UNIVERSITÉ DU QUÉBEC

Distribution de l'épifaune associée à l'aquaculture de moule et estimation du flux génique de *Mytilus edulis* à l'aide de marqueurs microsatellites.

MÉMOIRE

PRÉSENTÉ À

L'UNIVERSITÉ DU QUÉBEC À RIMOUSKI

comme exigence partielle

du programme de maîtrise en gestion de la faune et de ses habitats

PAR

Nathaël Bergeron

Juillet, 2005

UNIVERSITÉ DU QUÉBEC À RIMOUSKI Service de la bibliothèque

Avertissement

La diffusion de ce mémoire ou de cette thèse se fait dans le respect des droits de son auteur, qui a signé le formulaire « *Autorisation de reproduire et de diffuser un rapport, un mémoire ou une thèse* ». En signant ce formulaire, l'auteur concède à l'Université du Québec à Rimouski une licence non exclusive d'utilisation et de publication de la totalité ou d'une partie importante de son travail de recherche pour des fins pédagogiques et non commerciales. Plus précisément, l'auteur autorise l'Université du Québec à Rimouski à reproduire, diffuser, prêter, distribuer ou vendre des copies de son travail de recherche à des fins non commerciales sur quelque support que ce soit, y compris l'Internet. Cette licence et cette autorisation n'entraînent pas une renonciation de la part de l'auteur à ses droits moraux ni à ses droits de propriété intellectuelle. Sauf entente contraire, l'auteur conserve la liberté de diffuser et de commercialiser ou non ce travail dont il possède un exemplaire.

RÉSUMÉ

Cette étude porte principalement sur les espèces épifauniques associées à l'aquaculture de moule. La présence et la biomasse de ces espèces vont varier selon les régions géographiques et la connectivité entre ces sites dépend en partie du potentiel de dispersion des espèces ainsi que des caractéristiques hydrographiques du milieu. Le but de cette étude est de déterminer l'importance du développement de l'épifaune sur les structures d'élevages de moules dans le golfe du Saint-Laurent et d'évaluer le potentiel de dispersion entre les différents sites étudiés. Nous avons mis l'emphase sur la macrofaune sessile avant un stade larvaire pélagique. Les sites à l'étude sont Belles-Amours (Qc), Havre-aux-Maisons (Qc), Tracadie Bay (IPE), St.Mary's Bay (IPE), Miramichi (NB) et Lamèque (NB). Afin de déterminer la dynamique temporelle, trois sessions d'échantillonnage ont eu lieu au cours de l'été et ont permis l'identification des espèces ainsi que leur biomasse retrouvée sur les boudins de moules adultes. Le flux génique a été mesuré a l'aide de microsatellites sur Mytilus edulis. En tout, 14 espèces ont été retrouvées sur les boudins. Seul le naissain de moules (Mytilus edulis) se retrouve partout alors que Tubularia larynx, Balanus crenatus et Crepidula fornicata sont les autres espèces les plus largement distribuées. On retrouve une biomasse plus importante et une plus grande biodiversité en novembre. Le maximum de biodiversité se retrouve à St-Mary's Bay (indice de Shannon de 0,752) en novembre. Les sites qui ont la plus grande biodiversité sont ceux où l'aquaculture est pratiquée de façon intensive depuis une plus longue période. L'optimisation des microsatellites s'est révélée plutôt décevante. Seulement deux des sept locus ont révélé un polymorphisme utile pour l'étude du flux génique entre les populations du Canada Atlantique. La valeur globale du Fst de 0,0066 indique un flux génique important entre les sites. L'analyse des microsatellites sur Mytilus edulis montre un déficit en hétérozygote au locus mg μ -6 avec un F_{1S} de 0,3384 alors que la valeur du F_{1S} au locus mg μ -5 est de 0,1227. L'absence de structure génétique chez les moules du golfe du Saint-Laurent devra cependant être confirmé par un plus grand nombre de marqueurs hypervariables.

TABLE DES MATIÈRES

RÉSUMÉ	II
TABLE DES MATIÈRES	III
LISTE DES TABLEAUX	IV
LISTE DES FIGURES	V
LISTE DES ANNEXES	VI
INTRODUCTION GÉNÉRALE	1
MYTILICULTURE	1
La moule bleue	1
ÉPIFAUNE	2
DISTRIBUTION SPATIALE	4
BUT ET OBJECTIFS	6
CHAPITRE 1	7
DISTRIBUTION AND DEVELOPMENT OF EPIFAUNA ASSOCIATED WITH BLUE MU CULTURE AND GENE FLOW IN <i>MYTILUS EDULIS</i> FROM THE GULF OF ST-LAWRE	SSEL NCE.
ABSTRACT	8
INTRODUCTION	9
MATERIALS AND METHODS	11
Study area	12
Epifauna sampling	12
Epifauna data analysis	13
SEED MUSSELS SAMPLING	14
GENETIC DATA ANALYSES	15
RESULTS	16
	14
EPIFAUNA	10
DISCUSSION	
DISTRIBUTION OF SPECIES	21
Composition and succession	
The blue mussel	23
GENE FLOW RETWEEN STUDIED SITES	24
AKNOWLEDGMENTS	26
CONCLUSION GÉNÉRALE	38
BIBLIOGRAPHIE	40
ANNEXE 1	47

LISTE DES TABLEAUX

Table 1: Facteurs physiques et biologiques influençant les communautés benthiques.27
Table 2: Presence-absence of epifaunal species found on mussels socks at Havre-aux-
maisons, Lamèque, Belles-Amours, St. Mary's Bay, Miramichi and Tracadie. The
grey columns indicate the sites where the biomass of each species is available28
Table 3: Average biomass (g) of organisms found on a thirty centimeters section of
mussel sock sampled in July and November at each site
Table 4: Significance level of the factors site, month and position based on permutation
test for the two analyses: the first including the three factors and their interactions
and treating only the sites of Tracadie Bay, St.Mary's Bay and Belles-Amours Bay.
The second analysis excluding the factor of position but treating the upper section
of the sites Miramichi Bay, Tracadie Bay, St.Mary's Bay and Belles-Amours Bay.
Each test was done using 1 000 permutations (* indicates a significant difference,
** highly significant)
Table 5: Shannon's diversity index at the sites of Tracadie Bay, St.Mary's Bay, Belles-
Amours Bay and Miramichi Bay, in July and November. (1 = maximum of
diversity)
Table 6: Proportion of each species of mussel found in juveniles and adults. 32
Table 7: Pairwise F _{st} including both loci
Table 8: Sample size (n), number of alleles (Na), expected heterozygosity (H_E) and
observed heterozygosity (H_0) , F_{1S} , embodied values indicates samples which deviate
significantly from Hardy-Weinberg's expectation after sequential Bonferroni
corrections (p<0.005)

LISTE DES FIGURES

Figure 1: Sampling sites: Belles-amours (BA), Lamèque (LM), Miramichi (MM),
Havre-aux-Maisons (HM), Tracadie (TR) and St.Mary's Bay (SM)35
Figure 2: Temporal variation of the biomass (proportion of each species on the total
biomass) of the most widely distributed species; seed mussel (Mytilus spp.),
Tubularia larynx and Balanus crenatus as well as the dominant species of each site.
a) Bugula turrita at Tracadie Bay, b) Bugula turrita and Styela clava at St.Mary's
Bay, c) Alcyonidium gelatinosum at Belles-Amours Bay, d) the three most common
species at Miramichi
Figure 3: Multidimensional analysis of the epifaunic communities found at the sites of
Belles-Amours, Miramichi, St. Mary's Bay and Tracadie. The circled areas
represent samples from the same date, July and November

LISTE DES ANNEXES

Annexe 1 : Schéma du système de boudin suspendus utilisé au Canada Atlantique pour	
l'aquaculture	

INTRODUCTION GÉNÉRALE

Mytiliculture

L'aquaculture revêt une importance croissante au Canada comme partout au monde. En 15 ans, la part du marché mondial des produits de la mer fournie par l'aquaculture est passée de 15% à 31%. Au Canada, la production aquacole est de l'ordre de \$600 millions. Toutefois, la conchyliculture représente seulement 10% de la production nationale, le reste relevant de la pisciculture. La production de moules pour l'année 2003 était de \$30,7 millions représentant la moitié de la production totale nationale de mollusque. La mytiliculture au Canada est principalement pratiquée dans l'est, avec comme chef de file l'île du Prince-Édouard (77% de la production) (Ministère des Pêches et Océans Canada 2004).

Les structures traditionnelles d'élevage de moules dans l'Est du Canada sont appelées « boudins » (voir annexe 1). Ils sont suspendus dans la colonne d'eau sur une ligne ancrée à chaque bout et retenue à la surface par des bouées. Les boudins sont généralement mis à l'eau par les producteurs à la fin de l'automne. On utilise, pour la fabrication de ces boudins, des juvéniles d'environ 20 à 25 mm, appelés naissain, capté pendant l'été précédent sauf en Basse Côte-Nord, où le naissain est maintenu durant plus d'un an sur les collecteurs. Les moules sont récoltées entre un à trois ans après la mise à l'eau, selon les sites et la croissance des moules.

La moule bleue

On retrouve deux espèces de moules bleues dans l'Atlantique nord, Mytilus edulis et M. trossulus. Ces deux espèces faisant partie du complexe M. edulis se retrouvent souvent en sympatrie et peuvent s'hybrider (Gosling 1992a). M. edulis se retrouve aux latitudes tempérées de l'hémisphère Nord alors que *M. trossulus* a une répartition beaucoup plus nordique dans l'hémisphère nord. La mytiliculture privilégie *M. edulis*, *M. trossulus* étant reconnue pour sa coquille mince et fragile ainsi que pour une plus faible quantité de chair (Mallet et Carver 1999).

La période de ponte chez les moules de l'est du Canada est observée entre la mi-mai et la fin juin, suivi parfois d'une deuxième ponte en août. Les larves peuvent passer entre trois et quatre semaines dans le plancton avant la fixation (Mallet et Myrand 1995). Comme pour la plupart des bivalves, les moules ont tendance à se fixer à deux reprises. Les larves compétentes vont préférablement choisir un substrat filamenteux pour la première fixation (Harvey et Bourget 1997) et ensuite se relâcher afin d'atteindre un substrat dur (e.g. lit de moules) pour la deuxième fixation (Mallet et Myrand 1995).

Épifaune

La connaissance des communautés épifauniques associées aux structures d'élevage de la moule permet de jouer un rôle important dans le cadre des pratiques aquacoles, notamment lors de transfert. Le transfert de naissain entre les différents sites aquacoles est une pratique couramment utilisée et la présence d'épifaune associée aux juvéniles peut entraîner l'introduction accidentelle d'espèces indésirables et nuisibles aux élevages et à l'environnement. En plus de l'impact sur le milieu qu'ont les espèces exotiques, certaines espèces peuvent entrer directement en compétition avec les moules. Les moules sont maintenues à de très hautes densités dans les élevages ce qui entraîne une compétition intraet interspécifique pour l'espace et la nourriture (Fréchette *et al.* 1992; Lohse 2002). Cette compétition entraîne un ralentissement de la croissance ou le dégrappage massif de moules, dont l'ampleur varie selon la résistance individuelle associée au génotype (Brichette *et al.* 2001).

Le substrat nu qu'offrent les structures d'élevage de moule favorise la fixation de plusieurs invertébrés sessiles ayant un stade de vie larvaire pélagique. Ces structures en immersion constante offrent quelques avantages supplémentaires par rapport à la zone intertidale, favorisant du coup la croissance de ces individus, souvent au détriment des moules. Ainsi, les individus fixés sur les boudins de moules vont subir un stress physiologique moins important, ont une plus grande accessibilité à la nourriture et sont à l'abri de plusieurs prédateurs benthiques (Poirier et Myrand 1982; Dardignac-Corbeil 1986).

Plusieurs études se sont penchées sur la succession des communautés épifauniques. Elles ont démontré que les premières espèces colonisatrices seraient généralement des espèces à croissance rapide comme les hydraires, les balanes et quelques ascidies. Ces espèces préparent le substrat pour la fixation des bivalves et autres espèces à croissance plus lente (Seed *et al.* 1981; Sutherland 1981; Ardisson *et al.* 1990; Ardisson et Bourget 1992; Claereboudt *et al.* 1994; Butler et Connolly 1996; Grecian *et al.* 2000; Khalaman 2001; Ross *et al.* 2002).

La biomasse, la richesse spécifique et la productivité d'un milieu peuvent varier en fonction de paramètres physiques et biologiques. Ces facteurs affectent de plusieurs façons la composition des communautés benthiques (Tableau 1). Ces études mentionnent plusieurs facteurs qui ont un impact sur le stock de larves et qui agissent sur la structure des communautés. Certains facteurs limitent la fixation (prédation, hydrographie, qualité et comportement des larves), alors que d'autres exercent une pression de sélection sur les individus adultes (compétition intra- et interspécifique, parasites, maladies, interactions

biotiques et abiotiques). Pour ce qui est des assemblages épifauniques retrouvés sur des substrats solides comme les boudins de moules, les processus pré- et post-fixation sont tous les deux d'une importance capitale (Todd 1998). Ils agissent à plus ou moins grande échelle et toujours en interaction (Edgar et Barrett 2002). En somme, une combinaison de ces facteurs permet d'obtenir des assemblages différents selon les milieux.

Distribution spatiale

L'hydrographie du milieu et la durée de vie larvaire sont deux principaux facteurs affectant la distribution et la dispersion des invertébrés marins. Par exemple, les entrées massives d'eau douce, les résurgences marines, les gyres et les courants présents dans l'estuaire du Saint-Laurent peuvent modeler les assemblages et les communautés benthiques retrouvés sur les bouées de navigation (Ardisson et Bourget 1992). Ces auteurs ont démontré une corrélation entre ces structures hydrographiques particulières et les discontinuités dans les assemblages. Par conséquent, la dispersion larvaire est aussi fortement corrélée à l'hydrographie (Goldson *et al.* 2001) et il importe de tenir compte de la bathymétrie et des structures hydrodynamiques et océanographiques pour expliquer la structure génétique des populations (Ruzzante *et al.* 1999).

Plusieurs organismes marins sessiles possèdent un stade de vie planctonique, ce qui permet, en plus de la dispersion allélique, la colonisation de nouveaux sites (Scheltema et William 1983). La durée de vie larvaire des invertébrés sessiles joue un rôle prédominant dans l'amplitude de dispersion et façonne la structure génétique des populations (Crisp 1978; Hedgecock 1986; Ruzzante *et al.* 1999; Todd *et al.* 1998). Les larves dites planctotrophes ont un séjour pélagique variant entre une journée à plusieurs semaines et peuvent potentiellement parcourir des distances plus grandes que les larves lécithotrophes, qui ne passe que quelques heures sous forme larvaire. À l'autre extrême, les larves téléplaniques, peuvent effectuer des déplacements à l'échelle des océans (voir Jablonski et Lutz 1983). Cependant, la mesure directe du flux génique chez les organismes marins, dont les larves peuvent passer quelques semaines dans le plancton avant de devenir compétentes, est généralement limité dans le temps et l'espace (Slatkin 1987),

Les larves planctotrophes favoriseraient un flux génique important entre les populations et donc une faible structure génétique en comparaison avec des espèces ayant un stade de vie larvaire lécithotrophe (Crisp 1978; Hedgecock 1986). Plusieurs études démontrent un lien direct entre le type de larve et le degré de différenciation entre les populations (Goldson et al. 2001; Todd 1998; Todd et al. 1998). Les larves avec un long séjour planctonique, donc un fort potentiel de dispersion, permettent généralement d'assurer une cohésion entre les populations et d'éviter l'isolement reproducteur (Scheltema et William 1983). Toutefois, la relation entre la durée de dispersion et le flux génique n'est pas toujours claire. Hedgecock (1986) a montré une différentiation génétique entre les populations de Homarus americanus et de Balanus glandula malgré leur stade larvaire pélagique. Une différenciation génétique est également observée chez un crustacé pélagique, Meganyctiphanes norvegica (Zane et al. 2000). Alors que la diversification est généralement reconnue comme étant le fruit de l'isolation et qu'elle est facilement freinée même par un faible niveau de flux génique (Slatkin 1987), un nombre grandissant de travaux démontrent l'impact de la sélection chez les espèces marines (Bierne et al. 2003; Luttikhuizen et al. 2003; Maltagliati et al. 2004).

BUT ET OBJECTIFS

Le but de cette étude est de déterminer l'importance du développement de l'épifaune sur les structures d'élevages de moules dans le golfe du Saint-Laurent et d'évaluer la connectivité entre les différents sites à l'étude. Nous avons mis l'emphase sur la macrofaune sessile ayant un stade larvaire pélagique.

Le premier objectif vise à déterminer la dynamique temporelle de développement de l'épifaune sur les boudins de moules. Dans un premier temps, nous avons identifié à l'espèce toute la macrofaune sessile retrouvée sur les boudins de moules en juillet, septembre et novembre aux sites de Belles-Amours, St.Mary's Bay, Miramichi, Lamèque, Havre-auxmaisons et Tracadie Bay (Figure 1). Dans un second temps, nous avons mesuré la biomasse et le nombre d'individus de chaque espèce de la macrofaune sessile sur certains sites et à certaines dates sélectionnées, soient les sites de Belles-Amours, St.Mary's Bay et Miramichi, en juillet et novembre 2002. Cette étude s'intéresse par ailleurs à l'effet de la profondeur sur la biomasse et la richesse spécifique présente sur les boudins de moules.

Finalement, le dernier objectif vise l'exploration de techniques moléculaires permettant d'évaluer le potentiel de dispersion naturelle des espèces à l'intérieur du golfe du Saint-Laurent. Étant donné que *Mytilus edulis* se retrouve sur tous les sites à l'étude, c'est l'espèce qui a été utilisée pour l'estimation du flux génique. Pour y arriver, il a fallu d'abord identifier chaque moule à son espèce (*M. edulis* et *M. trossulus*), puis tester et optimiser les microsatellites développés pour le complexe *Mytilus* (Presa *et al.* 2002) sur les populations de *M. edulis* retrouvées dans le golfe du Saint-Laurent.

CHAPITRE 1

DISTRIBUTION AND DEVELOPMENT OF EPIFAUNA ASSOCIATED WITH BLUE MUSSEL CULTURE AND GENE FLOW IN *MYTILUS EDULIS* FROM THE GULF OF ST-LAWRENCE.

Bergeron, N¹., R. Tremblay², F. Dufresne¹, G. Miron³ et T. Landry⁴

¹ Département de Biologie, de chimie et des sciences de la santé, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1.

² ISMER, Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec, Canada, G5L 3A1.

³ Département de Biologie, Université de Moncton, Moncton, Nouveau-Brunswick, Canada, E1A 3E9.

⁴ Département of Fisheries and Oceans Canada, Science Branch Gulf Fisheries Centre, Moncton, Nouveau-Brunswick, Canada, E1C 9B6.

ABSTRACT

This aims to study the epifaunic species associated with mussel farming industry. Biomass and presence of these species vary according to specific biogeographic areas. The connectivity between biogeographic regions depends in part on dispersal potential of species as well as on hydrographic features. The goal of this study was to quantify the development of epifauna on farming mussel structure in the Gulf of St. Lawrence and to estimate dispersal potential between the studied sites. The emphasis has been put on sessile macrofauna with a pelagic larval stage. The studied sites were Belle-Amours (Quebec), Havre-aux-Maisons (Quebec), Tracadie (Prince-Edward Island), St. Mary's Bay (Prince-Edward Island), Miramichi (New-Brunswick) and Lameque (New-Brunswick). In order to determine the temporal dynamics on epifauna settlement, we sampled in July and November and estimated species biomass for each sampling time. Gene flow was measured using microsatellites on Mytilus edulis. Fourteen species were found on mussel socks. Only the seed mussel (Mytilus edulis) was found everywhere, whereas Tubularia larynx, Balanus crenatus and Crepidula fornicata were the other most commonly found species. Generally, we found a greater and more diverse biomass in November. The highest biodiversity was found at St. Mary's Bay (Shannon's index of 0.752). The sites with the greatest biodiversity were the ones where aquaculture has been intensively practiced for the longest time. Only two of the seven microsatellites loci were variable in our populations. The global F_{sT} value was 0.0066 suggesting high gene flow among sites. Microsatellites analyses on M. edulis showed a deficit of heterozygotes for the locus mg μ -6 with F_{IS} value ranging from 0.256 to 0.440 whereas F_{IS} for the locus mg μ -5 is from 0.051 to 0.310. Hardy-Weinberg expectation was rejected for one site at the locus mg μ -5 and at all the sites at mg μ -6. The absence of genetic structure for the mussels of the Gulf of St. Lawrence needs to be confirmed with a higher number of hypervariable markers.

The structures used for suspended mussel aquaculture provide a new solid substrate for the settlement of sessile species with a pelagic larval stage. The study of these structures is important for aquaculture in order to understand the impact of epifauna on farmed mussel production as well as at the fundamental level in order to determine the connectivity between sites and biodiversity. It is also important to know the distribution of invasive species in order to avoid transferring them along with seed mussels among aquaculture sites. The knowledge of epifaunic communities in the St. Lawrence estuary was assessed by studies of Ardisson *et al.* (1990) and Ardisson and Bourget (1992, 1997) using navigation buoys as well as an inventory at Tracadie Bay by Leblanc *et al* (2003a) on mussel socks. However, there have been no studies performed in the Gulf area, where aquaculture is commonly practiced.

The most common group of organisms found on the mussel farming structures are ascidians, hydroids, bryozoans, polychaetes, barnacles and bivalves, including mussels (Leblanc 2003 and references therein). Macrofauna found on the structures can be in competition for space and food or predatory towards farming mussels. The presence of epifauna and a high density of mussels could increase intra and interspecific competition and have a negative effect on mussel growth (Fréchette *et al.* 1992) but see Leblanc *et al.* (2003b).

Several studies have examined the succession of epifaunic communities (Seed *et al.* 1981; Sutherland 1981; Ardisson *et al.* 1990; Ardisson and Bourget 1992; Claereboudt *et al.* 1994; Butler and Connolly 1996; Grecian *et al.* 2000; Khalaman 2001; Ross *et al.* 2002). They generally showed that the first colonizing species are the fast growing ones, such as hydroids, barnacles and some ascidians and these species in turn set the stage for the

settlement of bivalves and other species with slower growth. Succession can be defined as a directional sequence of change, resulting in a distinct pattern of change in the abundance and composition of species in the assemblages. Conversely, seasonal progression is characterized by the abundance of competent larvae and varies according to the reproductive cycles. If succession is the principal mechanism, each site should follow the same sequence of species settlement.

Epifaunic communities change along the St. Lawrence River. Ardisson and Bourget (1992) showed a correlation between particular hydrographic structures and discontinuities in species assemblages. In general, the communities vary in function of environmental (e.g. Ardisson and Bourget 1997; Callaway *et al.* 2002; Bourget *et al.* 2003; Khalaman 2001) genetic (e.g. Koehn *et al.* 1976; Koehn and Bayne 1989) and biological factors (e.g. Mann 1988; Crisp 1978; Sutherland 1990; Possingham and Roughgarden 1990; Edgar and Barrett 2002) and each of these factors influence biomass, specific richness and communities structure.

Although biomass can be an indicator of dispersion, connectivity between sites requires a more precise estimator. The planktonic larval stage allows colonization of new sites and movement can be estimate by genetic markers between sites (Scheltema and William 1983). The lifespan of invertebrate larvae plays a crucial role in the dispersion amplitude and it shapes the genetic structure of populations (Crisp 1978; Hedgecock 1981; Ruzzante *et al.* 1999; Palumbi 1995; Bohonak 1999). The direct measurement of gene flow is, however, generally impossible (Slatkin 1994) especially for marine organisms, since larvae can spend several weeks in plankton before becoming competent to settle. Genetic markers used to estimate the distance covered during larval dispersion reveals a positive correlation between dispersal capacity (measured by the larval lifespan) and the real distance traveled (Bohonak 1999). Nevertheless, the real distances traveled by larvae are sometimes lower than those suggested by the life cycle, meaning that the relationship between the duration of dispersion and gene flow is not always clear. Some studies show strong population structure for species with a pelagic larval stage (Hedgecock 1986; Hillbish 1996; Zane *et al.* 2000). In some cases, this structure can be attributed to local retention of planktonic larvae (Jones *et al.* 1999; Swearer *et al.* 1999; Barber *et al.* 2000) or to hydrographic particularities, preventing or modifying dispersion (Hohenlohe 2004; Sotka *et al.* 2004). These differences can also be explained by selection rather than a weak gene flow. Recent studies have shown the importance of selection to explain the maintenance of diversity between populations and adaptation to local conditions (Dufresne *et al.* 2002; Luttikhuizen *et al.* 2003; Maltagliati *et al.* 2004).

The main goal of this study was to determine the development and distribution of epifauna on structures used for mussel farming and the connectivity among site in the Gulf of St-Lawrence. The distribution and biomass of species provide valuable information regarding dispersal among sites. The other objective of this study was to measure gene flow among farming sites in the Gulf. We chose the seed mussel, *Mytilus edulis*, which is widely distributed in the Gulf of St. Lawrence and for which microsatellite markers have been isolated.

MATERIALS AND METHODS

Study area

A number of mussel-farming sites were selected for study in the Gulf of St-Lawrence (figure 1) spanning a 745 km area from Belles-Amours (northern shore of the St. Lawrence, Quebec) to Miramichi (New Brunswick). Other sampling sites, Lameque (NB), Havre-aux-Maisons (Qc), Tracadie (PEI) and St. Mary's Bay (PEI) are shown in figure 1.

Epifauna sampling

The mussel socks in the water column served as substrate for the settling of sessile species with a planktonic larval stage. The socks used as epifauna collectors were placed in the water during September 2001. Their length varied from 1,5 and 3 m depending on the depth of the bay. We performed three sampling sessions during 2002 (July, September and November). During each session, five socks were taken at each of the following sites: Tracadie, Miramichi, Lameque, Havre-aux-Maisons, Belles-Amours and St. Mary's Bay exceptionally in November while only three socks were taken at Tracadie and St. Mary's Bay.

On each sock, two 30 cm sub-samples were taken, a first section corresponding to the upper section of the sock (15-45 cm under the surface) and a second section to the lower part (135-165 under the surface). However, since the length of the Miramichi sock was much shorter than the other socks, only the upper sections were used at that site.

To answer the first objective, we first proceeded to do a qualitative analysis of all the sessile species found for each of the 30 cm sections sampled in July, September and November. Second, samples from July and November were used to follow the variation of abundance of epifauna for the sites of Miramichi, Belles-Amours, St. Mary's Bay and

Tracadie. We originally planned to estimate the biomass in September inclusively, but an important data lost required us to analyze data from July and November only. Biomass was used as an indicator of abundance since the number of individuals was difficult to assess in colonial species.

Epifauna data analysis

There was little species overlap among sites. As the normality of data required for the parametric measures was not respected, due to many zeros in the data set, nonparametric analyses were applied. Analysis of variance by permutations allowed testing the effect of date, site and the position on the species biomass most often present. Indeed, it was not possible to test the effect of site on species found in only one site. The designated species were the seed mussel (*Mytilus* sp.), *Tubularia larynx* and *Balanus crenatus*. Due to the fact that Miramichi had shorter socks, only the upper section was collected. In order to incorporate Miramichi in our analysis, two types of analyses were performed. The first one included the factor of position (depth) as well as date and site, but only dealt with the samples from Belles-Amours, Tracadie and St. Mary's Bay. The second analysis included the samples from the upper sections of each site (Belles-Amours, Tracadie, St. Mary's Bay and Miramichi) and dealt with the factors of date and site, omitting the effect of position. Each test of permutation was done with 1000 iterations.

A multidimensional scaling (MDS) analysis of the biomass of all species allowed for a more global image of the similarities between sites based on the influence of date and site on the biomass of the species found on mussel socks. Furthermore, MDS is a non-parametric analysis and tolerates zeros in the database. It is therefore well indicated for our data analyses. The program PRIMER was used to perform the MDS. The species biomass data was transposed by distance matrix using the Bray and Curtis similarity coefficient and by applying an application of the fourth root, generally recommended by the program PRIMER for the analysis of a community. The biomass data was standardized in order to allow a better relationship between the wet biomass of the shell vs. the lighter organisms. The analyses were done based on the biomass of the epifauna and also took into account the biomass of the adult mussels.

Seed mussels sampling

Seed mussels used for genetic analysis were taken from the socks from the sites of Lameque, Miramichi, Belles-Amours, Havre-aux-Maisons and St. Mary's Bay during the month of November. One hundred individuals per site were taken except for Belles-Amours, where 180 individuals were taken in order to increase the probability of having enough *Mytilus edulis*, since *Mytilus trossulus* was the most abundant species in this site. All the seed mussels found were from the summer recruitment. Nevertheless, the smallest were chosen to ensure that all of the individuals came from the same cohort and not from older ones with a slower growth rate, while still ensuring enough tissue for DNA extraction. All of the individuals were conserved in 95% ethanol until DNA extraction.

Genetic Analysis

Total genomic DNA was extracted from 580 seed mussels using a Qiagen DNA extraction kit (Qiagen, Mississauga, Canada) and Millipore system following the manufacturer's protocol.

Since *Mytilus edulis* is difficult to distinguish morphologically from *Mytilus trossulus* we used the nuclear Glu-5' polymerase chain reaction (PCR) marker based on Rawson et al. (1996) protocol. A 25 μ l PCR reaction was carried out using 2,0 μ l DNA, 2,0 μ l 10X PCR buffer, 2,0 mM MgCl₂, 200 μ M dNTP's, 1 U *Taq* polymerase and 0,4 μ M each primers. The cycling profile was an initial denaturation at 94°C for 3 min, 35 cycles of denaturation at 94°C for 20 sec, annealing at 53°C for 30 sec, extension at 72°C for 2 min and a final extension at 72°C for 20 min. Individuals identified as *M. trossulus* were removed from further analysis.

Microsatellite amplifications were conducted in 25 μ l volume using 10-100 ng DNA, 2.5 μ l 10X PCR buffer, 120 μ M of each dNTP, 0.6 μ M fluorescent labeled forward primer, 0.6 μ M unlabeled reverse primer, 0.5 U *Taq* Polymerase, 1,4 mM of MgCl₂ in Mgu-6 and 1,7 mM in Mgu-5. Cycling parameters were an initial denaturation of 1 min at 95°C, 35 cycles of denaturation at 95°C for 60 s, annealing temperature of 59°C for Mgu-5 and 60°C for Mgu-6 for 60 sec, extension at 72°C for 50 s and a final extension at 72°C for 20 min. Fragments were visualized on Hitachi FM-BIO® II scanner and scored using IMAGE ANALYSIS program.

Genetic data analyses

GENEPOP software (version 3.3; Raymond et Rousset 1995) was used to measure intraspecific genetic variability (Ho, He, A) and Hardy-Weinberg equilibrium. Genetix software, version 4.05, was used to calculate *F-statistics*. F_{IS} was calculated by estimating *f* (Weir & Cockerham, 1984). The degree of genetic structuring was investigated using Wright's *F-statistics* (Wright, 1978) with the estimator θ of Weir and Cockerham (1984). Mentel tests were performed to estimate the relationship between genetic and geographic distances using Genetix, version 4.05. Geographic distance was calculated in straight line between populations using Nobeltec software. The Software Micro-checker was used to identify possible scoring errors or the presence of null alleles in the data set.

RESULTS

Epifauna

Fourteen species were identified on the various socks (table 2). However, one other specie can be added if we consider the fact that *Mytilus trossulus* was found in Belles-Amours, Lameque and Miramichi. Nevertheless, since *M. edulis* and *M. trossulus* are difficult to tell apart based on morphological criteria, we referred to them as seed mussels. Of the fourteen species, only the juvenile mussels were found at all sites. *Tubularia larynx*, *Balanus crenatus* and *Crepidula fornicata* were the other common species. Little overlap was observed among the sites and some species dominated at a single site. For example,

Styela clava was dominant in St. Mary's Bay and Alcyonidium gelatinosum at Belles-Amours (figure 3).

Among sites the total biomass found on the 30 cm samples (table 3) showed high variation among sites. The greatest biomass was found at Miramichi (686.9g). Indeed, most of the biomass was largely due to seed mussels. At Miramichi, a fall-off happened in August and removed all the epifauna that had already settled, explaining the drop in Shannon's index (0.335 in July and 0.060 in November). The maximum number of species (10), but the lowest biomass was found at St. Mary's Bay. The total biomass in November is roughly ten times higher than July for all the sites.

Figure 2 shows the temporal variation of the biomass of the species found most frequently at the sites of Belles-Amours, Tracadie Bay, Miramichi and St. Mary's Bay. The hydroid *T. larynx* is comprised a greater proportion of the relative abundance in July than in November whereas the opposite was found for seed mussels. Although widespread, *B. crenatus* only accounted for a small proportion of the biomass. Figure 2 also shows changes in communities and in species dominance. At Tracadie Bay, the seed mussels accounted for nearly all of the epifauna biomass in July, although the total biomass was low (5.14g near the surface and 7.96g at depth) whereas *Bugle turret* comprised nearly 50% of the total biomass in November. At St. Mary's Bay, seed mussels and *T. larynx* were sharing dominance in July, and in November 66% of the biomass was from *Styela clava*. At Belles-Amours, the recruitment of the seed mussels (on average 4.14g in July and 10.9g in November by 30cm section) was hidden by the very strong dominance of *Alcyonidium gelatinosum* (149.65g representing 87% of the biomass in November). At Miramichi, *T. larynx* was very abundant in July but was replaced by seed mussels in November.

The effect of the factors of site, month, depth and their interactions on biomass of the targeted species was analyzed by a variance analysis with repeated measures using permutations. Significance levels for each source of variation are given on table 3. The first analysis (including the three factors) showed a statistically significant triple interaction for seed mussels (<0.001) and B. crenatus (0.0020) whereas there was a significant double interaction between the site and the month for T. larynx (0.0020). To find where the factors varied we fixed each factors sequencely (test of effect slices). With the variable seed mussels, the depth had a significant effect at Tracadie in November only (<0.0001), site was significant in November at both position (<0.0001) while month was significant at Tracadie only (<0.0001). Depth had a significant effect on B. crenatus at St. Mary's Bay in July (0.0068) and Tracadie in November (<0.0001), site was significant in November for both depth (upper <0.0001, lower 0.0159) and month was significant at both position (upper <0.0001, lower 0.0067). The factor depth had no effect on the variable T. larynx, while the factor site was significant in July (0.0191) and November (0.0019) and month is significant at Belles-Amours (0.0037) only.

The second analysis including the four sites (Belles-Amours, Tracadie, St. Mary's Bay and Miramichi) showed a double interaction statistically significant for both seed mussels and *B. crenatus*. None of the factor had a significant effect on *T. larynx*. The test on effect slices with the variable seed mussels showed a significant effect of month at Miramichi (<0.0001) and Tracadie (0.0004), while the factor site was significant in July (0.0107) and November (<0.0001). Finally, with *B. crenatus*, month is significant at Miramichi (<0.0001) only and the site was significant in July (<0.0001) only

A multidimensional analysis of the biomass allows for the exploration of the effect of date, position and site on community structure. The MDS relative to the position showed that this parameter had little influence on the distribution of species (results not shown). With regard to the influence of date and site (figure 4) on the epifaunic community, some tendencies were observed. All of the samples taken on the same date were easily integrated in a group. The influence of date as a factor is nevertheless, more important for certain sites. Considering that the distance between two points reflects the degree of similitude between the communities, we noticed that the samples from St. Mary's Bay and Tracadie Bay in November were graphically distant from their homolog in July, contrary to Belles-Amours Bay and Miramichi Bay. This allows one to suppose an influence of date on the community, but this varies with each site. Similarly, the different samples from the same sites were generally grouped together according to date and there was no mixing, with the exception of Tracadie Bay and St. Mary's Bay in July, both of which are located on Prince-Edward Island. We also noticed that the sites in July were relatively close to one another whereas they were distinct in November (figure 3). In July, there were very few species fixed on the socks (table 2); this explains the similitude between the very simple macrofaunic sessile communities. The values of Shannon's diversity index (table 5) point in the same direction. The rise in November of Shannon's diversity index for the sites of St. Mary's Bay and Tracadie Bay demonstrates that there is rise in the diversity but only a slight variation is noted at the site of Belles-Amours.

Genetics

The results from the nuclear glu5 marker showed the presence of mixed populations at Belles-Amours and Miramichi (Table65). The percentage of *Mytilus edulis* was greater in the seed mussels compared to the adults of Belles-Amours (44% juveniles and 26% adults) and Miramichi (99% juveniles and 88% adults). The more southern sites were essentially composed of *M. edulis*. In Lameque, 1% of the juveniles were *M. trossulus*, but 100% of the adults were *M.edulis*, which accounted for 100% of both juveniles and adults in St. Mary's Bay and Havre-aux-Maisons.

We initially planned to optimize the seven microsatellite loci developed by Presa (2002). However, three of them (mg μ -2, mg μ -4 and mg μ -7) proved difficult to amplify. Mg μ -1 was also omitted since it only amplified the DNA of 60-70% of all individuals possibly due to a high frequency of null alleles at this locus (Presa, pers. comm.). Mg μ -3 was monomorphic in our populations (but polymorphic on *M. trossulus*). Mg μ -5 and mg μ -6 were amplified using a modified protocol.

Nine alleles were found at the locus mg μ -5 and 37 alleles at mg μ -6. F_{ST} value (table 7) of 0.006 was low, indicating a high dispersal and no significant divergence amongst sites. The level of observed heterozygosity varied from 0.383 to 0.602 (table 8). The null hypothesis of Hardy-Weinberg equilibrium (HWE) was rejected for all samples at mg μ -6 due to a heterozygosity deficit, but was not rejected for four out of five sites at mg μ -5. F_{IS} values at mg μ -5 varied from 0.051 and 0.310, where only St. Mary's bay was significatif. F_{is} values at mg μ -6 were higher, ranging from 0.256 to 0.440. There was no clear evidence of isolation by distance based on Mantel test (r = -0.548, p > 0.05)

DISCUSSION

Distribution of species

Mussel socks can be considered as good representative of species assemblages at each site. Indeed, the assemblages found on socks are mostly the result of the local production (Davis and Butler, 1989), not dominated by teleplanic larvae (Butler and Keough, 1990). Our results show that the six sites were very distinct in assemblage and biomass. The data we have is not sufficient to explain these differences, but many possibilities exist. These differences could be maintained by physico-chemical parameters of the area, that can be advantageous for some species while acting as an agent of selection on larvae, juveniles or adults. For example, Mytilus trossulus, which is dominant in Newfoundland, Labrador and Basse Côte-Nord (Comesana et al. 1999; Mallet and Carver 1999; Thomas and Tremblay 1999; Toro et al. 2004), is completely absent from our southernmost sites, despite a larval stage very similar to *M. edulis* (Qiu et al. 2002). The aquaculture practices may also explain differences among sites. The maximum of biodiversity (Shannon's index and a high number of species presents) was found at St. Mary's Bay and Tracadie Bay. Aquaculture has been practiced for a long time at these sites and has high production. The farming structures have long offered a solid and abundant substrate contributing to the long-term development of an epifaunic community (Arakawa 1990; Khalaman 2001; Butler and Connolly 1996). Finally, geographical variability reflects a whole spectrum of adaptive capacity and the species having a great dispersion are mainly those who have a greater capacity of adaptation.

The species most commonly found on all sites were the barnacle *Balanus crenatus*, the hydroid Tubularia larynx, the slipper limpet Crepidula fornicata and the blue mussel Mytilus edulis. These species were also the most common ones on the buoys analyzed by Ardisson and Bourget (1992) and belong to the group of "foundation" species (Sutherland, 1981). Moreover, the species found at Tracadie Bay are similar with those mentioned by Leblanc et al. (2003a). Hydroids, barnacles and some ascidians are the first species to settle on a solid substrate, after the microperiphyton. These fast-growing first succession species prepare the substrate available for the settlement of bivalves, which represent the second phase of development (Khalaman and reference therein, 2001). It is known that the first settlement of mussels is done preferably on arborescent species (Genzano et al. 2003) and a chemical cue from the biofilm could play a determinant role in settlement (Dobretsov 1999). In September, we collected most of the mussels on dead Tubularia larynx and Obelia longissima at Havre-aux-Maisons, Miramichi, St. Mary's Bay and Belles-Amours. Our results suggest the first stages of a succession pattern at those sites. Conversely, the recruitment of seed mussel was very weak on socks from Tracadie Bay and very few hydroids were previously found. However, it is difficult, with our results, to attribute this weak recruitment to the absence of hydroid in the process of succession or to the lack of larvae of those two species in the water column. This could likely be an effect of seasonal progression on the settlement sequence obtained. Turner and Todd (1993) describe the seasonal progression as being the result of the availability of larvae and this is closely dependent upon reproductive period. This complicates the process of succession described by Scheer (1945). If all the sites follow the same succession pattern, they should all have a

similar assemblage. Our results suggest the opposite. The variation found between the sites in November may be related to the availability of the larvae in the water.

The blue mussel

The most common species of blue mussels found in Atlantic Canada is M. edulis, which is sympatric with *M. trossulus*. Previous studies report the presence of pure populations of *M. trossulus*, in Brador Lake, Nova-Scotia (Mallet and Carver 1999) at the river mouth of Belles-Amours, in the bay of Gaspe, bay of Jacques-Cartier and Rivière-auxrenards in Gaspésie (Thomas and Tremblay 1999). Our results show sympatric populations in Bays of Belles-Amours and Miramichi and pure populations of *M. edulis* at St. Mary's bay, Tracadie Bay, Havre-aux-Maisons and the adults of Lameque. The environmental conditions, such as salinity, help the pure populations of *M. trossulus* to be maintained. Unless these are modified, those populations should maintain themselves (Qiu et al. 2002). The first ontogenetic stages of Mytilus sp. are sensitive to salinity and M. edulis does not tolerate low salinity well (Qiu et al. 2002). This could explain why we found two species as apposed to Thomas and Tremblay (1999) at Belles-Amours. The mussels taken for our study come from the farming structures located in the middle of the bay, whereas the pure population of *M. trossulus* has been found at the river mouth. Moreover, the studied sites show a higher proportion of *M. trossulus* at the adults level. This difference can be attributed to either a variable recruitment or selection pressure on *M. edulis*.

Gene flow between studied sites

The low level of differentiation (total F_{sT} of 0,0066) among the sites suggests an important gene flow. This is what is generally expected with marine species with a long pelagic larval stage (Palumbi 1995) such as mussels. There have been few genetic studies on invertebrate in the Gulf of St. Lawrence. However, some studies report genetic differentiation among population using allozyme markers with the barnacle *Semibalanus balanoïdes* (Holm and Bourget 1994; Dufresne *et al.* 2002; Véliz *et al.* 2004), microsatellites markers with the scallop *Placopecten magellanicus* (Roy 2004), isoenzymes markers with blues mussels (Gartner-Kepkay *et al.* 1983). Moreover, Luttikhuizen *et al.* (2003) showed the effect of selection on hereditary morphological characteristics in *Macoma balthica*, in spite of a very high gene flow. It is important to remember that the low level of differentiation with marine organisms is sometimes due to a lack of resolution rather than the true reflection of the structure of populations (Pogson and Zouros 1995).

Microsatellite analyses revealed a deficit in heterozygosity at locus mg μ -6 in all studied sites. Several other studies have shown heterozygote deficits on mollusks (Zouros and Foltz 1984; Gaffney 1994; Raymond *et al.* 1997; Tremblay *et al.* 1998). Null alleles (McGoldrick *et al.* 2000), inbreeding (Gaffney 1994), Walhund effect and selection at the larval stages (Tremblay *et al.* 1998; Mallet *et al.* 1985; Launey and Hedgecock, 2001; Toro and Vergara, 1995) could explain this phenomenon. The Microchecker software, used to test microsatellites, suggests the possibility of null alleles to explain the deficit in heterozygosity at the locus mg μ -6. The microsattelite results cast doubt on the possibility of using the markers developed by Presa *et al.* (2002) on North American populations of *M. edulis.* A single locus out of seven potential ones can be used. The mussel culture is expanding rapidly in Eastern Canada but one of the limiting factors is the supply of quality seed mussels (Gosling 1992b). Presently, some growers will supply themselves with reputable seed mussels coming from various sites. Generally, seed mussel quality is based on the judgment of the growers, although some studies clearly showed the importance of stocks on mussel mortality in the Gulf of St-Lawrence (Tremblay *et al.* 1998; Mallet *et al.* 1990). In this context, it becomes relevant to better assess genetic differentiation in mussels from various sites in the Gulf of St. Lawrence. Other genetic markers, such as AFLP, sequencing a mitochondrial DNA hypervariable region or other microsatellites markers should be isolated for use on the North American populations.

For most growers, the harvest of seed mussels is done at the same site as the farming (Thomas Landry, pers. comm.). However, the transfer of seed mussels between mussel farming operations is commonly done. For example, Acadian peninsula (New-Brunswick, Canada) growers provide some farms on Prince-Edward Island and Nova-Scotia with their seed mussels (Thomas Landry, pers. comm.). The definition of transfer given by Beaumont (2000) is the movement of a sample from one area to another within the natural range of the species. These transfers of organisms have genetic consequences on populations already present and the only way to estimate the consequences of such transfer is through a thorough understanding of the indigenous structures (Beaumont, 2000). With regards to mussels, some sites have been subject to transfers in the past. These transfers certainly help to decrease the divergence between sites, which shows the urgency to establish the genetic structure of the populations for a species with strong commercial value.

The weak genetic structure of mussel populations indicates that the Gulf represents an open area with few physical and natural barriers to prevent larval dispersion. Such systems

are sensitive to invasive species, where the only limit of dispersion is the capacity of adaptation. In conclusion, this study is a first step in the acquisition of knowledge concerning sessile epifaunic communities associated with mussel farming structures in the gulf of St-Lawrence and stresses the need to develop hypervariable markers for North American populations of *M. edulis*.

AKNOWLEDGMENTS

We would like to thanks G. D'aigle and E. Rény-Nolin from « Service de consultation statistique » of Laval university for their support in data analysis. L. Comeau, D. Bourque, F. Bourque, M. Ouellet and B. Dumas for field support, B. Fortune, B. Dumas, STMIM, M. Noël and S. Steward for mussel supply and sampling. Financial support was from MAPAQ.

		*
Facteur	Niveau d'influence	
Quantité de nutriments et production primaire	Biomasse et productivité des estuaires	Fréchette et Bourget 1985a, 1985b; Heip <i>et al.</i> 1995; Howard <i>et al.</i> 1989; Heck <i>et al.</i> 1995; Hovel <i>et al.</i> 2002
Prédation et compétition	Biomasse, richesse spécifique et productivité	Dare 1976; Edwards <i>et al.</i> 1982; Sousa 1985; Edgar et Barrett, 2002
Salinité	Biomasse, richesse spécifique et productivité	Dare 1976; Bourget 1983; Ardisson et Bourget 1997; Weisshappel et Svavarsson 1998; Edgar et Barrett 2002
Période d'anoxie	Biomasse, richesse spécifique et densité	Diaz et Rosenberg 1995
Taille des sédiments	Biomasse, richesse spécifique et diversité	Mannino et Montagna 1997; Callaway et al. 2002
Température	Biomasse, richesse spécifique et diversité	Bourget et al. 2003; Callaway et al. 2002
Profondeur	Richesse spécifique Biomasse	Colloca et al. 2003; Bourget et al. 2003
Hydrographie	Biomasse, structure des communautés	Butler et Connoly 1996; Ardisson et Bourget 1992
Abondance larvaire, Dynamique de recrutement et fixation	Structure des communautés	Sutherland 1990; Possingham et Roughgarden 1990
Dispersion larvaire		Mann 1988; Crisp 1978
Traits génétiques et physiologiques	Réponse individuelle et biomasse	Koehn <i>et al.</i> 1976; Koehn et Bayne 1989

Table 1: Facteurs physiques et biologiques influençant les communautés benthiques.

Species	July	September	November
	Lamèque Miramichi St-Mary Tracadie Belies-Amours Havre-aux-Maisons	Lamèque Miramichi Şt.Maiy Tracadié Béllès:Amours Havre-aux-Maisons	Lamèque Miramichi St-Mary Tracadie Belles-Amours Havre-aux-Maisons
Seed mussel (Mytilus sp.)	* * * * * *	* * * * *	* * * * * *
Alcyonidium gelatinosum			*.
Styela clava		*	*• • • • •
Metridium senile	*	* * *	* * * *
Anomia simplex		*	* * * *
Crepidula convexa		* * * *	* * * * *
Crepidula fornicata		* * *	* .*.`.*.`.*
Tubularia larynx	* * * * *	* *** *** ****	* * * * * *
Molgula manhattensis	*		* * * * * * * * * * * * * * * * * * * *
Bugula turrita		· · · · · · · · · · · · · · · · · · ·	*** ***
Obelia longissima	********	· · · · · · · · · · · · · · · · · · ·	
Balanus crenatus	* * *.	* * * *	* * * * *
Hippothoa hyalina		* * *	*
sponge		*	· · · · · · · · · · · · · · · · · · ·

Table 2: Presence-absence of epifaunal species found on mussels socks at Havre-auxmaisons, Lamèque, Belles-Amours, St. Mary's Bay, Miramichi and Tracadie. The grey columns indicate the sites where the biomass of each species is available.

Table 3: Average biomass (g) of organisms found on a thirty centimeters section of mussel sock sampled in July and November at each site.

	Tracadie					St.Ma	ry's Bay	
	July		Novembre		July		Novembre	
	Near surface	Bottom						
Alcyonidium gelatinosum	0	0	0	0	0	0	0	0
Anomia simplex	0	0	0.2	0.4	0	0	0.03	0.1
Balanus crenatus	0	0	0.8	0.3	0.04	0.3	0.1	0
Bugula turrita	0	0	48.1	34.4	0	0	0.5	1.3
Crepidula convexa	0	0	0	0	0	0	0	0
Crepidula fornicata	0	0	4.2	5.0	0	0	0.1	0.1
Hippothoa hyalina	0	0	0	0	0	0	0.4	0.1
Metridium senile	0	0	0	0	0	0	0.3	0.5
Molgula manhattensis	0	0	0	0	0	0	0.2	2.5
seed mussel (Mytilus sp.)	10.6	6.3	70.0	26.9	2.2	2.0	3.4	2.3
Obelia longissima	0	0	0	0	0	0	0	0
sponge	0	0	0	0	0	0	7.8	5.6
Styela Clava	0	0	0	0	0	0	30.6	8.9
Tubularia larynx	0.01	0.02	0	0	4.8	0.7	0	1.7
Total	10.6	6.3	123.4	67.1	7.0	3.1	43.4	23.0

	Belles-Amours Miramichi								
	July Novembre		nbre	July		Noven	Novembre		
	Near surface	Bottom	Near surface	Bottom	Near surface	Bottom	Near surface	Bottom	
Alcyonidium gelatinosum	19.7	5.4	230.7	68.6	0	n/a	0	n/a	324.4
Anomia simplex	0	0	0	0	0	n/a	0	n/a	0.8
Balanus crenatus	0	0	0.1	0.01	12.9	n/a	1.2	n/a	15.8
Bugula turrita	0	0	0	0	0	n/a	0	n/a	84.3
Crepidula convexa	0	0	0	0	0	n/a	1.6	n/a	1.6
Crepidula fornicata	0	0	0	0	0	n/a	0.1	n/a	9.5
Hippothoa hyalina	0	0	1	1.6	0	n/a	0	n/a	3.1
Metridium senile	0	0	0	0	0	n/a	1.8	n/a	2.7
Molgula manhattensis	0	0	0	0	0.6	n/a	0	n/a	3.3
seed mussel (Mytilus sp.)	4.5	3.8	11.3	10.5	89.5	n/a	665.4	n/a	908,5
Obelia longissima	0	0	7.8	5.0	0	n/a	0	n/a	12.7
sponge	0	0	0	0	0	n/a	0	n/a	13.4
Styela Clava	0	0	0	0	0	n/a	0,0	n/a	39.5
Tubularia larynx	1.0	0.1	3.5	4.7	148.4	n/a	16,8	n/a	181.8
Total	25.1	9.4	254.3	90.4	251.4		686.9		1601.4

Table 4: Significance level of the factors site, month and position based on permutation test for the two analyses: the first including the three factors and their interactions and treating only the sites of Tracadie Bay, St.Mary's Bay and Belles-Amours Bay. The second analysis excluding the factor of position but treating the upper section of the sites Miramichi Bay, Tracadie Bay, St.Mary's Bay and Belles-Amours Bay. Each test was done using 1 000 permutations (* indicates a significant difference, ** highly significant).

	3 factors (position, month and site)			2 factors (month and site)		
	Seed	Tubularia	Balanus	Seed	Tubularia	Balanus
	mussels	larynx	crenatus	Mussels	larynx	crenatus
Month	< 0.001	0.594	0.001	<0.001	0.536	0.053
Site	<0.001	0.048	0.002	<0.001	0.068	< 0.001
Site*Month	<0.001	0.020*	< 0.001	<0.001**	0.051	0.037*
Position	< 0.001	0.847	< 0.001			
Position*Month	< 0.001	0.149	<0.001			
Position*Site	< 0.001	0.818	<0.001			
Position*Site*Month	<0.001**	0.324	0.002*			

Site	July	November	
Tracadie	0.005	0.342	
St.Mary's Bay	0.310	0.752	
Belles-Amours	0.204	0.230	
Miramichi	0.335	0.060	

Table 5: Shannon's diversity index at the sites of Tracadie Bay, St.Mary's Bay, Belles-Amours Bay and Miramichi Bay, in July and November. (1 = maximum of diversity).

	Juv	venile	A	dult
	M. edulis (%)	M. trossulus (%)	M. edulis (%)	M. trossulus (%)
Belles-Amours	44	56	26	74
St.Mary's Bay	100	0	100	0
Havre-aux-Maisons	100	0	100	0
Lamèque	99	1	100	0
Miramichi	99	1	88	12
Tracadie			100	0

 Table 6: Proportion of each species of mussel found in juveniles and adults.

	Havre-aux-maisons	Belles-Amours	Lamèque	St.Mary's Bay	Miramichi
Havre-aux-maisons					
Belles-Amours	0.0059				
Lamèque	0.0168	0.0032			
St.Mary's Bay	0.0074	0.0035	0.0198		
Miramici	0.0044	0.0014	~0.0027	0.0073	

Table 7: Pairwise \mathbf{F}_{ST} including both loci.

	Sites					
Locus	HM	BA	LM	SM	MM	
N	88	49	60	50	87	
mgµ-5						
Na	7	7	6	6	7	
H_{E}	0.559	0.517	0.463	0.607	0.569	
H _o	0.511	0.449	0.413	0.420	0.540	
F _{IS}	0.086	0.133	0.101	0.310	0.051	
mgµ-6						
Na	25	22	18	22	26	
H_{E}	0.827	0.793	0.622	0.828	0.859	
Ho	0.602	0.592	0.383	0.600	0.483	
F _{IS}	0.273	0.256	0.386	0.277	0.440	

Table 8: Sample size (n), number of alleles (Na), expected heterozygosity (H_E) and observed heterozygosity (H_O), F_{IS} , embodied values indicates samples which deviate significantly from Hardy-Weinberg's expectation after sequential Bonferroni corrections (p<0.005).



Figure 1: Sampling sites: Belles-amours (BA), Lamèque (LM), Miramichi (MM), Havre-aux-Maisons (HM), Tracadie (TR) and St.Mary's Bay (SM).



Figure 2: Temporal variation of the biomass (proportion of each species on the total biomass) of the most widely distributed species; seed mussel (*Mytilus* spp.), *Tubularia larynx* and *Balanus crenatus* as well as the dominant species of each site. a) *Bugula turrita* at Tracadie Bay, b) *Bugula turrita* and *Styela clava* at St.Mary's Bay, c) *Alcyonidium gelatinosum* at Belles-Amours Bay, d) the three most common species at Miramichi.



Figure 3: Multidimensional analysis of the epifaunic communities found at the sites of Belles-Amours, Miramichi, St. Mary's Bay and Tracadie. The circled areas represent samples from the same date, July and November.

CONCLUSION GÉNÉRALE

La présente étude avait pour but premier de déterminer le développement temporel des espèces sessiles associées aux élevages de moules et d'estimer la connectivité entre différents sites d'élevage dans la région du Golfe du St-Laurent. Les résultats ont démontré que la présence des espèces et leur biomasse variaient beaucoup d'un endroit à l'autre et selon le site et la date d'échantillonnage, alors que la profondeur (3m) n'agit pas de façon significative sur les communautés d'épifaune. Le nombre d'espèce de macrofaune sessile retrouvé sur les boudins (14 espèces) est faible mais correspond aux études antérieures. La diversité et la biomasse étaient beaucoup plus importantes en novembre qu'en juillet.

Nous avions prévu inclure septembre dans nos analyses de biomasse, mais des problèmes techniques majeurs nous ont obligé à laisser tomber cette date. L'ajout de cette session d'échantillonnage aurait permis un meilleur suivi du développement des communautés sur les boudins. Les données récoltées dans le cadre de cette étude ajoutent tout de même une meilleure connaissance des espèces d'épifaune sessile associées aux sites à fort potentiel aquacole.

J'ai utilisé des microsatellites développés sur *Mytilus sp.* provenant de la Méditerranée pour mesurer la connectivité entre les différents sites. Après un laborieux travail d'optimisation, nous avons constaté que cinq des sept loci n'étaient pas variables ou interprétables aux populations du Canada Atlantique et a limité notre étude à l'interprétation de deux loci. Les résultats sur les deux loci montrent un flux génique important entre les populations. L'absence de structure génétique des populations suggère qu'aucune barrière physique ou naturelle ne limite la dispersion des moules dans cette région. Cependant, cette homogénéité peut également être le résultat du faible nombre de marqueurs utilisés. Il est généralement recommandé d'utiliser 5 loci microsatellites pour une étude des populations. Finalement, la présence d'un flux génique entre les sites permet de croire au potentiel de dispersion des espèces dans les limites de leur potentiel physiologique.

Cette étude est un premier pas dans la connaissance des communautés épifauniques sessiles associées aux structures d'élevages de moules propres au golfe du St-Laurent. De plus cette étude a démontré qu'il n'existe pas à l'heure actuelle, d'outils moléculaires assez puissants pour déterminer le flux génique entre les moules de différents site d'élevage.

BIBLIOGRAPHIE

- Ardisson, P.L., E. Bourget et P. Legendre. 1990. Multivariate approach to study species assemblages at large spatio-temporal scales: the community structure of the epibenthic fauna of the Estuary and Gulf of St.Lawrence. Canadian Journal of Fisheries and Aquatic Sciences. 47: 1364-1377.
- Ardisson, P.L., et E. Bourget. 1992. Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna. Marine Ecology Progress Series. 83: 15-34.
- Ardisson, P.L. et E. Bourget. 1997. A study of the relationship between freshwater runoff and benthos abundance: A scale-oriented approach. Estuarine, Coastal and Shelf Science. 45: 535-545.
- Arawaka, K.Y. 1990. Competitors and fouling organisms in the hanging culture of the pacific oyster, *Crassostrea gigas* (Thunderg). Marine Behaviour and Physiology. 17: 67-94.
- Barber, P.H., S.R. Palumbi, M.V. Erdmann et M. Kasim Moosa. 2000. A marine Wallace's line. Nature. 406 (6797): 692-693.
- Beaumont, A. 2000. Genetic considerations in transfers and introductions of scallops. Aquaculture International. 8: 493-512.
- Bierne, N., F. Bonhomme et P. David. 2003. Habitat preference and the marine speciation paradox. Proceeding of the Royal Society of London (B). 270: 1399-1406.
- Bohonak, A.J. 1999. Dispersal, gene flow, and population structure. The Quarterly Review of Biology. 7 (1): 21-45.
- Bourget, E. 1983. Seasonal variations of cold tolerance in intertidal mollusks and relation to environmental conditions in the St. Lawrence Estuary. Canadian Journal of Zoology. 61: 1193-1201.
- Bourget, E., P.L. Ardisson, L. Lapointe et G. Daigle. 2003. Environmental factors as predictors of epibenthic assemblage biomass in the St-Lawrence system. Estuarine, Coastal and Shelf Science. 57: 641-652.
- Brichette, I., M.I. Reyero et C. Garcia. 2001. A genetic analysis of intraspecific competition for growth in mussels cultures. Aquaculture. 192: 155-169.
- Butler, A.J. et M.J. Keough. 1990. A comment on short-supply lines. Trends in Ecology and Evolution. 5: 97.
- Butler, A.J. et R.M. Connolly. 1996. Development and long term dynamics of a fouling assemblage of sessile marine invertebrates. Biofouling. 9 (3): 187-209.
- Callaway, R., J. Alsvag, I. de Boois, J. Cotter, A. Ford, H. Hinz, S. Jennings, I. Kröncke, J. Lancaster, G. Piet, P. Prince et S. Ehrich. 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. Journal of Marine Science. 59: 1199-1214.
- Claereboudt, M.R., D. Bureau, J. Côté et J.H. Himmelman. 1994. Fouling development and its effect on the growth of juvenile giant scallops (*Placopecten magellanicus*) in suspended culture. Aquaculture. 121: 327-342.
- Colloca, F., M. Cardinale, A. Belluscio et G. Ardizzone. 2003. Pattern of distribution and diversity of demersal assemblages in the central Mediterranean sea. Estuarine Coastal and Shelf Science. 56: 469-480.
- Comesana ,A.S., J.E. Toro ,D.J. Innes et R.J. Thompson. 1999. A molecular approach to the ecology of a mussel (*Mytilus edulis M.trossulus*) hybrid zone on the east coast of Newfoundland, Canada. Marine Biology. 133: 213-221.

- Crisp, D.J. 1978. Genetic consequences of different reproductive strategies in marine invertabrates. In :Battaglia B, Beardmore J.A. (eds) Marine organisms : genetics, ecology and evolution. Plenum, New York. pp. 257-273.
- Dardignac-Corbeil, M.J. 1986. La mytiliculture traditionnelle. In G. Barnabé (Ed). Aquaculture. Paris : Tec. and Doc.-Lavoisier. T.1 pp.285-343.
- Dare, P.J. 1976. Settlement, growth and production of the mussel, Mytilus edulis L., in Morecambe Bay, England. Fish. Invest. Minist. Agric. Fish. Food (G. B.) (2 Sea Fish.). 28 (1).
- Davis, A.R. et A.J. Butler. 1989. Direct observations of larval dispersal in the colonial ascidian *Podoclavella molluccensis* Sluiter : evidence for closed populations. Journal of Experimental Marine Biology and Ecology. 127: 189-203.
- Diaz, R.J. et R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology. An annual review. 33: 245-03.
- Dobretsov, S.V. 1999. Effect of Macro algae and biofilm on settlement of blue mussel (*Mytilus edulis* L.) larvae. Hydrobiologia. 445 (1-3): 27-35.
- Dufresne, F., E. Bourget et L. Bernatchez. 2002. Differential patterns of spatial divergence in microsatellite and allozyme alleles: further evidence for locus-specific selection in the acorn barnacle, *Semibalanus balanoides*? Molecular Ecology. 11(1): 113-123.
- Edgar, G.J. et N.S. Barrett. 2002. Benthic macrofauna in Tasmanian estuaries :scale of distribution and relationships with environmental variables. Journal of Experimental Marine Biology and Ecology. 270: 1-24.
- Edwards, D.C., D.O. Conover et F. Sutter. 1982. Mobile predators and the structure of marine intertidal communities. Ecology. 63: 1175-1180.
- Fréchette, M. et E. Bourget. 1985a. Energy flow between the pelagic and the benthic zones : factors controlling particulate organic matter available to an intertidal mussel bed. Canadian Journal of Fisheries and Aquatic Science. 42: 1158-1165.
- Fréchette, M. et E. Bourget. 1985b. Food limited growth of *Mytilus edulis* L. in relation to the benthic boudary layer. Canadian Journal of Fisheries and Aquatic Science. 42: 1166-1170.
- Fréchette, M., A.E. Aitken et L. Page. 1992. Interdependence of food and space limitation of a benthic suspension feeder consequences for self-thinning relationships. Marine Ecology Progress series. 83 (1): 55-62.
- Gaffney, P.M. 1994. Heterosis and heterozygote deficiencies in marine bivalves: more light? In A.R. Beaumont, ed. Genetics and evolution of aquatic organisms, London: Chapman & Hall, pp. 146-153.
- Gartner-Kepkay, K.E., E. Zouros, L.M. Dickie et K.R. Freeman. 1983. Genetic differentiation in the face of gene flow: A study of mussel populations from a single Nova Scotian embayment. Canadian Journal of Fisheries and Aquatic Sciences. 40: 443-451.
- Genzano, G.N., A.C. Excoffon, F.H. Acuña et M.O. Zamboni. 2003. Hydroid colonies as primary substrata for recruits of the mussel *Mytilus edulis* Platensis front off Mar Del Plata, Argentina. Ophelia. 57 (2): 53-61.
- Goldson 1992

- Goldson, A.J., R.N. Hughes et C.J. Gliddon. 2001. Population genetic consequences of larval dispersal mode and hydrography : a case study with bryozoans. Marine Biology. 138: 519-528.
- Gosling, E.M. 1992a. Systematics and geographic distribution of *Mytilus*. In: Gosling E.M.
 (ed). The mussel *Mytilus*: ecology, physiology, genetics and culture. Developments in aquaculture and Fisheries Science. No 25. Elsevier, Amsterdam. pp. 309-382.
- Gosling, E.M. 1992b. Genetics on *Mytilus*. In: Gosling E.M. (ed). The mussel *Mytilus*: ecology, physiology, genetics and culture. Developments in Aquaculture and Fisheries Science. No 25. Elsevier, Amsterdam. pp. 309-382.
- Grecian, L., G. Parsons, P. Dabinett et C. Couturier. 2000. Influence of season, initial size, depth, gear type and stocking density on the growth rates and recovery of sea scallop, *Placopecten magellancius*, on a farm-based nursery. Aquaculture Internationale. 8: 183-206.
- Harvey, M. et E. Bourget. 1997. Recruitment of marine invertebrates onto arborescent epibenthic structures : active and passive processes acting at different spatiale scales. Marine Ecology Progress Series. 153: 203-215.
- Heck, K.L., K.W. Able, C.T. Roman et M.P. Fahay. 1995. Composition, abundance, biomass and production of macrofauna in a New England estuary : comparisons among eelgrass meadows and other nursery habitats. Estuaries. 18: 379-389.
- Hedgecock, D. 1981.Genetic consequences of larval retention: Theoretical and methodological aspects. Estuaries. 4: 239.
- Hedgecock, D. 1986. Is gene flow from pelagic larval dispersion important in the adaptation and evolution of marine invertebrates? Bulletin of Marine Science. 39 (2): 550-564.
- Heip, C.H.R., N.K. Goosen, P.M.J. Herman, J. Kromkamp, J.J. Middelburg et K. Soetaert. 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanography. 33: 1-14.
- Hilbish, T.J. 1996. Population genetics of marine species: The interaction of natural selection and historically differentiated populations. Journal of Experimental Marine Biology and Ecology. 200: 67-93.
- Holm, E.R. and E. Bourget. 1994. Selection and population genetic structure of the barnacle *Semibalanus balanoides* in the Nortwest Atlantic and Gulf of St. Lawrence. Marine Ecology Progress Series. 113: 247-256.
- Hohenlohe, P.A. 2004. Limits to gene flow in marine animals with planktonic larvae: models of Littorina species around Point Conception, California. Biological Journal of the Linnean Society. 82: 169-187.
- Hovel, K.A., M.S. Fonseca, D.L. Myer, W.J. Kenworthy et P.E. Whitfield. 2002. Effects of seagrass landscape structure, structural complexity and hydrodynamic regime on macrofaunal densities in North Carolina seagrass beds. Marine Ecology Progress Series. 243: 11-24.
- Howard, R.K., G.J. Edgar et P.A. Hutchings. 1989. Faunal assemblages of seagrass beds. In. Larkum, A.W.D., A.J. McComb and S.A. Shepherd (Eds.), Biology of seagrasses : A treatise on the biology seagrasses with special reference to the Australian region. Elsevier, Amsterdam, Netherlands. pp.536-564.
- Jablonski, D.J. et R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates : palebiological implications. Biological Review. 58: 21-89.

- Jones, G.P., M.J. Milicich, M.J. Emslie et C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature. 404 (6763): 802-804
- Khalaman, V.V. 2001. Succession of fouling communities on an artificial substrate of a mussel culture in the White Sea. Russian Journal of Marine Biology. 27 (6): 345-352.
- Koehn, R.K., R. Milkman et J.B. Mitton. 1976. Population genetics of marine pelecypods.
 4.Selection, migration and genetic differentiation in the blue mussel *Mytilus edulis*. Evolution. 30: 2-32.
- Koehn, R.K., B.L. Bayne, M.N. Moore et J.F. Siebenaller. 1980. Salinity related physiological and genetic differences between populations of *Mytilus edulis*. Biological Journal of the Linnean Society. 14: 319-334.
- Koehn, R.K. et B.L. Bayne.1989. Towards a physiological and genetical understanding of the energetics of the stress response. Biological Journal of the Linnean Society. 37: 157-171.
- Launey, S. et D. Hedgecock. 2001. High genetic load in the Pacific oyster Crassostrea gigas. Genetics. 159: 255-265.
- Leblanc, A.R. 2003. Effet de l'épifaune sur la production de moule bleu (*Mytilus edulis*) en aquaculture. Mémoire de maîtrise. Université de Moncton
- Leblanc, A.R., T. Landry, G. Miron. 2003a. Identification of fouling organisms covering mussel lines and impact of a common PEI defouling method on the abundance of foulers. Canadian Technical Repport of Fisheries and Aquatic Sciences. 2477, vii + 18p.
- Leblanc, A.R., T. Landry, G. Miron. 2003b. Fouling organisms of the blue mussel *Mytilus edulis*: Their effect on nutrient uptake and release. Journal of Shellfish Research. 22: 633-638.
- Luttikhuizen, P.C., J. Drent, W. Van Delden et T. Piersma. 2003. Spatially structured genetic variation in a broadcast spawning bivalve: quantitative vs. molecular traits. Journal of Evolutionary Biology. 16 (2): 260-272.
- Lohse, D.P. 2002. Relative strenghts of competition for space and food in a sessile filter feeder. Biological Bulletin. 203: 173-180.
- Mallet, A.L., E. Zouros, K.E. Gartner-Kepkay, K.R. Freeman et L.M. Dickie. 1985. Larval viability and heterozygote deficiency in populations of marine bivalves: evidence from pair mating of mussels. Marine Biology. 87: 165-172.
- Mallet, A.L., C.E.A. Carver et K.R. Freeman. 1990. Summer mortality of the blue mussel in eastern Canada: spatial, temporal, stock and age variation. Marine Ecology Progress series. 67: 35-41.
- Mallet, A.L. et B. Myrand. 1995. The culture of blue mussel in Atlantic Canada. In A.D. Boghen (ed.). Cold-Water aquaculture in Atlantic Canada. 2nd ed. Moncton, NB. pp. 257-296.
- Mallet, A.L., C.E. Carver. 1999. Maritime distribution and commercial production performance of *Mytilus edulis* and *Mytilus trossulus*. Bulletin Aquaculture Association Canada. 99 (3): 7-13.
- Maltagliati, F., M. Casu et A. Castelli. 2004. Morphological and genetic evidence supports the existence of two species in the genus Ophelia (Annelida, Polychaeta) from the Western Mediterranean. Biological Journal of the Linnean Society. 83: 101-113.

- Mann, R. 1988. Distribution of bivalve larvae at a frontal system in the James River, Virginia. Marine Ecology Progress Series. 50 :29-44.
- Mannino, A. et P.A. Montagna. 1997. Small-scale spatial variation of macrobenthic community structure. Estuaries. 20 (1): 159-173.
- McGoldrick, D.J., D. Hedgecock, L.J. English, P. Baoprasertkul et R.D. Ward. 2000. The transmission of microsatellite alleles in Australian and North American stocks of the Pacific oyster (*Crassostrea gigas*): Selection and null alleles. Journal of Shellfish Research. 19 (2): 779-788.
- Ministère des Pêches et Océans. 2004. Production aquacole du Canada en 2003. http://www.dfo-mpo.gc.ca/communic/statistics/aqua/aqua03_f.htm
- Palumbi, S.R. 1995. Using genetics as an indirect estimator of larval dispersal In: L. McEdward, ed. Ecology of Marine Invertebrate Larvae, Crc Press, Boca Raton, Fl. (USA). pp. 369-387.
- Pogson, G.H. et E. Zouros. 1995. Genetic population structure and gene flow in the Atlantic cod Gadus Morhua, A comparaison of allozyme and nuclear RFLP loci. Genetics. 139 (1): 375-385.
- Poirier, L. et B. Myrand. 1982. Élevage de la moule bleue, *Mytilus edulis* dans les lagunes des îles-de-la-Madeleine (Québec) Travaux sur les pêcheries du Québec 49. Ministère de l'Agriculture, des Pêcheries et de l'Alimentation, Gouvernement du Québec.
- Possingham, H.P. et J. Roughgarden. 1990. Spatial population dynamics of a marine organism with a complex life cycle. Ecology. 71 (3): 973-985.
- Presa ,P., M. Perez ET A.P. Diz. 2002. Polymorphic microsatellite markers for blue mussels (*Mytilus sp.*). Conservation Genetics. 3 (4): 441-443.
- Qiu, J.W., R. Tremblay, E. Bourget. 2002. Ontogenic changes in hyposaline tolerance in the mussels *Mytilus edulis* and *M. trossulus* implications for distribution. Marine Ecology Progress Series. 228: 143-152.
- Raymond, M., Rousset, F. 1995. Genepop, version 1.2. Population genetics software for exact test and ecuminicisms. Journal of Heredity. 86: 248-249.
- Raymond, M., R.L. Vaeaentoe, F. Thomas, F. Rousset, T. de Neeus et F. Renaud. 1997. Heterozygote deficiency in the mussel *Mytilus edulis* species complex revisited. Marine Ecology Progress Series. 156: 225-237.
- Rawson, P.D., K.L. Joyner, K. Meetze et T.J. Hilbish. 1996. Evidence for intragenic recombination within a novel genetic marker that distinguishes mussels in the Mytilus edulis species complex. Heredity, 77: 599-607.
- Ross, K.A., J.P. Thorpe, T.A. Norton et A.R. Brand. 2002. Fouling in scallop cultivation: help or hindrance? Journal of Shellfish Research. 21: 539-548.
- Roy, M.A. (2004) Caractéristiques génétiques des principaux gisements de pétoncle géant (*Placopecten Magellanicus*) à l'échelle du golfe du Saint-Laurent: Analyse à l'aide de marqueurs microsatellites. Mémoire de maîtrise. Université du Québec à Rimouski.
- Ruzzante, D.E., C.T. Taggart, D. Cook. 1999. A review for the evidence for genetic structure of cod *Gadus morhua* populations in the NW Atlantic and population affinities of larval cod of Newfoundland and the gulf of St. Lawrence. Fisheries Research. 43: 79-97.
- Scheer, B.T. 1945. The development of marine fouling communities. Biological Bulletin. 89: 103-121.

- Scheltema, R.S. et I.P. William. 1983. Long distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and Western Pacific molluscs. Bulletin of Marine Science. 33: 545-565.
- Seed, R., M.N. Elliott, P.J.S. Boaden et R.J. O'Connor. 1981. The composition and seasonal changes amongst the epifauna associated with fucus serratus L. in transford lough, Northern Ireland. Cahiers de Biologie Marine, Pêches et Océans XXII: 243-266.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science. 236: 787-792.
- Slatkin, M. 1994. Gene flow and the geographic structure of natural populations. Science. 236: 787-792.
- Sotka, E.E., J.P. Wares, J.A. Barth, R.K. Grosberg et S.R. Palumbi. 2004. Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. Molecular Ecology. 13 (8): 2143-2156.
- Sousa, W.P. 1985. Disturbance and patch dynamics on rocky intertidal shores. In Pickett, S.T.A. et P.S. White (eds). The ecology of natural disturbance and patch Dynamics. pp.101-124.
- Sutherland, J.P. 1981. The fouling community at Beaufort, North Carolina : a study in stability. The American Naturalist. 118: 499-519.
- Sutherland, J.P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. Ecology. 71: 955-972.
- Swearer, S.E., J.E. Caselle, D.W. Lea and R.R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature. 404(6763): 799-802.
- Thomas, B. et R. Tremblay. 1999. Distribution of *Mytilus edulis* and *Mytilus trosslus* in Quebec and the vicinity of the Maritimes, Canada. MAPAQ-DIT- Doc. rech. R99/01: 1-24.
- Todd, C.D. 1998. Larval supply and recruitment of benthic invertebrates: Do larvae always disperse as much as we believe? Hydrobiologia. 376: 1-21.
- Todd, C.D., W.J. Lambert, J.P. Thorpe. 1998. The genetic structure of intertidal populations of two species of nudibranch molluscs with planktotrophic and pelagic lecithotrophic larval stages: are pelagic larvae "for" dispersal? Journal of Experimental Marine Biology and Ecology. 228: 1-28.
- Toro, J.E. et M. Vergara. 1995. Evidence for selection against heterozygotes: post-settlement excess of allozyme homozygosity in a cohort of the Chilean Oyster, Ostrea chilensis Philippi, 1845. The Biological Bulletin. 188: 117-119.
- Toro, J., D.J. Innes et J. Thompson. 2004. Genetic variation among life-history stages of mussels in a *Mytilus edulis–M. trossulus* hybrid zone. Marine Biology. 145: 713–725.
- Tremblay, R.M., B. Myrand et J.-M. Sevigny, 1998. Genetic characterization of wild and suspension-cultured blue mussels (*Mytilus edulis* Linneaus, 1758) in the Magdalen Islands (southern Gulf of St. Lawrence, Canada). Journal of Shellfish Research 17: 1191-1202.
- Turner, S.J. et C.D. Todd. 1993. The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews, N.E. Scotland. Journal of Experimental Marine Biology and Ecology. 166: 251-272.
- Véliz, D., E. Bourget et and L. Bernatchez. 2004. Regional variation in the spatial scale of selection at MPI* and GPI* in the acorn barnacle Semibalanus balanoides (Crustacea). Journal of Evolutionary Biology. 17: 953–966.

- Weir, B.S. et C.C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38: 1358-1370.
- Weisshappel, J.B.F. et J. Svavarsson J. 1998. Benthic amphipods (Crustacea: Malacostrata) in Icelandic waters: diversity in relation to faunal patterns from shallow to intermediate deep Artic and North Atlantic Oceans. Marine Biology. 131: 133-143.
- Wright, S. 1978. Evolution and the genetic of populations, vol. 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago.
- Zane, L., L. Ostellari, L. Maccatrozzo, L. Bargelloni, J. Cuzin-Roudy, F. Buchholz et T. Patarnello. 2000. Genetic differentiation in a pelagic crustacean (*Meganyctiphanes norvegica : Euphausiacea*) from the North East Atlantic and the Mediterranean Sea. Marine Biology. 136 (2): 191-199.
- Zouros, E. et D.W. Foltz. 1984. Possible explanations of heterozygote deficiency in bivalve molluscs. Malacologia. 25: 583-591.

ANNEXE I

Shéma du système de boudin suspendus utilisé au Canada Atlantique pour l'aquaculture de



moule (tiré de Mallet et Myrand, 1995).