropper lines (socks) in shallow bays and rivers (depth approximately 4 m; (Drapeau *et al.* 2006)), mainly on the north and east coasts. In addition to mussels, oysters are also cultured in many bays. Mussel aquaculture production has been increasing on PEI since the early 1980s and the majority of the bays studied have been used for mussel aquaculture since the early-mid 1980s. However, in Malpeque Bay (Bideford River) and Rustico, mussels have been cultured since the late 1980s and early 1990s respectively (personal communication cited in Shaw, 1998, personal communication D. Small).

In 2004, total mussel landings were 15.6 million kg, with mussel leases covering a total area of approximately 43 km² (Department of Fisheries and Oceans Canada, Gulf Region Statistics Division and Charlottetown). Bivalve aquaculture sites (leases) occupy a significant area of the 8 bays selected in this study: the mean area covered by mussel leases was 2.57 km² (\pm 1.06 SD), equivalent to a mean of 13.77% of total bay

surface area (Table 1). These values are similar to those for all 30 bays containing mussel grow-out leases in 2005 (mean of $1.44 \text{ km}^2 \pm 1.71 \text{ SD}$ covered by mussel leases, equivalent to a mean of 12.52% of total surface area). Maps of all areas leased for shellfish culture are available online from the Department of Fisheries and Oceans Canada (2008) (<http://www.glf.dfo-mpo.gc.ca/ao-bl/pei-ipe/leasing-baux/maps-cartes-e.php>). Drapeau *et al.* (2006) completed a survey of mussel leases across PEI in 2003, and reported an average density of 23.3 socks per 100 m^2 within mussel leases ($n=111 \pm 18.3 \text{ SD}$), with an average sock length of 2 m ($n=111 \pm 0.3 \text{ SD}$). These values will be used in subsequent calculations.

Table 1. Estimated total bay area, area leased for mussel grow-out in 2005 and % of bay leased for mussel grow-out, for each bay sampled (data from Fisheries and Oceans Canada, Charlottetown, 2007). (S) indicates bays with *Styela clava*.

Bay	Bay area (km^2)	Area leased for mussel grow-out (km^2)	% of bay area leased for mussel grow-out
Malpeque (Bideford River)	133.06	4.34	3.26
Marchwater	7.84	1.51	19.29
New London	15.29	2.54	16.58
Rustico	12.16	2.05	16.87
Cardigan	55.70	2.33	4.18
Brudenell (S)	8.45	1.20	14.23
Saint Marys (S)	16.66	2.86	17.17
Murray River (S)	19.95	3.71	18.60

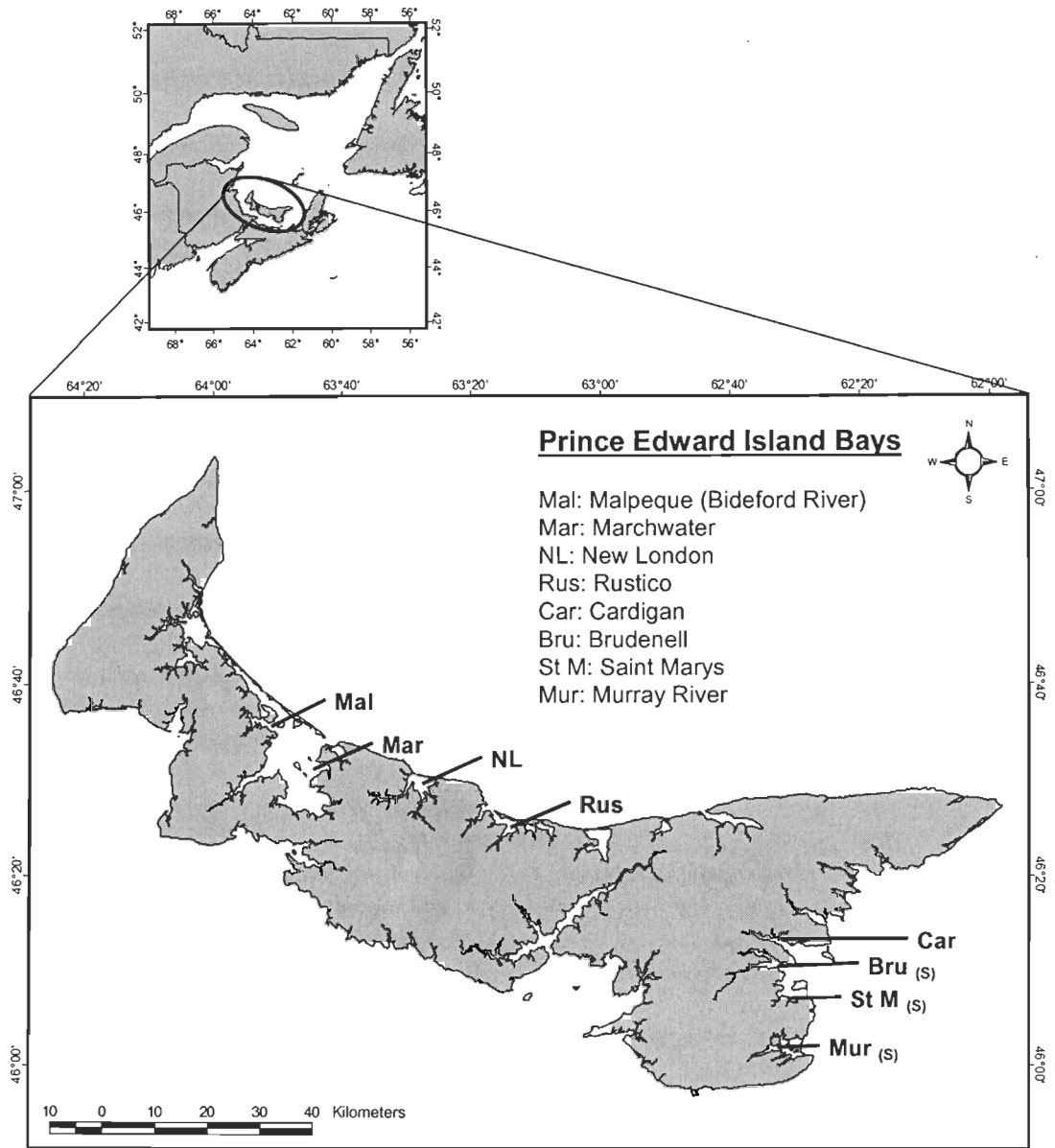


Figure 1. The Maritime Provinces of Canada, with insert of Prince Edward Island showing bays sampled. (S) indicates bays with *Styela clava*.

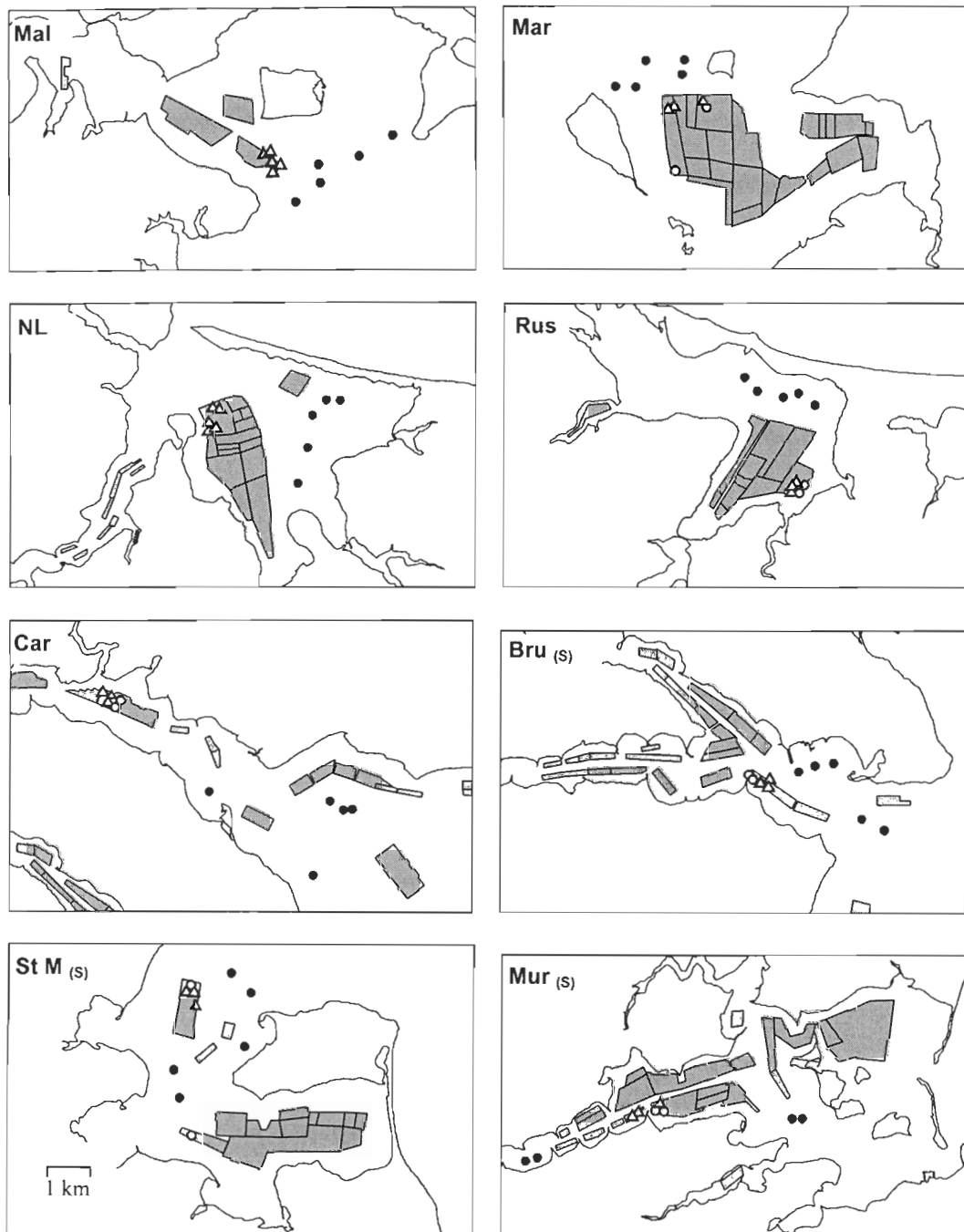


Figure 2. Sampling locations in bays shown in Fig. 1. Shaded areas are mussel leases. ●: control samples (sediment) ○: sediment samples inside leases Δ: sediment and mussel sock samples inside leases (separated by approximately 30 m). (S) indicates bays with *Styela clava*. Note that the scale is consistent throughout.

All bays included in this study had control sites at least 300 m from aquaculture sites and of similar depth. Control sites at this distance, while being of similar depth and having similar oceanographic conditions to culture sites, were not expected to be under the direct influence of sedimentation from mussel aquaculture (Grant *et al.* 2005, Callier *et al.* 2006, Callier *et al.* in press). The mean depth of locations sampled inside leases was 4.58 m (± 1.42 SD) vs a mean depth of 4.52 m (± 1.64 SD) outside leases. The bays sampled included 3 bays where adult *S. clava* were observed *in situ* and were abundant during sampling (Bays with *S. clava*: Brudenell, Saint Marys, Murray River), and 5 bays where no adult *S. clava* were observed (Bays without *S. clava*: Malpeque (Bideford River), Marchwater, New London, Rustico, Cardigan) (Figure 1). Mean annual bottom temperature in all bays was estimated at 8.6°C, based on data collected over 1 year in Malpeque and Covehead bays on PEI (mean bottom temperature of 8.4°C and 8.9°C respectively; Fisheries and Oceans Canada Gulf Region, Aquatic Ecosystems Section, personal communication).

1.3.2 Field sampling methods

Sampling was done from August 16 to 25, 2005. Two types of macroinvertebrate communities were sampled 1) macroinvertebrates living in association with mussel socks (=mussel sock macroinvertebrates) and 2) macroinvertebrates living in and on the sediment (=sediment macroinvertebrates). In each bay, 5 sediment samples were collected inside of mussel leases and a further 5 sediment samples were collected at least 300 m outside of mussel leases. As well, in each bay 3-5 samples of 1+ age class mussel socks were collected from leases of mussel growers

participating in this study (Figure 2). Mussels in this age class had typically been placed in socks for grow-out in autumn 2003. Sampling locations within each zone were randomly selected, as were sampling positions on mussel socks. Depths sampled ranged from approximately 1-2.7 m.

All sediment samples were collected by SCUBA divers using PVC sediment corers 10 cm in diameter, to a depth of 10 cm. Mussel socks were sampled using 50 cm mesh (1 mm) bags that seal on 3 sides with Velcro. These were sealed around a portion of the mussel socks *in situ* and the mussels and associated organisms were loosened by hand from the mussel sock within the bag. The bag and its contents were removed from the sock by, starting from one corner, simultaneously opening and resealing the sides of the bag until it was freed from the sock.

The mean length of mussels per subsample ranged from 49.1-67.6 mm with an overall mean length of 56.7 mm (subsample $n=1116$, ± 9.6 SD), excluding mussels shorter than approximately 3 cm which was considered to be secondary set (i.e., to have settled on the socks). *Styela clava* collected in mussel sock samples were up to 145 mm long. The total number of *S. clava* per sample ranged from 25-658, while biomass ranged from 1.92-334.83 g per sample (Table 2), although these measures of biomass are probably underestimated because large *S. clava* were frozen and became dehydrated after thawing. Although no adult *S. clava* were observed in Marchwater, 112 small *S. clava* individuals were observed in one sample upon processing (total biomass=1.24 g). Only socks containing *S. clava* were sampled in bays infested by this species. Water depths for individual sediment samples were estimated from hydrographic charts using

GPS points taken in the field. Depths of mussel sock samples were estimated from their relative positions on the socks.

Table 2. Total number and biomass of *Styela clava* per 50 cm mussel sock sample (totals calculated from subsamples of juveniles and full samples of adults). Averages (\pm SE) are indicated in bold.

Bay	Number of <i>S. clava</i> per sample	Biomass¹ of <i>S. clava</i> per sample (g)
Brudenell	237	117.88
	25	2.1
	352	63.07
	205 (96)	61.02 (33.44)
Murray River	170	28.08
	60	28.89
	658	334.83
	296 (184)	130.60 (102.11)
St Marys	128	7.04
	517	5.03
	54	1.92
	233 (144)	4.67 (1.49)

¹Biomass of large *S. clava* is underestimated as these individuals were frozen and became dehydrated after thawing.

1.3.3 Laboratory methods

All macroinvertebrate samples were sieved through a 1 mm mesh. Some organisms, including Asteroidea and Cirripedia, were frozen because of their large size, while the rest were fixed in formaldehyde (4% in a buffered saline solution) and transferred to 70% ethanol for conservation within the following month. Before sorting, samples of epifauna from mussel socks were split into subsamples using an aggregate sample splitter (Humboldt Materials Testing Solutions Model H-3985). Benthic macroinvertebrates were then sorted using a dissection microscope and identified to the lowest taxonomic level possible. Ascidiaceans, bivalves and gastropods were generally identified to genus; echinoderms, polychaetes and crustaceans were generally identified to family (see Annex 1 for a list of taxa identified from each bay). The taxa Nemertea, Nudibranchia and Oligochaeta were rare and were excluded from analyses. Colonial organisms (hydrozoans and bryozoans) were also excluded from all analyses because they could not be enumerated and as such, their productivity could not be estimated using the method employed in this study (see below). Sediment macroinvertebrates weighing more than 2 g were excluded from analyses (excluded n=1 Nereididae weighing 2.46 g). Mussels and *S. clava* were excluded from all analyses. Note that the organisms excluded from the analyses were largely associated with mussel sock samples.

Abundance and biomass

Biomass was measured as blotted wet weight (with shells). Weight-to-weight and weight-to-energy ratio conversion factors compiled by Brey (2001) and Ricciardi

and Bourget (1998) were used to convert wet-weights to KJ. When reliable conversion factors for identified taxa were not available, factors for the closest taxonomic levels were used. Abundances included heads of incomplete organisms. For biomass calculations, for each taxon in each sample, the number of heads of incomplete organisms was multiplied by the mean individual body mass (of complete individuals), and added to the total biomass of complete organisms. For each sample, the abundance and biomass of each taxon was standardized to 1 m² and pooled to obtain total macroinvertebrate abundance and biomass. Mussel sock samples were standardized to m² of bottom area using the average mussel sock length and density as given in Drapeau *et al.* (2006).

Productivity

Secondary productivity of each taxon identified in each sample was estimated using an empirical model proposed by Brey (2001) for benthic macroinvertebrate populations (based on global data from freshwater and marine populations).

$$\text{LogP} = 7.947 + \log B - 2.294 \log W_{\text{mean}} - 2409.856 * 1/(T + 273) + 0.168 (1/D) + 0.194 D_{\text{subt}} + 0.180 D_{\text{inf}} + 0.277 D_{\text{moti}} + 0.174 DM - 0.188 D_{\text{echi}} + 582.851 \log W_{\text{mean}} * 1/(T + 273),$$

where \underline{B} is mean annual biomass (KJ m⁻²); $\underline{W}_{\text{mean}}$ is mean body mass (KJ ind⁻¹); \underline{T} is mean annual bottom temperature (°C); \underline{D} is depth (m); and the remaining variables

are dummy variables (no = 0, yes = 1) for: subtidal species (D_{subt}); infauna (D_{inf}); motile epifauna (D_{moti}); Annelida or Crustacea (DM); Echinodermata (D_{echi})

Dummy variables to describe ecological characteristics of families were determined using available literature (e.g. Ruppert & Barnes 1995, Rouse & Pleijel 2001). Taxa not determined to be exclusively infaunal or epifaunal were considered epifaunal if they were found on mussel socks and infaunal if they were found in sediment samples. Productivity estimates for each taxon in each sample were standardized to 1 m² of bottom area. Mussel sock samples were standardized to m² of bottom area using the average mussel sock length and density as given in Drapeau *et al.* (2006). Estimates of productivity of individual taxa were pooled to obtain total macroinvertebrate productivity for each sample.

1.3.4 Statistical methods

Abundance, biomass and productivity of macroinvertebrates

A split-plot ANOVA model with 3 factors was used to analyse macroinvertebrate abundance, biomass and productivity: Bay type (fixed with two levels, with and without *S. clava*), Bay (random with 8 levels, 3 with *S. clava* and 5 without, nested in Bay type) and Position (fixed with two levels, inside and outside mussel leases). Separate analyses were done for sediment samples and mussel sock samples, and contrasts were used to compare macroinvertebrates sampled inside mussel leases (mussel socks + sediment) to sediment macroinvertebrates sampled outside leases. All data were log

$x+1$ transformed to meet assumptions of homogeneity and normality. Analyses on abundance, biomass and productivity of macroinvertebrates were done using SAS (MIXED procedure, SAS 1999).

Diversity

Taxonomic richness of sediment and mussel sock samples was evaluated using the ANOVA model described above. Sediment data were $\log(x+1)$ transformed to meet the assumptions of this test, whereas mussel sock data was not transformed. Because mussel sock samples were split into various fractions prior to laboratory analysis, organisms were randomly resampled in order to compare the richness of a standard fraction of each mussel sock sample. As such, taxonomic richness was calculated from $\frac{1}{4}$ of each sample, with the exception of one mussel sock sample from New London, for which taxonomic richness was calculated from only $\frac{1}{8}$ of the sample (sample with extremely large abundance of organisms).

Total taxonomic richness of macroinvertebrates sampled inside leases (mussel socks + sediment) was compared to taxonomic richness outside leases for the same unit bottom area, using a non-parametric Wilcoxon paired-sample test with bays as replicates. For this analysis, the number of taxa inside leases was calculated by pooling sediment samples from inside leases (total bottom area sampled= 0.039 m^2 , except Murray River bottom area sampled= 0.031 m^2) and adding to this total any additional species found in mussel sock samples of equivalent length, based on the average density of mussel socks on PEI. However, the length of the mussel sock samples collected was

greater than the length required for this analysis. Therefore, in addition to standardising mussel sock samples to $\frac{1}{4}$ as described above, a reduced proportion of mussel sock organisms were randomly selected for this analysis: a fraction equivalent to a 0.039 m^2 area, based on average density of mussel socks on PEI (measured by Drapeau *et al.* (2006)). In bays where $n=3$, 1.3% of each mussel sock sample was selected. In bays where $n=5$, 0.78% of each mussel sock sample was selected. The number of taxa outside leases was calculated by pooling sediment samples taken outside leases.

Multivariate community structure

The multivariate structure of sediment macrobenthic assemblages was compared using Distance-Based Multivariate Analysis (DISTLM) (Anderson 2001). A zero-adjusted Bray-Curtis coefficient (Clarke *et al.* 2006) was employed because of the presence of blank samples. The Bray-Curtis coefficient was adjusted by adding a dummy taxon with equal abundance, biomass, and productivity in each sample (dummy taxon abundance = 1 ind. m^{-2} ; dummy taxon biomass and productivity = $1.2732 \times 10^{-5} \text{ g m}^{-2}$ and $5.67 \times 10^{-4} \text{ KJ m}^{-2} \text{ yr}^{-1}$ respectively, corresponding to the lowest observed values). To facilitate multivariate analyses, one missing control sediment sample replicate from Murray River was replaced by the average of remaining replicates at that treatment and location.

Non-metric multidimensional scaling (nMDS), analysis of similarities (ANOSIM) and similarity percentages (SIMPER) analyses were done in PRIMER using the Bray-Curtis similarity measure (Clarke & Warwick 2001). For all multivariate

analyses, data were square-root transformed to decrease the influence of dominant taxa (Clarke & Warwick 2001).

1.4 Results

1.4.1 Sediment macroinvertebrates

When sediment macroinvertebrates were classified into general taxonomic groups (see Table 3), Polychaeta had the highest abundance, biomass and productivity both inside and outside mussel leases. Inside mussel leases, Polychaeta accounted for up to 92.3%, 90.9% and 96% of mean total abundance, biomass and productivity per bay, respectively. Outside leases, Polychaeta accounted for up to 93.8%, 63.5% and 83.4% of mean total abundance, biomass and productivity per bay, respectively. A full list of taxa identified from sediment samples from each bay is included in Annex 1.

Mean total abundance ranged from 280-12452 ind. m⁻² inside mussel leases and from 3743-8123 ind. m⁻² outside of leases, and was significantly lower inside mussel leases (Fig. 3, Table 4). Although ANOVA results comparing biomass and productivity inside vs outside leases were marginally not statistically significant (Table 4), biomass and productivity were lower inside mussel leases in 7 of 8 bays (Fig. 3). The taxonomic richness and the structure of assemblages did not differ significantly by position (inside vs outside of leases) (Fig 4, Table 5; Table 6).

Abundance, biomass and productivity of sediment macroinvertebrates did not differ significantly between bays with and without *S. clava* or as a function of Position \times Bay type (Fig. 3, Table 4). As well, the diversity (number of taxa) and structure of assemblages of sediment macroinvertebrates did not differ significantly for these factors (Fig. 4, Fig. 5, Table 5, Table 6).

Table 3. Mean a) abundance, b) biomass and c) productivity of macroinvertebrates in 7 taxa, and means of totals from sediment samples outside mussel leases (C), sediment samples under mussel leases (M_{sed}), and mussel socks (M_{socks}). Bay abbreviations are as in Figure 1. Actinaria were absent from sediment samples (C and M_{socks}), Asteroiidae were absent from sediment samples outside leases.

a) Abundance (ind. m^{-2})

Bays	Actiniaria	Ascidiacea			Asteroiidae		Bivalvia			Crustacea			Gastropoda			Polychaeta			Mean total ind m^{-2}		
	M_{socks}	C	M_{sed}	M_{socks}	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}
Bru	19		968	4260		76	25	51	185	153	102	1068	76	25	62	3820	789	528	4074	1935	6199
St M	33	51		287		18	484	560	271	3361	407	3939	204	102	112	4023	1019	468	8123	2088	5128
Mur	3		25	2869		96	1846	153	59	446		1973	541	25		4011	942	84	6844	1146	5083
Mal	22		76	246	25	40	713	2725	21	255	1146	394	917	1401	133	4380	7079	216	6264	12452	1073
Mar	17			1943		40	891	433	88	280	102	290	1044	968	672	2750	891	399	4966	2394	3448
NL	23	76	76	386		15	2419	484	29	382	280	793	484	280	75	4456	3896	365	7818	5017	1687
Rus	5			1814		4	433	51	9	306	25	949	586	25	137	2445	1222	407	3769	1324	3325
Car	20			766	32	60	789	64	135		64	448	382	64	23	2572	127	417	3743	280	1870

b) Biomass (g m^{-2})

Bays	Actiniaria	Ascidiacea			Asteroiidae		Bivalvia			Crustacea			Gastropoda			Polychaeta			Mean total g m^{-2}		
	M_{socks}	C	M_{sed}	M_{socks}	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}
Bru	1.85		4.38	73.47		5.01	0.11	0.86	4.06	4.22	0.07	1.03	2.93	1.69	3.07	5.83	3.47	6.56	13.09	10.48	95.07
St M	11.41	0.98		6.20		3.86	2.26	3.23	1.56	6.32	3.34	5.73	0.55	2.02	0.18	7.28	3.45	6.34	17.39	12.05	35.28
Mur	0.08		0.01	55.67		10.50	8.96	2.38	3.22	0.27		0.93	3.41	0.05		6.94	8.13	1.49	19.59	10.57	71.89
Mal	0.25		1.96	2.42	0.28	4.86	1.05	6.61	0.12	0.16	1.01	0.23	5.42	2.28	0.48	11.53	8.86	3.24	18.16	20.99	11.61
Mar	0.28			25.14		2.32	4.11	1.07	0.85	0.20	0.04	0.14	5.47	2.26	3.25	13.07	7.17	3.51	22.85	10.54	35.48
NL	1.15	0.60	0.27	0.93		10.01	11.63	4.64	0.34	0.42	0.22	0.37	3.94	3.82	0.11	16.64	10.94	11.19	33.24	19.89	24.10
Rus	0.14			19.08		36.46	4.20	0.29	0.11	0.15	0.01	23.27	3.28	0.04	3.55	5.04	3.37	11.18	12.68	3.70	93.78
Car	0.27			7.02	0.42	5.41	3.82	0.02	4.66		0.21	1.46	9.07	0.12	3.61	18.32		3.41	31.20	0.77	25.84

Table 3. (continued)

c) Productivity ($\text{KJ m}^{-2} \text{yr}^{-1}$)

Bays	Actiniaria	Ascidiacea			Asteroiidae		Bivalvia			Crustacea			Gastropoda			Polychaeta			Mean total $\text{KJ m}^{-2} \text{yr}^{-1}$		
	M_{socks}	C	M_{sed}	M_{socks}	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}	C	M_{sed}	M_{socks}
Bru	2.53		3.48	44.84		14.10	0.23	1.33	6.21	25.36	0.87	8.43	9.81	4.95	1.94	61.83	28.75	53.69	97.23	39.38	131.74
St M	12.27	1.03		2.87		8.01	4.97	6.23	2.16	78.70	18.17	48.22	2.92	8.05	1.41	68.67	26.36	46.66	156.30	58.81	121.60
Mur	0.17		0.03	34.35		28.81	19.14	3.18	4.81	3.38		10.93	15.54	0.35		64.64	40.67	8.94	102.70	44.22	88.01
Mal	0.56		1.95	1.80	1.01	11.60	2.98	15.89	0.25	1.62	12.06	2.53	15.29	13.42	2.11	100.20	76.78	21.95	120.09	121.10	40.80
Mar	0.58			19.12		6.17	9.02	2.52	1.70	2.56	0.41	1.58	25.96	13.55	16.85	77.18	37.40	28.86	114.73	53.88	74.85
NL	1.72	0.80	0.23	0.93		13.83	26.02	12.17	0.59	3.68	2.41	4.05	17.30	15.44	0.81	115.88	95.38	42.02	163.68	125.62	63.95
Rus	0.28			16.24		34.66	6.28	0.77	0.24	1.06	0.07	36.12	16.27	0.28	13.36	44.72	27.10	71.99	68.34	28.22	172.90
Car	0.57			5.37	1.36	12.56	7.56	0.07	5.36		1.19	4.86	28.72	0.70	1.35	113.74		36.27	150.03	3.33	66.34

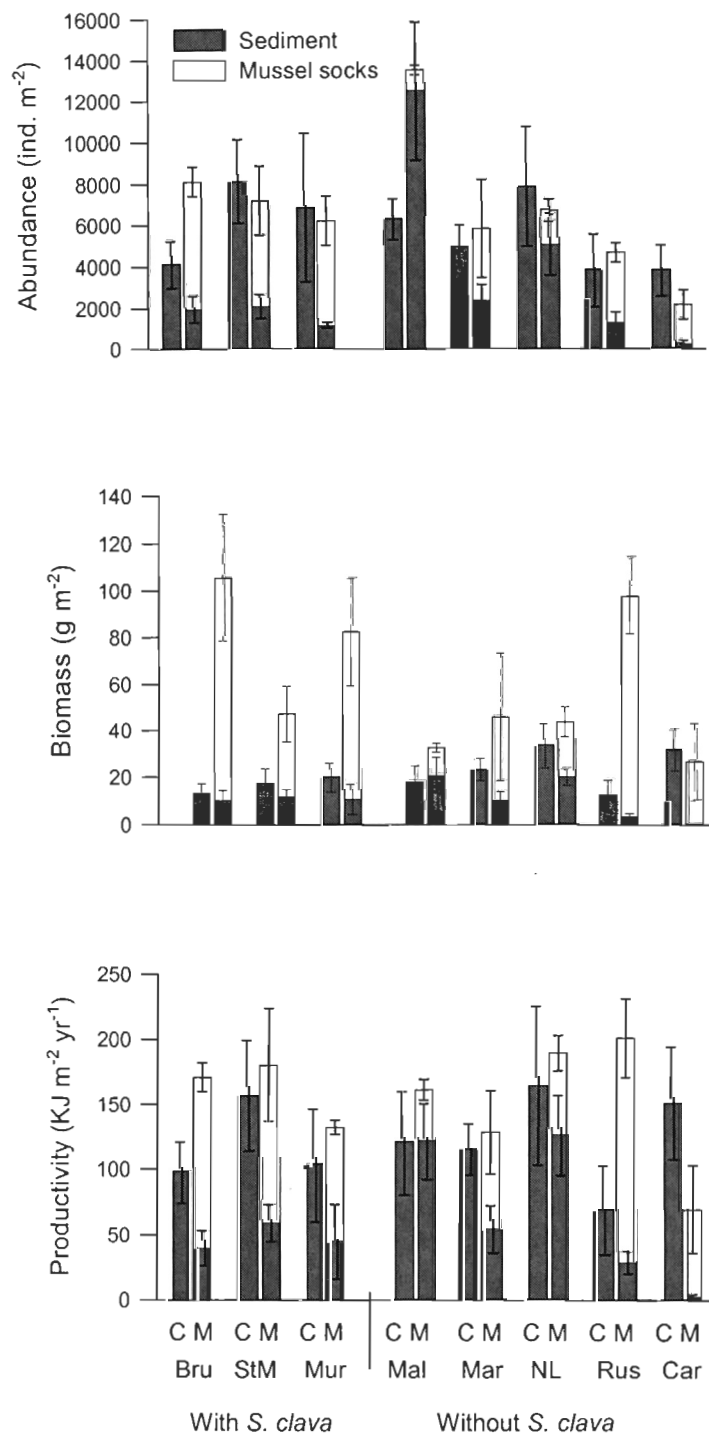


Figure 3. Mean (\pm SE) total abundance, biomass and productivity of sediment and mussel sock macroinvertebrates in control sites (C) and mussel leases (M) in 3 bays with *Styela clava* and 5 bays without *S. clava* (see Fig. 1 for bay abbreviations). $n=5$ for sediment samples except Mur where $n=4$; $n=3$ for mussel sock samples except NL and Mal where $n=5$.

Table 4. Results of ANOVAs to test fixed effects a) Bay type (with vs without *Styela clava*) and Position (inside vs outside mussel leases) on log (x+1) transformed sediment macroinvertebrate abundance, biomass and productivity, and b) Bay type on log-transformed mussel sock macroinvertebrate abundance, biomass and productivity. Random effects Bay (Bay type) and Bay (Bay type) × Position are also shown.

Source of variation	df, df _{error}	Abundance		Biomass		Productivity	
		F	P	F	P	F	P
a) Sediment							
Bay type	1, 6	0.01	0.9360	0.02	0.8934	0.00	0.9968
Bay (Bay type)	6, 6	1.32	0.3736	0.14	0.9856	0.14	0.9841
Position	1, 6	6.64	0.0420	4.85	0.0698	5.88	0.0515
Bay type × Position	1, 6	0.21	0.6658	0.36	0.5688	0.01	0.9425
Bay (Bay type) × Position	6, 63	2.06	0.0710	2.63	0.0244	3.68	0.0034
Error	63						
b) Mussel socks							
Bay type	1, 6	15.21	0.0080	2.73	0.1495	2.08	0.1990
Bay (Bay type)	6, 20	0.42	0.8599	1.90	0.1307	2.02	0.1100
Error	20						

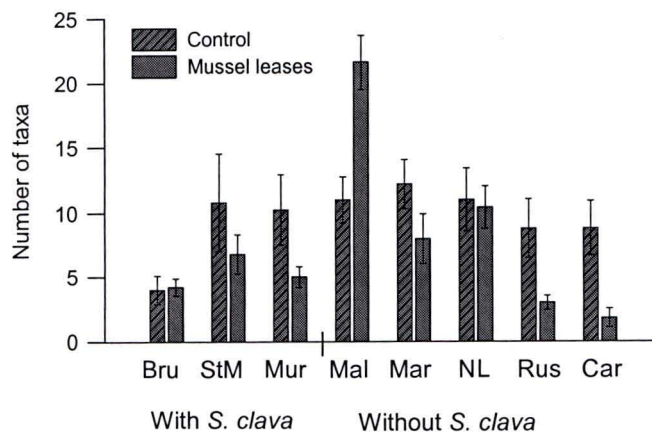


Figure 4. Taxonomic richness (\pm SE) of sediment macroinvertebrates sampled inside and outside mussel leases in bays with and without *Styela clava*.

Table 5. Results of ANOVA to test fixed effects Bay type (with vs without *Styela clava*) and position (inside vs outside mussel leases), on a) log- (x+1) transformed taxonomic richness of sediment macroinvertebrates and b) taxonomic richness of mussel sock macroinvertebrates. Random effects Bay (Bay type) and Bay (Bay type) \times Position are also shown.

Source of variation	df, df _{error}	Number of taxa	
		F	P
a) Sediment			
Bay type	1, 6	0.61	0.4623
Bay (Bay type)	6, 6	0.95	0.5236
Position	1, 6	1.92	0.2149
Bay type \times Position	1, 6	0.04	0.8419
Bay (Bay type) \times Position	6, 63	3.72	0.0032
Error	63		
b) Mussel socks			
Bay type	1, 6	3.09	0.1291
Bay (Bay type)	6, 20	1.73	0.1665
Error	20		

Table 6. DISTLM (Distance-based multivariate analysis) results testing fixed effects Bay type and Position on sediment macrobenthic assemblages using parameters a) abundance, b) biomass and c) productivity. Data for all 3 parameters were $\sqrt{}$ -transformed prior to analysis. Random effects Bay (Bay type) and Bay (Bay type) \times Position are also shown.

a)				
Source of variation	df, df _{error}	Abundance		
		MS	Pseudo- <i>F</i>	Permutation <i>P</i>
Bay type	1, 6	7897.82144	1.08196	0.30450
Bay (Bay type)	6, 64	7299.54653	2.39036	0.00010
Position	1, 6	4652.66779	0.88776	0.52320
Bay type \times Position	1, 6	2903.65398	0.55403	0.75770
Bay (Bay type) \times Position	6, 64	5240.92445	1.71623	0.00240
Error	15, 64	6032.97326		

b)				
Source of variation	df, df _{error}	Biomass		
		MS	Pseudo- <i>F</i>	Permutation <i>P</i>
Bay type	1, 6	7258.22714	1.06136	0.32300
Bay (Bay type)	6, 64	6838.59488	1.93065	0.00040
Position	1, 6	6532.76881	1.50263	0.17030
Bay type \times Position	1, 6	3130.04306	0.71995	0.66610
Bay (Bay type) \times Position	6, 64	4347.56690	1.22739	0.11830
Error	15, 64	5589.38594		

c)				
Source of variation	df, df _{error}	Productivity		
		MS	Pseudo- <i>F</i>	Permutation <i>P</i>
Bay type	1, 6	7520.04269	1.06731	0.32540
Bay (Bay type)	6, 64	7045.78492	1.96716	0.00040
Position	1, 6	5490.66495	1.21915	0.30220
Bay type \times Position	1, 6	3295.25327	0.73168	0.65440
Bay (Bay type) \times Position	6, 64	4503.66677	1.25741	0.09070
Error	15, 64	5690.67689		

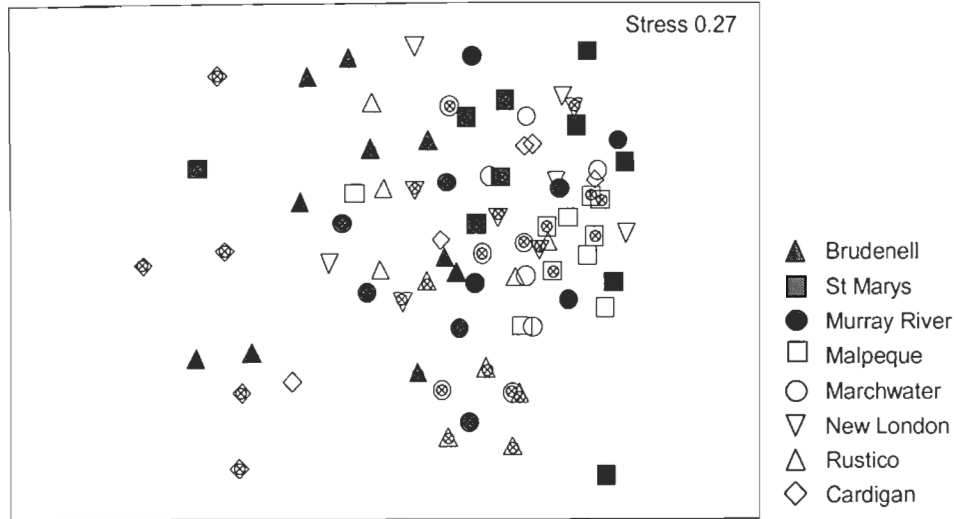


Figure 5. nMDS plot of abundance of sediment macroinvertebrate assemblages in 8 bays on PEI. A zero-adjusted Bray-Curtis dissimilarity coefficient was used to calculate dissimilarity among samples. Data were $\sqrt{}$ -transformed prior to analysis. Filled symbols indicate samples from bays infested by *Styela clava*, open symbols indicate samples from bays without *S. clava*. ⊗ Indicates samples from inside mussel leases. Multivariate patterns were similar for biomass and productivity of sediment macroinvertebrates and thus, for brevity, are not shown.

1.4.2 Mussel sock macroinvertebrates

Among the general mussel sock macroinvertebrate taxa shown in Table 3, Ascidiacea (excluding *S. clava*) were most abundant and had the greatest biomass, accounting for up to 68.7% and 77.4% of mean mussel sock abundance and biomass per bay respectively. Polychaeta had the highest productivity, contributing up to 65.7% of the mean total productivity per bay. A full list of taxa identified from mussel sock samples in each bay is included in Annex 1.

The mean abundance of mussel sock invertebrates ranged from 5083-6199 ind. m⁻² in bays with *S. clava* and abundance was significantly higher overall than in bays without *S. clava*, where abundance ranged from 1073-3448 ind. m⁻² (Fig. 3, Table 4). Mussel sock macroinvertebrate biomass and productivity did not vary significantly with Bay type (Fig. 3, Table 4). Taxonomic richness of mussel sock invertebrates did not differ among bays with and without *S. clava* (Table 5, Fig. 6).

Multivariate mussel sock macroinvertebrate assemblages in bays with and without *S. clava* varied significantly in terms of abundance ($R=0.508$, $P=0.02$ Fig. 7), but were marginally non-significant in terms of the other two metrics (Biomass $R=0.374$ $P=0.071$, Productivity $R=0.426$ $P=0.054$, Fig. 7). In terms of abundance, overall, mussel sock macroinvertebrate assemblages had 45.48% dissimilarity between bays with and without *S. clava*. The taxa *Molgula* sp., Corophiidae and Caprellidae were at least twice as abundant in samples with *S. clava* and together they accounted for 45% of this total dissimilarity (Table 7).

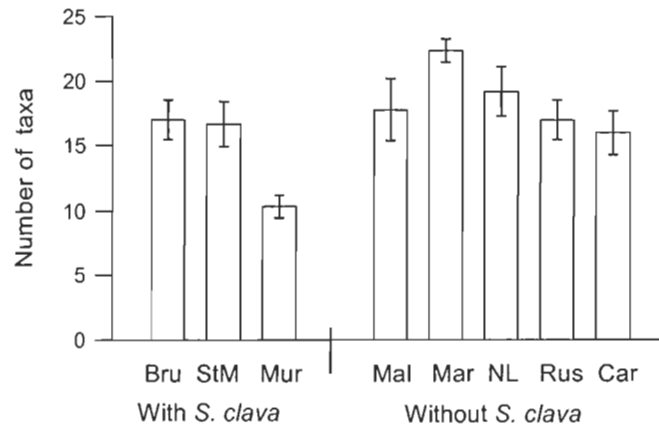


Figure 6. Taxonomic richness (\pm SE) of mussel sock macroinvertebrate samples from mussel leases in bays with and without *Styela clava*.

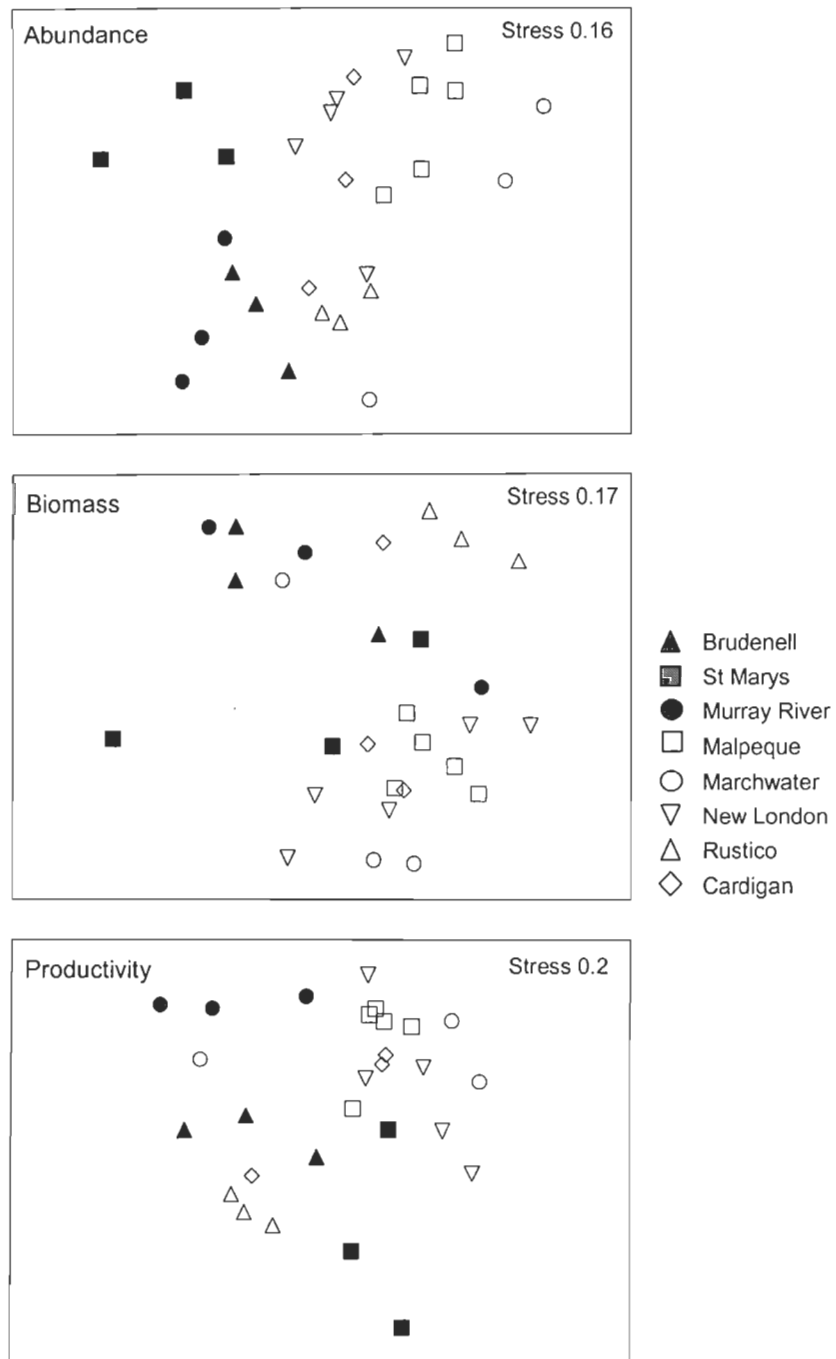


Figure 7. nMDS plots of abundance, biomass and productivity of mussel sock macroinvertebrate assemblages in 8 bays on PEI. All data were $\sqrt{\cdot}$ -transformed prior to analysis. Filled symbols indicate bays infested by *Styela clava*, open symbols indicate bays without *S. clava*.

Table 7. Results of SIMPER analysis of $\sqrt{}$ -transformed mussel sock macroinvertebrate abundance, indicating taxa contributing most to total dissimilarity between assemblages in bays with and without *Styela clava*.

Taxa	Average in bays with <i>Styela clava</i>	Average in bays without <i>Styela clava</i>	Contribution to dissimilarity (%)	Cumulative contribution (%)
<i>Molgula</i> sp.	2469.83	880.14	21.56	21.56
Corophiidae	1891.88	497.57	15.67	37.23
Caprellida	419.73	37.48	8.34	45.56

1.4.3 Sediment and mussel sock macroinvertebrates

As expected, the patterns observed with respect to macroinvertebrate abundance, biomass and productivity within as compared to outside of mussel leases changed when mussel sock macroinvertebrates were included in the calculation of these parameters. Significantly higher abundance, biomass and productivity were observed inside mussel leases when mussel sock macroinvertebrates were combined with sediment macroinvertebrates and compared to sediment macroinvertebrates outside leases (Fig. 3, Table 8). However, like sediment macroinvertebrate taxonomic richness, total macroinvertebrate taxonomic richness per unit of bottom area did not differ significantly between positions inside and outside mussel leases (Table 9, $P=0.234$).

As well, neither Bay type nor Bay type \times position were significant for macroinvertebrate abundance, biomass or productivity when mussel sock and sediment data were combined to calculate these parameters.

Table 8. Results of ANOVAs with contrasts to test fixed effects Bay type (with vs without *Styela clava*) and position (inside vs outside mussel leases) on abundance, biomass and productivity of all macroinvertebrates sampled: sediment + mussel sock macroinvertebrates in mussel leases, and sediment macroinvertebrates outside leases. Random effects Bay (Bay type) and Bay (Bay type) × Position are also shown. All data were log (x+1) transformed.

Source of variation	df, df _{error}	Abundance		Biomass		Productivity	
		F	P	F	P	F	P
Bay type	1, 6	0.94	0.3707	0.70	0.4345	0.22	0.6544
Bay (Bay type)	6,12	0.20	0.9717	0.01	0.9999	0.01	0.9999
Position	2, 12	237.95	<0.0001	96.63	<0.0001	113.23	<0.0001
Bay type × Position	2, 12	1.66	0.2214	0.23	0.6394	0.28	0.6033
Bay (Bay type) × Position	12, 83	2.79	0.0031	3.09	0.0012	3.58	0.0003
Error	83						

Table 9. Number of taxa observed per 0.039 m² of bottom area inside and outside mussel leases in 8 bays on PEI. (S) indicates bays with *Styela clava*.

Bay	Inside leases (sediment+socks)	Outside leases (sediment)
Brudenell (S)	13	10
St Marys (S)	23	29
Murray River (S)	16	27
Malpeque (Bideford River)	46	25
Marchwater	23	31
New London	25	29
Rustico	12	21
Cardigan	9	20

1.5 Discussion

This observational experiment replicated in 8 bays on PEI indicated overall significantly lower abundance of macroinvertebrates in sediments inside leases, along with a trend towards smaller biomass and productivity. Contrary to this effect on the bottom, when sediment and mussel sock macroinvertebrates were considered together, their combined abundance, biomass and productivity was greater inside mussel leases than in areas outside of mussel leases. This combined effect on mussel sock and sediment macroinvertebrates was not increased by the presence of *S. clava*, in contrast to *a priori* predictions. However, considering mussel sock macroinvertebrates only, a greater abundance of macroinvertebrates was observed when *S. clava* was present on mussel socks and macroinvertebrate assemblages were altered relative to macroinvertebrate communities on mussel socks without *S. clava*.

1.5.1 Effect of mussel aquaculture on sediment macroinvertebrates

In PEI and elsewhere, as noted above, a primary focus of research on the influence of bivalve aquaculture on the environment has been potential disturbances to underlying sediments and associated benthic infaunal communities. However, such effects have not been clearly shown on PEI. It has been proposed that effects of mussel aquaculture on PEI could be bay-wide in many cases, and therefore observable both outside and inside mussel leases (Shaw 1998, Cranford *et al.* 2003, Grant *et al.* 2005, Miron *et al.* 2005). This is in contrast to studies from other locations that suggest that benthic effects of mussel aquaculture may be limited to an area extending several

metres beyond mussel lines (Chamberlain *et al.* 2001, Callier *et al.* 2007). Although a short-term study by Grant *et al.* (2005) showed increased sedimentation in a mussel culture site in Tracadie bay on the North Shore of PEI (not included in this study), a study by Miron *et al.* (2005) in the same bay showed that macroinvertebrate diversity and community structure did not change in relation to the density or age of mussel culture. Further, Shaw (1998) observed high levels of organic matter both inside and outside of mussel leases during a survey that included 10 bays used for mussel aquaculture on PEI. In this study, no significant differences in macroinvertebrate abundance, biomass and diversity were observed inside leases, relative to locations outside leases. Bay-wide effects on PEI could be explained by the extent of mussel culture, which occupies a significant proportion of the total volume and surface area of bays, as well as the physical characteristics of bays and oceanographic features (Grant *et al.* 2005). As well, other factors in addition to mussel aquaculture are suspected to influence organic loading in bays on PEI (Cranford *et al.* 2003). For example, organic enrichment in general appears to be increasing through time as shown by Shaw (1998) by comparing the % organic matter of sediments in 4 bays in 1998 to levels from 1971. Eutrophication of bays on PEI seems to be well-explained by surrounding land use (Meeuwig 1999), suggesting that terrestrial farming and other practices may be better indicators of increased sediment organic content.

That the present study showed no consistent differences in diversity and structure of assemblages of sediment macroinvertebrates inside and outside of leases is therefore consistent with previous studies examining the benthic influence of mussel culture in PEI (Shaw 1998, Miron *et al.* 2005). However, this study also describes a

pattern of decreased total sediment macroinvertebrate abundance inside leases (with non-significant decreases in total biomass and productivity). This trend has been observed in other mussel culture sites (e.g. Stenton-Dozey *et al.* 1999), although recent studies done in the Magdalen Islands (approximately 100 km north east of PEI) report equal or higher abundance and biomass inside mussel leases (Callier *et al.* 2007, Richard *et al.* 2007).

Decreases in macroinvertebrate abundance in mussel leases have generally been associated with increased sedimentation of organic matter. However, a further explanation for lower sediment macroinvertebrate abundances in mussel leases could be a local increase in predators of these organisms. SCUBA transects under mussel leases in PEI, done as part of a parallel study (D'Amours *et al.* in revision), have shown increased abundances of fish and large mobile macroinvertebrates (crabs, seastars, etc.) in mussel leases, relative to areas outside leases. As well, Callier *et al.* (2007) observed lobsters feeding on benthic infauna in mussel sites in the Magdalen Islands. Previous work suggests that such local increases in reef-associated predators may decrease infaunal macroinvertebrate abundance (Posey & Ambrose 1994, Langlois & Anderson 2005).

1.5.2 Effect of mussel aquaculture on sediment and mussel sock macroinvertebrates

Extending this survey beyond sediment macroinvertebrates to include all “benthic” macroinvertebrates within a mussel lease (i.e. both mussel sock-associated macroinvertebrates and those in the sediment below) revealed a different pattern than

previously observed for macroinvertebrates in mussel leases. As predicted, both structural (abundance, biomass) and functional (productivity) aspects of the community were enhanced by the presence of mussel aquaculture.

Natural bivalve populations have previously been associated with large and diverse benthic macroinvertebrate communities (Nixon 1971, Tsuchiya & Nishihira 1985). Bivalves in culture, however, are often suspended in the water column, creating a new habitat for benthic macroinvertebrates that may function as artificial reefs (Tenore & Gonzalez 1975, Shumway *et al.* 2003). Artificial reefs often increase the biomass of macroinvertebrates by increasing the surface area available for settlement (Relini & Relini 1997, Svane & Petersen 2001). However, studies including invertebrates both on reefs as well as in the surrounding sediment are rare. Steimle *et al.* (2002) showed that when both these components were included overall productivity could be increased by up to 2 orders of magnitude by an artificial reef, although their results were variable such that the productivity increase may not have consistently compensated for the infaunal habitat covered by the reef.

In comparison, mussel socks do not directly cover the sediment, but may alter underlying benthic habitats. However, this study shows that macroinvertebrate communities associated with mussel socks on PEI are large enough to compensate for observed decreases in sediment macroinvertebrate abundance and increase overall abundance, biomass and productivity. Other studies have also shown significant macroinvertebrate communities living in association with cultured bivalves. Notably, Tenore and Gonzalez (1975) also described a scenario where mussel sock epifaunal

growth on Spanish mussel rafts compensated for sediment infauna losses.

Macroinvertebrate biomass on Spanish mussel rafts was greater than values observed in the present study, ranging from 4.14-429.45 g ash-free dry weight per m of rope, though these values included small mussels (which were not included in analyses in the present study).

The macroinvertebrate communities living on the pelagic hard-bottom habitat (*sensu* McKindsey *et al.* 2006) provided by mussel socks were generally different from sediment communities. The mussel sock community was mainly composed of hard-bottom epifaunal organisms, some of which were absent or nearly absent from sediments (e.g. Asteroidea, Ascidiacea, Actinaria, Table 3). However, some infaunal polychaetes were observed in mussel sock samples (e.g. Capitellidae, Spionidae, Maldanidae), since sediments can accumulate between suspended bivalves in culture, creating a novel infaunal soft-bottom-like community (Mazouni *et al.* 2001, Richard *et al.* 2006).

The estimates of biomass and productivity associated with mussel sock macroinvertebrates shown here are conservative. The biomass of *S. clava* and newly recruited and juvenile mussels on mussel socks was great but was not included in calculations, nor were colonial organisms such as hydroids, although they may contribute greatly to energy transfer (Gili & Coma 1998).

Increased macroinvertebrate productivity associated with habitats created by mussel aquaculture, as shown in this study, may be accompanied by changes to other

biological components of coastal ecosystems. For example, Steimle *et al.* (2002) suggested that an increase in benthic productivity due to the presence of artificial reefs might result in lower availability of organic matter for other communities. On the other hand, mussel sock invertebrates may provide food for higher trophic levels such as fish and large mobile macroinvertebrates (McKindsey *et al.* 2006). For example, macroinvertebrates associated with mussel culture in Spain contributed to diets of fish and crabs (Lopez-Jamar *et al.* 1984, Freire *et al.* 1990). As previously mentioned, the effect of mussel aquaculture on mobile macroinvertebrates and fish in PEI and the Magdalen Islands has been investigated by parallel studies (Clynick *et al.* in revision, D'Amours *et al.* in revision) which showed that the abundance of macroinvertebrates was high in mussel leases. Further, Anderson *et al.* (2006) suggest that mussel aquaculture may increase total productivity in areas where habitat is limiting, while this activity would more likely cause trophic changes in areas where primary productivity limits overall productivity (Anderson *et al.* 2006).

1.5.3 Effect of *Styela clava* on sediment and mussel sock macroinvertebrates

The ecological role of bivalve aquaculture pests such as *S. clava* is poorly known (McKindsey *et al.* 2007). While efforts are being made to remove this species from mussel aquaculture sites in PEI due to the economic impacts it causes, this study confirms that macroinvertebrates can use *S. clava* as habitat (Whitlatch *et al.* 1995, Thompson & MacNair 2004, Dijkstra *et al.* 2007). When *S. clava* was present on mussel socks, a greater abundance of macroinvertebrates was observed, with potentially further cascading effects on the rest of the environment.

Solitary ascidians in natural habitats may support diverse communities of macroinvertebrates (e.g. Castilla *et al.* 2004). While the diversity of macroinvertebrates did not increase when *S. clava* was present on mussel socks, macroinvertebrate assemblages were significantly different, largely a function of a greater abundance of another ascidian *Molgula* sp., as well as the crustaceans Corophiidae and Caprellidae.

No change in infaunal benthic communities was observed in bays with *S. clava*. However, it should be noted that as this study was done relatively soon following invasion by *S. clava* (the first observation of *S. clava* in PEI was 7 years prior to the present study). In contrast to the effects observed on macroinvertebrates that live in association with *S. clava*, it may take longer before more indirect effects on sediment macroinvertebrates can be observed (Strayer *et al.* 2006).

1.6 Conclusion

This study shows that anthropogenic habitat modifications through mussel aquaculture and invasive species have altered benthic macroinvertebrate communities on PEI. In particular, it is shown quantitatively that bivalve aquaculture can change energy flows in aquatic ecosystems. By increasing the overall abundance and biomass of macroinvertebrates, mussel aquaculture has increased energy flow (productivity) through this community. Studies of changes in productivity associated with aquaculture are rare (McKindsey *et al.* 2006), although key to analysing ecosystem dynamics (Odum 1968, Benke 1993). Therefore, the results obtained in this study contribute to a

greater understanding of the effects of bivalve aquaculture on ecosystem function. Such information is important for the management of bivalve aquaculture in Canada under the *Fisheries Act*. The *Act* prohibits harmful alteration, disruption or destruction of fish habitat and a guiding principle of the Department of Fisheries and Oceans *Policy for the Management of Fish Habitat* is “no net loss” of natural productive capacity of fish habitat (Department of Fisheries and Oceans Canada 1986). The results of this study, showing a net increase of macroinvertebrate productivity in mussel aquaculture sites, are of great significance in this management context.

Increased productivity was observed when both sediment and mussel sock macroinvertebrates were included in the estimation of productivity. Including mussel sock macroinvertebrates clearly changed patterns of abundance, biomass and productivity, in comparison to negative impacts commonly observed on infaunal benthic macroinvertebrates. When compared with unstructured seabeds, bottom oyster culture sites have also been found to increase abundances and biomass of macroinvertebrates (Ferraro & Cole 2007). As well, increased abundances of fish and mobile macroinvertebrates have been observed in both oyster and clam sites (Dealteris *et al.* 2004, Powers *et al.* 2007). These studies, in addition to the present study, show the importance of bivalves as habitat for macroinvertebrates and indicate that this influence of bivalve culture should be included in any attempts to understand and manage aquaculture from a holistic or ecosystem approach.

However, as noted by O'Beirn *et al.* (2004), organisms attached to bivalves will eventually be harvested, which may minimize their contribution to the ecosystem. In

addition, as this study included only commercial size mussels (1+ age class), the influence of mussels in their first year of culture (0+ age class) should also be examined. Macroinvertebrates living in association with 0+ mussels will likely be smaller which may affect changes in their productivity, and the influence of 0+ mussels on sediment macroinvertebrates may be different from that of 1+ mussels (Callier *et al.* 2007). As such, further work may be done to look at patterns in macroinvertebrate productivity over time at the scale of a bay, given that large variations in macroinvertebrate biomass may occur with husbandry practices and harvesting, in addition to seasonal variations. The present work is an important first step towards developing a more complete understanding of the role of bivalve culture in coastal ecosystems.

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CONCLUSION GÉNÉRALE

L'objectif de ce projet de maîtrise était de déterminer l'influence de la mytiliculture et de l'espèce envahissante *Styela clava* sur les communautés de macroinvertébrés benthiques. À cette fin, les macroinvertébrés associés au sédiment ainsi que ceux associés aux moules cultivées en suspension ont été échantillonnés à l'intérieur et à l'extérieur de sites mytilicoles dans 8 baies à l'Île-du-Prince-Édouard (ÎPÉ) : 3 avec *S. clava* et 5 sans *S. clava*. Les résultats de cette étude suggèrent que la modification anthropique de l'habitat par la mytiliculture et par l'invasion de l'ascidie envahissante *S. clava* facilitent le développement des communautés de macroinvertébrés à l'ÎPÉ. Cette facilitation pourrait être expliquée par la structure complexe que les moules et les ascidies peuvent créer dans la colonne d'eau, en tant qu'espèces structurantes [« ingénieurs » (Jones *et al.* 1994) ou « fondatrices », (Dayton 1972)].

En ce qui concerne les macroinvertébrés dans les sédiments, ceux-ci étaient significativement moins abondants dans les sites mytilicoles, sans changements significatifs de leur biomasse et de leur productivité. L'abondance, la biomasse et la productivité totale de l'ensemble des macroinvertébrés benthiques dans les sites mytilicoles ont par la suite été calculées en combinant les données des deux types d'échantillons prélevés : les échantillons de macroinvertébrés prélevés du sédiment et les échantillons de macroinvertébrés prélevés des boudins de moules en suspension. Ces résultats ont montré un patron différent de celui décrit plus haut : l'abondance, la biomasse et la productivité secondaire des macroinvertébrés étaient significativement

plus élevées à l'intérieur des sites mytilicoles. Contrairement aux résultats prédits, la présence de *S. clava* n'a pas augmenté l'effet de la mytiliculture sur la productivité secondaire totale (fond et boudins combinés). Cependant, les communautés de macroinvertébrés associés aux boudins de moules étaient plus abondants dans les baies envahies par *S. clava* que dans les baies sans *S. clava*.

Il importe de souligner que si les effets de la culture de bivalves sur l'abondance et la biomasse des macroinvertébrés qui vivent dans le sédiment, tel qu'observé dans le cadre de la présente étude, sont bien connus (Kaiser *et al.* 1998, Cranford *et al.* 2003), la productivité secondaire a quant à elle été estimée pour la première fois. De plus, l'estimation de la productivité de l'ensemble des macroinvertébrés benthiques dans les sites mytilicoles (macroinvertébrés dans le sédiment et sur les moules en suspension), à l'aide d'un modèle empirique, a démontré quantitativement un effet de cette activité sur les flux d'énergie dans les écosystèmes. L'influence de l'ascidie envahissante *S. clava* sur les macroinvertébrés dans les sites mytilicoles est aussi estimée pour la première fois.

Les changements concomitants de la productivité des autres composantes biologiques de l'écosystème restent toutefois à être investigués. Steimle *et al.* (2002) ont suggéré qu'une augmentation de la productivité des macroinvertébrés associés à un récif artificiel puisse diminuer la matière organique disponible pour d'autres communautés. Par contre, les macroinvertébrés sont aussi des proies pour d'autres organismes comme les macroinvertébrés mobiles et les poissons. Des études conjointes à la présente étude (Clynick *et al.* en révision, D'Amours *et al.* en révision) se sont

intéressées aux effets de la mytiliculture sur la productivité de ces organismes. Plus généralement, Anderson *et al.* (2006) ont suggéré que la présence de structures mytilicoles puisse augmenter la productivité totale dans les écosystèmes où l'habitat est limitant, tandis que la présence de structures mytilicoles entraînera seulement des modifications dans les réseaux trophiques lorsque la production primaire est limitante.

En plus de la présente étude sur les bivalves élevés en suspension, l'importance de l'habitat créé par les bivalves en culture sur le fond, ou à proximité de celui-ci, a été démontré pour les macroinvertébrés mobiles en surface (crabes, crevettes, homards, etc.) et les poissons (Dealteris *et al.* 2004, Powers *et al.* 2007), ainsi que pour les macroinvertébrés en surface et à l'intérieur des sédiments (Ferraro & Cole 2007). Ces études indiquent qu'il est important de considérer les invertébrés qui vivent en association avec les bivalves en culture, en plus de ceux dans les sédiments, pour dresser un portrait réaliste quant aux effets de la conchyliculture.

Les résultats présentés dans le cadre de ce mémoire contribuent à combler un manque de connaissance par rapport à la compréhension et à la gestion de la culture de bivalves dans les milieux côtiers. Au Canada, les activités aquacoles, comme toutes autres activités anthropiques dans le milieu aquatique, sont sujettes aux évaluations décrétées par la *Politique de gestion de l'habitat du poisson* (Department of Fisheries and Oceans Canada 1986). Le principe d'« aucune perte nette » de la capacité de production des habitats, tel que décrit dans cette politique, est appliqué pour conserver les habitats existants. La mise en pratique de ce principe aux activités aquacoles dépend

donc de connaissances scientifiques des effets de cette industrie sur la productivité secondaire (Minns 1997). Les résultats de la présente étude sont importants dans ce contexte puisqu'ils ont montré une augmentation nette de la productivité des macroinvertébrés « benthiques » dans les sites mytilicoles. Cependant, d'autres études seront nécessaires pour compléter nos connaissances à ce sujet.

Les estimations de productivité secondaire obtenues dans le cadre de cette étude à l'aide d'un modèle empirique se sont avérées très utiles pour faire des comparaisons entre différents habitats. Cependant, il est possible que la productivité secondaire associée aux boudins de moules soit sous-estimée par rapport aux autres communautés échantillonnées (échantillons de sédiment), puisqu'il n'a pas été possible d'inclure les organismes coloniaux dans les analyses et ceux-ci étaient présents sur les boudins seulement. De plus, d'autres sources d'erreur ont pu affecter les estimations de productivité secondaire de façon générale (sédiment et boudins de moules). Par exemple, il est probable que la production secondaire est sous-estimée puisque plusieurs autres organismes ont été exclus des analyses. De plus, l'application du modèle empirique à des taxons plus élevés que l'espèce peut sous-estimer la productivité secondaire totale des communautés (Nilsen, 2006). L'utilisation de facteurs de conversion est une autre source d'erreur possible.

Afin d'obtenir des valeurs plus exactes que celles obtenues avec un modèle empirique, des mesures directes de la production secondaire pourraient aussi être effectuées (méthodes basées sur les cohortes ou sur les classes de taille), malgré que ces

méthodes soient plus coûteuses. Ces mesures pourraient aussi être utilisées afin de développer de meilleurs modèles empiriques et de les adapter à des régions spécifiques.

La présente étude a été effectuée à une période de l'année seulement : au mois d'août, quand la biomasse des macroinvertébrés est maximale sur les boudins de moules à l'ÎPÉ (LeBlanc *et al.* 2003b). De futurs travaux pourraient examiner la productivité des macroinvertébrés en fonction du temps, prenant en considération les cycles saisonniers ainsi que les cycles d'élevage et de récolte des bivalves dans chaque site. Il est important de souligner que les organismes fixés aux bivalves en culture seront récoltés avec les bivalves, ce qui pourrait minimiser leur contribution au fonctionnement de l'écosystème, notamment parce qu'il est possible qu'ils soient récoltés avant de se reproduire (O'Beirn *et al.* 2004). Aussi, les traitements employés pour contrôler les ascidies dans les sites mytilicoles (ex. traitements de chaux, vinaigre) provoquent la chute des ascidies et des autres macroinvertébrés sur le fond, ce qui pourrait engendrer d'autres changements liés à la productivité des macroinvertébrés. De plus, l'influence de la mytiliculture sur la productivité peut dépendre de la taille des moules échantillonnées. La présente étude a décrit les communautés de macroinvertébrés associés à la culture de moules de taille commerciale seulement (classe d'âge 1+) donc il pourrait être intéressant de répéter cette expérience en échantillonnant des moules en première année de culture (classe d'âge 0+). Les macroinvertébrés sur les moules 0+ seront probablement plus petites, ce qui pourra modifier leur productivité. De plus, l'influence de ces moules sur les macroinvertébrés dans le sédiment sera probablement différente de celle des moules 1+ (Callier *et al.*

2007). De futurs travaux pourraient déterminer les effets de ces facteurs sur la productivité des macroinvertébrés à l'échelle d'une baie.

L'effet des espèces envahissantes peut aussi varier dans le temps, suivant l'établissement et la propagation de ces espèces. Comme décrit plus haut, plusieurs espèces envahissantes se sont établies à l'ÎPE suite à l'arrivée de *S. clava*. L'ascidie *Ciona intestinalis* fut rare dans les échantillons prélevés pour la présente étude, mais des populations de *C. intestinalis* ont envahi plusieurs baies à l'ÎPE depuis l'échantillonnage. De plus, *C. intestinalis* a remplacé *S. clava* à plusieurs endroits (Communication personnelle, C. McKindsey, Ramsay *et al.* 2008). La tunique molle et gélatineuse de *C. intestinalis* offre un substrat très différent de celui épais et rugueux de *S. clava* (Ramsay *et al.* 2008) et il sera donc intéressant d'étudier l'influence de *C. intestinalis* sur les autres macroinvertébrés dans les sites mytilicoles.

L'importance de l'habitat créé par les bivalves en culture s'ajoute à d'autres effets de la conchyliculture qui sont généralement considérés positifs pour l'environnement. Par exemple, Shumway *et al.* (2003) soulignent que la biofiltration par les bivalves peut améliorer la qualité de l'eau, et plus particulièrement, que l'élevage et la récolte de bivalves peut réduire les niveaux d'azote et d'autres éléments nutritifs dans la colonne d'eau. De plus, la biofiltration par les bivalves peut améliorer la transmission de la lumière dans les milieux aquatiques, ce qui peut favoriser la survie de plantes aquatiques. Cependant, comme décrit plus haut, l'ensemble des effets positifs et négatifs possibles de la conchyliculture doit être considéré à l'échelle de l'écosystème afin de comprendre les effets réels de cette industrie sur l'environnement.

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ANNEXE 1

**LISTE DE TAXONS IDENTIFIÉS DANS CHAQUE BAIE ET LEURS
ABONDANCES**

Annexe 1. Liste des taxons identifiés et leurs abondances par m² dans les 3 positions échantillonnées dans 8 baies à l'Île-du-Prince-Édouard :
Échantillons de sédiment à l'intérieur de sites mytilicoles (=sediment inside mussel leases) et à l'extérieur de sites mytilicoles (=sediment outside mussel leases) et échantillons prélevés des boudins de moules (=mussel socks).

a) Brudenell

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V108	V110	VO45	V014	V109	C1 _(near)	C31 _(near)	C4	C _(near) 21	Cnear51	V014	VI	V110
Actiniaria											11.97		43.88
Amphipoda							127.32	509.30					3.99
Anomiidae: <i>Anomia</i>											101.72	333.08	11.97
Asciacea: <i>Ciona</i>											11.97		3.99
Asciacea: <i>Molgula</i>			1273.24	3565.07							4443.70	5337.23	2983.74
Asteriidae											79.78	8.98	139.61
Calyptraeidae: <i>Crepidula</i>												27.92	
Capitellidae			254.65					254.65		127.32	31.91	59.83	15.96
Caprellida					127.32						111.69	31.91	319.12
Cirratulidae													3.99
Cirripedia											3.99	36.90	
Columbellidae: <i>Mitrella lunata</i>											79.78	71.80	7.98
Corophiidae				127.32							1100.95	650.20	937.41
Crustacea		127.32			127.32								3.99
Dorvilleidae													3.99
Flabelligeridae							127.32						3.99
Gammaridae								127.32					
Glyceridae									127.32				
Hiatellidae: <i>Hiatella arctica</i>											52.85	31.91	19.94
Ischyroceridae													3.99
Nassariidae: <i>Nassarius trivittatus</i>				127.32			127.32		127.32				127.32

Annexe 1 : a) Brudenell (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V108	V110	VO45	V014	V109	C1 _(near)	C31 _(near)	C4	C _(near) 21	Cnear51	V014	VI	V110
Nephtyidae	127.32		127.32		254.65	4329.01	5602.25		6875.49				
Nereidae								127.32			7.98	7.98	
Pectinariidae					127.32					127.32			
Pectinidae: <i>Argopecten irradians</i>												3.99	
Phyllodocidae			381.97					127.32			55.85	59.83	67.81
Polynoidae	127.32				127.32						450.75	454.74	243.33
Spionidae	1782.54	127.32		127.32	381.97		127.32	381.97		763.94	3.99	7.98	
Tellinidae: <i>Tellina agilis</i>	127.32			127.32			127.32						
Terebellida											43.88	55.85	3.99
Total	2164.51	254.65	2291.83	4074.37	891.27	4456.34	6111.55	1655.21	6875.49	1273.24	6600.73	7192.09	4802.71

Annexe 1: b) St Marys

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V121	V123	VO139	VO323	VO232	C1	C2	C3	C4	C5	V121	V123	VO232
Actiniaria											27.92	31.91	39.89
Ampeliscidae		381.97							2673.80	1400.56			
Amphipoda	254.65										3.99		
Anomiidae: <i>Anomia</i>	127.32										19.94	31.91	28.92
Asciacea									254.65				
Asciacea: <i>Ciona</i>													3.99
Asciacea: <i>Molgula</i>											311.14	402.88	143.60
Asteriidae											23.93	30.91	
Bivalvia	127.32					254.65			127.32				
Bivalvia <i>Hiatella striata?</i>											3.99	47.87	
Calyptraeidae: <i>Crepidula</i>										127.32	11.97	11.97	
Capitellidae	127.32	127.32		381.97	127.32	127.32	127.32	254.65	509.30				
Caprellida					127.32						390.92	1575.64	1216.63
Cardiidae: <i>Cerastoderma pinnulatum</i>	127.32			381.97					381.97		3.99	19.94	
Cirratulidae									127.32	127.32			
Cirripedia												48.86	19.94
Columbellidae: <i>Mitrella lunata</i>											163.55	83.77	27.92
Corophiidae	127.32	254.65		254.65	127.32	763.94			1018.59	381.97	2556.92	4927.36	1072.03
Cylichnidae: <i>Acteocina canaliculata</i>									381.97				
Diastylidae: <i>Oxyurostylis</i>					127.32			127.32	127.32	381.97			
Flabelligeridae									254.65				
Gammaridae							509.30						
Gastropoda									254.65			19.94	
Gastropoda non-id 1									127.32				
Glyceridae									254.65				
Hiatellidae: <i>Hiatella arctica</i>											27.92	590.37	36.90

Annexe 1 : b) Saint Marys (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V121	V123	VO139	VO323	VO232	C1	C2	C3	C4	C5	V121	V123	VO232
Idoteidae					127.32		7766.76		254.65				
Ischyroceridae												3.99	
Isopoda									254.65				
Lottiidae: <i>Tectura testudinalis</i>													3.99
Lumbrineridae								127.32	254.65	127.32			
Mollusca													3.99
Nassariidae:													
<i>Nassarius trivittatus</i>		509.30							127.32			3.99	
Nephtyidae		127.32											
Nereidae	254.65		127.32			127.32					7.98	7.98	
Orbiniidae		254.65											
Paraonidae				127.32					3692.39	2164.51			
Pectinariidae						254.65							
Phoxocephalidae		254.65				254.65			254.65	636.62			
Phyllodocidae	127.32			127.32					254.65	127.32	19.94	47.87	3.99
Polychaeta non-id								127.32					
Polynoidae	763.94				254.65	1527.89	127.32		1145.92	636.62	339.06	422.83	251.30
Pyramidellidae:													
<i>Odostomia</i>												3.99	
Sabellidae									127.32				
Spionidae		1273.24		381.97	509.30	3947.04		2291.83	381.97	254.65			
Syllidae								127.32					
Tellinidae: <i>Tellina agilis</i>	1018.59	127.32		891.27					1655.21				
Terebellida									509.30		187.48	111.69	3.99
Total	3055.77	3310.42	127.32	2546.48	1400.56	7257.47	8530.70	3055.77	15406.20	6366.20	4100.65	8425.68	2857.09

Annexe 1 : c) Murray River

Taxa	Sediment inside mussel leases					Sediment outside mussel leases				Mussel socks		
	N218	N59	V0414	VO518	V317	C1	C129	C130	C4	V218	N59	V0414
Actiniaria										3.99		5.98
Ampeliscidae									509.30			
Anomiidae: <i>Anomia</i>										51.86	115.68	1.99
Asciacea		127.32										
Asciacea: <i>Molgula</i>										4387.86	2947.84	1270.48
Asteriidae										43.88	39.89	205.43
Bivalvia					127.32		127.32	127.32				
Bivalvia: <i>Mysella?</i>			127.32	127.32								
Calyptraeidae: <i>Crepidula</i>									127.32			
Capitellidae	254.65		254.65	127.32		1273.24	891.27		127.32			
Caprellida										43.88	27.92	59.83
Cardiidae: <i>Cerastoderma pinnulatum</i>							127.32			3.99		1.99
Cirratulidae		127.32		127.32								
Columbellidae: <i>Mitrella lunata</i>							127.32					
Corophiidae									1145.92	2532.99	1938.63	1310.37
Cylichnidae: <i>Acteocina canaliculata</i>							381.97		254.65			
Flabelligeridae									254.65			1.99
Gammaridae										3.99		
Gastropoda	127.32						127.32					
Gastropoda non-id 0							127.32					
Mactridae: <i>Mulinia lateralis</i>				127.32					127.32			
Maldanidae									636.62			
Nassariidae: <i>Nassarius trivittatus</i>									381.97			
Nephtyidae		127.32										
Nereidae	254.65			127.32	127.32		381.97	254.65		27.92	15.96	29.92
Opheliidae						127.32						
Orbiniidae	636.62	763.94	509.30		381.97		509.30	254.65				
Paraonidae						1909.86	127.32		3692.39			

Annexe I : c) Murray River (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases				Mussel socks		
	N218	N59	V0414	VO518	V317	C1	C129	C130	C4	V218	N59	VO414
Pectinariidae							127.32					
Phoxocephalidae									127.32			
Phyllodocidae				254.65					763.94		3.99	1.99
Polychaeta non-id						127.32						
Polynoidae									127.32	23.93	51.86	57.84
Pyramidellidae: <i>Turbonilla</i>							381.97		254.65			
Spionidae	127.32	254.65		254.65		254.65		254.65	2801.13	7.98	7.98	
Syllidae									763.94	3.99		
Tellinidae: <i>Tellina agilis</i>				127.32	127.32	636.62	763.94		5474.93			
Terebellida								381.97			3.99	11.97
Total	1400.56	1400.56	891.27	1273.24	763.94	3055.77	4456.34	2291.83	17570.71	7136.25	5153.74	2959.81

Annexe 1 : d) Malpeque (Bideford River)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Actiniaria											41.88	23.93	6.98	17.95	18.95
Ampeliscidae	509.30	891.27		1018.59	636.62		254.65	254.65							
Amphipoda											1.99				1.99
Anomiidae: <i>Anomia</i>											19.94	4.99	1.00	12.96	7.98
Aphroditidae		127.32													
Asciacea					381.97										
Asciacea: <i>Molgula</i>											604.33	261.28	38.89	148.59	177.51
Asteriidae					127.32						29.92	40.89	27.92	36.90	66.82
Bivalvia	2164.51		127.32		1655.21		254.65	127.32			13.96		1.00		
Calyptraeidae: <i>Crepidula</i>			127.32							127.32	19.94	1.99	1.00		13.96
Capitellidae	7512.11	4838.31	1400.56	1018.59	4710.99	1655.21	1655.21		3819.72	3310.42	33.91	2.99	1.00	1.00	21.94
Caprellida		127.32	127.32								65.82	12.96	25.93	37.90	31.91
Cardiidae:															
<i>Cerastoderma pinnulatum</i>	381.97			127.32	636.62			254.65			5.98		4.99	8.98	3.99
Cirratulidae	254.65				127.32										
Cirripedia											3.99		4.99		
Columbellidae:															
<i>Mitrella lunata</i>	127.32			127.32				127.32			89.75	53.85	13.96	134.63	27.92
Corophiidae		254.65	254.65								420.84	115.68	275.24	258.29	696.07
Crustacea		254.65													
Cylichnidae:															
<i>Acteocina canaliculata</i>	763.94	127.32	254.65	1145.92	1018.59	1782.54	127.32	381.97		636.62				1.00	
Diastylidae:															
Oxyurostylis		381.97										1.00			
Dorvilleidae	254.65											1.00			3.99
Flabelligeridae	381.97	254.65	127.32	127.32	1145.92						1.99	1.00	1.00	1.00	31.91
Gastropoda		381.97	254.65	254.65	381.97					127.32					
Gastropoda non-id 0	891.27														
Gastropoda non-id 1														1.00	7.98

Annexe 1 : d) Malpeque (Bideford River) (suite)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Glyceridae				127.32			254.65		127.32						
Haminoeidae:															
<i>Haminoea solitaria</i>	127.32			254.65	127.32	254.65				254.65					
Hesionidae					127.32										
Hiatellidae: <i>Hiatella arctica</i>												1.00			
Idoteidae														1.99	
Ischyroceridae															1.99
Isopoda				127.32					127.32						
Lumbrineridae		509.30	254.65		381.97		2037.18		254.65	1527.89		1.99			7.98
Mactridae: <i>Mulinia lateralis</i>								381.97							
Maldanidae	381.97	254.65	636.62	0.00	254.65		1909.86		381.97	254.65	1.99				7.98
Mollusca			254.65								7.98			1.00	3.99
Nassariidae:															
<i>Nassarius trivittatus</i>			127.32		127.32		254.65	127.32							
Nephtyidae	127.32	381.97	127.32	127.32	127.32	254.65	254.65	1018.59	127.32	127.32					
Nereidae	254.65		636.62		381.97						7.98	4.99	3.99		5.98
Orbiniidae	509.30	127.32		127.32	127.32		127.32								
Ostracoda		127.32				254.65	254.65	127.32							
Paraonidae	127.32	254.65			381.97		254.65			127.32					
Pectinariidae	127.32	127.32	127.32	254.65						127.32					
Phoxocephalidae	509.30	254.65			254.65							1.00	1.00		9.97
Phyllodocidae	127.32	127.32			381.97		127.32		127.32		1.99	1.99	1.00	2.99	13.96
Polychaeta non-id					127.324										1.99
Polynoidae	381.9719		254.6479	127.324	509.2958						239.34	118.67	121.66	124.66	219.39
Pyramidellidae:															
<i>Odostomia</i>											73.80	24.93	19.94	9.97	69.81
Pyramidellidae:															
<i>Turbonilla</i>					127.324		381.9719				1.99	19.94	12.96	1.99	35.90

Annexe 1 : d) Malpeque (Bideford River) (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Sabellidae	127.32														
Sigalionidae					127.32		127.32								
Spionidae	1273.24	127.32	127.32	127.32	1527.89	381.97	381.97		891.27		3.99	1.00			3.99
Syllidae	127.32														
Tellinidae:															
<i>Tellina agilis</i>	3310.42	381.97	127.32	509.30	4074.37			254.65	1782.54	381.97	3.99	2.99	1.99		7.98
Terebellida					127.32		127.32		127.32		7.98	8.98	10.97	16.95	33.91
Triphoridae:															
<i>Triphora nigrocincta</i>											13.96			1.00	
Yoldiidae			127.32					127.32							
Total	20753.80	10313.24	5474.93	5602.25	20117.18	4583.66	8785.35	3183.10	7766.76	7002.82	1719.24	709.04	577.40	820.73	1537.74

Annexe 1 : e) Marchwater

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V3	V2	V1
Actiniaria											27.92	7.98	13.96
Ampeliscidae						127.32		127.32					
Amphipoda	127.32												
Anomiidae: <i>Anomia</i>											163.55	7.98	9.97
Asciacea												3.99	
Asciacea: <i>Molgula</i>											5668.31	135.62	19.94
Asteriidae											52.85	31.91	33.91
Bivalvia								127.32		127.32	3.99		
Bivalvia: <i>Mysella?</i>										127.32			
Calyptraeidae: <i>Crepidula</i>				127.32				127.32			63.82	43.88	17.95
Capitellidae	127.32	254.65		1273.24	127.32	509.30	1655.21		127.32	254.65	7.98	107.70	13.96
Caprellida											79.78	15.96	15.96
Cardiidae: <i>Cerastoderma pinnulatum</i>				509.30		254.65		509.30	254.65		23.93	19.94	1.99
Cirripedia											3.99		
Columbellidae: <i>Mitrella lunata</i>				127.32							1232.59	63.82	131.64
Corophiidae		127.32	127.32			127.32					402.88	251.30	95.74
Cylichnidae: <i>Acteocina canaliculata</i>	1273.24	381.97		1145.92	891.27	381.97	1527.89			1273.24			
Diastylidae: <i>Oxyurostylis</i>							127.32						
Dorvilleidae						127.32							
Flabelligeridae							127.32					11.97	3.99
Gastropoda	127.32					381.97	127.32		127.32		3.99		
Gastropoda non-id 1					127.32	254.65							
Glyceridae				127.32				127.32	127.32			3.99	
Idoteidae								127.32					
Ischyroceridae													3.99
Lumbrineridae										127.32			
Maldanidae			127.32			891.27		127.32		1145.92		7.98	3.99
Mollusca											7.98		

Annexe 1 : e) Marchwater (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V3	V2	V1
Nassariidae: <i>Nassarius</i>													
<i>trivittatus</i>	127.32	127.32		127.32	127.32			381.97		254.65	59.83		
Nephtyidae	127.32						127.32		127.32				
Nereidae			127.32	127.32	127.32	509.30					27.92	35.90	17.95
Orbiniidae				127.32	891.27					127.32			
Ostracoda				127.32		127.32	127.32						
Paraonidae						1018.59		127.32	891.27				
Pectinariidae								127.32					1.99
Phoxocephalidae						509.30							
Phyllodocidae				127.32	127.32	509.30		254.65	254.65		3.99	23.93	3.99
Polynoidae			127.32								275.24	422.83	171.53
Pyramidellidae: <i>Odostomia</i>											59.83	19.94	17.95
Pyramidellidae: <i>Turbonilla</i>				127.32		254.65				127.32	11.97	3.99	11.97
Spionidae			127.32	127.32	127.32	1782.54	254.65	1145.92	509.30	254.65		11.97	1.99
Syllidae						127.32						3.99	
Tellinidae : <i>Tellina agilis</i>			509.30	509.30	636.62	1018.59		1273.24	636.62	127.32		19.94	13.96
Terebellida				127.32		127.32		127.32			11.97	3.99	15.96
Triphoridae: <i>Triphora</i>													
<i>nigrocincta</i>											19.94	127.65	117.67
Total	1909.86	891.27	1145.92	4838.31	3183.10	9040.00	4074.37	4583.66	3183.10	3947.04	8214.27	1388.16	741.95

Annexe 1 : f) New London

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Actiniaria											8.98	20.94	51.86	15.06	15.96
Ampeliscidae	127.32				254.65		381.97								
Amphipoda												3.99	15.96	11.97	3.99
Anomiidae: <i>Anomia</i>											7.98	8.98	15.96	20.94	39.89
Asciidiacea							381.97						1.00		
Asciidiacea: <i>Molgula</i>					381.97						95.74	167.54	263.27	1061.06	341.06
Asteriidae											26.93	14.96	8.98	19.94	5.98
Bivalvia				127.32		254.65					3.99	3.99		7.98	
Bivalvia <i>Hiatella striata?</i>		127.32													
Calyptraeidae: <i>Crepidula</i>							127.32				3.99			27.92	5.98
Capitellidae	1655.21			381.97				7257.47	509.30		3.99		15.96	19.94	
Caprellida					127.32		127.32				11.97	59.83	79.78	39.89	13.96
Cardiidae : <i>Cerastoderma pinnulatum</i>			127.32				254.65								
Cirratulidae				509.30	763.94						19.94			139.61	11.97
Columbellidae : <i>Mitrella lunata</i>							381.97				19.94	11.97	63.82	171.53	5.98
Corophiidae					381.97		127.32		127.32		311.14	514.58	981.28	1527.77	382.94
Crustacea															1.99
Cylichnidae : <i>Acteocina canaliculata</i>		127.32							127.32						
Diastylidae : <i>Oxyurostylis</i>		127.32	127.32						381.97						
Flabelligeridae							1018.59				3.99	3.99		11.97	
Gastropoda			127.32	127.32	127.32				127.32		7.98				3.99
Haminoeidae: <i>Haminoea solitaria</i>						127.32		381.97		509.30					
Hesionidae					127.32		127.32							3.99	
Hiatellidae: <i>Hiatella arctica</i>											3.99	3.99	15.96		1.99

Annexe 1 : f) New London (suite)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Hydrobiidae: <i>Hydrobia</i>															
<i>minuta</i>								127.32							
Idoteidae														3.99	
Lumbrineridae		127.32													
Mactridae: <i>Mulinia</i>															
<i>lateralis</i>								127.32							
Maldanidae							381.97		254.65				7.98	3.99	
Mollusca													7.98	15.96	3.99
Nassariidae: <i>Nassarius</i>															
<i>trivittatus</i>	127.32	254.65	509.30				127.32		127.32						
Nephtyidae										127.32					
Nereidae	127.32	636.62		127.32							3.99			51.86	1.99
Orbiniidae	127.32	381.97	891.27	763.94	2037.18		254.65	127.32	127.32	127.32				15.96	
Ostracoda						127.32	254.65	254.65		127.32					
Paraonidae									1145.92						
Pectinariidae		381.97	509.30		127.32			254.65							
Petricolidae: <i>Petricolaria</i>										127.32					
<i>pholadiformis</i>										127.32					
Phoxocephalidae		127.32			127.32										1.99
Phyllodocidae			127.32		381.97				127.32			11.97	15.96	23.93	3.99
Polychaeta non-id											3.99				
Polynoidae					127.32	127.32	763.94		127.32		187.48	191.47	215.40	382.94	161.55
Pyramidellidae:															
Odostomia											3.99			11.97	
Pyramidellidae:															
Turbonilla							254.65						7.98		
Sigalionidae					127.32		127.32						7.98		
Spionidae	254.65	1909.86		2164.51	4710.99		381.97	5856.90	2928.45		19.94	3.99	31.91	67.81	5.98
Syllidae														11.97	
Tellinidae: <i>Tellina agilis</i>	254.65	254.65	127.32	381.97	127.32	254.65	3183.10	1018.59	4074.37	381.97				7.98	

Annexe 1 : f) New London (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks				
	V1	V2	V3	V4	V5	C1	C2	C3	C4	C5	V1	V2	V3	V4	V5
Terebellida							127.32				11.97	7.98	79.78	47.87	9.97
Yoldiidae	254.65		509.30		127.32	509.30		1273.24		636.62					
Total	1273.24	6111.55	3055.77	4583.66	10058.59	1400.56	8785.35	17188.73	9803.94	1909.86	761.89	1030.15	1888.77	3726.69	1025.16

Annexe 1 : g) Rustico

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V1	V3	V4	V5	vV2	C1	C2	C3	C4	C5	V3	V4	V5
Actiniaria											7.98	3.99	3.99
Anomiidae: <i>Anomia</i>												3.99	11.97
Asciacea: <i>Molgula</i>											945.38	1874.81	2620.75
Asteriidae											5.98	4.99	1.99
Bivalvia			127.32							127.32			3.99
Bivalvia <i>Hiatella striata?</i>											3.99		
Calyptraeidae: <i>Crepidula</i>											35.90	107.70	43.88
Caprellidae	891.27	127.32	127.32	1400.56	381.97		509.30			1909.86			3.99
Caprellida						127.32					35.90	51.86	95.74
Cirratulidae												3.99	3.99
Cirripedia											177.51	114.68	209.42
Columbellidae: <i>Mitrella lunata</i>											91.75	19.94	15.96
Corophiidae				127.32							829.70	682.11	642.22
Cylichnidae: <i>Acteocina canaliculata</i>							1782.54		127.32	127.32			
Diastylidae: <i>Oxyurostylis</i>							254.65						
Gammaridae											7.98		
Gastropoda					127.32								
Haminoeidae: <i>Haminoea solitaria</i>							381.97			254.65			
Idoteidae										127.32			
Mactridae: <i>Mulinia lateralis</i>							891.27						
Maldanidae										509.30			3.99
Mollusca											7.98	19.94	
Nassariidae: <i>Nassarius trivittatus</i>											7.98		
Nephtyidae							509.30			127.32			
Nereidae			127.32			127.32					3.99	15.96	19.94
Orbiniidae	1782.54	127.32	381.97	636.62			254.65	381.97	127.32	891.27	3.99		
Ostracoda						127.32	509.30		127.32	254.65			
Pectinariidae							381.97			254.65			

Annexe 1 : g) Rustico (suite et fin)

Taxa	Sediment inside mussel leases					Sediment outside mussel leases					Mussel socks		
	V1	V3	V4	V5	vV2	C1	C2	C3	C4	C5	V3	V4	V5
Phyllodocidae						254.65	254.65			127.32	11.97		3.99
Polynoidae											382.94	247.32	478.68
Pyramidellidae: <i>Odostomia</i>											39.89	7.98	11.97
Sigalionidae										127.32			
Spionidae			127.32			127.32	509.30	254.65	254.65	3692.39	7.98		11.97
Tellinidae: <i>Tellina agilis</i>	127.32						254.65			381.97			3.99
Terebellida									254.65	381.97			15.96
Yoldiidae						127.32		127.32	254.65				
Total	2801.13	254.65	891.27	2164.51	509.30	891.27	6493.52	891.27	1145.92	9421.97	2608.78	3159.26	4208.35

Annexe 1 : h) Cardigan

Taxa	Sediment inside mussel leases				Sediment outside mussel leases					Mussel socks		
	V95	V98	V1	V3	C1	C2	C3	C4	C5	V3	V98	V1
Actiniaria										10.97	35.90	13.96
Amphipoda												1.99
Anomiidae: <i>Anomia</i>										14.96	214.41	33.91
Asciacea: <i>Molgula</i>										322.11	1120.90	855.63
Asteriidae				127.32						26.93	87.76	63.82
Bivalvia					127.32	127.32			127.32			
Bivalvia <i>Hiatella striata?</i>											15.96	
Bivalvia: <i>Mysella?</i>								636.62				
Calyptraeidae: <i>Crepidula</i>			127.32								24.93	3.99
Capitellidae					127.32	127.32		254.65			43.88	3.99
Caprellida		127.32								16.95		19.94
Cardiidae: <i>Cerastoderma pinnulatum</i>		127.32	127.32							9.97	11.97	3.99
Cirratulidae						254.65			127.32			
Cirripedia											237.34	
Columbellidae: <i>Mitrella lunata</i>										1.00	19.94	7.98
Corophiidae										242.33	574.41	249.31
Crustacea		127.32										
Cylichnidae: <i>Acteocina canaliculata</i>								127.32	509.30			
Flabelligeridae										1.00	3.99	
Gammaridae												1.99
Gastropoda non-id 2			127.32									
Glyceridae						127.32		127.32				
Hiatellidae: <i>Hiatella arctica</i>								127.32		14.96	71.80	9.97
Lumbrineridae								127.32				
Maldanidae								891.27	381.97			
Nassariidae: <i>Nassarius trivittatus</i>					381.97	127.32	127.32	127.32	381.97			1.99
Nephtyidae	127.32	381.97			127.32		127.32					
Nereidae					127.32					2.99		

Annexe 1 : h) Cardigan (suite et fin)

Taxa	Sediment inside mussel leases				Sediment outside mussel leases					Mussel socks		
	V95	V98	V1	V3	C1	C2	C3	C4	C5	V3	V98	V1
Opheliidae								127.32				
Ophiuridae												1.99
Orbiniidae					127.32							
Paraonidae									254.65			
Pectinidae: <i>Chlamys islandica</i>											3.99	
Phyllodocidae						127.32			254.65	3.99	31.91	
Polynoidae						127.32		254.65		143.60	654.19	291.19
Pyramidellidae: <i>Odostomia</i>												1.99
Pyramidellidae: <i>Turbonilla</i>								127.32			7.98	
Sabellidae												1.99
Spionidae					509.30	4710.99		1909.86	891.27	1.00	3.99	1.99
Syllidae						127.32		254.65	127.32			
Tellinidae: <i>Tellina agilis</i>					127.32			1782.54	891.27			
Terebellida								127.32		11.97	31.91	15.96
Total	127.32	763.94	381.97	127.32	1655.21	5856.90	254.65	7002.82	3947.04	824.72	3197.15	1587.61