VARIABILITÉ DE LA CONNECTIVITÉ ET DU RECRUTEMENT AU SEIN D'UNE MÉTAPOPULATION MARINE

Thèse

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Résumé

La connectivité des populations marines est un élément majeur de la démographie des métapopulations, car elle constitue le lien entre les sous-populations. Chez les invertébrés marins ayant un cycle vital bentho-pélagique, la connectivité se produit au cours de la dissémination larvaire, laquelle est principalement dirigée par les courants marins. L'objectif principal de cette étude est de mettre en évidence la variabilité de la connectivité dans les métapopulations marines, et particulièrement pour les populations de *Mytilus* spp. dans l'estuaire maritime du Saint-Laurent. L'objectif secondaire consiste à analyser les variations spatiotemporelles de la colonisation et du recrutement dans ce système, car ils représentent des processus essentiels de la connectivité. (1) Les différentes méthodes pour mesurer la connectivité et sa variabilité sont exposées, ainsi que leur applicabilité dans différents systèmes. Après avoir décrit les principaux facteurs influençant la connectivité, les éléments moteurs d'une telle variabilité et leurs implications pour les métapopulations marines et la gestion de la biodiversité sont discutés. (2) Par ailleurs, des études sur le terrain ont été effectuées et ont révélé une variabilité saisonnière et interannuelle de la colonisation de *Mytilus* spp. dans l'écosystème boréal du Saint-Laurent. Ces observations ont montré que la colonisation, faisant suite à la phase initiale de dissémination larvaire (c.-à-d. large échelle spatiale), se déroule sur une ou deux courtes périodes (de 1 à 2 semaines) au cours de la saison de reproduction. De plus, une phase de colonisation secondaire effectuée par des stades post-métamorphiques (juvéniles) a été démontrée tout au long de la saison de reproduction. Cette phase constitue une part importante de l'ensemble de la colonisation observée, particulièrement dans les semaines suivant les évènements de recrutement primaire larvaire et les périodes de tempête. (3) Finalement, une méthode géostatistique, basée sur la relation entre la biomasse d'adultes et le recrutement dans les différentes sous-populations, a permis de mettre en évidence un couplage démographique homogène à une distance de 12-24 km au cours des cinq années d'études, dans la direction du courant dominant. Dans l'ensemble, cette étude confirme de manière empirique l'importance des fluctuations de la biomasse d'adultes, de la colonisation et du recrutement

pour déterminer la variabilité de la connectivité des métapopulations marines et supporte ainsi les études théoriques considérant ces fluctuations.

Abstract

Connectivity of marine populations represents a key element of metapopulation demography, as it links local populations. For marine invertebrates with a bentho-pelagic life cycle, connectivity occurs during the dispersive larval stage, which is primarily driven by marine currents. The main objective of this study was to show the variability of connectivity within marine metapopulations, especially for *Mytilus* spp. populations in the St. Lawrence maritime estuary. The secondary objective was to further analyse the spatiotemporal variations of settlement and recruitment in this system, since these processes are essential for connectivity. (1) Different methods to assess the variability of connectivity are described, as well as their applicability to different systems. Following a description of the main factors influencing connectivity, the drivers of variability and their implications for marine metapopulations and biodiversity management are discussed. (2) In addition, field studies were conducted and revealed seasonal and inter-annual variability of *Mytilus* spp. settlement in the boreal St. Lawrence marine ecosystem. These observations showed that settlement, following the initial larval dispersal phase (i.e. large spatial scale), occurred during one or two short periods of time (1 to 2 weeks) during the reproductive season. Moreover, there was also evidence for a secondary post-metamorphic settlement phase (juneniles) that extended over the entire reproductive season and represented a major part of the total settlement, particularly during weeks following primary larval settlement events and storms. (3) Finally, a geostatistic method, based on the relationship between adult biomass and recruitment in different local populations, identified homogeneous demographic coupling at scales from 12-24 km over a five year study, in the direction of the main current. Overall, this study empirically confirms the importance of variations in adult biomass, settlement, and recruitment in determining the variability of connectivity in marine metapopulations and supports theoretical studies considering such fluctuations.

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Avant-propos

Cette thèse comprend une introduction et une conclusion générale (Chapitres 1 et 5), ainsi que trois chapitres principaux (2 à 4) rédigés sous forme d'articles scientifiques en anglais dont je suis le premier auteur, et dont deux sont publiés à ce jour.

Le chapitre 2 constitue un chapitre dans le livre *Oceanography*, il est publié sous la référence : **Le Corre N.**, Guichard F., Johnson L.E. (2012). Connectivity as a management tool for coastal ecosystems in changing oceans. M. Marcelli (éditeur), édition InTech Science : p. 235-258, DOI 10.5772/27704.

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Le chapitre 4 sera soumis à une revue internationale d'écologie. Les coauteurs sont Frédéric Guichard, Ladd E. Johnson et Geneviève K. Smith qui m'a fourni les données pour l'année 2005.

J'ai effectué la collecte et l'analyse des données (laboratoire et statistiques) de chaque expérience, ainsi que la rédaction de chaque chapitre, sous la supervision de mon directeur Ladd Johnson et de mon codirecteur Frédéric Guichard.

Chapitre 1. Introduction Générale

"Metapopulations are systems of local populations connected by dispersing individuals"

Hanski et al. 1991

En écologie, les phénomènes étudiés opèrent à des échelles spatiotemporelles variées. Il est donc essentiel de bien définir les échelles auxquelles opèrent les différents processus (Levin 1992). Les nombreux principes qui influencent la démographie des populations (ex. : distribution, abondance et interactions entre espèces) s'appliquent à différentes échelles, varient en fonction de celles-ci et sont même parfois intégrés sur plusieurs échelles (Levin 1992; Chase & Leibold 2002). Aux variations dues à l'échelle d'observation, il faut ajouter la variabilité inhérente aux processus écologiques, qui nécessite de réaliser des études à des échelles temporelles et spatiales variées afin de mieux connaître les processus et leurs fluctuations (Levin 1992). Chaque échelle d'étude permet donc d'identifier des concepts qui lui sont propres (Wiens 1989; Levin 1992; Hubbell 2001). Jusqu'à récemment en écologie, la plupart des études empiriques étaient menées à l'échelle locale (moins de 1 km), pour des raisons techniques, pratiques ou financières, sur des populations considérées « ouvertes », car les relations avec les populations environnantes étaient méconnues. Les théories qui en découlent ne sont donc souvent valables qu'à une échelle locale (Leibold et al. 2004). Pour une population, on peut ainsi observer une certaine dynamique à l'échelle locale, mais celle-ci est susceptible de varier si on considère une échelle plus grande (Dayton et al. 1992; Levin 1992).

1.1 Les métapopulations

Tout comme les populations permettent d'étudier un ensemble d'individus occupant un territoire donné dont les individus interagissent (Waples & Gaggiotti 2006), les métapopulations permettent de considérer plusieurs populations (ou sous-populations) qui interagissent entre elles par le biais de déplacements d'individus entre les populations (Hanski 2004). Cette théorie s'applique à des régions regroupant plusieurs populations (ex. : îles, forêts fragmentées) et permet donc d'étudier des processus écologiques qui opèrent à plus grande échelle spatiale (échelle régionale) que les études de populations locales (Kritzer & Sale 2004). Le concept de métapopulation s'applique à de nombreuses espèces occupant en permanence ou périodiquement des habitats pouvant être hétérogènes, séparés les uns des autres (ex. : île ou « patch ») et connectés entre eux (Hanski 2004). Cependant, pour être appliquée à de plus nombreux systèmes, cette approche théorique de métapopulation est également utilisée pour des espèces ayant une distribution spatiale moins clairement définie, mais montrant des échanges d'individus entre les différentes sous-populations (Hanski 2004). Les populations locales ont généralement une démographie dynamique (c.-à-d. : en non-équilibres) dans l'espace et le temps, elles peuvent persister malgré des extinctions de populations locales par le biais, notamment, de recolonisations provenant de la dissémination d'individus d'autres populations connectées (Husband & Barrett 1996; Ellner & Fussmann 2003). Chaque sous-population a donc une probabilité réelle d'extinction à l'échelle locale, mais la métapopulation peut persister à l'échelle régionale; néanmoins, cette condition d'extinction est facultative (Hanski 2004). La théorie des métapopulations, qui a un rôle primordial dans l'écologie actuelle, s'est développée principalement au début des années 1990 avec des études menées sur des populations terrestres présentant des dispersions d'individus (Ims & Steen 1990; Stacey & Taper 1992; Heikkila et al. 1994). Dans un contexte où la fragmentation des habitats est largement répandue, la perspective des métapopulations permet d'étudier la dynamique d'une population dans son ensemble, et ainsi permettre une gestion plus adaptée à grande échelle spatiale (Cushman 2006). Par conséquent, cette théorie des métapopulations a été adaptée à divers systèmes ayant des sous-populations isolées, dynamiques et connectées entre elles (Hanski 1999).

Les écologistes marins ont adapté le concept de métapopulation dans les années 1990 afin de mieux étudier, comprendre et gérer les populations marines (Grimm et al. 2003; Kritzer & Sale 2004). L'assouplissement de certains critères du concept de métapopulation (voir paragraphe précédent) ont permis l'adaptation de ce concept aux milieux marins et de l'appliquer à de nombreux systèmes. Notamment, la nécessité d'extinction des populations locales, ainsi que le besoin de considérer des habitats et des populations homogènes et précisément délimitées ont été nuancés, car elles ne s'appliquent que très rarement à des systèmes marins (Kritzer & Sale 2006). En effet, les phénomènes d'extinction sont plus difficilement observables en milieu marin, car les mécanismes impliqués sont nombreux et agissent à des échelles de temps importantes (Hixon et al. 2002; Smedbol et al. 2002). Aussi, la fragmentation est moins claire dans le domaine marin que dans le domaine terrestre et donc les limites de certains habitats peuvent être moins évidentes (Kritzer & Sale 2006). De plus, le rôle capital des migrations d'individus par le biais des phénomènes de dissémination a été confirmé dans les écosystèmes marins (Kritzer & Sale 2004). Comme le vent en milieu terrestre, l'eau offre peu de barrières à la dissémination dans le milieu marin et permet une grande dissémination des individus et donc du flux génique pouvant s'étendre à grandes échelles (> 100 km) (Kinlan & Gaines 2003; Kritzer & Sale 2006). Par ailleurs, l'eau va également permettre des perturbations anthropogéniques de grandes ampleurs (ex. : marée noire, réchauffement climatique, pêche, introduction d'espèce), pouvant entraîner d'importantes pertes d'habitats et une forte mortalité pouvant mener jusqu'à l'extinction de certaines populations (Connell et al. 2004). Le concept de métapopulation, appliqué au domaine marin, permet donc de considérer des processus agissant à grandes échelles par rapport aux théories plus « classiques » qui considèrent une échelle plus petite et les sous-populations séparément. Ce réseau de sous-populations s'avère prépondérant dans la dynamique des métapopulations et la gestion des écosystèmes (Hanski 1999; Palumbi 2003; Kritzer & Sale 2004; Gilarranz & Bascompte 2012).

1.2 La connectivité démographique

La connectivité démographique représente l'ensemble du réseau d'échange d'individus entre des sous-populations géographiquement séparées formant la métapopulation (Hansson 1991; Cowen & Sponaugle 2009). Les individus échangés entre les populations permettent de conserver des similarités génétiques et favorisent la persistance de la métapopulation en influant, par exemple, sur les taux de colonisation, l'abondance ou la structure d'âge de chacune des sous-populations (Bell et al. 2001). Au sein de ce réseau de sous-populations connectées, les sous-populations vont avoir des rôles variables dans le temps en fonction de leur influence sur l'ensemble de la métapopulation (ex. : populations sources, puits). L'importance de la dispersion d'individus sur la démographie de la métapopulation est variable au cours du temps et le rôle des sous-populations peut ainsi être remanié (Kritzer & Sale 2004). L'ensemble des évènements de dissémination (colonisation) qui se terminent par un succès (recrutement), couplé aux perturbations démographiques (émigration, mortalité) et à la disponibilité en habitats vont ainsi structurer la métapopulation au fil des générations qui se succèdent (Bell et al. 2001; Cowen et al. 2006). Les différentes cohortes vont influencer différemment la démographie des populations locales en fonction du schéma de dispersion et de la distance entre les populations et avoir un rôle prépondérant sur la persistance des métapopulations marines (Bell et al. 2001; Cowen et al. 2006).

L'échelle de connectivité démographique des métapopulations est variable dans l'espace et dans le temps en fonction des caractéristiques de dissémination de l'espèce, des particularités de chaque sous-population et du système étudié (Kinlan & Gaines 2003; Shanks et al. 2003). En écologie marine, la connectivité est souvent liée aux phases de dissémination entre les sous-populations, qui sont en partie ou complètement guidées par les courants marins. Le lien direct joignant les populations adultes et leurs impacts sur le recrutement local ont été peu étudiés, (Hughes et al. 2000) car il existe peu de méthodes pour analyser ces phénomènes ayant des échelles spatiotemporelles très variables et montrant une forte hétérogénéité (Raffaelli et al. 2003). La durée des phases de dissémination peut être très variable en milieu marin, allant de quelques minutes à plusieurs mois en fonction des espèces et de leur cycle vital (Shanks et al. 2003). Par conséquent, les échelles de dispersion sont tout aussi variables, allant de quelques centimètres à plusieurs centaines de kilomètres (Kinlan & Gaines 2003; Shanks et al. 2003). Cependant, malgré cette possibilité de disséminations à grandes échelles spatiales, de récentes études ont montré que ce type d'évènements est plus limité qu'on le pensait auparavant, montrant même des possibilités d'autorecrutement (c.-à-d. rétention locale des recrues sur un même site) ayant un rôle important sur la persistance des sous-populations (Caley et al. 1996; Warner & Cowen 2002; Cowen et al. 2006; Levin 2006). Selon les espèces, la phase de dissémination est liée aux particularités des différents stades de vie permettant le déplacement des organismes, couplé aux caractéristiques hydrodynamiques du milieu et à leur variabilité spatiotemporelle (Cowen & Sponaugle 2009).

1.3 La connectivité chez les invertébrés marins

Les invertébrés marins ont majoritairement un cycle vital complexe avec une phase benthique et une phase pélagique. C'est généralement la phase larvaire planctonique qui permet la dissémination, les adultes et les juvéniles étant majoritairement sessiles dans la zone benthique. L'importance de la phase larvaire dans la dissémination est due, d'une part à l'action des courants dispersant les larves sur potentiellement de grandes distances, et d'autre part à la faible mobilité des phases benthiques adultes et juvéniles. Pour la plupart de ces espèces, l'échelle spatiale de dispersion est corrélée à la durée de la phase larvaire planctonique qui peut durer plusieurs semaines (Thorson 1950) et ainsi permettre la dispersion à plusieurs dizaines de kilomètres de la population source (McQuaid & Phillips 2000; Siegel et al. 2003). Malgré son rôle clé en écologie benthique, les estimations des distances de dissémination larvaire sont très difficiles à mesurer en raison de la petite taille des individus (< 1 mm) en comparaison à l'étendue du milieu marin.

Face à la difficulté d'estimer la connectivité et sa variabilité spatiotemporelle en effectuant un traçage direct des larves, la plupart des estimations de la connectivité sont le fruit d'études théoriques ou empiriques indirectes (Cowen et al. 2006; Cowen & Sponaugle 2009). Ces récentes études sont souvent basées sur la génétique des populations qui intègrent plusieurs générations ou des simulations de modèles physiques hydrodynamiques (Gilg & Hilbish 2003; Palumbi 2004; Kinlan et al. 2005). Ces types d'études ont notamment permis de réviser les estimations antérieures associées à la théorie des océans « ouverts » qui surévaluaient les distances de dispersion et donc la connectivité au sein des populations d'invertébrés marins (Roughgarden et al. 1985; Gaines & Bertness 1992). Depuis, diverses théories ont vu le jour afin d'expliquer les variations et la provenance du recrutement dans les populations de différents systèmes (Hughes et al. 2000; Smith et al. 2009). À l'opposé de la théorie des populations « ouvertes », considérant que le recrutement proviendrait d'un « pool » larvaire commun créé par l'ensemble des populations de la métapopulation, il y a la théorie des populations « fermées » qui stipule que le recrutement dans une population serait uniquement issu de la même population; on parle aussi d'autorecrutement (Hixon et al. 2002). Entre ces deux concepts, on retrouve, par exemple, la théorie du couplage démographique qui reconnait le rôle des populations adultes connectées sur l'apport larvaire et le recrutement reçu par les populations situées à une distance donnée (*spatial lag*) (Smith et al. 2009). Cependant, ces diverses théories sur la connectivité entre les populations ne sont pas exclusives entre elles et sont généralement fonction de l'échelle d'étude. Les différentes méthodes utilisées pour déterminer les schémas de connectivité s'intéressent principalement au processus de connectivité dans son ensemble, en l'intégrant parfois sur plusieurs années. Cependant, pour mieux cerner les sources de variabilité, il serait intéressant de décomposer la connectivité en différentes phases. La connectivité au sein des populations bentho-pélagiques peut être décomposée en trois phases distinctes : l'apport larvaire des populations sources, la dissémination larvaire et les effets post-colonisations qui aboutissent au recrutement d'individus (Pineda et al. 2007; Cowen & Sponaugle 2009).

1.3.1 **Reproduction et dissémination larvaire**

Si la phase de dissémination larvaire est généralement considérée comme la plus importante, la première étape visant à connecter deux populations d'invertébrés marins est l'émission de gamètes ou de larves par les populations sources. De multiples facteurs entrent en jeu lors de cette phase, qui peut commencer plusieurs mois avant la ponte, et influencent l'intensité des évènements de ponte et ultimement le recrutement dans la population d'accueil. L'apport larvaire est sujet à une grande variabilité puisque divers facteurs (ex. : condition des parents, nourriture disponible) opèrent à différentes échelles spatiotemporelles en fonction de l'espèce et du système. Malgré la relative stabilité à moyen terme des populations locales adultes, d'importantes fluctuations temporelles sont observées entre les différents évènements de reproduction dont la fréquence et l'intensité varient au cours du temps (ex. : Harris et al. 1998; Lipcius & Stockhausen 2002). De plus, l'hétérogénéité des populations (ex. : abondance, densité) provoque de larges fluctuations spatiales de l'apport larvaire provenant des différentes sous-populations. L'ensemble des variations constatées à différentes échelles spatiotemporelles en amont de la phase de dissémination larvaire contribue donc à augmenter les variations du processus de connectivité.

Les schémas de dispersion larvaire, étroitement associés à la connectivité entre les sous-populations, sont principalement dirigés par les courants océaniques et, dans une moindre mesure, par le comportement des larves (Cowen et al. 2006). Malgré une certaine influence (Kingsford et al. 2002), le comportement des larves est souvent considéré comme négligeable par comparaison aux courants qui jouent un rôle prépondérant dans la dissémination larvaire, les larves sont donc souvent considérées comme des particules passives pendant la phase planctonique (McQuaid & Phillips 2000; Gilg & Hilbish 2003; Siegel et al. 2003). Cette phase de dissémination larvaire est donc étroitement liée aux phénomènes physiques ou biologiques qui régissent les courants océaniques et le développement larvaire; elle dépend donc du système et de l'espèce étudiée (Cowen & Sponaugle 2009). Bien que le régime océanique soit plutôt constant dans la plupart des systèmes, la dispersion larvaire est soumise à la variabilité des processus physiques. Les variations hydrodynamiques peuvent ainsi faire varier les schémas de dispersion en les influençant depuis le déclenchement de la ponte jusqu'au recrutement dans la population d'accueil.

1.3.2 La colonisation et le recrutement

Chez les invertébrés marins, la phase de dissémination larvaire dans la colonne d'eau se termine par le passage à un mode de vie benthique. Lorsque la larve est devenue compétente, elle va pouvoir chercher et coloniser un substrat d'accueil. Cette première fixation est généralement accompagnée d'une métamorphose de l'organisme qui va lui permettre d'acquérir de nouvelles fonctions morphologiques adaptées à ce nouveau mode de vie benthique; on parle alors de post-larve (*post-larva*) ou recrue primaire (*primary settler*). Suite à la métamorphose, l'organisme peut explorer (de manière volontaire ou involontaire) et tester le substrat à la recherche d'un habitat plus approprié à son établissement à long terme; les individus issus de ces déplacements exploratoires sont appelés des recrues secondaires (*secondary settlers*). Le recrutement est complété dans la population d'accueil quand le nouvel individu a atteint une certaine taille et qu'il est bien établi dans la population, on parle alors de juvénile (*juvenile*). La différenciation entre ces stades est importante, car les processus impliqués peuvent être très variables et mettre en jeu des échelles spatiotemporelles différentes (Rodriguez et al. 1993).

Faisant suite à la phase de dissémination, la colonisation du substrat menant au recrutement dans la population d'accueil constitue la fin du processus connectant deux sous-populations (Pineda et al. 2007; Cowen & Sponaugle 2009). Pendant la phase post-métamorphose, les organismes sont plus matures qu'au stade larvaire et le comportement des individus (ex. : reptation, dérive du byssus, délogement volontaire) a donc une influence plus importante sur les déplacements. Cependant, chez la majorité des organismes le processus de colonisation est principalement dirigé par des processus physiques (ex. : courants, vagues) qui sont propres aux sites (Wing et al. 2003) et dont l'influence est variable en fonction des espèces (Rodriguez et al. 1993). Toutefois, la disponibilité d'habitat et les processus biologiques (ex. : prédation, compétition) agissant immédiatement après la colonisation primaire vont aussi être primordiaux lors de l'établissement des individus dans la population d'accueil (Rodriguez et al. 1993; Caley et al. 1996). Chaque population ayant ses particularités, les mécanismes impliqués entre la colonisation et le recrutement sont très variables dans l'espace (ex. : site, région) dans le temps (ex. : saisons) et en fonction des espèces (Rodriguez et al. 1993; Gosselin & Qian 1997; Hunt & Scheibling 1998).

La connectivité démographique affiche donc de multiples sources de variations au cours des différentes phases qu'elle comporte et elles sont principalement liées aux processus biotiques et abiotiques régissant l'ensemble des schémas de connectivité. En plus de ces variations inhérentes à la connectivité, il est nécessaire de considérer la variabilité entre les différentes études. En effet, l'échelle temporelle utilisée et le système étudié vont avoir des rôles essentiels sur l'estimation de la connectivité et sa variabilité (Wiens 1989). Cependant, la faisabilité de ce type de recherche est récente et les ressources nécessaires pour mesurer la connectivité sont importantes, la variabilité de la connectivité n'a donc que très rarement été évaluée de manière empirique sur plusieurs années (Levin 2006; Cowen & Sponaugle 2009; Jones et al. 2009). La plupart des récentes études de connectivité se sont concentrées sur la provenance des individus et l'influence de l'autorecrutement sur certaines populations au cours d'un seul évènement de dissémination (ex. : Thorrold et al. 2002; Almany et al. 2007; Becker et al. 2007; Christie et al. 2010). Malgré des avancées importantes sur les mesures de connectivité, il n'y a que très peu d'études (Miller & Shanks 2004; Carson 2010; Hogan et al. 2012) qui ont répété ce type de travaux pendant plusieurs années afin d'estimer la stabilité de la connectivité et l'ampleur de sa variabilité au cours du temps au sein de métapopulations marines. La variabilité de la connectivité demeure donc encore méconnue et l'impact de telles variations sur la dynamique des métapopulations pourrait donc être capital pour la gestion des écosystèmes et des aires marines protégées (Aiken & Navarrete 2011).

1.4 **La moule bleue : *Mytilus* spp.**

Le modèle biologique utilisé pour réaliser cette étude sur la dynamique d'une métapopulation marine est le complexe *Mytilus* spp., communément appelé la moule bleue. Comme la plupart des invertébrés marins, son cycle vital montre une phase adulte sessile et une phase larvaire pélagique durant plusieurs semaines qui permettent une dissémination potentielle de plusieurs kilomètres. Chez les moules marines de la famille des Mytilidés, incluant les espèces du genre *Mytilus*, cette phase adulte sessile implique une fixation à des substrats principalement rocheux par le biais de filament de byssus. Par ailleurs, la moule bleue a une très importante aire de répartition; elle est présente dans les zones tempérées du monde entier, jusque dans les zones boréales et subarctiques. Aussi, cette espèce occupe un rôle majeur d'ingénieur écologique au sein de la communauté benthique de l'étage médiolittoral; il s'agit donc d'une espèce bien étudiée (Seed 1976; Menge et al. 1994; Gutierrez et al. 2003). Ces caractéristiques font que les moules bleues constituent d'importantes métapopulations benthiques, dont la connectivité entre les sous-populations et le recrutement sont assurés par la phase larvaire de l'organisme (Gosling 1992; Caley et al. 1996). Par conséquent, la moule bleue constitue un excellent modèle pour étudier la variabilité de différents aspects de la connectivité au sein des métapopulations marines.

Pendant la phase benthique, les moules bleues sont présentes dans les étages infralittoraux et médiolittoraux (zone basse et moyenne), ce qui permet d'observer directement l'évolution démographique des sous-populations et leur variabilité spatiotemporelle. Les juvéniles deviennent matures environ un an après leur fixation (Seed 1976) et pondent directement dans la colonne d'eau des gamètes qui, après fécondation, donnent rapidement naissance à des larves. Les capacités natatoires limitées des larves de moules permettent d'assimiler la dispersion des larves aux courants de surface (McQuaid & Phillips 2000; Gilg & Hilbish 2003), mais elles demeurent trop petites (< 250 µm) pour être techniquement traçables directement dans la colonne d'eau. La durée de la phase larvaire dépend de différents paramètres propres à chaque système et peut s'étirer sur plusieurs semaines (Seed & Suchanek 1992). Le cycle vital s'achève par la colonisation et la métamorphose sur un substrat approprié (recrue primaire). Cependant, l'individu fixé peut encore se détacher si l'endroit n'est pas propice à un bon développement et se fixer ailleurs (recrue secondaire) à la suite de déplacements exploratoires à l'échelle locale (Bayne 1976; Lutz & Kennish 1992; Seed & Suchanek 1992; Newell et al. 2010; Shanks & Shearman 2011). Les caractéristiques de ces recrues secondaires (ex. : durée de l'exploration, comportement actif ou passif) sont mal connues chez *Mytilus* spp. car ces individus sont difficiles à suivre en raison de leur petite taille (< 2 mm) (Newell et al. 2010). À l'âge adulte, les déplacements des moules s'effectuent principalement sur de faibles distances (< 160 m; Petrovic & Guichard 2008).

Dans l'estuaire et le golfe du Saint-Laurent (EGSL) situé dans l'est du Canada (Québec), l'influence des marées, dont le marnage semi-diurne peut atteindre quatre mètres, offre aux populations médiolittorales un vaste habitat sur les rives de l'EGSL. En revanche, les moules bleues sont très peu représentées dans la zone infralittorale de l'EGSL (Hamdi H., Le Corre N. et al., données non publiées). Le substrat rocheux occupe les rives de l'EGSL en alternance avec des étendues sableuses, la proportion de chaque type de substrat varie en fonction des régions dans l'EGSL. Les surfaces rocheuses sont principalement occupées par des algues et des invertébrés marins, dominés par le complexe *Mytilus* spp.. Les moules bleues sont généralement absentes des zones de sédiment meuble dans l'EGSL (Le Corre N., données non publiées). On distingue sur les rives de l'EGSL différentes populations de moules de tailles variables qui sont séparées géographiquement les unes des autres en fonction des habitats disponibles et de la dynamique des populations (Ardisson & Bourget 1991; Bélanger 2009; Smith et al. 2009). On y retrouve deux espèces génétiquement distinctes, *Mytilus edulis, M. trossulus*, ainsi que leurs hybrides. À l'état pur, *Mytilus edulis* et *M. trossulus* sont très difficilement différentiables morphologiquement (McDonald et al. 1991), et ainsi en est-il de leurs hybrides qui sont vastement répandus le long des rives de l'EGSL (Thomas et al. 2004, Turgeon J. & Roby C., données non publiées). De plus, tant les espèces pures que les hybrides montrent des caractéristiques écologiques semblables, malgré quelques différences lors de la reproduction (Toro et al. 2002; Thomas et al. 2004; Toro et al. 2004). Dans ce contexte, le complexe *Mytilus* spp. est considéré dans son ensemble dans la présente étude. Par ailleurs, l'EGSL étant situé dans les zones subarctique et boréale, les propriétés physiologiques (ex. : développement larvaire, taux de croissance des adultes) de la moule bleue sont ralenties, entre autres paramètres, par les faibles températures (Sprung 1984; Widdows 1991). La présence de glace en hiver, de décembre à avril (Saucier et al. 2003), peut également influencer la phase benthique en causant des perturbations influençant la démographique des sous-populations à l'échelle du système (Bergeron & Bourget. 1984). La structure spatiale des populations est donc susceptible de changer au fil des années et donc d'influencer la connectivité (Underwood 2000; Gutt 2001). Bien qu'il existe de nombreuses études sur le recrutement de la moule bleue, il n'y a que peu d'étude sur la connectivité et la dissémination de cette espèce (ex. : Navarrete et al. 2005; Broitman et al. 2008; Menge et al. 2011), et encore moins dans l'EGSL (Smith et al. 2009).

1.5 **Le système d'étude**

En raison de sa taille importante, l'EGSL est un système dans lequel la circulation est complexe et offre des conditions environnementales variées, avec de forts gradients physico-chimiques régissant les limites de dispersion des espèces (Ardisson & Bourget 1991). L'estuaire maritime, situé dans la partie amont de l'EGSL, est soumis à l'influence des marées et montre donc des salinités allant de 0 à 34 ‰ entre l'amont (Québec) et l'aval (le golf du Saint-Laurent). En surface, les températures varient de –1,7 à 20 °C au cours de l'année. Par ailleurs, la largeur de l'estuaire sur la zone d'étude est de 20 à 50 km, on y observe notamment des phénomènes à grandes échelles comme des tourbillons de plusieurs dizaines de kilomètres, des remontées d'eau (*upwelling*), des jets de rives ou des fronts de densité et de marée (El-Sabh 1990; Koutitonsky et al. 1990; Mertz et al. 1990; Sheng 2001). La variabilité de ces phénomènes peut-être importante, car ils dépendent de différents facteurs comme le débit d'eau douce, les vents ou la marée (Benoit et al. 1985; El-Sabh 1990; Mertz et al. 1990). Par ailleurs, la morphologie des rives de l'estuaire maritime est hétérogène et montre des différences entre le nord et le sud. Au nord, la côte est généralement plus abrupte et montre une zone médiolittorale moins étendue qu'au sud et on y observe plus de zones de substrat meuble (sable). Au sud, la topographie est plus plane et d'une composition plus rocheuse (Le Corre N., données non publiées).

La zone d'étude des travaux présentés dans cette thèse se situe sur la rive sud de l'estuaire maritime du Saint-Laurent où le courant de surface principal est celui de Gaspé. Il est généré par l'apport d'eau douce du fleuve Saint-Laurent et de ses affluents. Il s'agit d'un courant côtier de surface qui est principalement unidirectionnel vers l'aval (transport net), parcoure plus de 1 m.s^{-1} en été et montre des salinités moyennes comprises entre 24 et 33‰ entre juin et septembre (Benoit et al. 1985; données Obsersatoire Global du Saint-Laurent, 2013). La majorité des études de cette thèse ont été réalisées sur la côte de la Gaspésie entre Pointe Mitis et Ste-Anne-des-Monts. Malgré l'importante variabilité qui existe à l'échelle de l'EGSL, il s'agit d'une côte principalement rocheuse d'environ 100km de long où la topographie et les conditions environnementales sont homogènes (Ouellet et al. 2011). Cependant, la présence de quelques baies peut influencer la distribution des populations benthiques, et notamment la moule bleue (Archambault & Bourget 1999), tout comme les légères variations du substrat qui existent à de plus faibles échelles spatiales (Archambault & Bourget 1996; McKindsey & Bourget 2000; Guichard et al. 2001).

1.6 **Objectifs**

Cette thèse a trois objectifs principaux, il s'agit : (1) d'identifier les différentes sources de variabilité de la connectivité démographique et d'évaluer les conséquences de ces variations au sein de métapopulations marines, (2) de caractériser le rôle des processus de colonisation et de recrutement sur la connectivité et (3) de mesurer empiriquement les échelles spatiales de la connectivité démographique et leur variabilité. Le premier objectif décompose le processus de connectivité démographique en plusieurs sections afin de mieux distinguer les sources de variation chez les invertébrés marins, alors qu'ensuite (chapitre 3 et 4) j'étudie la variabilité de la colonisation et de la connectivité au sein d'une métapopulation de *Mytilus* spp..

Le chapitre 2 a pour but de dresser le tableau des connaissances actuelles sur la connectivité démographique en écologie marine et sa variabilité dans les métapopulations. La connectivité étant un processus essentiel dans la dynamique des populations, elle soulève beaucoup d'intérêt dans différents domaines en lien avec l'écologie et différentes méthodes peuvent être utilisées pour l'estimer. Dans un premier temps, nous décrivons les différentes méthodes permettant de mesurer la connectivité et sa variabilité sur une seule génération et discutons leur applicabilité, points forts et faibles. Une distinction a été effectuée entre les méthodes spécifiques à certaines espèces et celles spécifiques aux systèmes étudiés. Cette nouvelle classification a été jugée nécessaire, car les classifications existantes ne permettaient pas de distinguer l'ensemble des différentes méthodes existant pour mesurer la variabilité de la connectivité. Par exemple, Jacobson & Peres-Neto (2010) suggèrent la distinction entre les méthodes directes qui suivent les organismes individuellement et les méthodes indirectes qui retracent la provenance des individus une fois qu'ils sont arrivés à destination. Cependant, la majorité des techniques identifiées pour mesurer la connectivité dans ce chapitre seraient classées comme des méthodes indirectes. La nouvelle classification permet de classer toutes les méthodes en fonction de leur limite d'applicabilité. Les méthodes spécifiques aux espèces peuvent être utilisées dans plusieurs systèmes, mais sont applicables à un groupe d'espèces en particulier en raison des caractéristiques requises à l'application de la méthode (ex. : otolithes des poissons de récifs). Les méthodes caractéristiques des systèmes peuvent s'appliquer à toutes les espèces du système d'intérêt (ex. : modèle hydrodynamique des courants en Californie).

Une méthode géostatistique est discutée plus en détail dans ce chapitre, car il s'agit de celle employée dans le chapitre 4 de cette thèse pour étudier le type et les distances de connectivité au sein du système d'étude. L'objectif étant de mettre en avant les possibilités de cette méthode, différents scénarios de recrutement sont évoqués et des prédictions utilisant cette technique de géostatistique sont proposées (voir aussi le chapitre 4). Cette technique permet d'examiner la force de la relation statistique (ex. : covariance) entre les populations adultes et les recrues dans différentes populations (covariance croisée ou *cross-covariance*) et évalue les distances auxquelles les deux variables sont corrélées (Rossi et al. 1992). Les résultats sont présentés graphiquement en fonction de la distance entre les deux variables (*cross-covariogram*) afin d'identifier l'échelle spatiale de connectivité au sein de la population étudiée (Smith et al. 2009). Le scénario des populations « ouvertes » associé à des effets post-recrutement prédominants (ex. : effet de la densité-dépendance) est présenté en comparaison à un scénario de couplage démographique, ainsi qu'un scénario basé sur la théorie du « *supply-side* » dans lequel le recrutement est directement basé sur l'apport larvaire des populations situées à proximité (Hughes et al. 2000).

Dans une seconde partie, ce chapitre a pour but d'identifier les facteurs influant la variabilité de la connectivité démographique, car le processus de connectivité peut impliquer un large panel de facteurs agissant à différentes échelles. Par ailleurs, malgré le peu d'études empiriques (ex. : Carson 2010; Hogan et al. 2012) ayant mis en évidence des variations du processus de connectivité, quelques études théoriques en tiennent compte et nous ont permis d'estimer ses impacts sur la dynamique des populations. Finalement, en se basant sur de récentes études théoriques incluant une connectivité variable, les nouvelles orientations quant à la gestion des réseaux d'aires marines protégées sont discutées, ainsi que les implications pour la gestion de la biodiversité et la conservation d'espèces. La théorie des métapopulations est souvent utilisée dans les programmes de gestion et de conservation, mais la connectivité démographique y est fréquemment considérée comme statique.

Si le chapitre 2 concerne l'ensemble des métapopulations marines montrant une phase de dissémination larvaire, les deux chapitres suivants considèrent les invertébrés marins et plus particulièrement un complexe de bivalves répandus dans le monde entier : la moule bleue, *Mytilus* spp.. Ainsi, je me suis intéressé à cette espèce dans l'estuaire du Saint-Laurent (Québec, Canada) où j'ai réalisé les études empiriques exposées dans le deuxième et le troisième chapitre de ma thèse. Les travaux présentés ont été réalisés sur la côte gaspésienne, qui représente une partie de la métapopulation de moules de l'EGSL.

Dans le chapitre 3, je traite trois différents aspects en lien avec le premier objectif de cette thèse : la variabilité temporelle de la colonisation, l'importance de distinguer les types de recrues en termes de connectivité et la variabilité de la phase larvaire chez les recrues primaires. Comme les schémas de colonisation de *Mytilus* spp. et leur variabilité sont méconnus dans notre système d'étude, nous avons examiné le schéma temporel de la colonisation dans ce système boréal. De plus, afin d'obtenir des indices sur la variabilité du processus à différentes échelles temporelles et l'importance du choix de l'échelle d'étude, nous avons répété le même protocole en changeant la fréquence d'échantillonnage au cours de la saison de reproduction de *Mytilus* spp. et répété l'expérience deux années consécutives. Dans une seconde partie de ce chapitre 3, les deux types de recrues sont distingués (voir la section : 1.4 : Mytilus *spp.*) afin d'identifier les processus de dispersion mis en cause lors des différents évènements de colonisation au cours de la saison (dispersion à grande échelle ou locale). Finalement, dans la troisième partie du chapitre 3 j'ai estimé la durée de la phase larvaire planctonique et ses variations au cours de la saison de reproduction à l'aide d'une méthode indirecte basée sur la morphologie des coquilles de recrues (Martel et al. 1999). L'ensemble de ce chapitre 3 permet ainsi d'évaluer la variabilité de différentes caractéristiques essentielles dans la connectivité démographique au sein d'une métapopulation marine.

Dans le chapitre 4, la variabilité interannuelle des populations de moule et du recrutement a été estimée, ainsi que les échelles spatiales de la connectivité démographique et leur variabilité. Bien qu'en apparence les populations médiolittorales d'invertébrés semblent afficher une certaine stabilité, plusieurs facteurs peuvent avoir une influence significative sur les populations et entraîner d'importantes fluctuations (ex. : Sagarin et al. 1999; Menge et al. 2011). Le premier objectif du chapitre 4 est donc d'évaluer la stationnarité interannuelle de la distribution des populations adultes et du recrutement de *Mytilus* spp. à l'échelle de l'estuaire du Saint-Laurent en se basant sur l'important jeu de données qui a été récolté (5 ans, 29 sites, 100km). Dans la deuxième partie du chapitre 4, la nature et la distance auxquelles la connectivité se matérialise dans l'estuaire du Saint-Laurent ont été évaluées indirectement en utilisant la même méthode géostatistique que celle utilisée par Smith et al. (2009), brièvement décrite précédemment (voir p. 13). Cette méthode est basée sur le lien entre les populations adultes sources et leurs impacts sur le recrutement dans les populations d'accueil et permet de déterminer le type de connectivité qui prédomine entre les populations et estimer les distances moyennes de dispersion des individus. Cette technique a déjà permis de mettre en évidence un couplage démographique au cours de l'année 2003, mais la variabilité de la connectivité dans ce système demeure inconnue (Smith et al. 2009). En répétant ces estimations plusieurs années, on a pu ainsi estimer de manière empirique la variabilité de la connectivité à l'échelle régionale et estimer l'échelle de dispersion d'une espèce ayant une phase planctonique de plusieurs semaines.

Les travaux présentés dans cette thèse contribuent aux sujets clés et actuels en écologie marine que sont la connectivité démographique et le recrutement chez les populations marines. En se basant sur une étude du recrutement à l'échelle locale il a été possible de mettre en évidence l'importance du recrutement secondaire chez *Mytilus* spp. et ainsi souligner le fait que le recrutement primaire peut être surestimé. Ce biais a notamment des conséquences importantes lors de l'évaluation de la provenance des recrues et du taux de recrutement, qui constituent des caractéristiques essentielles de la connectivité. Aussi, la nature « nordique » du recrutement a pu être mise en évidence et suggère que la fenêtre de recrutement est restreinte et variable dans le temps et en amplitude. Par ailleurs, la connectivité étant souvent très complexe à mesurer dans le domaine marin en raison de la durée de la phase de dissémination, cette étude constitue l'une des premières à caractériser la connectivité démographique sur plusieurs années. Une stationnarité globale du schéma de dispersion, assortie d'une variabilité extraordinaire de ce schéma en 2008, a été observée sur une période de cinq années malgré la variabilité des structures spatiales du recrutement et des populations de moules dans ce système. Cette variabilité de la connectivité, bien que limitée dans ce système, constitue un phénomène important en regard de la dynamique des populations. En effet, les récentes avancées en écologie théorique traitant de la variabilité de la connectivité ont pu montrer qu'il s'agissait d'un processus essentiel pour la gestion de la biodiversité et des écosystèmes.

Chapitre 2. Connectivity as a Management Tool for Coastal Ecosystems in Changing Oceans

2.1 Résumé

Les espèces qui se dispersent via une phase planctonique sont très répandues dans les systèmes marins où beaucoup d'organismes ont un cycle vital bentho-pélagique. De récentes études considèrent les larves planctoniques comme des agents de dissémination, liant les populations benthiques dans des environnements spatialement structurés. Un tel couplage entre les populations dirige la dynamique des populations à grande échelle à travers la connectivité; celle-ci étant l'intégration de tous les processus se produisant pendant la phase de dissémination et leurs impacts sur la population d'accueil. Dans cette étude, nous examinons les récentes avancées dans notre compréhension de la connectivité des populations dans les systèmes marins et son implication pour la persistance des populations et des écosystèmes à grandes échelles temporelles et spatiales. Notre but est d'approfondir l'intégration de l'écologie larvaire et celle des écosystèmes et de suggérer comment notre connaissance de la connectivité peut aider à la gestion durable à long terme des écosystèmes marins. Nous avons dans un premier temps révisé les outils développés récemment qui permettent de révéler l'hétérogénéité spatiotemporelle des distances de dispersion et du recrutement à une échelle temporelle écologique, en se concentrant sur une méthode de géostatistique basée sur des études écologiques à faible coût. Nous examinons par la suite les processus primaires affectant et causant la variabilité spatiotemporelle de la connectivité et puis nous discutons comment une telle hétérogénéité au cours de la période larvaire peut augmenter l'ampleur des fluctuations spatiotemporelles de l'abondance des populations adultes et des fonctions des écosystèmes. Finalement, nous révisons et proposons de nouvelles théories de connectivité marine qui intègrent l'hétérogénéité à plusieurs échelles des processus de dispersion aux stratégies à long terme de gestion et de conservation de la biodiversité et des écosystèmes. Une telle approche fournit des outils pour améliorer notre compréhension et nos capacités à prévoir les distributions régionales

des populations marines et les services écosystèmiques en se basant sur notre compréhension et notre gestion actuelle de la connectivité marine.

2.2 **Abstract**

Species that disperse via a planktonic phase are widespread in marine systems where many organisms have a bentho-pelagic life cycle. Recent studies have considered planktonic larvae as dispersing agents, which link benthic populations within a spatially-structured environment. Such coupling between populations drives large-scale population dynamics through connectivity; the integration of all processes that occur during the dispersal phase and the impact these have on the recipient populations. Here we examine recent advances in our understanding of population connectivity in marine systems and its implication for the persistence of populations and ecosystems over large temporal and spatial scales. Our goal is to further the integration of larval and ecosystem ecology and suggest how our understanding of connectivity can help the management of long term sustainability of entire ecosystems. We first review recently developed tools that can reveal spatiotemporal heterogeneity in dispersal distance and recruitment at an ecological temporal scale, by focusing on a geostatistical method based on low-cost ecological surveys. We then examine the primary processes affecting and causing spatiotemporal variability in connectivity and then discuss how such heterogeneity during the larval period can scale up to spatiotemporal fluctuations of adult population abundance and ecosystem functions. Finally, we review and propose new theories of marine connectivity which integrate multi-scale heterogeneous processes of dispersal into long term management and conservation strategies of biodiversity and ecosystems. Such an approach provides tools that enhance our understanding of and ability to predict regional distributions of marine populations and ecosystem services based on our current understanding and management of marine connectivity.

2.3 Introduction

Recent theoretical management research has focused on systems from species to ecosystem at large scales (i.e. metapopulations and metaecosystems), and the links between habitats patches and subpopulations are of crucial importance to understand, predict, and manage resource dynamics. One of the key characteristics affecting the dynamics and demography of metapopulations is thus connectivity (Hanski 1999; Moilanen & Nieminen 2002; Kritzer & Sale 2004), the exchange or flux of material between different locations (Cowen & Sponaugle 2009). Because of its broad definition and growing relevance, "connectivity" is now employed in a number of fields, including metapopulation ecology. Consequently, several definitions of connectivity exist with the main differences between them lying in the spatial scale of study (Kadoya 2009). In this review, we consider connectivity in its broadest sense of demographic or population connectivity: the exchange of individuals among geographically separated subpopulations in a metapopulation (Cowen & Sponaugle 2009).

2.3.1 Connectivity in marine ecology

In a marine context, metapopulation structure is defined as populations occupying discrete patches, demographically connected according to a dispersal kernel (the function of propagule abundance vs. distance from the parental source) and potentially affecting the dynamic of the entire ecosystem (Kritzer & Sale 2004). The main difference from equivalent terrestrial systems is that local extinctions rarely occur in marine systems (Kritzer & Sale 2004) as the diverse regulation processes operating in the ocean and their inherent stochasticity lead to lower extinction rates (Hixon et al. 2002). Connectivity is one of these processes and tends to operate over larger spatial scales in marine metapopulations, due to fewer dispersal barriers and a more favorable medium for long distance movement of propagules. However, the potential for self-recruitment, i.e. the retention of propagules within a population, has recently been highlighted in many marine systems and may act as an additional mechanism to prevent extinction (Cowen et al. 2006; Levin 2006; Almany et al. 2007).

In marine ecology, ideas have historically ranged from the extremes of demographically-open systems (fully connected) to closed populations (not connected)(Hixon et al. 2002). For example, fisheries stock recruitment models generally ignored connectivity among populations, and local density-dependent factors were considered the most important parameters in the regulation of the populations. At the other end of the spectrum, recruitment into local populations was thought to occur from a general pool of propagules with new settlers arriving from unknown source populations. These simplifications of immigration and emigration processes were imaginable due to the spatial scales of studies that were either large enough (in the former case of some fisheries) or sufficiently small enough (open populations) to avoid dealing with the more realistic intermediate situations that characterize most marine systems. Connectivity is now, however, recognized to be a primary driver of most large-scale marine population dynamics. This is particularly true for the large number of marine species that are bentho-pelagic, with a stationary phase (e.g. sessile or sedentary juveniles and adults) and a planktonic stage (e.g. larvae, spores) during which dispersal occurs. Thus, marine ecologists have more recently focused on the dispersing agents (i.e. propagules) themselves and how they serve to connect populations. Here we focus on coastal marine invertebrate species with both a stationary and planktonic (dispersive) phase although the principles apply as well to reef fish and seaweeds.

Generally, connectivity is assumed not only to be a function of larval dispersal but also of post-larval survival (Pineda et al. 2007). It implies a large range of scales of connectivity, which are variable between and within species and locations (Kritzer & Sale 2004; Cowen & Sponaugle 2009). Thus, for a species in a specific area, once one knows the pattern of dispersal (i.e. dispersal kernels) and post-settlement processes, patterns of connectivity can then be derived. Unfortunately, this is often more simply said than done as dispersal parameters, such as pelagic larval duration (PLD) and post-settlement processes, that were historically considered to be stable over time (i.e. implying invariant connectivity) can be, in fact, quite variable. Indeed, several recent genetic studies have shown substantial spatial heterogeneity between life stages and temporal variability in genetic structure within metapopulations (Hogan et al. 2010; Selkoe et al. 2010). Likewise, several studies have explored hypotheses of oceanographic variability to explain fine-scale genetic patchiness (Banks et al. 2007) or chaotic genetic patchiness (Hogan et al. 2010), and certain larval transport models suggest that large variations in PLD and recruitment patterns could even be linked to hydrodynamic variability (Bolle et al. 2009; Connolly & Baird 2010). Indeed, even knowledge of the PLD is not sufficient to predict scale of dispersal and gene flow among populations (Mitarai et al. 2009; Weersing & Toonen 2009). Regardless, all these studies emphasize the importance of variation in larval dispersal on the resulting spatial patterns observed in different systems and, consequently, we should investigate connectivity as a varying feature of natural systems. Levels of variation (seasonality, annual variation, and periodicity) need to be examined in depth and methods to assess connectivity should take these variations into account. Connectivity then should be thought of as the net result of all dispersal that has been observed over a given period, and the actual connectivity of the system will arise from the integration of all dispersal processes (Jacobson & Peres-Neto 2010).

2.3.2 **Measurement of connectivity**

As the awareness of connectivity as a crucial characteristic for understanding ecosystems has emerged, a number of methods have been developed to explore and estimate connectivity within metapopulations and metaecosystems. These can differ, however, in their ability to assess variability in connectivity and can be further distinguished by their specificity in measuring dispersal between subpopulations and their applicability to other systems (Cowen et al. 2006; Levin 2006; Cowen & Sponaugle 2009; Jones et al. 2009). Other reviews about connectivity have utilized a classification based on two main categories: direct and indirect methods (Jacobson & Peres-Neto 2010) or natural & artificial markers (Thorrold et al. 2002). Because each method targets a different goal and is often applied to a specific scale, we have chosen instead to classify methods by assessing their specificity to a species or system. The former concentrates on the connectivity of a specific species, giving information on dispersal patterns of the species in the study area. The latter focuses on the dispersal processes (e.g. hydrodynamics) and its variations in a specific study region and can thus be applied to co-occurring species having similar characteristics.

Both types can include methods for assessing connectivity over multiple years (integrative) or for a single event (punctual).

Although using different methods to assess patterns of connectivity of a species in a particular system inevitably leads to different estimates, such predictions should ideally be similar. Regardless, to compare results among methods, the scale at which connectivity is evaluated ought to be the same for all methods (Palumbi 2004; Weersing & Toonen 2009). For example, dispersal distance of blue mussel larvae has been estimated through different methods in various systems, and ranges from <5km to <100km (McQuaid & Phillips 2000; Gilg & Hilbish 2003; Smith et al. 2009). A part of this variability is inherent to the analysis of distinct systems with different methods; more significantly, however, the methods did not estimate the connectivity at the same spatiotemporal scale. For example, Gilg and Hilbish (2003) used a genetic method that averaged over several generations whereas Smith et al. (2009) estimated the pattern of connectivity within a single year. Consequently, when connectivity estimates are compared, attention should be given to the temporal scale employed in the method. The use of multiple methods at different temporal scales may be necessary, however, to completely understand a system, and the application of several methods in a given system should permit measures at different spatiotemporal scales and lead to a better knowledge of the crucial connections between populations.

When comparing different methods of measuring connectivity, it is important to evaluate not only differences in mean connectivity, but also to measure variability in the pattern of connectivity within a specific system. Such variation can arise from biotic or abiotic factors and can affect the connectivity and the dynamics of the system at different scales. Depending on the system, variability of connectivity can result in periodicity, stationarity or more complex behavior of individual populations or the entire ecosystem. Therefore, the range of variation in dispersal patterns needs to be better understood to improve model predictions and management strategies, ideally using a single method over different temporal scales (e.g. day, season or year). However, because assessing connectivity employs newly developed tools, most efforts concentrate on simply evaluating the principal patterns of connectivity; only a few studies have tried to empirically estimate the variability of connectivity itself (Botsford et al. 2009; Jones et al. 2009). Moreover, in spite of the vast choice of methods, only a few are appropriate to assess potential variability of connectivity.

Beyond academic interest in ecosystem functioning, a knowledge of connectivity and its variability is essential for applied environmental problems. It is particularly important for the design of marine protected areas (MPAs) to preserve biodiversity. As reserves integrate many species, it becomes important to consider the dispersal networks of all targeted species to improve coastal management. In this case, multi-scale studies are necessary because of the potential for different species to disperse at different scales, and respond differently to settlement variation.

In this chapter, we examine recent progress in our understanding of population connectivity in coastal marine systems and discuss the implications of variability of connectivity in the persistence of populations and ecosystems over large temporal and spatial scales. We hope to demonstrate how understanding connectivity and its variability can help the long-term sustainable management of entire ecosystems in a variable world. We divide our treatment into three parts. Firstly, we review the recently developed tools from different scientific disciplines concerned with connectivity and classify them as species- or system-specific as well as on their scale of applicability. Secondly, we examine evidence on the variability of observed patterns of connectivity and its causes. Finally, we discuss considerations for management and conservation of ecosystems. In particular, we review different theories and strategies related to populations and ecosystem dynamics that integrate the variability of connectivity in the context of marine protected areas (MPAs).

2.4 **Methods to assess variability in connectivity**

As the interest in population connectivity has grown, so too has the number of methods to estimate connectivity patterns. Several scientific disciplines, including physics, genetics, and microchemistry, have contributed to our improved understanding of dispersal in marine systems. These approaches were originally developed for other reasons, but they can also be applied to estimate the dispersal of individuals and the flux between populations. However, as mentioned above, the diverse life histories, PLD and mobility of different species require that temporal and spatial scales be taken into account, making comparisons among methods tenuous.

The high mortality rate and high diffusion of larvae during the dispersive stage make direct measurements of larval dispersal nearly impossible. Therefore most methods measure dispersal patterns indirectly, e.g. through successful settlers (= recruits). Previous reviews of the methodologies used to measure connectivity distinguished between direct or indirect, or artificial or natural methods (Thorrold et al. 2002; Jacobson & Peres-Neto 2010). Rather than following these dichotomies, we classify connectivity methods according to their applicability to different species or other systems. The first category groups methods that provide results for a particular species. The second includes techniques relevant to particular systems (e.g. bay, reef, or shoreline), and can be applied to other species. For each category, we briefly describe several methods that allow the measurement of variability in connectivity among populations, describe their scale of applicability, and discuss their potential utility. To conclude, we discuss scenarios where several complementary methods can be used within the same system.

2.4.1 Species-specific methods

The three methods presented here have been developed recently to evaluate the dispersal kernel of individual key or representative species. They can be applicable to other species, but require further development to fit the species of interest. The two first methodological approaches rely on sampling individuals for genetic or geochemical markers.

2.4.1.1 Parentage analysis and assignment tests

Population genetics is the most widely used approach for making inferences about dispersal and connectivity in marine organisms (Hellberg 2009). Traditionally, spatial variation in frequencies of alleles and genotypes (F_{st} and G_{st}) was the most common indirect method to genetically assess genetic divergence and long-term connectivity among populations

(Hedgecock 2010). However, limitations in the resolution of temporal scales, especially the inherent integration of dispersal over multiple generations, made it impossible to assess connectivity patterns over shorter ecological scales (Hedgecock et al. 2007). Recently new more direct genetic methods, such as population and parentage analysis, have been developed to more precisely estimate connectivity among populations (Manel et al. 2005; Christie et al. 2010; Hedgecock 2010). These methods are based on the multilocus genotype of individuals at different locations (Manel et al. 2005). Assignment tests provide the probability that an individual originated from one of a number of different known source populations. However, precise assignment of a given individual to a population requires that populations are genetically distinct and is unsuccessful when populations are too similar (Saenz 2009; Christie et al. 2010). Parentage analysis is a particular type of assignment test used to determine the parents of an individual or group of individuals based on shared alleles between individuals (Manel et al. 2005). As populations of marine invertebrates are usually comprised of large numbers of individuals with possibly long dispersal phases, the fraction of sampled individuals is usually too small for precise parental assignment (Hedgecock et al. 2007), and a persistent challenge associated with these techniques is the necessity for genotyping many individuals, both adults and recruits, from all of the different populations within the metapopulation. However, a promising new technique of parentage assignment (Christie et al. 2010) requires fewer individuals from a given population than previous techniques. Using a Bayesian classification approach for the kind of organisms, this approach has been used successfully to document connectivity patterns of marine organisms with long PLD (Richards et al. 2007; Underwood et al. 2007; Christie et al. 2010).

The spatial scale over which these methods can be used depends on the characteristics of the species (e.g. PLD, larval behaviour) and of the system (e.g. currents, topography) in question. In addition, the temporal scale of the sampling will depend on the frequency of reproduction of the species and on the variability of the oceanographic conditions encountered by the larvae. Consequently, the assessment of the variability of connectivity pattern necessitates an extensive sampling of all the potentially connected populations over different cohorts. Despite the high costs of these methods, they offer very precise techniques to measure connectivity pattern. Unfortunately, estimating the variability of connectivity requires multi-year studies.

2.4.1.2 Geochemical signatures in calcified structures

While genetic assignment tests measure connectivity by determining the natal origin of juveniles that are collected from different sites within a region, calcified structures (e.g. otoliths, statoliths or shells) can retain chemical traces of the environment (due to spatial and temporal variations of seawater) encountered by individuals during their entire life. Researchers are using such chemical signatures (e.g. isotope ratios, trace elements) of calcified structures formed during early development to identify the region or site of origin of individuals (Thorrold et al. 2002; Zacherl 2005). These structures are either naturally marked by the environment or artificially “tagged” by transgenerational isotope labelling (TRAIL) at their origin. Natural markers can be found in the otoliths of fish and in the statoliths or shells of molluscs. This process is usually bipartite – first, the microchemistry of the calcareous parts corresponding to early life is analysed to define the trace elemental profile of a location of interest. Then, the trace elemental fingerprint of post-dispersal individuals is compared with the elemental profiles of individuals from which the original location is known (Becker et al. 2005; Becker et al. 2007). The source identification is obviously more reliable when differences in elemental composition are great among possible source locations (Thorrold et al. 2007). However, this method necessitates identifying the elemental profiles from all potential sources (Berumen et al. 2010), and moreover, it can be variable in time (seasonally, yearly) (Walther & Thorrold 2009; Cook 2011; Fodrie et al. 2011). Even though some statistical methods can be used to increase the precision of assignments (White et al. 2008), some limitations of this method appear for marine organisms because chemical distinctions among origin areas are sometimes too small to enable accurate assignment of individuals (Berumen et al. 2010), and the processes of integration of these trace elements in the hard parts of these organisms is not fully understood (Warner et al. 2005; Thorrold et al. 2007). The applicability of these techniques over multiple years has been shown recently and has provided new insights on the variability in connectivity. In particular, multi-year studies on fish otoliths (Clarke et al. 2010), oyster and mussel shells (Carson 2010) have revealed seasonally and yearly variations in connectivity and the importance of self-recruitment in different systems. This variability underscores the need to identify the source elemental profiles over appropriate temporal scales if needed.

The second approach involves directly tagging individuals with enriched isotopes at possible source populations (Thorrold et al. 2006). Stable isotopes at concentrations an order of magnitude higher than those found in nature are injected into gravid females and are subsequently incorporated into internally developing embryos, thereby acting as unequivocal tags (Thorrold et al. 2006). This method permits the marking of many individuals at one time, and at low doses does not alter larval and juvenile behaviour (Williamson et al. 2009). TRAIL has been used mostly to assess the self-recruitment hypothesis in cephalopods (Pecl et al. 2010) and reef fishes (Almany et al. 2007; Planes et al. 2009). However, because of high mortality rates during the larval dispersal stage, this technique cannot be employed to assess connectivity at large scales. Moreover, as a large part of the population needs to be marked at one time, it is almost impossible to use this method with benthic invertebrates or large populations of reef fishes. Finally, the use of this method is limited by the different markers available and question regarding the incorporation process of markers (Pecl et al. 2010). Thus, this method appears to be most useful in assessing variability of connectivity at limited spatial scales of dispersal in system where larval retention and self-recruitment are thought to be important.

2.4.1.3 Invasive species

The establishment and subsequent spread of non-indigenous species (“invasive species”) is an emerging environmental problem of global extent, but a “silver lining” of biological invasions is a relative easy opportunity to examine rates and patterns of dispersal (Johnson & Padilla 1996). Estimates of rates of spread can be made from sequential observations at the edge of the range (Grosholz 1996; McQuaid & Phillips 2000; Lyons & Scheibling 2009) assuming that sampling efforts are reasonably constant over time. Such information has already been used in the planning for MPA (Shanks et al. 2003) for comparison with the range shifts associated with climate change (Sorte et al. 2010). Unfortunately, the monitoring of most past invasions has been a rather piecemeal affair with different observers using different techniques and/or effort to document the distribution of the invasive species over time. Current interest in aquatic invasive species has, however, provided better information and interest in documenting the secondary spread of established invaders.

Measures of the rates of spread of invasive species are not, however, exact equivalents of either dispersal or connectivity in metapopulations. First, invasive species often spread by both natural (e.g. currents) and human-mediated (boat hull fouling) vectors (Goldstien et al. 2010), and the latter can give artificially high estimates of dispersal. Second, population densities at the edge of an invader's range are likely to be lower than in sites where the species is well established. This attribute may reduce the propagule supply available for dispersal and lead to underestimates of the normal dispersal that occurs within a fully developed metapopulation. Finally, given the number of propagules that are likely to settle will diminish with increasing distance from the edge of an invader's range, there are likely to be sites where populations will not become established due to demographic limitations such as "Allee effects" (Leung et al. 2004) which would not exist if dispersal was simply occurring between populations within a metapopulation. Thus, estimates of range expansion for either invasive or native species are likely to underestimate dispersal distances. Such measures can serve, however, as first approximations for dispersal within metapopulation of similar species and provide information on pathway of transport within coastal ecosystems.

2.4.2 System specific methods

System-specific approaches depend primarily on properties of the physical system to assess connectivity patterns in the study area. These methods are developed to fit to a specific system but can be applied to similar systems or other organisms within the same system.

Two such methods are particularly useful in evaluating variability in connectivity: geostatistics and biophysical models.

2.4.2.1 Geostatistics

Geostatistics, the statistical analysis of spatially-referenced data over large spatial extents, represents a powerful new tool to assess connectivity in marine ecosystems. These analyses are based on estimates of the adult abundance and the number of recruits at different sites within the study area. Significant coupling between sites at a particular distance gives an estimate of the distance at which a given population has an impact on the recruitment elsewhere in the system. Appropriately oriented and homogeneous coastal systems (e.g. estuaries, rivers, straight shoreline) are currently the preferred systems for the application of this method because such coastal configurations facilitate the detection of significant signals between adult populations and their impact on juvenile recruitment. This method has already been used to estimate the distance of demographic coupling of blue mussels in the St. Lawrence estuary (Smith et al. 2009). Depending on the different dispersal properties of the species, distinct signals can be distinguished, ranging from no association at all to significant relationships at a given distance between adults and recruits. Different theories can be tested (Fig. 2.1, e.g. post-recruitment effects, supply-side limitations, demographic coupling), and the covariogram developed from the data provides an estimation of the dispersal characteristics of the species within the system being studied (Fig. 2.2). Also, this approach can avoid difficulties in separating different kind of variability (e.g. environmental variation among sites versus pure connectivity variations) by using detrended data to partition the variance (chapter 4 of this thesis).

Although system-specific by nature, this method is less expensive as the data are relatively easy to collect and analyse. Consequently, it permits the repeated sampling necessary for evaluating the temporal variability of the connectivity pattern of the study species. Depending on the frequency of reproductive/dispersal events, the analysis can be repeated yearly or even seasonally to estimate the effective scale of connectivity, to infer dispersal patterns, and to capture the temporal variability of connectivity. This method is particularly useful for estimating the scale of connectivity and dispersal pattern variability in regions with strong alongshore currents and can be used to identify complementary methods (e.g. genetic analyses) that can be employed subsequently to provide higher resolution of the dispersal patterns within the study system.

2.4.2.2 Coupled biophysical models

With advances in computational abilities, many three-dimensional hydrodynamic models have been developed to better understand geochemical processes, hydrology, and sedimentology. In recent years, ecologists have started exploring the power of these tools to better comprehend dispersal of larvae which are almost impossible to track directly (Cowen et al. 2007; Thorrold et al. 2007; Werner et al. 2007). These powerful tools can model entire coastal ecosystems, incorporating diverse attributes such as coastal geometry and the influence of wind. The spatial scale of the model is a key parameter for coastal marine species because of the important interaction between dispersing larvae and of nearshore physical processes, but depending on the complexity required, their spatial resolution can be adjusted accordingly (Greenberg et al. 2007). For example, models with high resolution are preferred to simulate coastal processes like eddies or waves.

The best way to model the dispersal of larvae appears to be the Lagrangian dispersal process (Siegel et al. 2003), particularly through the use of Individual Based Modeling (IBM) (Werner et al. 2007). At its simplest, Lagrangian dispersal assumes that larvae are transported advectively as passive particles (Siegel et al. 2003; Mitarai et al. 2009), and thus the process consists of following a parcel of water that is characterized by a particular set of conditions (e.g. initial density, PLD). Movements of the Lagrangian particles are then viewed as proxies for passively dispersing larvae and the analysis of the trajectories of several particles (used to create probability density functions) allows the estimation of dispersal kernels, the connectivity matrix, or potential connectivity (Siegel et al. 2003; Cowen et al. 2006; Watson et al. 2010). Recently, IBMs have also been able to integrate behavioural traits of organisms (e.g. diel migration, mortality, feeding; Ayata et al. 2010; Utne et al. 2012).

In a context of marine coastal species, the most important factors influencing dispersal, in addition to physical currents, are species properties such as timing of spawning, PLD, and duration of competence period, i.e. development to a stage able to settle back into the benthic environment (Mitarai et al. 2009). Integration of the interaction between individuals and their physical environment into physical oceanographic models, including the addition of specific larval behaviours, will certainly increase the precision of estimates of dispersal kernels and connectivity. IBMs have already permitted researchers to explore and integrate the role of specific behaviours during the dispersal phase and better explain diverse phenomena such as self-recruitment and limited dispersal (Werner et al. 2007). Depending on the species, the incorporation of processes such as the relationship between growth and water temperature (O'Connor et al. 2007), diel migration (Cowen et al. 2006; Ayata et al. 2010), chemical cues (Gerlach et al. 2007), and attraction by turbulence and waves (Fuchs et al. 2007) can have large impacts on resulting dispersal patterns. The added complexity due to the integration of such processes can be mitigated by the judicious identification and selection of behaviours that are found to be most critical in the dispersal of the individual species in question.

The development of 3-D hydrodynamic models necessitates high level programming capacities, good calibration before and after development of the model, and extensive validation before they are used by ecologists to run simulations. Also, larval behaviours require considerable effort to be properly integrated into the model and a strong understanding by the programmer of the processes most critical to accurately describing the behaviour. Consequently, the development of a good hydrodynamic model requires substantial time and associated costs. However, once appropriately developed and validated these models offer a powerful tool to explore a given system and enable researchers to test hypotheses with increasing realism. In particular, the low costs associated with exploring different environmental scenarios provide a fantastic tool to assess population connectivity and its variability across different spatiotemporal scales. The modeled patterns can then be used to generate testable hypotheses regarding connectivity which can, with the use of targeted experiments, provide data critical for model refinement, increasing our ability to understand the mechanisms driving patterns of connectivity. Ultimately, such coupled biophysical models will permit ecologists to test hypothesis of different scenarios of climate change and predict changes within the system of interest.

2.4.3 Use of multiple methods

Given the inherent limitations of any given approach, attempts have been made to compare different methodologies. In particular, several studies have confirmed predictions of biophysical models with genetic analysis (Galindo et al. 2010; White et al. 2010) or the inverse (Gilg & Hilbish 2003), and the comparison of these tools has permitted researchers to verify predictions and to identify the main genetic processes involved in marine dispersal. Perhaps more importantly, mismatches between theoretical predictions and empirical data have directed researchers to explore further the mechanisms involved (Galindo et al. 2010). A good example is that of Gilg and Hilbish (2003) who combined simulated hydrodynamic data (2D) and allele frequencies in a region with strong differentiation among populations to estimate the geographic scale of larval dispersal. The use of 3 years of averaged simulation data in combination with the genetic allele frequencies data enabled them to define the scale of dispersal distance. They were not, however, able to assess the variability in connectivity because the temporal resolution of connectivity assessed by these methods was too different. In the future, the use of multiple methodologies should provide more robust estimates of connectivity patterns by incorporating newly developed methods. As previously mentioned, it remains important to use multiple complementary methods with similar temporal resolution, especially when assessing the variability of connectivity patterns.

2.5 Variability of connectivity for populations: causes and consequences

As discussed above, variability in estimates of connectivity can be attributed to methodology alone, i.e. due simply to technical artifacts. However, there are many natural processes that result in connectivity being truly and inherently variable. At larger spatial and temporal scales, this variability has important impacts on different characteristics (e.g. demography, genetics) of populations, communities, and ecosystems. In this section we review the primary processes affecting and causing variability in connectivity and then discuss the implications of these variations in dispersal patterns at larger spatiotemporal scales.

2.5.1 **Main factors causing variability of connectivity**

Dispersal, which underlies connectivity, involves three distinct sequential steps (Fig. 2.3) – it begins with the release of propagules (e.g. gametes, spores or larvae), is followed by a pelagic dispersal phase and ends with settlement to an appropriate habitat (Cowen & Sponaugle 2009; Pineda et al. 2010). Each of these phases represents a potential source of variability because of the distinct suite of biological, physical, and biophysical processes involved in each period. Depending on species, region, and timing of a particular study, these phases of connectivity may differentially impact dispersal and consequently produce variability in connectivity patterns.

2.5.1.1 Spawning

The first phase, release of propagules, can be affected by variation in the abiotic environment (e.g. temperature), maternal condition, food availability, and local oceanographic conditions. All of these parameters can influence the timing and location of spawning (Levitan 2005). The importance of spawning, and its influence on connectivity depends greatly on the study species and their various modes of reproduction. Species-specific variation in offspring size reflects evolutionary strategies to deal with unpredictable variation of the environment (Marshall et al. 2008) and represents a compromise between quantity and quality as reflected by the number, size, and feeding strategy (e.g. lecithotrophic vs. planktotrophic) of propagules produced. Maternal condition can also be an important factor in terms of brood quality and is likely linked to the food available to parents prior to the spawning event. Spawning is influenced by both intrinsic (e.g. gonadal condition) and extrinsic (e.g. spawning cues) properties of the system (Starr et al. 1990), and as local oceanographic features are highly variable at small spatial and temporal scales (i.e. due to topography, bathymetry, waves, and tides), the timing of spawning will be a key factor influencing fertilization in broadcast spawners and larval dispersal trajectories of planktotrophic and lecithotrophic species (Largier 2003).

2.5.1.2 Larval dispersal

Once the planktonic phase begins, the spatial and temporal scales over which connectivity varies increase relative to the spawning phase. During this phase, many features influence larval dispersal: hydrodynamics of the system, larval behavior, prey availability, PLD and predation (Levin 2006). In the simplest case, many larvae can be thought of as passively dispersing particles subject to oceanographic dynamics (see above), but these complex processes vary enormously over all spatial and temporal scales. Certain hydrodynamic conditions may increase larval dispersal distances (e.g. alongshore currents, wind driven surface current), while others may act to reduce dispersal distance (e.g. eddies, waves, tides) (McQuaid & Phillips 2000; Largier 2003; Sponaugle et al. 2005; Mitarai et al. 2009). More realistically, larval behaviour, especially vertical swimming, can influence dispersal. Indeed, the swimming ability of many pelagic larvae often increases with ontogeny enabling complex swimming behavior in both horizontal and vertical directions, which in turn has associated impacts on dispersal trajectories (Cowen et al. 2006; Fuchs et al. 2007; Gerlach et al. 2007). Likewise, because many species have planktotrophic larvae which must feed and develop during the dispersive phase, there is an obligatory pelagic period (the PLD) of days to weeks during which dispersal is occurring. PLD can vary greatly both within and among species (Kinlan & Gaines 2003; Kinlan et al. 2005; Shanks & Eckert 2005), depending on abiotic and biotic conditions. In particular, temperature and prey availability play key roles in larval development due to their high spatiotemporal variability, resulting in large variation in mean PLD and mortality among cohorts (O'Connor et al. 2007). In addition, if a suitable substratum is not available when larvae become competent to settle down to benthic habitat, organisms can even delay metamorphosis, so that the PLD can extend significantly beyond the mean pelagic larval duration (Pechenik et al. 1990). Consequently, the dispersal phase can last a relatively long time with concomitant increases in possible dispersal trajectories. All of these factors, in addition to direct predation on larvae, result in very high mortality during the pelagic larval phase (Houde 1997).

2.5.1.3 Settlement

Even if larvae do survive the challenges of the pelagic realm and find suitable substrata, post-settlement processes can dramatically influence the chances of these “recruits” becoming part of the local population. First, post-settlement survivorship is closely tied to larval quality (Pechenik et al. 1998), and thus the diverse factors influencing larval life (see above) can produce variation as well in the quality of settlers (e.g. size, physiological conditions). This variability in quality has important demographic impacts, particularly on the growth and survival rate of individuals (Pechenik et al. 1998; Phillips 2002). Various selection processes occur early in the development of juveniles because high quality metamorphosed larvae have a higher probability of recruiting to the adult population (Cowan & Shaw 1988). Nevertheless, favorable larval traits do not necessary produce successful juveniles because the benthic environment can require different traits for survival. Quality of settlers then, as with quantity and quality of larvae, appears to be highly variable over spatial and temporal scales and consequently contribute to produce heterogeneous and highly variable recruitment patterns in changing locations (e.g. sink locations, areas of low recruitment). At smaller spatial scales, some species aggregate during the dispersal phase because of currents and differences among water masses (Natunewicz et al. 2001); larval delivery appears to be highly variable at spatial scales less than one hundred meters and necessitate additional sampling effort to characterize the population (Siegel et al. 2008; Pineda et al. 2010). Even if most long distance dispersal occurs during the pelagic larval stage of invertebrates, dispersal has been observed as post-larvae, juveniles and adults, which also contributes to variability exhibited across the three stages of the connectivity process (Bayne 1964; Petrovic & Guichard 2008).

2.5.2 Consequences and ecological implications of the variability of connectivity

All the phenomena described above can produce variability in connectivity. Therefore, the ecological consequences at larger spatiotemporal scales (metapopulation and ecosystem) are diverse. Only a few theoretical studies have been conducted to assess these impacts (e.g. variable dispersal kernels). In this section, we discuss the general implications of considering variable connectivity patterns on large scale demography and genetics.

As previously emphasized, marine systems are characterized by variability in environmental conditions. Stochasticity of dispersal kernels or the connectivity matrix is often used to incorporate this variability in models. When stochasticity of connectivity is increased, large increases occur in the mean abundance of individuals in the metapopulation as well as in its variance (Aiken & Navarrete 2011). Moreover, persistence of the metapopulation is logically enhanced by adding dispersal variability corresponding to what is observed in empirical studies (Aiken & Navarrete 2011). In practice, strong variations in recruitment occur at a regional scale due to variation in bathymetry and winds. Because of this, some areas can be identified as "hot spots" where recruitment is always higher than the regional average (Siegel et al. 2008), in spite of the large variation in recruitment observed among years (Shima et al. 2010). Since some species are reproducing all year round, important variations can be observed in the number of recruitment events. Depending on seasonality, certain patterns of dispersal at different scales can emerge during a given year (Siegel et al. 2008). Some systems are strongly oriented by ocean currents, causing asymmetrical dispersal, and higher sensitivity to climate change has been observed in simulations (Aiken & Navarrete 2011). The metapopulation system can then shift continually between stable and unstable states, according to variability in recruitment (Aiken & Navarrete 2011). However, long-term empirical evidence for variability in connectivity is rare, so the long-term analysis of its impact on the demography of populations remains unknown. However, some methods developed recently (e.g. biophysical model, geostatistics; see above) should allow a better assessment of connectivity patterns with previously collected data and permit better validation of theoretical work.

Variability in dispersal distance also leads to different levels of gene flow between populations; parent populations of different cohorts of recruits at a given location are therefore variable and gene flow may occur, in time, over various distances (O'Connor et al. 2007). High variability in connectivity can lead to unstable genetic structure at seasonal and annual temporal scales in adults and juveniles (chaotic genetic patchiness), each site consisting of an admixture of cohorts from multiple sources. Chaotic genetic patchiness nevertheless allows stability of the entire metapopulation and contributes as a buffer against strong fluctuations in population size (Hogan et al. 2010).

2.6 Implications for management and conservation of biodiversity and ecosystems

Management of biodiversity and conservation of ecosystems, often through the establishment of marine protected areas (MPAs), has been well studied in past decades, and agreement has been reached on the necessity of a solid knowledge of population size, genetic diversity, representativeness to the entire system, and connectivity pattern across the area for effective management (O'Connor et al. 2007; Sundblad et al. 2011). However, different goals exist in species management, so the benefits differ depending on the adopted strategy (e.g. specific fisheries protection or biodiversity conservation), opportunities, budget, and number and types of species targeted by the MPA network (e.g. homing or sessile vs. migratory species) (Kritzer & Sale 2004; McCook et al. 2010). Goals of MPA networks are evaluated and chosen by policy decisions and are often established according to the opportunities present in the region, rather than following strict ecological analysis (Kritzer & Sale 2004; Sundblad et al. 2011). In spite of the recent interest and extensive research on fisheries management on an ecosystem level, the effectiveness of MPAs to protect ecosystems and their biodiversity has unfortunately received relatively little attention (Jones et al. 2007).

2.6.1 Design of MPA networks

MPAs are generally established to help a given metapopulation or an ecosystem persist demographically. When defining a network of protected areas, the determination of the size and structure (e.g. a single or several areas, spacing, location) requires a good knowledge of the scale of dispersal and the size of discrete local populations (Kritzer & Sale 2004; Jones et al. 2007). In MPAs where the goal is to preserve biodiversity, several areas are normally required; if the goal is to protect a single species (e.g. fishery), fewer and larger areas are generally used (Jones et al. 2007). Size of reserves also depends on the effective number of individuals surviving to the next generation (Almany et al. 2009). With regard to the distance among reserves, the greater the dispersal range, the larger the protected areas should be and the longer the distances among them can be (Jones et al. 2007). For example, if the goal is the persistence of several species, Moffitt et al. (2011) recommended increasing the size of MPAs and diminishing distances among them to allow a higher number of species to persist via network connectivity rather than self-replenishment, particularly species with long dispersal. Additionally, the spacing among reserves to protect a given species is variable among regions because of local differences in larval development time. For example, because water is warmer in tropical regions relative to temperate ones, PLD is generally shorter and thus spacing among reserves in networks should be smaller in tropics to ensure connectivity (O'Connor et al. 2007).

Because low levels of larval exchange limit success of MPAs (Bell 2008), networks of protected areas should be designed as a function of observed connectivity patterns, but can also include potential connectivity among areas that can be linked and where suitable substrata exist. Consequently, some of the methods described above (part 2 of this chapter) that allow variability in connectivity to be estimated and used in determining locations that are potentially connected and can reinforce the MPA network. Moreover, a good description of the demography of the population (e.g. through statistical methods (Aiken 2011) or source/sink population analysis (Almany et al. 2009)) will help to define areas (sectors of the coast) which would have a greater impact if protected. For example, isolated populations or retention areas, which have high conservation values, should be preferred because they ensure the persistence of the metapopulation (Almany et al. 2009; White et al. 2010). However, in retention zones, connectivity is less important but sensitivity to stochastic disturbances might be higher. Therefore, such populations could go extinct, endangering the whole network because of its weaker connectivity (White et al. 2010). Generally, Jones (2007) suggests protecting source populations, isolated populations and spawning aggregation sites.

2.6.2 Management of biodiversity

When applied to whole ecosystems, management becomes more complex and reserves should be designed differently. Metacommunity levels should be considered in spatially-explicit models to manage effectively reserves in MPA networks (Guichard et al. 2004). More recently, MPAs have been designed to be large enough to protect a suite of populations and have emphasized the importance of protecting different functional groups in ecosystems (McLeod et al. 2009). Also, the protection of vulnerable or fragile species may necessitate focussing on the other species upon which they depend, perhaps at additional spatial and temporal scales (Almany et al. 2009). As dispersal distances occur at different scales among species, variability in spacing between reserves is desirable to reduce dependence of the system to a specific distance and better protect diverse groups of species (Kaplan 2006).

Conservation strategies have to be developed to reduce impacts on biodiversity and ecosystems because high environmental variability is an inherent part of marine systems. For example, in a context of global climate change, McLeod (2009) suggested “spreading the risk” to avoid coral reef extinction by protecting several replicates of all kinds of habitats. To identify potential habitats, he proposed to use past incidents of coral bleaching and sea surface temperature. Another risk-spreading strategy that limits the impact of variability of connectivity patterns and strong fluctuations in MPA networks involves using more, but smaller, reserves (Almany et al. 2009; Hogan et al. 2010). Also, under high environmental variability, Baeza & Estades (2010) have shown that enhancement of the habitat quality in small reserves has better effects on surrounding landscapes than large and costly enhancement of large reserves.

When a MPA network is designed, population genetics also need to be considered. Because panmictic populations are rare, it is important to study direction and strength of the gene flow (von der Heyden 2009). Gene flow should be maintained by frequent, medium and rare (long distance) dispersal of individuals among populations and its inclusion in MPA network designs is highly recommended (O'Connor et al. 2007). Also, Von der Heyden (2009) recommends favoring multiple MPAs to avoid excessive population genetic structuring and population isolation; spacing of reserves should be designed to ensure adequate demographic connectivity and maintenance of genetic diversity (Almany et al. 2009). Even if substantial self-recruitment has been observed in dispersal analyses and may permit the persistence of specific populations, the exchange of individuals among populations remains crucial from a perspective of genetic diversity.

2.7 **Conclusion**

Connectivity is now a recognized feature of metapopulations that are a part of coastal ecosystems. This overview of connectivity has revealed both the inherent shortcomings and future potential of applying this approach to the understanding and management of coastal ecosystems. There is clearly an emerging set of techniques that can now be applied to estimate and document dispersal between populations and the concomitant effects on metapopulation connectivity. There are, however, biases in these techniques in terms of the temporal and spatial scales over which they can be applied, and future effort will need to strive for the integration of these different approaches to better understand the role of connectivity in maintaining demographic stability and genetic diversity within metapopulations. Moreover, connectivity can no longer be considered a static, invariant property of metapopulations. It too is inherently variable, subject to intrinsic and extrinsic factors that can affect the dispersal and survival of propagules. The importance of documenting and incorporating this variability in our theoretical and empirical understanding of metapopulation dynamics and ecosystem function is a new challenge, but one that must be met to address the environmental challenges associated with the sustainable management of ecosystems threatened by overexploitation and climate change.

2.8 **Acknowledgements**

We thank G. Cook, C. Leroux, and E. Pedersen for critical reading of the manuscript. We acknowledge and appreciate the financial support provided by the Canadian Natural Science and Engineering Research Council (NSERC Strategic Grant Project 336324).

2.9 **Figures**

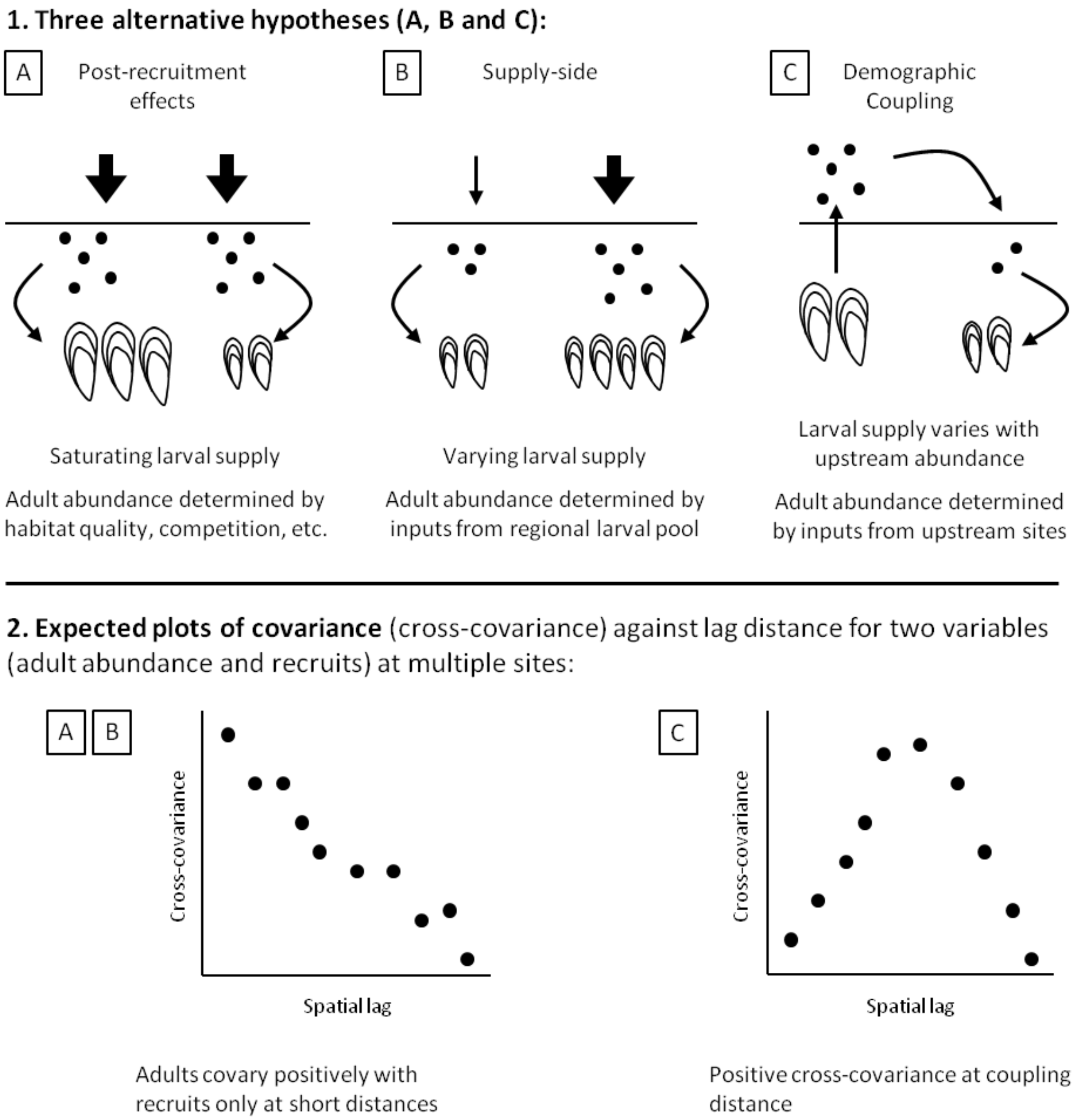

Figure 2.1 (1) Different scenarios of mussel recruitment (A, B, and C) that can be tested using cross-covariance geostatistics. (2) Expected cross-covariograms for each scenarios

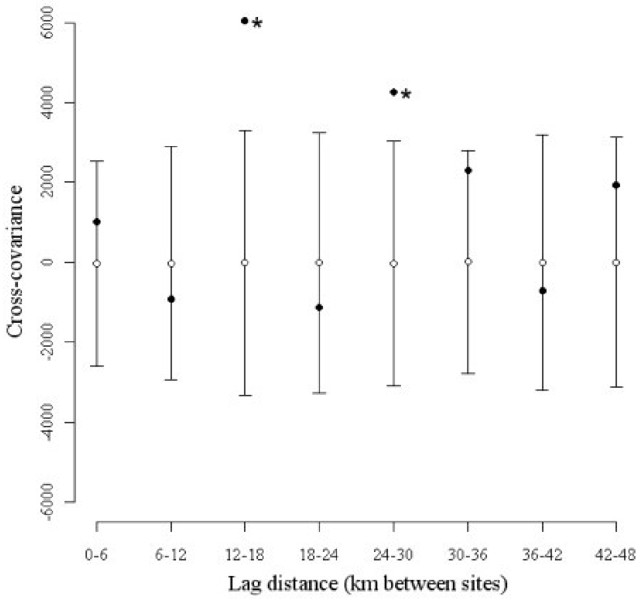

Figure 2.2 Example of demographic connectivity in marine mussel metapopulations: significant cross-covariances (filled circles with asterisk) were observed between upstream adult mussels and downstream recruitment, indicating spatial connectivity between sites at 12-18km and 24-30km apart from one another. Open circles indicate mean values of a random process in that system. This figure is modified from Smith et al. 2009 (Copyright (2009) by the Association for the Sciences of Limnology and Oceanography, Inc.)

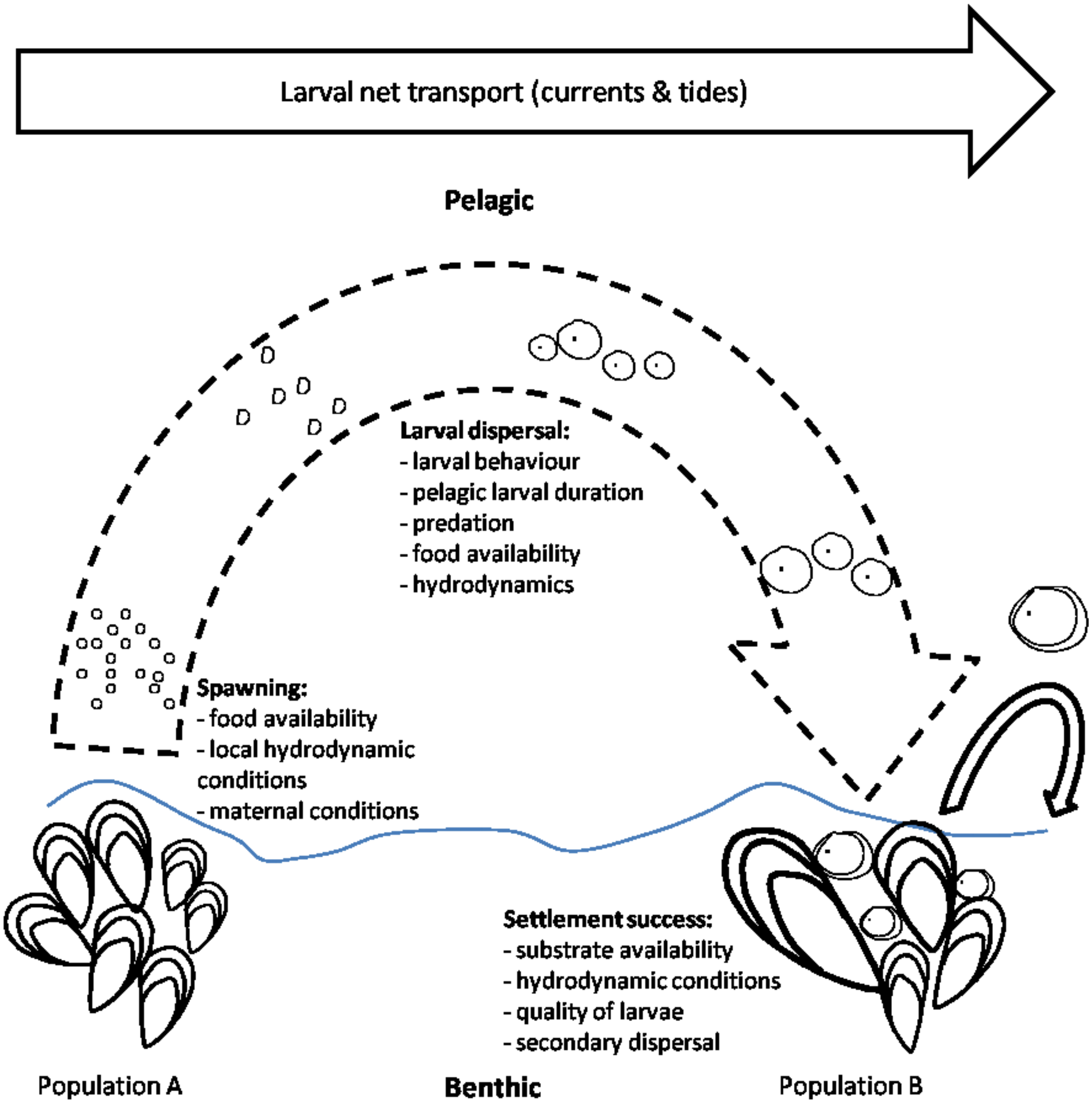

Figure 2.3 Overview of the different processes contributing to the variability in connectivity among populations (e.g. marine mussels)

Chapitre 3. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus* spp.

3.1 **Résumé**

Le recrutement a souvent été cité comme un facteur clé régulant l'abondance des populations et la structure des communautés dans les écosystèmes benthiques marins où le cycle vital de beaucoup d'espèces comporte une phase de dissémination planctonique. Cependant, les schémas et les causes de l'hétérogénéité temporelle du processus de recrutement, de l'échelle journalière à annuelle, sont méconnus pour beaucoup de taxons. Nous avons réalisé une évaluation hebdomadaire (2008) et bimensuelle (c.-à-d. chaque 2 semaines; en 2008-2009) de la colonisation de la moule bleue *Mytilus* spp. dans l'estuaire maritime du Saint-Laurent, puis différencié les recrues primaires (métamorphose) et secondaires (mouvements post-métamorphose). Avec une résolution temporelle bimensuelle, le recrutement en 2008 s'est produit sur une période de 2 mois avec un seul pic en aout. Un schéma de recrutement plus complexe impliquant de multiples pics de recrutement primaire et secondaire a cependant été révélé avec une résolution hebdomadaire. En 2009, le taux de colonisation bimensuel était réduit d'un ordre de grandeur, avec une fois encore un seul pic. Au cours des 2 années, le recrutement secondaire a été observé au cours de la plupart de la saison et a contribué autant, voir plus (50-81%), que le recrutement primaire dans plusieurs pics. Basée sur la taille de la prodissoconch II et une estimation des taux de croissance larvaire, la durée moyenne de la phase larvaire planctonique a été estimée à 38 jours, mais elle peut s'étirer de 27 à 67 jours en fonction du taux de croissance utilisé. L'importance du recrutement secondaire a augmenté au cours du temps et a été un contributeur majeur à la dynamique du recrutement local. La variation du recrutement primaire et secondaire, tout comme les variations interannuelles pourraient fortement affecter les estimations des taux de recrutement, la dynamique locale, les échelles spatiales de connectivité entre les populations côtières et

donc notre compréhension de la régulation des populations locales et de la dynamique des métapopulations.

3.2 **Abstract**

Recruitment has often been cited as a key factor regulating population abundance and community structure in benthic marine ecosystems, where the life cycle of many species includes a dispersive planktonic phase. Still, the patterns and causes of temporal heterogeneity in the recruitment process, from daily to annual scales, are poorly understood for most taxa. We conducted weekly (2008) and biweekly (i.e. every 2 weeks; 2008–2009) assessments of settlement of the marine mussels *Mytilus* spp. in the St. Lawrence maritime estuary, and differentiated between primary (metamorphosis) and secondary (post-metamorphosis movements) settlers. At a biweekly temporal resolution, recruitment in 2008 occurred over a 2-months period with a single peak in August. A more complex pattern of recruitment involving multiple peaks of primary and secondary settlement was, however, revealed at a weekly resolution. In 2009 the biweekly settlement rates were an order of magnitude lower, with again only a single peak. In both years, secondary settlement was observed throughout most of the season and contributed as much or more (50–81%) than primary settlement for several peaks. Based on prodissoconch II size and estimated larval growth rates, the mean planktonic larval duration was estimated to be 38 days, but may have ranged from 27 to 67 days depending on the actual growth rate. The importance of secondary settlement increased over time and was a major contributor to local recruitment dynamics. Variation in primary and secondary settlement as well as inter-annual variations could strongly affect estimates of recruitment rates, local dynamics and the spatial scales of connectivity among coastal populations, and thus our understanding of local population regulation and metapopulation dynamics.

3.3 **Introduction**

Temporal and spatial variation in the availability of planktonic larvae is recognized as a strong ecological driver of population dynamics in a wide range of marine systems (Roughgarden et al. 1988; Caley et al. 1996; Kinlan & Gaines 2003). Larval supply is particularly important for sessile and sedentary benthic invertebrates as dispersal after settlement is either limited or non-existent. Larval supply is controlled by many biotic (e.g. behavior, settlement cues, survival rates) and abiotic (e.g. waves, currents, topography) factors and, depending on the scale of observation, these factors influence larval dispersal and settlement differently and generate variability in settlement (Woodin 1986; Cowen & Sponaugle 2009; Pineda et al. 2010). For bivalves, important ecosystem engineers in many communities (Gutierrez et al. 2003), the supply of settlers can result from 2 disparate processes that operate over contrasting spatial scales: (1) primary settlement at the end of the larval phase, i.e. metamorphosis and initial attachment to a substratum, and (2) secondary settlement (post-metamorphosis). This latter process can involve post-settlement movements (drifting or crawling) presumably to select a more suitable substratum or microhabitat (Bayne 1964; Sigurdsson et al. 1976; Buchanan & Babcock 1997; Newell et al. 2010), sometimes far from the initial location of settlement (Shanks & Shearman 2011). Such movement can also result simply from dislodgment by water motion (Martel 1993). Regardless, it is only once a sessile organism is definitively established in an area that it can be considered a recruit (Rodriguez et al. 1993).

Although secondary settlement through juvenile drifting appears to be a widespread dispersal phenomenon in bivalves (Lane et al. 1985; Baker & Mann 1997; Bownes & McQuaid 2009), it is often ignored (e.g. Leonard et al. 1998; Connolly et al. 2001; Pelc et al. 2009), and in spite of its potential to contribute substantially to observed recruitment, the relative importance of secondary settlement is rarely well documented (e.g. Martel & Chia 1991; Martel 1993). Distinguishing the relative contribution of these 2 processes is, however, crucial for assessing the role of larval supply in determining the population dynamics of benthic species.

Because dispersal scales depend on the type of settlement, important differences can occur when assessing connectivity of populations, i.e. metapopulation dynamics (Kinlan & Gaines 2003). The spatial scale over which primary settlement will operate will depend in a large part on the duration of the dispersal phase prior to settlement (Shanks & Shearman 2011). For example, the dispersal event leading to the primary settlement (planktonic larval duration [PLD]) is generally thought to last for approximately 4 weeks for *Mytilus* spp. (Thorarinsdottir 1996), leading to dispersal distances on the order of 10s to 100s of kilometers (Kinlan & Gaines 2003; Becker et al. 2007; Smith et al. 2009). This contrasts with the much shorter secondary dispersal events that operate on the order of 10s to 100s of meters (Lane et al. 1985; Gunther 1992; Cáceres-Martínez & Figueras 1998), and in spite of the possible repetitiveness of such secondary dispersal events, the total distance covered should be orders of magnitude smaller than for primary settlers (Lane et al. 1985). Thus the distinction between primary and secondary settlers can provide more precise information on the dispersal of settlers (i.e. regional versus local). Demographically speaking, this will allow better estimates of settlement patterns for the different phases of dispersal rather than total recruitment, which normally combines all sizes of settlers and therefore primary and secondary phases of dispersal. The latter approach can result in overestimates of primary settlement, and thus the degree of connectivity of populations in time and space. The distinction between types of settlers will determine the importance of each dispersal process within observed peaks of settlement, and target main periods affecting connectivity patterns. Failing to distinguish between primary and secondary settlers will therefore bias measurements of dispersal, resulting in inaccurate estimates of the timing, magnitude, and duration of major dispersal events.

Many studies have shown that timing in reproduction and larval settlement of bivalves varies between regions, primarily because of differences in climate and hydrodynamic regime (Ramirez & Caceres-Martinez 1999; Jenkins et al. 2000; Philippart et al. 2003; Broitman et al. 2008; Porri et al. 2008). Dispersal during the planktonic larval stage depends largely on the PLD, which is principally influenced by environmental factors such as temperature and planktonic food availability (Sprung 1984; Widdows 1991). Moreover, in boreal and subarctic regions, reproduction occurs over a shorter period during the warm season than in temperate regions (Thorarinsdottir & Gunnarsson 2003; Frantzen 2007). The timing of reproduction can thus influence planktonic larval development.

Although the PLD is generally difficult to estimate, the end of the planktonic larval stage in bivalves is marked by a change in shell morphology and composition after metamorphosis, creating a distinct visual demarcation between the prodissoconch II (PII, or larval shell) and the dissoconch (D, or benthic shell) (Martel et al. 1999; Zardus & Martel 2002). The PII thus provides valuable information about the larval phase history, especially the size at metamorphosis (i.e. at the time of primary settlement). If larval growth rate is known or can be estimated, we suggest that the size at metamorphosis can then be used to determine the PLD (Martel et al. 1995). In systems where variations in plankton and temperature are relatively small over the spatial and temporal scales of the planktonic larval phase, PII shell morphometry can then be an efficient tool for estimating PLD at the level of individuals.

In this study, we documented spatial and temporal patterns of primary and secondary settlement by assessing the variation in blue mussel (*Mytilus* spp.) recruitment in a boreal ecosystem, the St. Lawrence maritime estuary. A previous study (Smith et al. 2009) documented substantial spatial along-shore variations in seasonal mussel recruitment in this region. However, short-term variations in this process and the relative importance of secondary settlement remain unexplored. Using size and larval shell characteristics, we estimated the primary and secondary settlement over the summer and thus obtained information about their relative contributions to recruitment patterns. We also used PII measurements to obtain information on size at metamorphosis as well to estimate the PLD of settlers. Our study provides valuable insights into dispersal scales among larvae (i.e. PII size variability and PLD estimates), recruitment rates and metapopulation connectivity (i.e. distinction between primary and secondary settlement) in *Mytilus* spp. in a boreal estuary.

3.4 Materials and Methods

3.4.1 Study area

Settlement and recruitment of *Mytilus* spp. were examined during the spring and summer of 2008 and 2009 on the southern shore of the St. Lawrence maritime estuary (Québec, Canada) at 3 intertidal sites (Pointe-Mitis, 48°40'N, 68°02'W;, Saint-Ulric, 48°46'N, 67°44'W; and Sainte-Félicité, 48°54'N, 67°17'W; Fig. 1) near the city of Matane on the Gaspé Peninsula. (NB although the terms 'settler/settlement' and 'recruit/recruitment' are used somewhat interchangeably in the literature, we try here to use the former terms for short-term observations where we are trying to infer settlement and the latter terms for longer-term demographic phenomena.) The study sites consist primarily of rocky shores (benches and boulders fields) that experience semi-diurnal tides ranging up to 4 m. The intertidal communities were largely dominated by *Mytilus* spp. (20–60% cover) in the mid and low zones. As seen elsewhere in the maritime regions of Canada (Toro et al. 2004; Moreau et al. 2005), these populations are mixtures of *M. trossulus*, *M. edulis*, and their hybrids (J. Turgeon, unpubl. data), and individuals cannot be readily distinguished morphologically. We thus considered this complex as a whole because environmental conditions are comparable among sites (Ouellet et al. 2011), and similar larval growth rates have been observed within this complex for temperatures typical of this region (Rayssac et al. 2010). The Gaspé Current, the dominant current in this area, runs downstream (west to east) along the shore towards the Gulf of St. Lawrence (Sheng 2001). Temperature and wind data for the region were obtained from an oceanographic buoy (IML-4) located 40 km upstream from Pointe-Mitis and 18 km offshore of Rimouski (48°40.000′N, 68°35.000′W; Fisheries and Oceans Canada, Oceanographic Data Management System [ODMS]; available at http://slgo.ca/app-sgdo/en/accueil.html). Salinity was not analyzed in this study because it was spatiotemporally homogeneous (24.5 ± 1.7 psu in 2008 and 25.8 ± 1.6 psu in 2009 [mean ± SD]; ODMS data).

3.4.2 **Settlement experiments**

Plastic multifilament nylon scouring pads (S.O.S. Tuffy) were used to collect mussel settlers (Menge 1992; Pulfrich 1996; Ramirez & Caceres-Martinez 1999) as larval mussels generally first attach to filamentous material (e.g. byssus threads of established mussels and filamentous algae; Yang et al. 2007). Collectors were anchored to bedrock with screws and wall anchors in the low mid-intertidal zone (the presence of the red alga *Porphyra* sp. was used as the tidal level indicator among sites). After collection, pads were preserved in 70% ethanol until laboratory processing. To extract settlers, a high-pressure jet of fresh water was used to detach them from the pad into a 150-µm mesh sieve that separated mussel settlers from smaller particles and organisms. Settlers were then identified and counted under a stereomicroscope (Olympus SZX 12). When more than 200 individuals were observed in a sample, samples were split using a Folsom splitter. Samples mainly contained mussels, but other taxa (e.g. bivalve settlers of *Mya* sp., *Macoma* sp., *Hiatella* sp., and the periwinkles *Littorina* spp.) were also collected. No apparent saturation of the collectors was observed.

For all experiments, 8 collectors were set out at the same tidal level at each site and replaced every 7 or 14 days from the end of June to mid-September depending on the time scale of interest. Experiments were conducted at 3 different combinations of spatio-temporal scales (Table 1): (experiment 1) biweekly (i.e. every 2 weeks) at all 3 sites (Fig. 1) in 2008 to compare spatial variation in the temporal pattern of recruitment; (experiment 2) weekly at one site (Pointe-Mitis) in 2008 to examine how temporal resolution of sampling affects patterns of recruitment (relative to the biweekly sampling at this site); and (experiment 3) biweekly at one site (Pointe-Mitis) in 2009 to examine interannual differences in the patterns of recruitment (relative to the 2008 sampling of this site). In parallel, 8 collectors were anchored for the whole summer (from mid-July to late-September) at all 3 study sites in 2008.

3.4.3 Size frequency and distinction of primary and secondary settlers

Variation of the size frequency of settlers throughout the summer was investigated using subsamples from the collections at Pointe-Mitis (experiment 2 and 3). At least 3 collectors from each date (late June to late September) were processed when sufficient numbers of settlers were present (11 sampling dates in 2008 [weekly] and 6 in 2009 [biweekly]). Because large settlers prefer natural substrates (Roughgarden et al. 1988; Porri et al. 2008), we measured shell length of all individuals in collectors that were less than 2000 µm (except when abundant, when 100 were haphazardly selected) with a range of 71 to 518 settlers per sampling date. We restricted the maximum shell length because larger settlers prefer attaching to hard natural substrata rather than filamentous substrata (Hunt & Scheibling 1996; Alfaro 2006). Individuals were measured using a stereomicroscope (Olympus SZX 12) with a PixeLink digital camera and the software iSolution. We measured the maximum length (anterior–posterior dimension) of the shells using a wet preparation (70% ethanol). Shells were carefully oriented to assure that they were in the ocular plane to avoid underestimation of their length.

To distinguish primary settlers from secondary settlers, we estimated a conservative size threshold (i.e. biased towards underestimating the abundance of secondary settlers compared with primary settlers) as a function of the size at metamorphosis and the potential growth on collectors after settlement. This threshold was estimated by using the maximum size at metamorphosis observed (370 µm) based on PII shell length and the maximum *in situ* post-settlement growth rate of mussels in this region (15 µm d^{-1}; N.L.C., unpubl. data) multiplied by the maximum number of days that settlers could have been in the collectors. This average growth rate corresponded to the slope of a linear regression using successive measurements of the size of settlers sampled from the same cohort in Pointe-Mitis during summer 2008. This calculation led to estimates of threshold sizes of 475 and 580 µm for collector deployments of 7 (experiment 2) or 14 days (experiment 3), respectively. The proportion of primary and secondary settlers in the subsample was then multiplied by the total settler count to estimate their total numbers in each sample.

To explore the influence of the physical environment on levels of primary and secondary settlement, we examined rates of settlement as a function of average wind speed and temperature during the preceding week, as calculated from measurements taken by the nearby oceanographic buoy (see above). Wind speed is a proxy for wave action along this relatively sheltered coastline where no oceanic swell occurs (L.E.J., unpubl. data). Data for both 2008 (weekly and biweekly) and 2009 (biweekly only) were analyzed separately for primary and secondary settlers.

3.4.4 **Prodissoconch II analysis and age at settlement**

We examined the PII region of the larval shell to determine the size of individual settlers at the time of settlement and metamorphosis. Since larval shell length changes linearly with time (Sprung 1984; Pechenik et al. 1990; Galley et al. 2010; Rayssac et al. 2010), we could thus estimate a range of the period of PLD based on the maximum and minimum planktonic growth rates observed in laboratory experiments at similar water temperatures (Bayne et al. 1975; Beaumont & Budd 1982; Sprung 1984; Pechenik et al. 1990; Beaumont et al. 2004; Hayhurst & Rawson 2009; Rayssac et al. 2010). Sixteen individuals (when available) less than 475 μm in total length were randomly chosen from each of 4 collectors used for the weekly samples in experiment 2 (the size criterion was applied to avoid including secondary settlers; see above). Maximum PII length was measured using a stereomicroscope (Olympus SZX 12, 90×1.2) equipped with a digital camera (6.6 megapixels, software: iSolution). To assess the age of primary settlers in 2009, the same method was used, but because it was a biweekly experiment only individuals less than 580 μm in total length were randomly chosen. For both years, we examined the relationship between PII size and average water temperature during the 38-days period before collection.

3.4.5 **Statistical analysis**

For the biweekly settlement analysis in 2008, a 2-way mixed model ANOVA was used with date (fixed) and site (random) as factors to determine whether differences in total recruitment (without distinguishing between primary and secondary settlers) occurred between sampling periods. Date was considered independent because collectors were replaced each time. A one-way ANOVA was used for the weekly recruitment analysis in 2008 and the biweekly recruitment analysis in 2009, and a parametric post hoc test was then used after ANOVA analysis to compare settling rates among dates or sites (alpha = 0.05). Log-transformed data were used in these analyses to respect ANOVA assumptions. The size frequency of settlers was analysed by using the percentage in each size class (from 250 to 2000 μm, in 50-μm classes, except for the last class, which ranged from 900 to 2000 μm) for each date in 2008 and 2009. Distributions were then compared among sampling dates chronologically using Kolmogorov-Smirnov tests on pairs of sequential dates and *F*-tests to compare variances. PII shell size analysis on individuals (log-transformed PII shell length) related to period of settlement was conducted using a one-way ANOVA and a post hoc Tukey's test. Linear regressions were used to examine the relationship between primary and secondary settlers and the average wind speed of the preceding week (weekly [2008] and biweekly [2008, 2009] at Pointe-Mitis and biweekly [2008] at the other sites). Linear regressions were also used to test for a relationship between average water temperature (during 35 days before settlement) and average PII size of primary settlers in 2008 and 2009. For the PII analysis of biweekly settlers in 2009, we used a non-parametric test (Kruskal-Wallis test) and then a post hoc multiple comparison test because of strong non-normality of the data. R software version 2.13 (R development core team, www.r-project.org) was used for all statistical analyses.

3.5 Results

3.5.1 Temporal variability in total settlement

In 2008, overall settlement rate of *Mytilus* spp. (all settlers) in experiment 1 (Fig. 2A–C) showed significant differences between biweekly periods ($p < 0.001$, ANOVA), with no or low mussel settlement in early/mid-July at the 3 sites (group d, Tukey's test), followed by a small, but significant, increase in late July (group c), August (group b) and a major peak in late August (group a). Subsequently, little settlement was observed in September (group b). This pattern was generally consistent among the 3 sites, although settlement was twice as high at Saint-Ulric (group a, Tukey's test among sites) relative to the other sites (group b, among sites), and the August peak began earlier at Sainte-Félicité. In 2009 (Pointe-Mitis only), settlement was an order of magnitude lower and generally occurred earlier in the summer (Fig. 2D; experiment 3). As in 2008, almost no settlement was observed in early July (group e, Tukey's test), but distinct settlement peaks were observed in both mid-July (group a) and mid-August (group ab), the latter corresponding approximately with the single peak observed in 2008.

The higher-resolution data from weekly sampling in 2008 (experiment 2, one site) revealed a more complex pattern of settlement relative to the single peak observed in biweekly sampling (experiment 1, 3 sites; see above). First, there was a minor but significant peak in settlement in early July (Fig. 3). Second, the August peak was composed of 2 significantly distinct peaks. In terms of total rates of settlement, the comparison of samples collected at Pointe-Mitis showed that total settlement per collector location (i.e. the sum of all settlers collected at a specific location throughout the 3-months experimental period) was strikingly similar regardless of the duration of deployment: 864 ± 179 and 907 ± 204 settlers location^{-1} (mean ± SD; n = 8) for the weekly and biweekly experiments, respectively. However, these numbers were significantly lower than those from collectors deployed for the entire 3-months period (1750 ± 378 recruits location^{-1}; n = 8). Cumulative totals for biweekly collector locations at the other 2 sites (2233 ± 557 and 1679 ± 337 settlers location^{-1} at Saint-Ulric and Sainte-Félicité, respectively) were much closer to the number of settlers observed in the 3-months collectors (2699 ± 439 and 1549 ± 445 recruits location^{-1}, respectively).

3.5.2 **Primary versus secondary settlement**

In 2008, mean shell length of settlers collected weekly at Pointe-Mitis varied from 325 ± 35 µm (mean ± SD, n = 297) in early July to 608 ± 199 µm (n = 82) in mid-September (Fig. 4). Two main periods with small settlers were seen, one in mid-July and another in mid-August, with average sizes less than 440 µm. After each of those periods, there was generally a gradual increase in the average size of settlers between each sampling date (p <

0.05, except between 1 and 8 September and between 15 and 21 September, Kolmogorov-Smirnov test). Using a 475-µm threshold, the percentage of secondary settlers was always ≥10% (except for the first sampling period) and exceeded 50% for 4 different periods. Percentages were generally low (0–29%) during periods of high settlement, with the exception of the 4 August peak, when one of the highest percentage of secondary settlers (73%) was observed. In 2008, secondary settlement measured weekly at Pointe-Mitis was positively correlated with the average wind speed of the preceding week (Fig. 5; adjusted $R^2 = 0.72$, $p < 0.001$; $n = 11$, linear regression analysis) whereas primary settlement was not (adjusted $R^2 = -0.06$, $p = 0.52$; $n = 11$, linear regression analysis). Neither primary nor secondary settlement was correlated with wind speed for biweekly collections at any of the 3 sites. Mean daily average wind speed was 5.2 ± 2.0 km h^{-1} (mean ± SD) from 1 June to 30 September in 2008.

In 2009, the mean (±SD) settler size ranged from 352 ± 46 µm in mid-July ($n = 299$) to 903 ± 281 µm in late-September ($n = 53$), and we observed a continuous increase in the average size and in the variation in shell length throughout the summer (Fig. 6; $p < 0.001$, Kolmogorov-Smirnov test), except between 16 and 21 September, when no significant difference was observed. The size of settlers became more heterogeneous as the season progressed, with a range of 250–550 µm in July and 300 to >900 µm in September ($p < 0.001$, *F*-test). Corresponding with this shift to larger sizes, our estimate of the proportion of secondary settlers also increased over the summer (from 0% of secondary settlers in July to 91% at the end of September). Once again the earliest peak in settlement (20 July) was exclusively primary settlers whereas the later peak (17 August) had a substantial portion (50%) of secondary settlers. Overall, in spite of the reduced settlement in 2009, a similar evolution of the settlement pattern was seen in both years, with an increase in the average size and a larger number of secondary settlers in the weeks following events of primary settlement. Neither primary nor secondary settlement was correlated with the preceding wind conditions for the biweekly collections at Pointe-Mitis in 2009. Mean daily average wind speed in 2009 (5.4 ± 1.7 km h^{-1}, mean ± SD) was very similar to that of 2008 for the same time period (see above).

3.5.3 **Prodissoconch II analysis**

For primary settlers collected weekly at Pointe-Mitis in 2008, mean (±SD) PII size ranged from 284 ± 16 μm (4 August, n = 51) to 319 ± 28 μm (25 August, n = 71), with individual values varying from 242 to 384 μm (Fig. 7). Using values of planktonic larval growth rates ranging from 3 to 8 μm day^{-1} (= water temperature from 6 to 15°C; see above) and an initial prodissoconch I shell ('D-shell') length of ≈110 μm after 3 days of post-fertilization development (Bayne et al. 1975; Sprung 1984; Pechenik et al. 1990; Beaumont et al. 2004; Hayhurst & Rawson 2009; Rayssac et al. 2010), we estimated PLD to be 38 days on average with a growth rate of 5.5 μm day^{-1} (range: 27 to 67 days for growth rates of 8 and 3 μm day^{-1}, respectively, for a 302 μm settler, the overall average size in 2008). In 2008, for the first 6 weeks, mean PII length did not vary significantly ($p > 0.05$, group d, Tukey's test), but by late August (25 August and 1 September) PII size was significantly larger than previously observed ($p < 0.001$, ANOVA; group a, Tukey's test). A progressive return to smaller PII size (median around 295–300 μm) occurred at the end of the season. Depending on the value of the larval growth rate used, the maximum variation between different weeks in the estimated larval period was 4.4 to 12 days. PII length and water temperature prior to settlement were not correlated in 2008.

In 2009 a similar pattern in PII size was detected in the biweekly samples collected at Pointe-Mitis, and PII shell lengths were significantly different (data not shown, $p \leq 0.02$, Kruskal-Wallis test) among certain periods. PII size generally increased throughout the summer from 20 July (290 ± 12 μm, n = 50) to 1 September (308 ± 24 μm, n = 22; $p < 0.05$, Kruskal-Wallis post hoc test), but was followed by a small decrease in September. In 2009 the mean PII shell length was 296 ± 20 μm (n = 162), corresponding to a mean PLD of 37 days (range: 26 to 65 days) when based on a growth rate of 5.5 μm day^{-1}. We estimated that the maximum differences in PLD among sampling periods ranged from 2.5 to 7.0 days. However, the increase in PII shell lengths occurred earlier in 2009 than in 2008 (as did overall settlement; see above). As in 2008, PII length and water temperature prior to settlement were not correlated in 2009.

3.6 **Discussion**

Except for a few earlier studies (Bayne 1964; Garcia et al. 2003; Bownes & McQuaid 2009; Newell et al. 2010), most previous studies of bivalve recruitment (e.g. Porri et al. 2006; Lagos et al. 2007; Smith et al. 2009) have not distinguished between primary and secondary settlers and thus have tended to overestimate levels of larval supply by including secondary settlers already *in situ* at the site. In the present study we measured settlement with the most common methods currently used, but then refined estimates by distinguishing between the 2 types of settlers depending on their size. Important differences were found, allowing us to distinguish among different scenarios of settlement over time. Neither a scenario of settlement as a relatively continuous process during the summer nor a simple peak of primary settlement was observed. Rather, when a distinction was made between the types of settlers (and thus the scale of dispersal), limited periods of large-scale dispersal (i.e. primary settlement) were observed followed by an increasing importance of secondary dispersal, especially within the first weeks after settlement and metamorphosis. Substantial variability in timing and magnitude of settlement between the 2 years was also observed, suggesting that long-term variability in connectivity also needs to be considered when examining population dynamics, especially at a metapopulation level (Le Corre et al. 2012). Finally, the duration of the planktonic larval phase appeared remarkably constant between the 2 years. Moreover, the observed sizes at settlement and metamorphosis during the summer were comparable to those from other boreal/subarctic studies (e.g. Kautsky 1982; Rodhouse et al. 1984).

3.6.1 **Temporal settlement patterns**

Studies in other boreal environments (Baltic Sea, northern Norway, Iceland, and Ireland) have usually revealed a single main event of spawning/settlement during the warm season (Kautsky 1982; Rodhouse et al. 1984; Thorarinsdottir 1996; Garcia et al. 2003; Thorarinsdottir & Gunnarsson 2003; Frantzen 2007), although a partial (i.e. smaller) spawning event can occur earlier during late spring (Rodhouse et al. 1984; Garcia et al. 2003; Frantzen 2007). Our settlement data, taken at a much higher resolution, showed that more complex patterns can occur. At a biweekly resolution, the typical pattern of one main recruitment event was observed in 2008 and occurred at all our sites with only small spatial differences in the magnitude and timing of recruitment. Low variability in recruitment at this spatial scale (30 km) along a relatively homogeneous shoreline is consistent with previous results reported from the same region (Smith et al. 2009). In contrast, the low recruitment in 2009 revealed the high temporal variability between years and could explain corresponding inter-annual variability in the scale and strength of population connectivity (Le Corre et al. 2012).

The higher resolution provided by weekly sampling showed that recruitment can be more complex, e.g. 3 peaks in 2008. Discrimination of primary settlers from secondary settlers revealed that only 2 of the peaks were due mainly to primary settlement, the first in mid-July and a second, higher peak, in mid-August. Those events may be the consequence of 2 separate spawning events, asynchronous spawning at 2 different places, or possibly biological differences between the 2 species that occur in the estuary (*Mytilus edulis* and *M. trossulus*). These results demonstrate the importance of proper temporal resolution for documenting key properties of recruitment patterns. For example, the bimodal settlement pattern observed in 2008 was only documented by our weekly sampling and was missed entirely by our biweekly sampling scheme.

3.6.2 **Primary versus secondary settlement**

Primary settlement occurred over the whole sampling period, but our analysis revealed a clear modal or bimodal distribution through that period. Secondary settlers were present throughout the summer and were relatively abundant at certain times during the season. However, secondary settlement was likely to have been underestimated because: (1) a few large settlers (>2000 μm) were excluded from the sampling, (2) large settlers are known to prefer natural substrata rather than artificial substrata (Roughgarden et al. 1988; Porri et al. 2008), and (3) the threshold size used to discriminate between primary and secondary settlement was intentionally biased towards overestimating primary settlement (i.e. maximum PII size, maximal period for growth, and maximal post-settlement growth rates were used to determine the threshold size). Secondary settlement may also be occurring throughout the year, as seen in some subarctic areas (Garcia et al. 2003), but ice cover during winter prevented us from sampling throughout the year in the St. Lawrence Estuary. After the 2 main settlement events of 2008, we observed a distinct increase in the size/age of settlers over time with individuals settling on the collectors through post-larval dispersal (Hunt & Scheibling 1998; Garcia et al. 2003). Our results thus demonstrate the high mobility of settlers, even weeks after first settlement, and support the idea that the transition between the planktonic and benthic phase is not as abrupt as generally thought (Lane et al. 1985; Newell et al. 2010). Despite important inter-annual variability in settlement peaks, the temporal sequence of primary and secondary settlement was consistent between years, with increasing secondary settlement occurring over time, likely due to the increasing pool of post-settlement individuals as primary settlement occurred and settlers accumulated.

Secondary dispersal and settlement can be the result of either active or passive processes. After settlement, the post-metamorphic stage can detach itself from the original substratum, drift or crawl on the substratum, and then reattach to an alternative substratum; thus active behavior by the organism itself can contribute to the occurrence of secondary settlers observed in collectors (Bayne 1964; Cáceres-Martínez et al. 1994; Hunt & Scheibling 1998). Alternatively, dislodgment by water motion is a more passive means of secondary dispersal, one that may even be undesirable for the organism (Cáceres-Martínez et al. 1994). Discriminating between these 2 possibilities is difficult, but the recruitment peak in 2008 that was dominated by secondary settlers (4 August) coincided with a storm in early August. Moreover, weekly secondary settlement in 2008 was positively correlated with regional wind speeds, a proxy for wave action in this system. Thus, in *Mytilus* spp., secondary settlement appears to be primarily a passive process controlled by water motion (i.e. wave action), as observed elsewhere (Martel 1993; Newell et al. 2010). In these studies, where primary settlement was distinguished from secondary settlement, rarely has each settler type been thoroughly teased out and their relative importance quantified through time. Newell et al. (2010) examined settlement of *Mytilus edulis* on eelgrass blades in tidal channels in Maine and reported a strong temporal component in the relative proportion of primary settlers (predominance early in the season) versus secondary settlers (predominance late in the season). Moreover, in a study on the bivalve *Dreissena polymorpha*, Martel (1993) distinguished between primary and secondary settlement and found that the secondary settlers (drifting juveniles) represent a high proportion of settlers. In that study, an average 46% of all individuals collected had arrived as drifting post-metamorphic stages, and, as in this study, peak periods of secondary settlement coincided with periods of high winds and associated high wave action.

Although water motion may redistribute settlers within a site, we did not observe any evidence of a net loss of settlers from collectors over time. The comparison of weekly versus biweekly recruitment showed that the cumulative numbers of recruits for any particular location were the same, i.e. there was no net loss over time from the collectors that were deployed for a longer period. This result contrasts with studies of algal and invertebrate recruitment, which have shown that post-settlement losses are high (e.g. Widdows 1991; Gosselin & Qian 1997; Lamote & Johnson 2008), but is similar to other studies on mussels (Hunt & Scheibling 1998; Bownes & McQuaid 2009). In our study, recruitment to collectors deployed over the entire season was consistent with these shorter-term results, as it was equivalent or greater than the cumulative totals for collectors deployed for 2-weeks periods, indicating low post-settlement mortality and importance of initial colonization in determining spatial distribution of mussels (Hunt & Scheibling 1998). Indeed, the much higher recruitment in collectors deployed for the entire season at 2 sites suggests that some type of substratum ‘conditioning’ (e.g. loss of chemical from the plastic, development of a biofilm; Dobretsov 1999; Bao et al. 2007; von der Meden et al. 2010; Shimeta et al. 2012) or possibly enhanced settlement was occurring in response to the presence of conspecifics (e.g. Chase & Bailey 1996; von der Meden et al. 2010).

Dispersal distances are very different between the 2 types of settlement, with primary settlers dispersing on a much larger scale than secondary settlers (Gunther 1992). When assessing connectivity among populations, the focus should be on primary settlers to determine large-scale dispersal and precise timing of the phenomenon. In contrast, secondary settlement is a more diffusive process with less impact on large-scale connectivity, which may occur for a few weeks and remain largely local because drifting periods are much shorter than the planktonic larval phase. Our results indicate that large-scale dispersal via primary settlement occurred mainly after 1 (2009) or 2 (2008) short spawning periods. Secondary dispersal in the following weeks then allowed further localized spreading of these more isolated events of large-scale dispersal. However, if only overall recruitment had been measured, with no distinction between primary and secondary settlement, then we may have erroneously concluded that settlement (and thus connectivity) was a more temporally diffuse process, occurring across the entire season.

3.6.3 Prodissoconch II analysis

The average PII shell length (or size at settlement and metamorphosis) of primary settlers (242 to 384 µm) was similar to what has been reported for *Mytilus* spp. elsewhere *in situ* (Seed 1976; Sprung 1984; Hendriks et al. 2005; Bownes & McQuaid 2009), and similar to what has been observed in one laboratory study in Germany (Sprung 1984), but slightly larger than in another in the Netherlands (Hendriks et al. 2005). The average temperature is approximately 10°C along the southern shore of the St. Lawrence maritime estuary where this study was conducted, which should produce slower larval development and thus a longer larval phase duration and greater size at metamorphosis than in more temperate climate zones (Bayne 1965; Beaumont & Budd 1982; Hodgson & Bourne 1988; Widdows 1991). In the St. Lawrence estuary, we estimated that mussel larvae spent an average of 38 days (range: 27 to 67 days) in the water column before attaching to the substratum, longer than most estimates of PLD in temperate regions (Seed 1976; Widdows 1991; Lutz & Kennish 1992) but similar to estimates from subarctic areas (Kautsky 1982; Thorarinsdottir 1996; Garcia et al. 2003; Thorarinsdottir & Gunnarsson 2003). Longer PLD increases planktonic mortality but is necessary to achieve adequate development, as size and health of the settlers at metamorphosis play a major role in juvenile growth. Recruitment success varies with individuals and cohorts (Gosselin & Qian 1997; Pechenik et al. 1998), and one potential source of variability is variation in larval condition, or quality, at metamorphosis (Phillips 2002). The larger primary settlers of late August may thus have had a better potential for survival. Further experimental studies (Phillips 2002) on settlement size and success across the season need to be pursued.

The consistent size at settlement and metamorphosis (i.e. PII) during the first half of the season suggests that there is either steady, low-level reproduction occurring regionally or different sub-populations that are asynchronously reproducing, but their larvae are then well distributed within the system. In 2008, the peak of small settlers observed on 18 August strongly suggests a single large and widespread spawning event occurring in early July, as seen elsewhere (Duinker et al. 2008). Indeed, increases in shell size at settlement (PII) in the subsequent weeks would then correspond to a simple delay in settlement (i.e. longer PLD), generating the larger individuals observed in late August 2008 (some individuals up to 370 µm). Greater PII values during August 2008 were not caused by higher water temperatures since there is a reverse correlation between PII size and water temperature (Bayne 1965; Hodgson & Bourne 1988; Schejter et al. 2010), but were rather due to longer PLD of those larvae prior to settlement and metamorphosis. The smaller PII shell length of settlers in September is suggestive of a minor, secondary spawning event in weeks prior (Duinker et al. 2008). Late-September settlers could also be secondary settlers that had slow post-settlement growth and thus were still counted as primary settlers based on our estimated size threshold (this size threshold was, however, quite conservative, i.e. largest PII size combined with maximal possible period of growth). More perplexing are the smaller early pulses of settlers (early July in 2008 weekly data, and mid-July in 2009) that demonstrate that minor spawning events consistently occur in these populations early in the season.

The planktonic larval phase is known to be influenced by several interacting biological and physical parameters operating at various scales (Cowen & Sponaugle 2009). Larval growth and development of *Mytilus* larvae is known to be largely influenced by water temperature (Widdows 1991). Seasonal and annual variability of water temperature and food availability might have a considerable impact on larval development rates and, therefore, PLD and PII shell length (Widdows 1991; Fotel et al. 1999). These sources of variation were not, however, a focus of our study, and we accounted for them by using a range of growth rates and PLD estimates. The variations of PII shell length observed within a single period (e.g. weekly collections) also suggest different origins of larvae within a recruitment event. This variation could be explained by the same combination of mechanisms: different spawning times (varying PLD) and/or different spawning locations. For the latter, different hydrological regimes encountered during the larval phase can generate variability in both PLD and size at metamorphosis due either to longer pathways taken by larvae (i.e. time) or to different environmental conditions encountered en route (i.e. growth). However, despite lower water temperatures in 2009 (Fig. 8; 10.1 ± 2.7°C in 2008 vs. 8.9 ± 2.3°C in 2009; mean ± SD of average daily temperature from 1 June to 30 September), no major variations in PII size were noticed between years. The seasonal variability in size at settlement and metamorphosis, coupled with different timing of settlement peaks, suggests that there are important variations in the dispersal patterns of *Mytilus* in the St. Lawrence Estuary, and thus high variability in connectivity within the region (Le Corre et al. 2012).

3.7 Conclusions

We have demonstrated the importance of distinguishing between primary and secondary settlement when assessing the scale and timing of dispersal. Using only primary settlement data, we have shown that large-scale dispersal of *Mytilus* spp. prior to primary settlement occurs for a limited period of time in the St. Lawrence maritime estuary, usually in mid-July and mid-August. However, secondary dispersal and settlement is not as limited and can take place throughout the whole summer, and therefore better knowledge of this latter process is necessary to understand local population dynamics. The large within-season and inter-annual variability in the timing and magnitude of primary settlement demonstrates, however, that the larger-scale metapopulation dynamics are also highly variable and may be driven by exceptional years of high settlement.

3.8 Acknowledgements

We acknowledge and appreciate the funding for this research (STPGP 336324) from the Natural Sciences and Engineering Research Council (NSERC) of Canada, the financial and logistic support from Québec-Océan and Canadian Museum of Nature (Zoology Section), as well as the student support from the Département de biologie, Université Laval. We are grateful to C. McKindsey and Fisheries and Oceans Canada for access to facilities at the Maurice Lamontagne Institute. Our thanks as well to L. Boutet, S. Collin, H. Hamdi, K. Hasegawa, C. Leroux, A. Marzouk, M. Morin, J. Ploquet, C. Robineau and C. Roby for the invaluable assistance provided during field and laboratory work and for comments on earlier versions of this manuscript.

3.9 **Table**

Table 3.1 *Mytilus* spp. Study sites where the settlement experiments were conducted along the St. Lawrence maritime estuary, Québec, Canada. Number, replacement frequency and deployment period (no. of sample periods) of collectors are indicated for each experiment. Dates are day/month/year; biweekly: every 2 weeks

Collector deployment

Experiment #	Locality	Year	Collector replacement	Number of sample periods (collectors)	Deployment period	
					Start	End
1	Pointe-Mitis	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
	Saint-Ulric	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
	Ste-Félicité	2008	Biweekly	6 (8)	27/06/2008	21/09/2008
2	Pointe-Mitis	2008	Weekly	11 (8)	7/07/2008	21/09/2008
3	Pointe-Mitis	2009	Biweekly	7 (8)	21/06/2009	30/09/2009

3.10 **Figures**

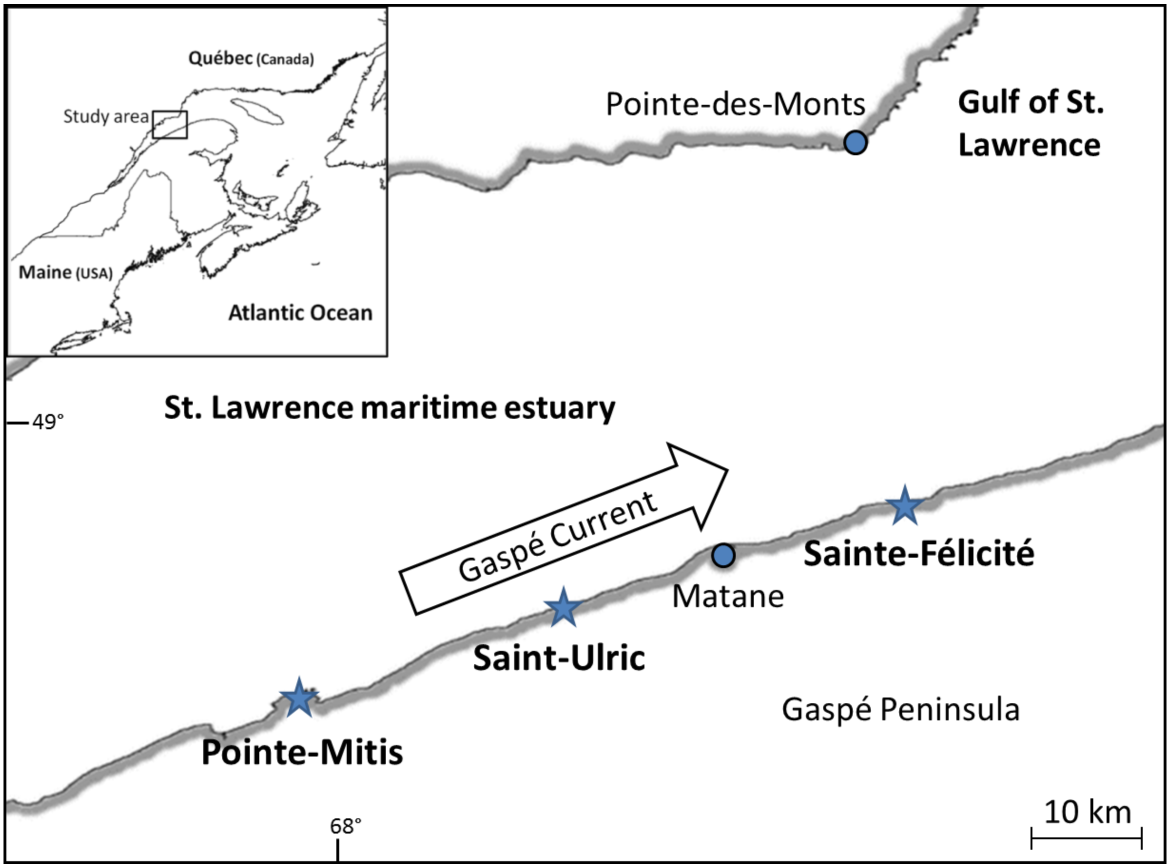

Figure 3.1 *Mytilus* spp. Study sites (stars) where mussel settlement was studied along the St. Lawrence maritime estuary, Québec, Canada. The arrow indicates the eastward net flow of the Gaspé Current

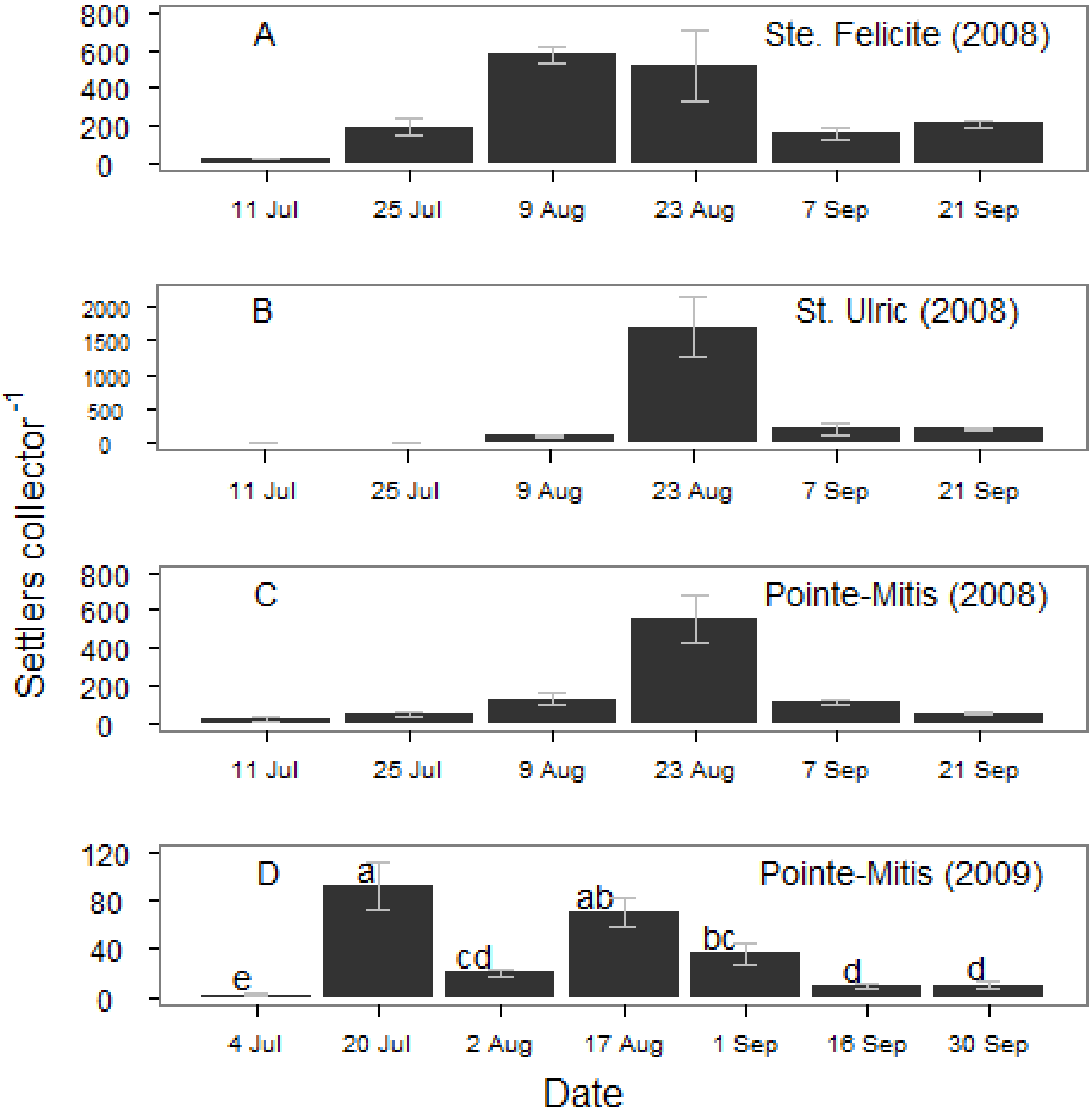

Figure 3.2 *Mytilus* spp. Mean (±SE) number of settlers in collectors replaced biweekly (i.e. every 2 weeks) from late June to late September on the south shore of the St. Lawrence maritime estuary, Québec, Canada, at Sainte-Félicité (A), Saint-Ulric (B) and Pointe-Mitis (C) in 2008 (experiment 1), and at Pointe-Mitis in 2009 (experiment 3, D). For 2009, periods with the same letter above the bar were not significantly different. Statistical results for 2008 are not shown here but are described in the results section. Note differences in *y*-axes scales

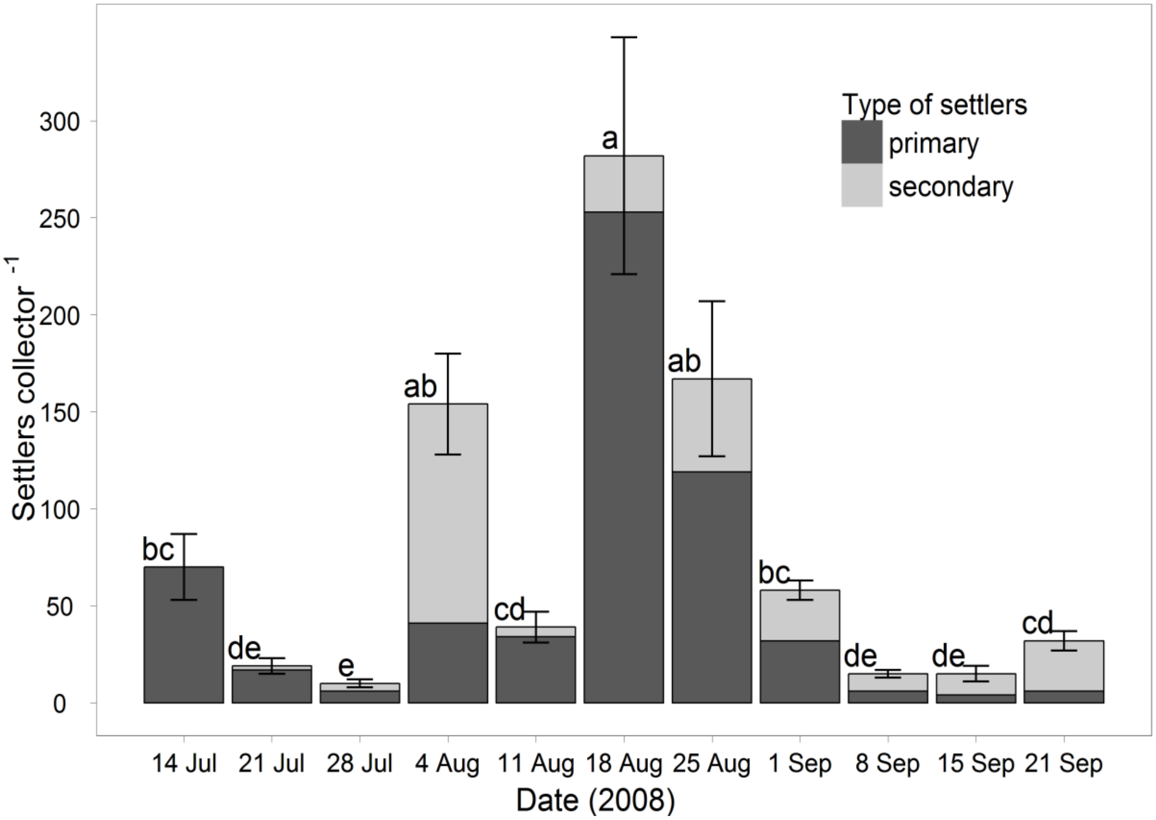

Figure 3.3 *Mytilus* spp. Mean (±SE) number of settlers in collectors replaced weekly from early July to mid-September 2008 at Pointe-Mitis (experiment 2). Primary settlement (dark grey) and secondary settlement (light grey) were differentiated by an analysis of size frequencies. Periods with common letters (above bars) are not significantly different

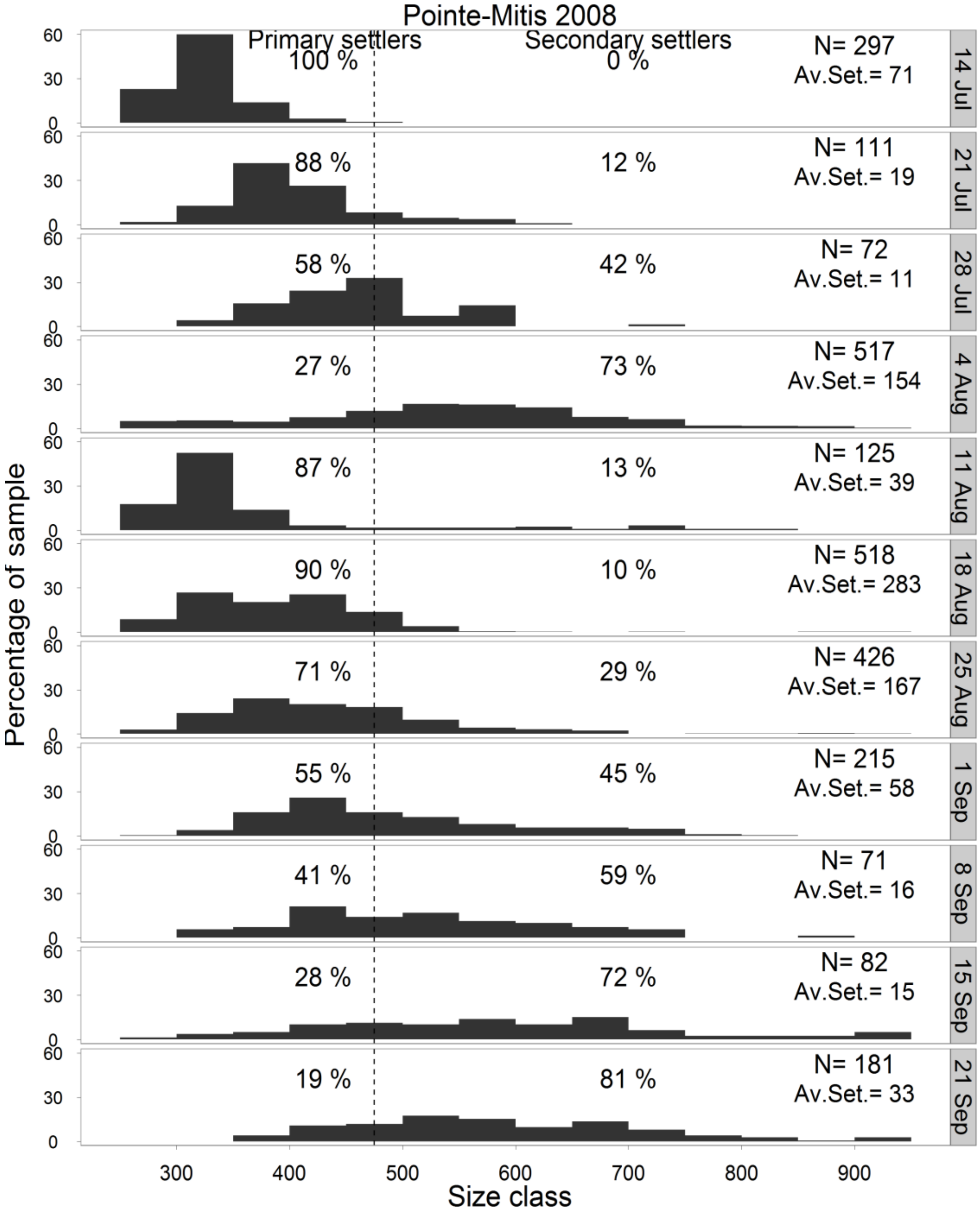

Figure 3.4 *Mytilus* spp. Temporal change in size–frequency distribution (250–2000 µm, the last size class ranges from 900 to 2000 µm) of settlers collected weekly at Pointe-Mitis, Québec, Canada, during summer 2008 (experiment 2). Vertical dashed line: threshold (475 µm total shell length) distinguishing primary and secondary settlers. N: the total number of ind. measured; Av.Set.: the mean number of mussel settlers per collector occurring during each period

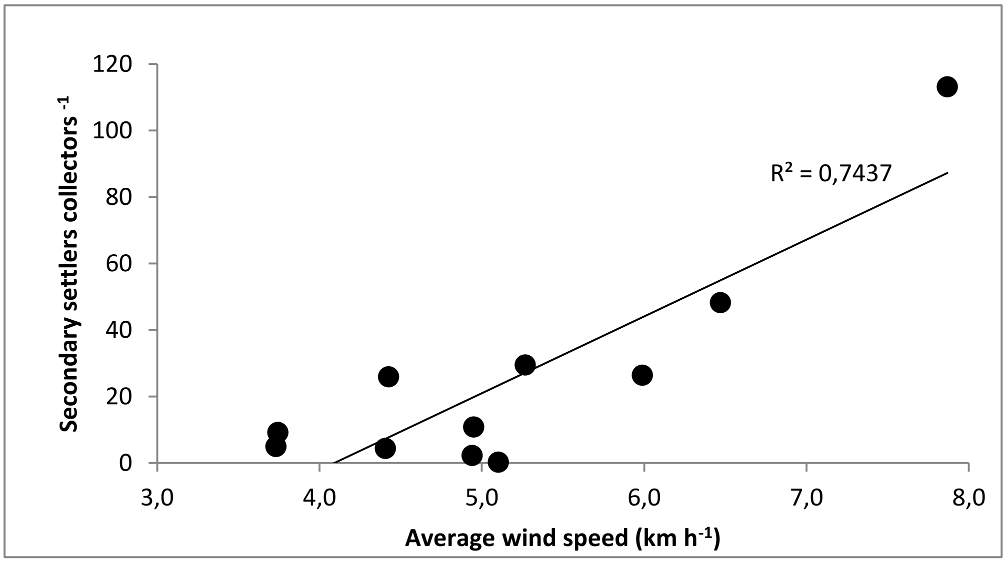

Figure 3.5 *Mytilus* spp. Average number of weekly secondary settlers as a function of the mean wind speed (km h^{-1}) during the week prior to replacement of collectors in summer 2008 at Pointe-Mitis, Québec, Canada. The significant linear regression and R^2 values are also shown

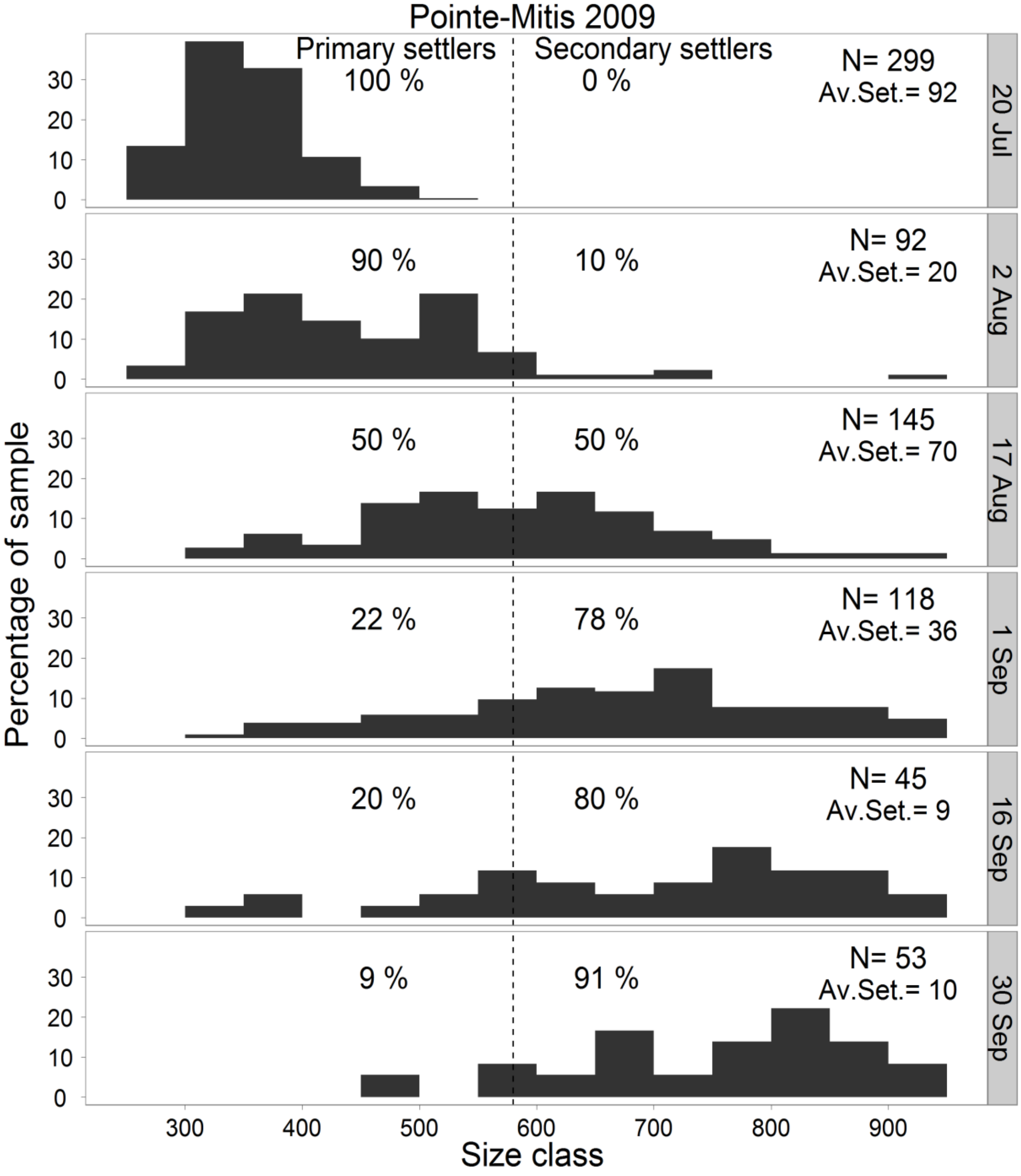

Figure 3.6 *Mytilus* spp. Temporal change in size–frequency distribution (250–2000 µm, the largest size class ranges from 900 to 2000 µm) of settlers collected biweekly at Pointe-Mitis, Québec, Canada, during summer 2009 (experiment 3). The vertical dashed line represents the threshold (580 µm total shell length) distinguishing primary and secondary settlers. N: the total number of individuals measured; Av.Set.: the mean number of mussel settlers per collector occurring during each period

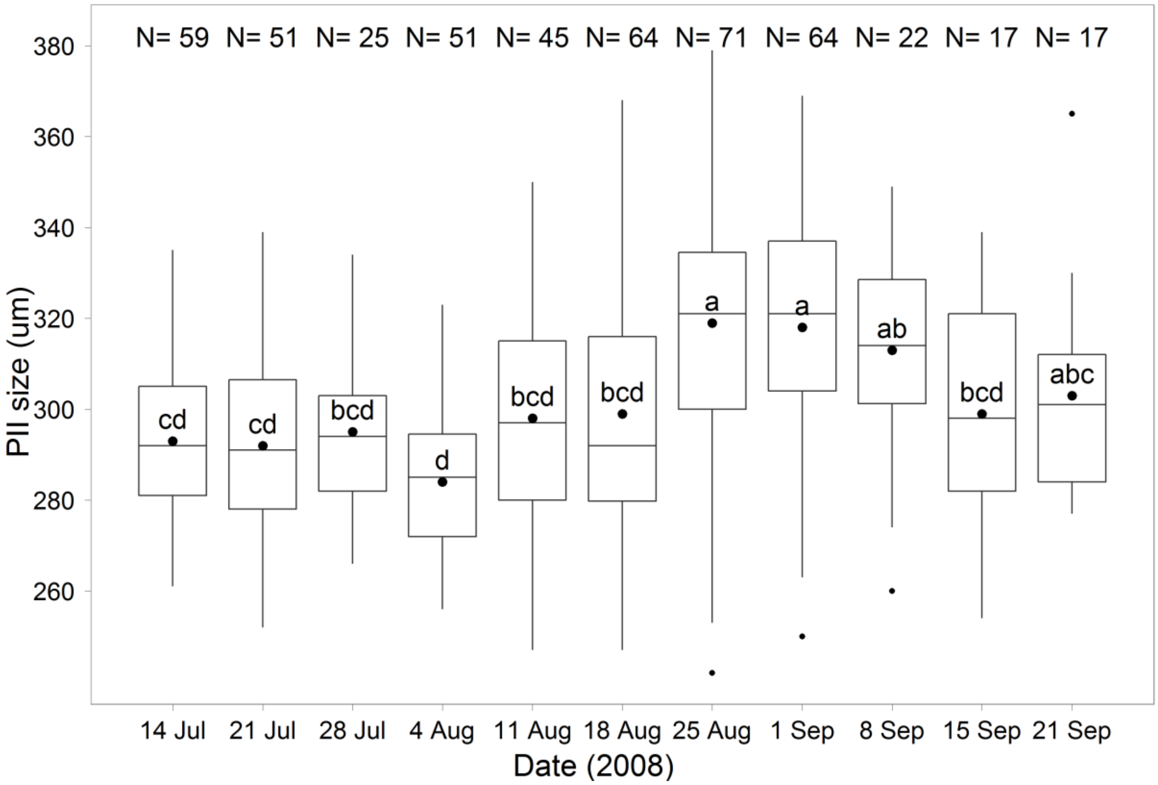

Figure 3.7 *Mytilus* spp. Mean size (large filled circle) and box-and-whisker diagram (central line: median; box: lower and upper quartiles; whiskers: smallest and largest observations; small circles: over-dispersed observations) of prodissoconch II (PII) shell length (µm) of weekly settlers at Pointe-Mitis (experiment 2) during summer 2008. Individuals were considered to be primary settlers if their total length was <475 µm. Letters represent significantly different groups. N: number of settlers measured

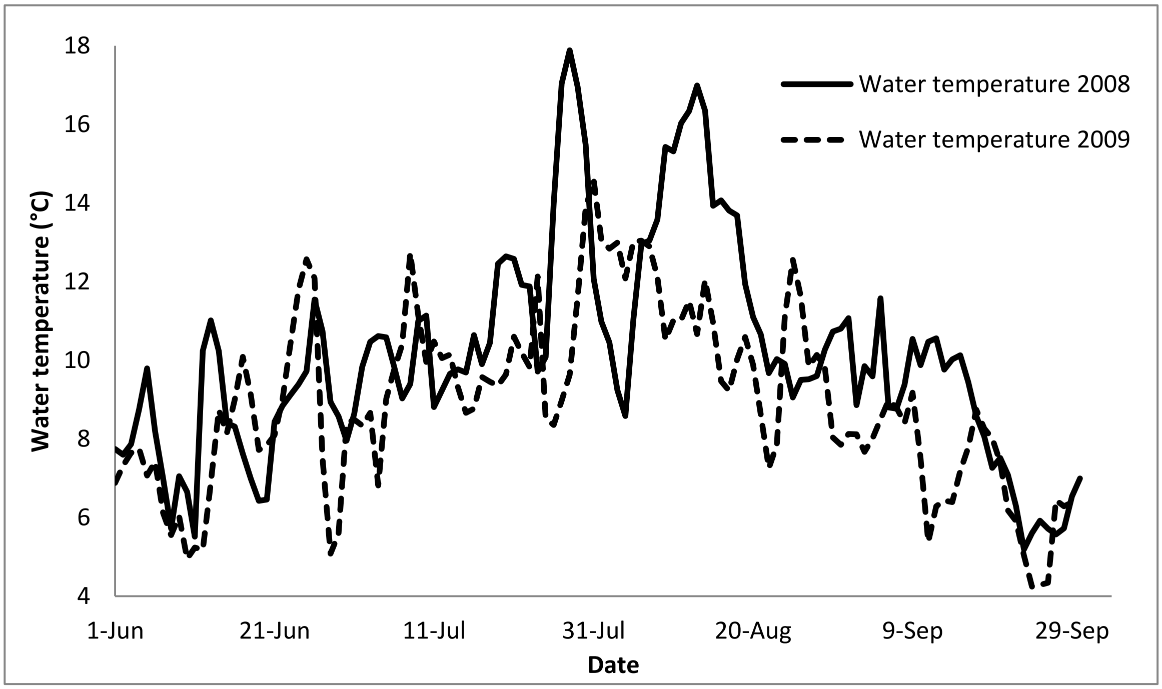

Figure 3.8 *Mytilus* spp. Time series of average daily water temperature (°C) observed from 1 June to 30 September in 2008 (line) and 2009 (dashed line) measured at the Fisheries and Ocean Canada oceanographic buoy (IML-4), located 40 km upstream from Pointe-Mitis at 48° 40’′N, 68° 35’′W

Chapitre 4. Inter-annual variability in demographic connectivity among blue mussel (*Mytilus* spp.) populations in the St. Lawrence estuary.

4.1 Résumé

Les processus de recrutement jouent un rôle fondamental en structurant les communautés marines benthiques et en contrôlant la persistance des métapopulations. Comme beaucoup d'invertébrés benthiques ont une phase de dissémination planctonique, les échelles de connectivité démographique entre les populations sont des éléments clés, mais difficile à cerner. Afin de mesurer la relation entre l'abondance des moules adultes et le recrutement larvaire au sein d'une métapopulation, nous avons réalisé une vaste étude entre 2005 à 2010 sur 100 km le long du littoral de la péninsule gaspésienne (Québec, Canada). La direction de la dispersion larvaire le long de cette côte est influencée par le courant de Gaspé (qui a un flux net vers l'est et le golfe du Saint-Laurent), permettant l'utilisation de statistiques spatiales pour faire le lien entre les populations adultes et le recrutement dans ce système (c.-à-d. le couplage démographique). Dans cette étude, nous avons examiné la dynamique d'une population de moules bleues (*Mytilus* spp.) au cours du temps pour estimer l'ampleur des variations spatiotemporelles de la biomasse et de recrutement, ainsi qu'évaluer la variabilité temporelle de l'échelle de connectivité entre les populations. Malgré une variabilité temporelle des abondances d'adultes et de recrues au cours des années, notre analyse a révélé, dans l'ensemble, une certaine stationnarité dans la distribution du recrutement et de l'abondance d'adultes et une absence de structures spatiales bien définies. Plus important encore, notre analyse a révélé la constance du couplage démographique entre les populations séparées par une distance de 12 à 24 km au cours de toutes les années étudiées, sauf une. Cette année exceptionnelle a démontré, cependant, que l'échelle de connectivité n'est pas une caractéristique fixe des métapopulations, et que les efforts pour modéliser ce type de systèmes nécessitent d'inclure ce paramètre dynamique pour adéquatement les décrire et les comprendre.

4.2 **Abstract**

Recruitment processes play a fundamental role in structuring benthic marine communities and controlling metapopulation persistence. As many benthic invertebrates have a dispersive planktonic phase, the scale of demographic connectivity among local populations remains a key, but elusive, element. To assess the relationship between the abundance of adult mussels and larval recruitment within a metapopulation, we conducted a large-scale survey from 2005 to 2010 along a 100-km section of coastline of the Gaspé Peninsula (Québec, Canada). The direction of net larval dispersal along this shore is influenced by the Gaspé Current (which has a net eastward flow toward the Gulf of St. Lawrence), allowing the use of spatial statistics to assess the linkage between adult populations and recruitment in this system (i.e. demographic coupling). Here, we examined the population dynamics of the blue mussel (*Mytilus* spp.) over time to estimate scales of spatiotemporal variation in biomass and recruitment and to assess temporal variability in the scale of connectivity among populations. Despite temporal variability in adult and recruitment abundances over multiple years, our analysis revealed an overall stationarity in distributions of recruitment and adult abundance and a lack of strong spatial structure. More importantly, our analysis revealed a consistent demographic coupling among populations at a distance ranging from 12 to 24 km in all but one of the five years studied. This exceptional year demonstrates, however, that the scale of connectivity is not a fixed feature of metapopulations, and efforts to model or manage such systems will need to include this dynamic attribute to adequate describe and understand them.

4.3 **Introduction**

Ecological processes act at various scales (Levin 1992) and impact population dynamics by creating variability within populations (Lima et al. 2000; Edwards & Stachowicz 2011). Such spatiotemporal variations of ecological and physical processes can create spatial structures in the abundance and distributions (e.g. gradient, patchiness) of species. Integrating these sources of variation in coastal ecosystems suggests that sessile marine populations remain generally stable (i.e. "stationary") at small temporal scales (e.g. seasonally), but vary at larger ones (e.g. annually) (Caley et al. 1996; Lima et al. 2000; Kraan et al. 2009; Frid 2011). Moreover, many natural populations can be characterized as metapopulations and spatiotemporal patterns of connectivity among local populations can thus interact with other ecological and physical processes to affect the regional distribution of abundance (Reed et al. 2000; Shima et al. 2010). In marine ecosystems, the scale of connectivity has been often estimated using planktonic larval duration (PLD) or other time-integrated variables (e.g. genetic isolation) as a proxy. As a result, our understanding of spatiotemporal patterns of abundance is still limited by assumptions of constant scale of connectivity between populations.

Demographic connectivity allows exchange of individuals within a metapopulation through movement of adults, larval or juvenile stages among populations (Hanski 2004; Kritzer & Sale 2004; Cowen & Sponaugle 2009). In marine environments, many invertebrate species are characterized by a planktonic larval stage and a sessile adult existence (i.e. low mobility), and connectivity between populations is thus driven by planktonic larval dispersal. Recent studies have improved our knowledge of larval dispersal distance, including cases of when self-recruitment (i.e. the local retention of larvae) occurs (e.g. Cowen et al. 2006; Levin 2006; Almany et al. 2007). Simulation studies predict that when dispersal is mostly driven by oceanographic regimes, dispersal patterns can show great variability due to the stochasticity of oceanographic transport processes (Gilg & Hilbish 2003; Siegel et al. 2003; Cowen et al. 2006; Werner et al. 2007). Because of this variability, the connectivity patterns might become more complex and variable than generally considered (Le Corre et al. 2012). However, connectivity is difficult to measure directly in marine systems, especially for the many invertebrate species characterized by long PLD, and variability in dispersal patterns is not typically amenable to empirical assessment (Cowen & Sponaugle 2009; Le Corre et al. 2012). Despite a few empirical and theoretical studies suggesting its importance (Botsford et al. 2009; Cowen & Sponaugle 2009; Jones et al. 2009; Carson 2010; Hogan et al. 2012), ecological theories still largely ignore variability in patterns of connectivity over ecological time scales.

The dynamics of intertidal populations has been studied under very contrasting assumptions of demographic connectivity, ranging from demographically open populations to metapopulations and, finally, to closed populations (Hixon et al. 2002). In a metapopulation, local populations are partially controlled demographically by adults from other populations through larval dispersal over spatial scales specific to the species and the system in which it occurred (Caley et al. 1996; Cowen et al. 2000; Hughes et al. 2000). In contrast, closed systems imply local density-dependence and self-recruitment as the most important process of population regulation (Caley et al. 1996; Cowen et al. 2000), and open populations theory involves recruitment from a well-mixed regional pool of individuals (Hixon et al. 2002). An important empirical assessment of metapopulation connectivity consists of using a stock-recruitment relationship across local populations, which can be used to infer the existence of a metapopulation and estimate scales of connectivity (Cowen & Sponaugle 2009; Smith et al. 2009). For example, metapopulation dynamics of the blue mussel (*Mytilus* spp.) is influenced by the relationship between larval production by adults (i.e. stock) and recruitment of larvae into the adult populations. This relationship drives demographic connectivity through larval dispersal among sites and allows estimating the scale of dispersal of mussel larvae. Examining the strength of the statistical relationship between local abundance of adults and downstream recruitment at a variety of spatial scales provides a statistical estimate of the characteristic scale(s) of the stock-recruitment relationship between populations, and allows testing different alternative hypothesis of demographic connectivity through their statistical signature (Smith et al. 2009; Le Corre et al. 2012). While such an assessment of demographic connectivity can be conducted over single, discrete recruitment events, it should also be repeated over several generations to quantify spatiotemporal variability in patterns of connectivity.

Here, we sampled adult mussel biomass and larval recruitment over multiple years and then conducted geostatistical analyses to assess inter-annual variability of spatial patterns and scales of connectivity among populations (Rossi et al. 1992; Hewitt et al. 1997; Smith et al. 2009). Specifically, (1) we examined the stability over time of a blue mussel metapopulation at a regional scale (> 100 km), and (2) looked for spatial structure within the distribution of adult biomass and recruitment and their variability. Using these data, we then (3) tested for the existence of demographic connectivity within a metapopulation and assessed the temporal variability in the scale of connectivity among populations. This study represents one of the first empirical assessments of marine population connectivity over several years (e.g. Carson 2010; Hogan et al. 2012), which has mostly been considered as a stable species characteristic. As opposed to earlier studies, our results suggest an overall stationarity in the scale of connectivity, despite variations in the spatial patterns of adult biomass distribution, and oceanographic conditions. However, the robustness of connectivity patterns may be compromised during years with strong deviations from the average scale of connectivity that may affect metapopulation dynamics. Our study provides empirical support for the development of a non-equilibrium theory on metapopulation connectivity.

4.4 Materials and methods

4.4.1 Study sites

The study area was located along 100 km of rocky shoreline in the Gaspé Peninsula (Québec, Canada) from Saint-Ulric [48.7725°N, 67.7559°W] to Sainte-Anne-des-Monts [49.1286°N, 66.5595°W] (Fig. 4.1). Along this shore, circulation is mainly driven by the tidal, wind-driven and longshore currents, the latter, the Gaspé Current, being driven by the freshwater discharge of the St. Lawrence River (Sheng 2001). This current thus generates a net eastward coastal flow at the surface with oscillations of current directions due to tidal effects. The combination of these hydrodynamic processes likely drives the dispersal of mussel larvae, as seen elsewhere (McQuaid & Phillips 2000; Gilg & Hilbish 2003). A few bays exist along this coast, but the shoreline is mainly straight and homogeneous at a large scale, and the impact of these bays on benthic populations and larval dispersal is likely to be small, except at local scales (Archambault & Bourget 1999; McKindsey & Bourget 2000). The water flow regime is known to be generally stable among years, but slight variations might occur depending on the wind and freshwater discharge (Senneville S., unpubl. data; Fradette & Bourget 1980). In the St. Lawrence Gulf and Estuary, tides are diurnal with mean and maximal fluctuations of approximately 2.6 and 4.1 m, respectively. Typical summer surface salinity is 27 ppt and temperature ranges between 5 and 18°C in summer (Fradette & Bourget 1980). Two species of mussel, *Mytilus edulis* and *M. trossulus*, are widespread along the Gaspé coast and are ecologically similar. Hybridization between the two species occur in this (Turgeon J., unpubl. data) and other systems (McDonald et al. 1991; Thomas et al. 2004; Toro et al. 2004; Moreau et al. 2005), but morphological techniques to distinguish the two species and their hybrids are unreliable (Innes & Bates 1999), and it appears that molecular techniques are required (McDonald et al. 1991; Toro et al. 2004). Consequently, we treated all individuals as a functional taxonomic group (i.e. *Mytilus* spp.).

We selected 27 (2007) to 29 sites (2005, 2008-2010), including the same 26 sites which were studied by Smith et al. (2009), to assess the spatial scale of demographic coupling between adults and recruits and its variability among years (see annexe 1 for precise locations). Study sites were 100-m long, and we used GPS to allow precise resampling from one year to the next. The primary criteria for site selection were (1) homogenous horizontal rock benches, (2) a cover of at least 50% of hard substratum, (3) no influence of freshwater run-off, and (4) a separation of 1-12 km from the nearest site.

4.4.2 **Sampling procedures**

At each site along the selected zone, we measured total mussel biomass and seasonal recruitment, using a protocol similar to that described in Smith et al. (2009). In brief, to collect mussel recruits, eight multifilament nylon cleaning pads (S.O.S. Tuffy Pad^{TM}) were anchored to rocks with screws (Menge et al. 2004) within a 100-m section of the site in the mid-intertidal zone for 2 months from mid-July to mid-September, the main period for mussel settlement in the St. Lawrence Estuary (see chapter 3 of this thesis). To extract recruits from collectors, a high-pressure jet of tap water was used to detach organisms into a 150-µm sieve. Mussel recruits were then counted under a stereomicroscope, and when high density of recruits was observed (> 200 individuals.collector^{-1}), a small Folsom splitter was used to subsample. The number of recruits per collector was then averaged per site (n = 8). Mussel biomass was estimated using transect-quadrat surveys (which differed slightly among years) in a 2000-6000-m^2 area in the mid-intertidal zone. For most years (2007 - 2010), we assessed percentage of mussel cover along 6 horizontal transects (length: 10 m) using visual estimates of three 0.25 m^2 gridded quadrats (total of 18 per site). Additionally, one smaller quadrats (15 x 15 cm) per transect was destructively sampled in the mid-intertidal zone at each site. Samples were frozen until treated at which time they were thawed, rinsed in a 3.2 mm sieve and then the retained mussels weighed (± 0.01g) after blotting. This sieve did retain some juvenile mussels, but their cumulative weight was negligible compared to that of the larger mussels which were mostly adults (i.e. >10 mm length; Le Corre N., unpubl. data, Gosling 1992). Total biomass of mussel was then averaged per site (n = 6), and this variable was used to represent the relative reproductive contribution of mussel stock from each site to the metapopulation. As adult biomass and percentage cover were highly correlated (data not shown), we used just biomass data to run statistical analysis as in the earlier study (Smith et al. 2009). However, in 2005 mussel populations were only estimated by using percent cover along 8 to 10 transects (5 quadrats of 50 x 50 cm per transect) in the mid-intertidal zone at each site. Adult biomass and percentage of mussel cover were then normalized to a scale from 0-100 (minimum to maximum values) for each year to compare results among years. Subtidal populations were not surveyed, but their abundance along this coast was insignificant compared to the intertidal zone (Hamdi H., unpubl. data).

4.4.3 **Statistical analysis**

We conducted stationarity and geostatistical analyses on adult biomass and recruitment data to assess the scale of auto-covariance and associated spatial structures (if any) for each variable and its among-year stationarity. We then conducted cross-covariance analysis between adult biomass and recruitment data of each year to infer the type and scale(s) of demographic connectivity, and its variability across years within our study area.

4.4.3.1 Stationarity and spatial patterns of adult biomass and recruitment

Stationarity in the data was measured by using Kendall's concordant analysis with data grouped by year (Legendre 2005, Buonaccorsi et al. 2001). For each year of study, sites were ranked in function of mussel biomass or recruitment, and then we tested for the concordance of ranks simultaneously among years. We selected only years and sites showing complete data sets (i.e. 27 sites during 5 years for both variables). Supplementary Pearson's correlation tests were conducted to assess the stationarity of demographic indicators (i.e. recruitment and mussel biomass) between successive years of study. We additionally investigated the relationship between recruitment and mussel biomass over successive years (e.g. recruitment in 2008 and adult biomass in 2009) at the same site to assess any effect of local recruitment on adult biomass. Moreover, large-scale spatial gradients within the spatial distributions of the adult biomass and recruitment were analyzed for each year using Pearson's correlation test between each variable and the along-shore distance from western to eastern sites.

4.4.3.2 Spatial analysis

We examined the spatial structures of the distributions of recruits and adults, separately, by calculating the auto-covariance between pairs of sites at specific distance classes (Legendre & Fortin 1989; Rossi et al. 1992). Then, we employed cross-covariance analysis to test for the type of connectivity pattern and scale the distance of connectivity among populations (Smith et al. 2009). Auto-covariance is a value of covariance between one variable (e.g. adult biomass) at two locations, whereas cross-covariance is a value of covariance between two different variables (e.g. adult biomass and recruitment) at two locations. These analyses were done with 6-km bins on half the spatial extent of our study area (i.e. from 0 to 48 km) to optimize the spatial resolution, and to include a sufficient set of pairs of sites in each bin for significance tests (Legendre & Fortin 1989; Rossi et al. 1992). We also tested for the sensitivity of the results to different spatial lag values and observed similar results. Only covariance analyses were presented here, but results using correlations were similar. The large dataset allowed us to control and partition the variance to remove trends (e.g. environmental gradient), that might mask any demographic coupling. To diminish the influence of the spatial gradients in further analysis, we used detrended data for both averaged and yearly data (Legendre & Fortin 1989; Fortin & Dale 2005). Data detrending was done by taking the residuals of a linear regression as values to remove any linear trend along the coastline of each variable (Legendre & Fortin 1989; Paradis et al. 2000; Ranta et al. 2005).

Spatial structure analysis

Different spatial structures (e.g. patchiness, periodicity, or gradients) can be observed at various scales within the spatial distribution of populations, despite an apparent homogeneity of the area. Such structures result from a combination of several biotic (e.g. conspecific attraction, food availability) or abiotic processes (e.g. local currents, coastal geomorphology) which influence the spatial distribution of individuals (Legendre 1993). In order to assess persistence of these spatial structures within distributions of each of these two key variables, we analyzed the spatial patterns of each year separately, and ran the analysis for averaged adult biomass and recruitment (averaged for years 2007-2010). Auto-covariance values described the spatial correlation within the distribution of the data at specific distances between sites (Radeloff et al. 2000). Resulting auto-covariograms provided the spatial scale(s) over which mussel biomass or recruitment co-varied among sites, positively or negatively (Rossi et al. 1992). For example, a patchy distribution would show high auto-covariance values at small distances and lower auto-covariance at larger distances (Rossi et al. 1992; Pastor et al. 1998; Radeloff et al. 2000; Fortin & Dale 2005; Kraan et al. 2009). Also, spatial periodicity linked to the regular distribution of high density patches could be observed in auto-covariograms, showing strong positive and negative auto-covariance values over regular intervals (Legendre & Fortin 1989; Rossi et al. 1992;

Radeloff et al. 2000; Kraan et al. 2009). We tested for significance (α = 0.05) of observed auto-covariances against the distribution values obtained after 10,000 randomization of geographical positions for both recruits and adults (Fortin & Dale 2005).

Scale of demographic connectivity

We adopted the geostatistical method described by Smith et al. (2009) to evaluate the pattern of connectivity and the average distance of larval dispersal over each separate year as well as the time-averaged value for all years combined and then compared the pattern and scale(s) of demographic connectivity among years to assess its inter-annual variability within the metapopulation. This method used the statistical relationships (i.e. cross-covariance) between two life stages, adult and recruits (i.e. the stock-recruitment relationship), to estimate the type of connectivity among populations and its scale(s). These statistics provided an integrated measure of demographic connectivity at different distances along the coastline (Rossi et al. 1992; Smith et al. 2009), and allowed us testing *a priori* hypothesis about the shape of resulting cross-covariograms (e.g. an open, self-recruitment, or demographically-coupled system; Le Corre et al. 2012). The distances showing the statistical mode(s) of cross-covariograms, corresponding to distance(s) of maximum coupling between adults and recruits along the coastline, were then quantified and interpreted when possible.

Because the area was characterized by a net residual downstream current (i.e. the Gaspé Current), we assumed that if demographic coupling was occurring, it would be observed as a significant positive cross-covariance between upstream adult biomass and recruitment downstream. The intermediate lag distances with significant positive cross-covariance could thus be interpreted as scales of demographic coupling. However, if a self-recruitment connectivity pattern occurred within the system, we assumed that significant positive cross-covariance would be observed at the smallest distance class, associated with a decrease of cross-covariances values when increasing distances. Also, if the connectivity pattern within the system is open, cross-covariances values should be randomly distributed and no significant cross-covariances observed at any lag distances. Moreover, significant negative values of cross-covariance could also be observed, but the processes involved in such relationships between the two demographic variables (e.g. periodic spatial structures of the variables) might be too complex to be clearly identified, and significant negative values of cross-covariance were thus ignored in this study. To evaluate the significance of cross-covariograms, a Monte Carlo method was employed with a restricted randomization test (Purves & Law 2002; Fortin & Dale 2005; Smith et al. 2009) in which the relative positions of adults and recruits values were shifted from each other. This controlled for any effect of spatial structure (monotonic or periodic auto-covariance) in the distribution of adults and recruits (see Smith et al. 2009 for details). To control for statistical artifacts of the analysis, we also analysed the data in the opposite manner, in other words, an examination of the cross-covariance for downstream adult biomass and recruits upstream (i.e. dispersal in the direction against the prevailing current).

4.5 **Results**

4.5.1 **Mussel distribution (adults and recruits)**

Adult biomass and recruitment varied over an order of magnitude among sites, and in some years gradients were observed in their spatial distribution (adult biomass 2007 vs. distance: $P = 0.01$, Pearson's $r = -0.47$; recruitment 2009 vs. distance: $P = 0.04$, Pearson's $r = 0.39$; recruitment 2010 vs. distance: $P = 0.009$, Pearson's $r = 0.47$) with abundances of adults decreasing from west to east and recruitment increasing (Fig. 4.2 and 4.3). Stationarity in spatial distributions of both adult biomass (Fig. 4.2) and recruitment (Fig. 4.3) was, however, observed among years. Indeed, for both stages significant concordances were observed among years of study when site abundances were ranked for each year of study (adult biomass: Kendall's $w = 0.69$, $P = 0.001$; recruitment: $w = 0.6$, $P = 0.001$; 5 years, 27 sites). Moreover, correlations between pairs of successive years were significant for both mussel stages, further confirming stationarity in the spatial distributions (adult biomass: $P \leq 0.001$, Pearson's $r \geq 0.77$ for all pairs; recruits: $P < 0.001$, Pearson's $r \geq 0.77$ for all pairs; n = 27 (for comparisons with 2007) or 29 sites). No significant relationship was seen between recruitment in one year and adult biomass in any subsequent year at individual sites.

4.5.2 Spatial analysis of covariance

Despite the overall temporal stationarity in the distributions of adults and recruits, there was high variability within and among sites, and auto-covariances of recruitment showed particularly high values. We did not, however, observe any clear and consistent spatial structures (e.g. patchiness, periodicity) in the distribution of adult biomass (Fig. 4.4 or recruitment (Fig. 4.5). Adult biomass did show negative auto-covariances at 6-12 km in 2010 and at 24-30 km in 2007, but no significant positive covariance was ever detected, except when data were averaged over the entire study period and a positive covariance was observed at 18-24 km. This latter result reflected periodicity in the distribution of the average population of adult mussels at this distance or, in other words, sites spaced by 18-24 km showed regular tendencies within the distribution of adult biomass (e.g. lag distance between sites of high or low adult populations). Recruitment showed positive auto-covariances in 2010 (6-12 and 30-36 km), and negative spatial auto-covariances in 2008 (0-6 km), 2009 (42-48 km), 2010 (12-18 and 42-48 km), and time-averaged data (42-48 km), suggesting that any spatial structure was highly variable. In particular, there was no auto-covariance at short lag distances which would have suggested patchiness. Instead, auto-covariance of recruitment indicated periodicity at intermediate scales during specific years (e.g. 2010), and variability in the scale of such periodicity among those years.

4.5.3 Spatial statistics and regional demographic connectivity

Stationarity of population connectivity was observed with consistent demographic coupling between upstream adults and downstream recruits over short distances (12-18 km or 18-24 km) during four of the five years of the study (Fig. 4.6). More specifically positive cross-covariances were observed at 12-18 km in 2005 and 2007 and at 18-24 km in 2009 and 2010. In 2008, a significant positive relationship at a 6-12 km was seen in our control analysis (i.e. recruitment upstream from adults), which suggests that factors other than from demographic coupling produced cross-covariance in that year. Consistent with the annual results, the time-averaged cross-covariance of adult and recruitment data was significantly positive at 18-24 km, but was also negative at 36-42 km, which was reflected in consistently large negative (although not significant) values for all the individual years.

4.6 **Discussion**

Our dataset of mussel abundance and recruitment over multiple years and sites allowed us to look for structure within the distribution of adults and recruits and estimate scales of dispersal among populations. Despite spatial variability over 100 km and temporal variability over five years in adult biomass and recruitment, our analyses revealed an overall stationarity in spatial patterns of recruitment and adult abundance, but a general lack of any distinct spatial structures (e.g. patchiness or periodicity). More importantly, our analysis revealed a consistent demographic coupling among adult populations with a lag distance ranging from 12 to 24 km, suggesting that the scale and intensity of demographic coupling can be a consistent feature of marine metapopulations, albeit interrupted in exceptional years.

4.6.1 **Spatial variability and stationarity of mussel population spatial structures**

Relative to recruitment, adult populations of marine benthic invertebrates are generally stable across space and time, a pattern observed in a variety of systems (Botsford et al. 1994; Sagarin et al. 1999; Van der Meer et al. 2001), and our results (e.g. values of correlations for the separate analyses of adult biomass and recruitment) were consistent with this idea. Invertebrate adult biomass is likely influenced by the stable, site-specific characteristics of benthic habitats that favor spatial stationarity (e.g. substrata, wave exposure; Archambault & Bourget 1999; Gaylord & Gaines 2000; McKindsey & Bourget 2000; Navarrete et al. 2005). Disturbance by ice scour is, however, a ubiquitous feature of intertidal shores in the St. Lawrence maritime estuary, and it is thus surprising that more variation was not observed. Variation in recruitment can also cause variation in adult benthic populations (i.e. “supply-side ecology”; Roughgarden et al. 1985; Roughgarden et al. 1988), but we found no link between recruitment and adult populations at the level of individual sites, a pattern that suggests that these populations are not recruitment limited, as opposed to other systems (e.g. Navarrete et al. 2005; Navarrete et al. 2008). However, although recruitment is less limited than in other systems, its role on population dynamics remains essential when major disturbance events occur (e.g. ice scouring) (Gouhier & Guichard 2007). This absence of direct relationship between recruitment and adult abundance might be explained by several factors occurring during the period between the two stages (e.g. habitat availability, post-recruitment mortality), which limit the impact of recruitment on adult populations in this system (Roughgarden et al. 1988; Menge et al. 2011). Moreover, several physical factors acting before larval settlement can contribute to the high temporal annual variability observed in recruitment (e.g. water temperature, food availability), particularly during the larval dispersal process (Roughgarden et al. 1988; Caley et al. 1996; Noda 2004; Porri et al. 2006; Broitman et al. 2008; Menge et al. 2011). Despite the striking persistence of recruitment spatial distributions through time suggesting the importance of processes acting at the site scale (1 km) (Navarrete et al. 2002; Broitman et al. 2008; Navarrete et al. 2008), high inter-annual variation occurred among years, as observed in many systems (e.g. Navarrete et al. 2005; Broitman et al. 2008), with 2008 being a year of exceptionally high recruitment (see below).

Although stationarity was a feature of both adult populations and recruitment, no clear and stable spatial structure (e.g. regular patchiness, periodicity) was revealed by our analyses of auto-covariograms: when observable, the various spatial patterns were inconsistent across the years, despite spatial concordances and correlations seen among years (see above). Any spatial structure observed in a marine invertebrate population could be expected to continue for years for adults given their sessile nature, whereas spatial structures within recruitment patterns should be more variable because it is more sensitive to annual variability in adult reproduction and oceanographic processes (Sagarin et al. 1999; Connolly et al. 2001; Kraan et al. 2009; Carson et al. 2011; Menge et al. 2011). However, our results suggest that there are no consistent processes that generate or maintain spatial structure of adult biomass at the metapopulation scale or that large-scale environmental (e.g. ice scouring) and ecological (e.g. predation, food availability) processes may highly impact any patchiness or periodicity within the population distribution across years (Hughes et al. 2002; Bandt 2005; Fortin & Dale 2005). Indeed, as noted above, the annual cycle of ice disturbance may strongly impact adult benthic populations (Bergeron & Bourget 1986; Hunt & Scheibling

2001). Spatial structures of benthic populations could also be generated by recruitment processes (Roughgarden et al. 1988; Gouhier & Guichard 2007; Broitman et al. 2008; Smith et al. 2009; Wing 2009; Sams & Keough 2012), but again no patterns of systematic or distinctly patchy recruitment were observed.

4.6.2 Scale of demographic coupling and variability of demographic connectivity

Our analyses revealed demographic coupling at similar lag distances over 5 years despite the lack of consistent spatial structures in the distribution of either adult biomass or recruitment. This result suggests that a characteristic dispersal distance is a robust component of metapopulations connectivity, although we did not observe consistent periodicity in spatial distributions of adults or recruits (the method adopted here is able to statistically control for this characteristic, which can have impacts on the long-term dynamics of metapopulations (David et al. 1997)). However, with the method used we could not determine what proportion of the recruitment was provided by such demographic coupling compare to the other potential sources of recruitment nor how important demographic coupling is for a metapopulation which is not recruitment limited (see above). However, alternative hypotheses of stock-recruitment relationships (e.g. open population, self-recruitment) were not support by our results. Adult abundance and recruitment were not significantly correlated over small distances (including within-site comparisons), and therefore local retention is not likely to be the primary mechanism explaining the distribution of adults and recruits in our study system (Legendre & Fortin 1989; Smith et al. 2009; Le Corre et al. 2012). Likewise, the cross-covariance of adults and recruits demonstrates that the population is not completely open (i.e. recruits have a higher probability of coming from specific sites, in this case those 12-24 km upstream). Such demographic coupling has been observed in other systems and has been suggested to depend on characteristics of the dispersal phase (e.g. pelagic larval duration, PLD) and local oceanographic circulation (Kinlan & Gaines 2003; Cowen & Sponaugle 2009). The spatial scale that we observed (12-24 km) is consistent with both previous work done in this system (Smith et al. 2009) and other estimates of dispersal scale of invertebrates with similar PLD (e.g. McQuaid & Phillips 2000; Gilg & Hilbish 2003; Kinlan & Gaines 2003; Becker et al. 2005; Becker et al. 2007). Interestingly, this estimated scale of demographic coupling matches the time-averaged value of spatial structure seen in the distribution of adult biomass (periodicity of 18-24 km) although again this was not seen for individual years.

This estimated dispersal scale is much smaller than that predicted by hydrodynamic models of the transport of passive particles in this system (i.e. dispersal distances > 100 km; Senneville S., unpubl. data, Saucier et al. 2003). This difference may be due to the complexity of hydrodynamics in shallow coastal zones where waves, tidal currents, shore configuration or bottom complexity can cause larval retention and thus reduce dispersal to scales smaller than those predicted by hydrodynamic models (Largier 2003; Siegel et al. 2003; Cowen et al. 2006; Werner et al. 2007; Cowen & Sponaugle 2009). Such methodological biases are important to recognize as they can affect estimates of dispersal distances. For example, genetic approaches can also provide estimates of connectivity, but because the temporal scales over which connectivity is estimated can highly affect results (Hedgecock et al. 2007), approaches based on dispersal over multiple generations (e.g. genetic tools; Gilg & Hilbish 2003; Palumbi 2003) will integrate multiple dispersal events. Moreover, as we have done here, single generation approaches allow documenting temporal variability in connectivity, which can have deep implications for population persistence, distribution, and species coexistence (Carson et al. 2011; Salau et al. 2012; Watson et al. 2012).

The consistency of our results (4 of 5 years) demonstrated that some statistical properties of demographic coupling (e.g. its scale) can be robust to expected inter-annual variations, including nearshore circulation patterns (Saucier et al. 2003). However, 2008 was the exception with no observed demographic coupling and anomalously high recruitment. Interestingly, in spite of the lack of any detectable coupling (the reverse coupling of the control analysis notwithstanding), the spatial variation in recruitment was both visually and statistically similar to other years (e.g. the site with the highest recruitment was still at the

40 km distance). Moreover, the much higher level of recruitment in this year suggests that such exceptional years may be more important demographically for the maintenance of populations, although again we did not observe any correlation between recruitment and adult population in this particular system (see above). The environmental processes behind this exceptional event are unknown but could include the unusual wind conditions and high water retention that was documented across our study system in that summer (M. Starr, unpubl. data; Fauchot et al. 2008). Explanations of such variability in the scale of demographic coupling usually invoke temporal variations of the oceanographic circulation regimes that drive larval dispersal (Bertness et al. 1996; McQuaid & Phillips 2000; Watson et al. 2010; Sponaugle et al. 2012). While we are in general agreement with this hypothesis, our results suggest that demographic coupling can be fairly robust to variation in nearshore current variations, at least in simple systems such as the St. Lawrence maritime estuary, and that significant deviations from average scales and magnitude of connectivity require exceptional events. Previous empirical studies were done on a similar spatial scale but in more complex oceanic systems (Carson 2010; Hogan et al. 2012), and openness of such systems might favor higher variations in coastal currents. However, our study, which stretches over a longer period than previous empirical studies, is the first to show an overall stability of connectivity patterns across years (i.e. demographic coupling), despite variability during an exceptional year. In general, variations in directions of demographic coupling, scales of dispersal and intensity of recruitment (see above), coupled to biotic factors, can create high variability of demographic connectivity within marine metapopulations. In regards to such variability, it is essential to expand our knowledge of the importance of recurrent demographic coupling relative to exceptional events on the structure and dynamics of metapopulations. Indeed, connectivity patterns and consequent recruitment represent two of the most important factors driving metapopulation dynamics (Carson et al. 2011).

4.7 **Conclusions**

This empirical study demonstrates that the distribution of adults and recruitment, despite apparent stationarity, exhibits variable spatial structures over time. Demographic connectivity in this area involves a consistent pattern of demographic coupling between adult populations and downstream recruitment at a system-specific scale; and exceptional deviations from expected demographic coupling may occur and suggest potentially strong variability in connectivity over longer time scales. The integration of intermittent variations in connectivity into metapopulation theory could have important implications for persistence (e.g. White et al. 2010; Carson et al. 2011), gene flow (e.g. O'Connor et al. 2007; Hogan et al. 2010; Aguirre & Marshall 2012) and patchiness (e.g. Gouhier et al. 2010; Aiken & Navarrete 2011) within metapopulations. All these considerations represent essential knowledge for the management of marine ecosystems, including the design of marine reserve networks (Botsford et al. 2001; Palumbi 2003; Palumbi 2004; Jones et al. 2007).

4.8 Acknowledgements

We acknowledge and appreciate the funding for this research (STPGP 336324) from the Natural Sciences and Engineering Research Council (NSERC) of Canada, the financial and logistic support from Québec-Océan, as well as student support from the Département de biologie, Université Laval. We are grateful to C. McKindsey and Fisheries and Oceans Canada for access to facilities at the Maurice Lamontagne Institute. Our thanks as well to L. Boutet, S. Briand, S. Collin, T. Gouhier, H. Hamdi, K. Hasegawa, C. Leroux, A. Marzouk, M. Morin, G. Parent, J. Ploquet, C. Robineau and C. Roby for the invaluable assistance provided during field and laboratory work.

4.9 **Figures**

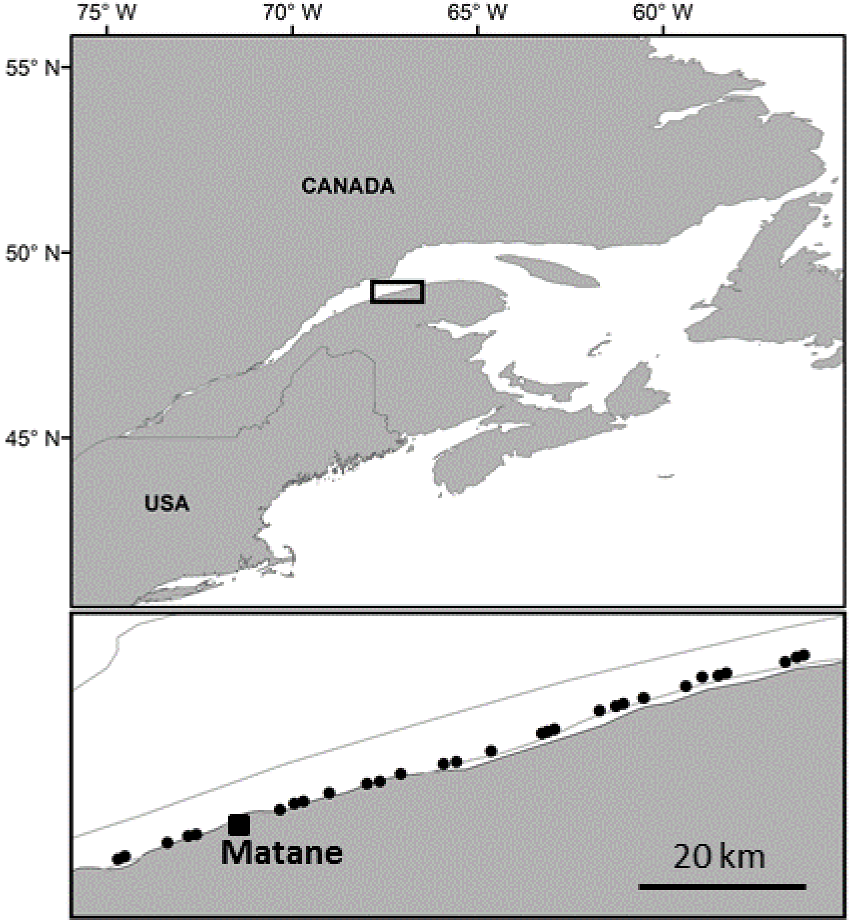

Figure 4.1 Map of the St. Lawrence Estuary and the Gulf of St. Lawrence (top). Spatial arrangement of study sites along the southern shore of the estuary (bottom). Filled circles represent sampling locations from West (site 1: 0 km) to East (site 29: 96km)

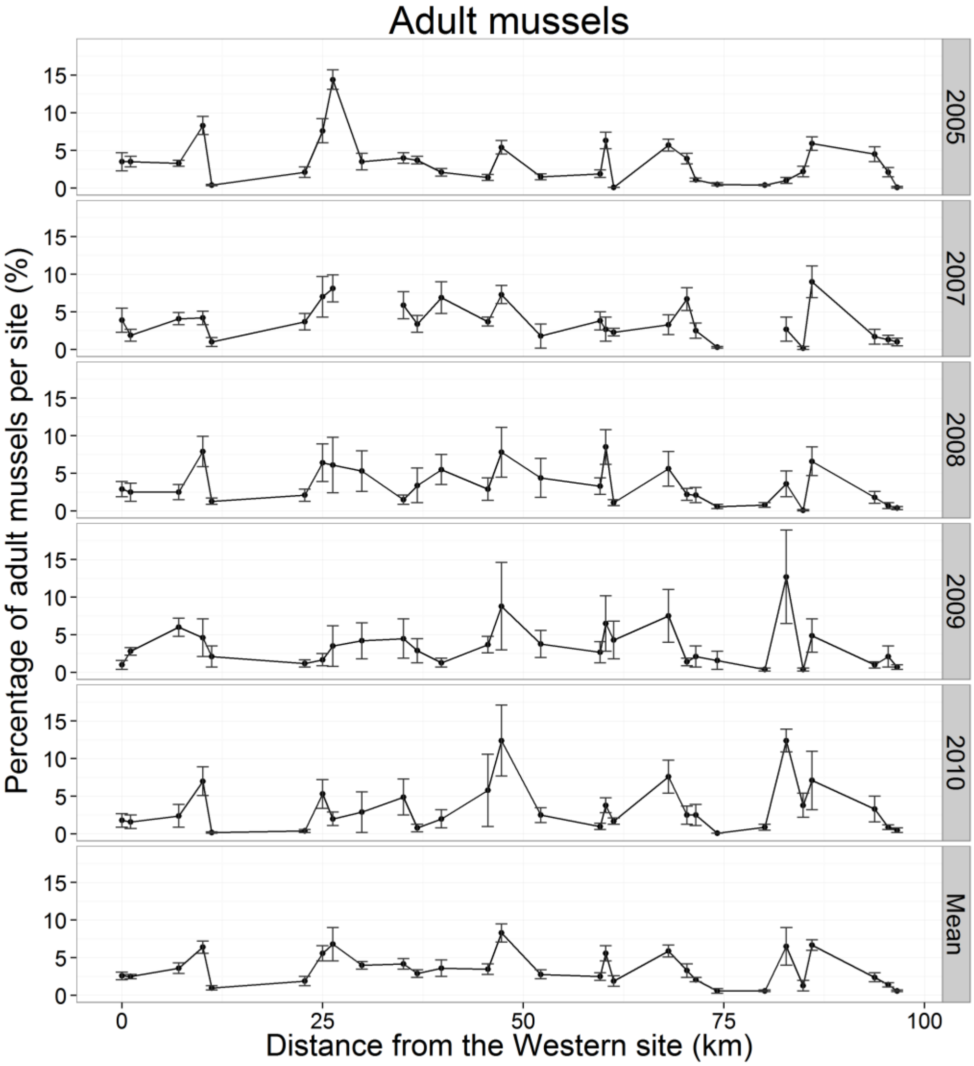

Figure 4.2 Normalized annual (2005-2010) and 5-years mean distributions of *Mytilus* spp. adult mussels across all study sites (mean ± standard error; n = 6 (2007-2010) or 10 (2005) quadrats per site)

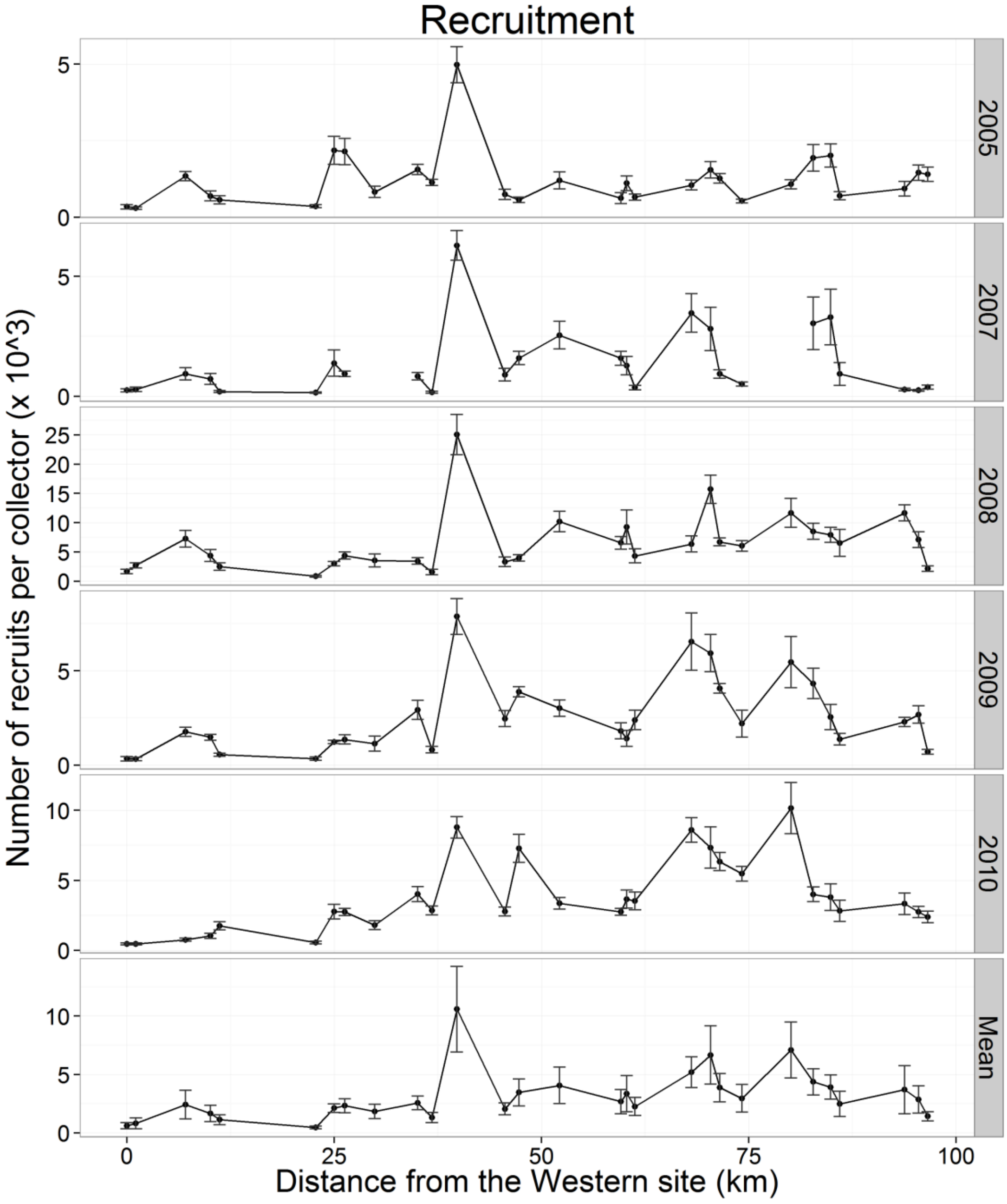

Figure 4.3 Annual (2005-2010) and 5-years mean distribution of *Mytilus* spp. recruitment over the 29 sites of the study system (mean ± standard error; n = 8 collectors per site)

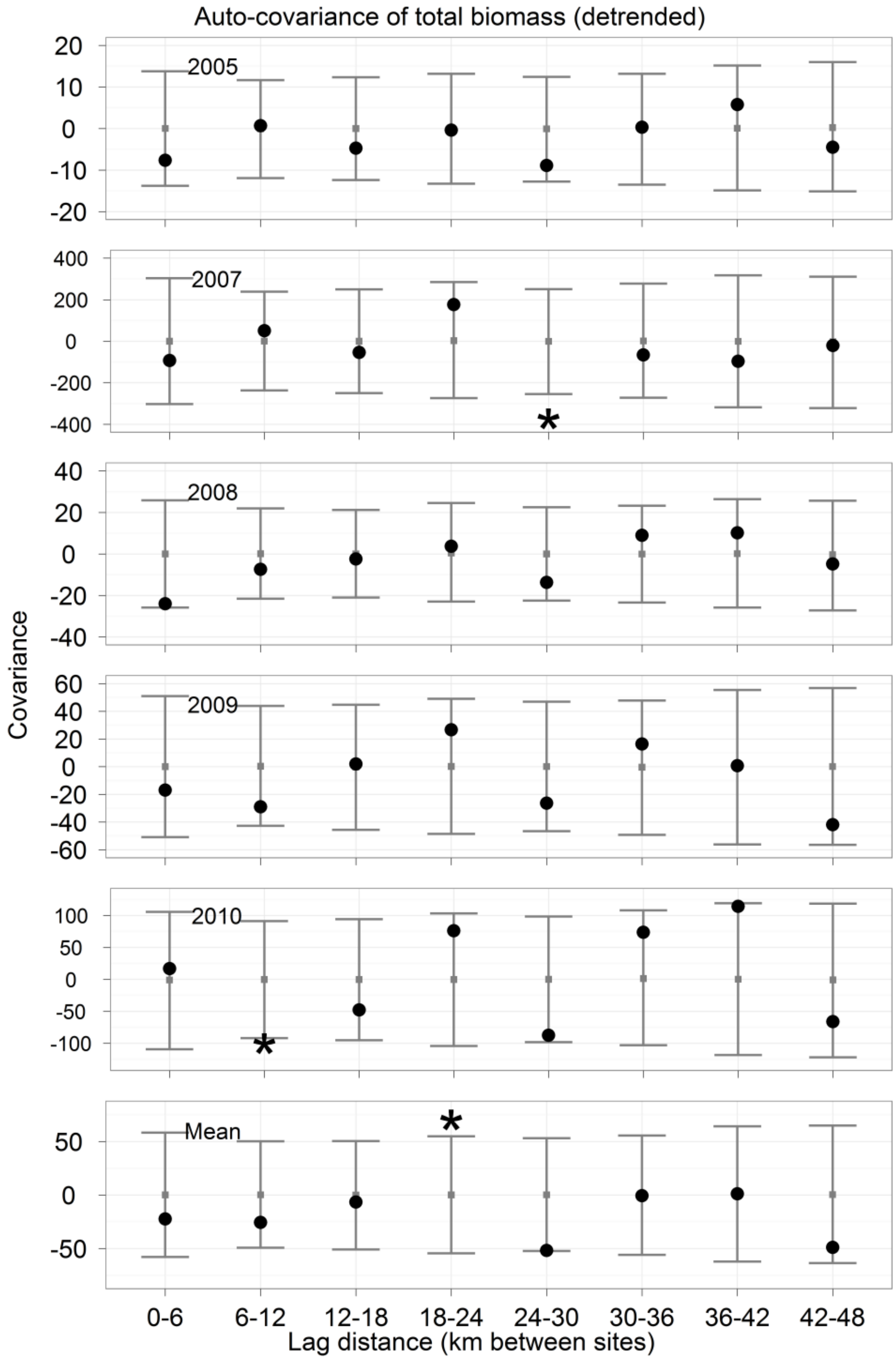

Figure 4.4 Auto-covariograms of annual (2005-2010) and averaged over all years (Mean) *Mytilus* spp. biomass. Filled circles indicate auto-covariance values for original data, grey squares indicate mean values generated from 10,000 randomized permutations, grey bars represent 95 % confidence intervals based on these randomizations, and significant auto-covariance values are noted with an asterisk. Sample sizes for each lag-distance class are 15+ pairwise comparisons

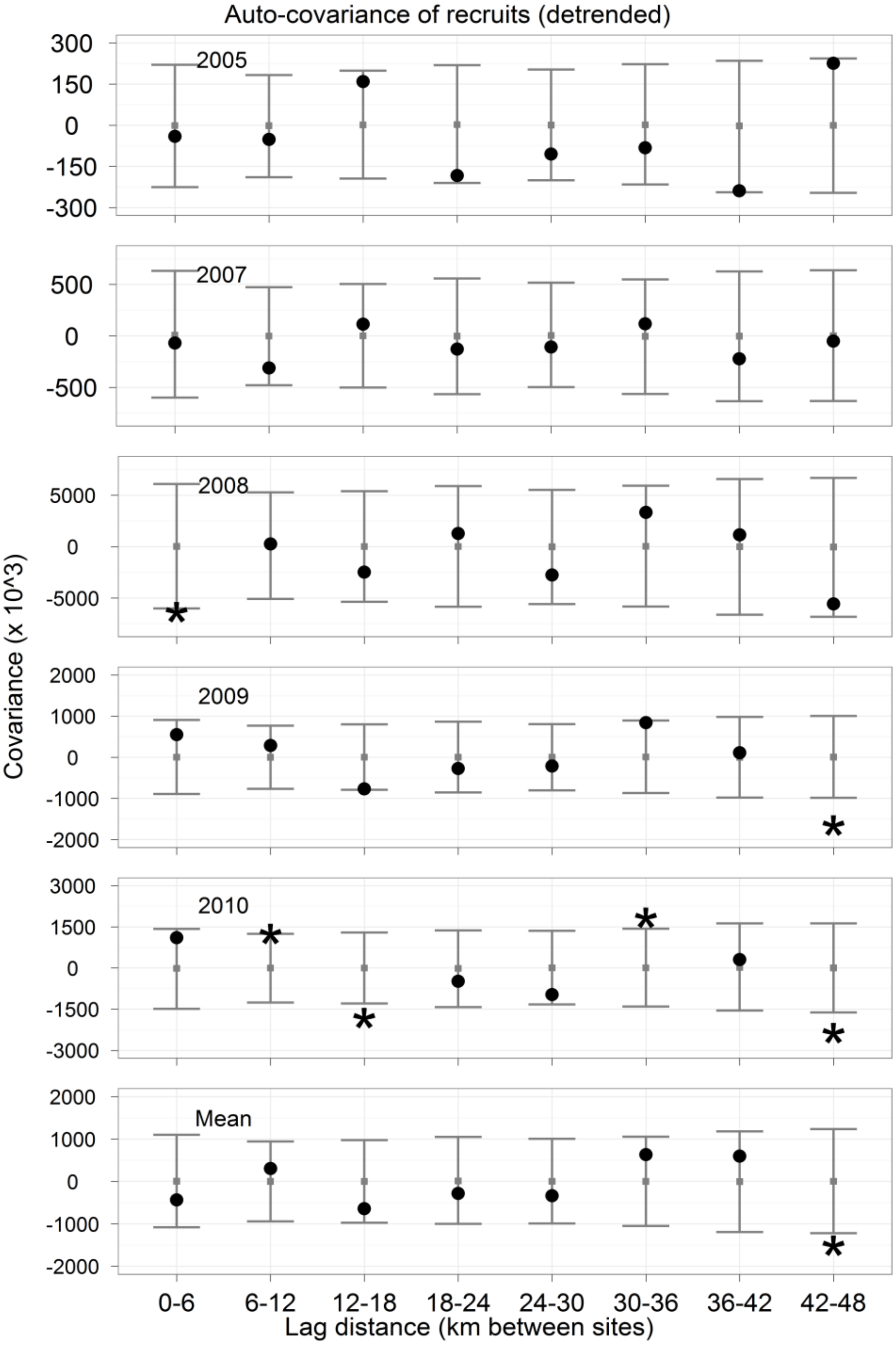

Figure 4.5 Auto-covariograms of annual (2005-2010) and averaged over all years (Mean) Mytilus spp. recruitment density. Filled circles indicate auto-covariance values for original data, grey squares indicate mean values generated from 10,000 randomized permutations, grey bars represent 95 % confidence intervals based on these randomizations, and significant auto-covariance values are noted with an asterisk. Sample sizes for each lag-distance class are 15+ pairwise comparisons

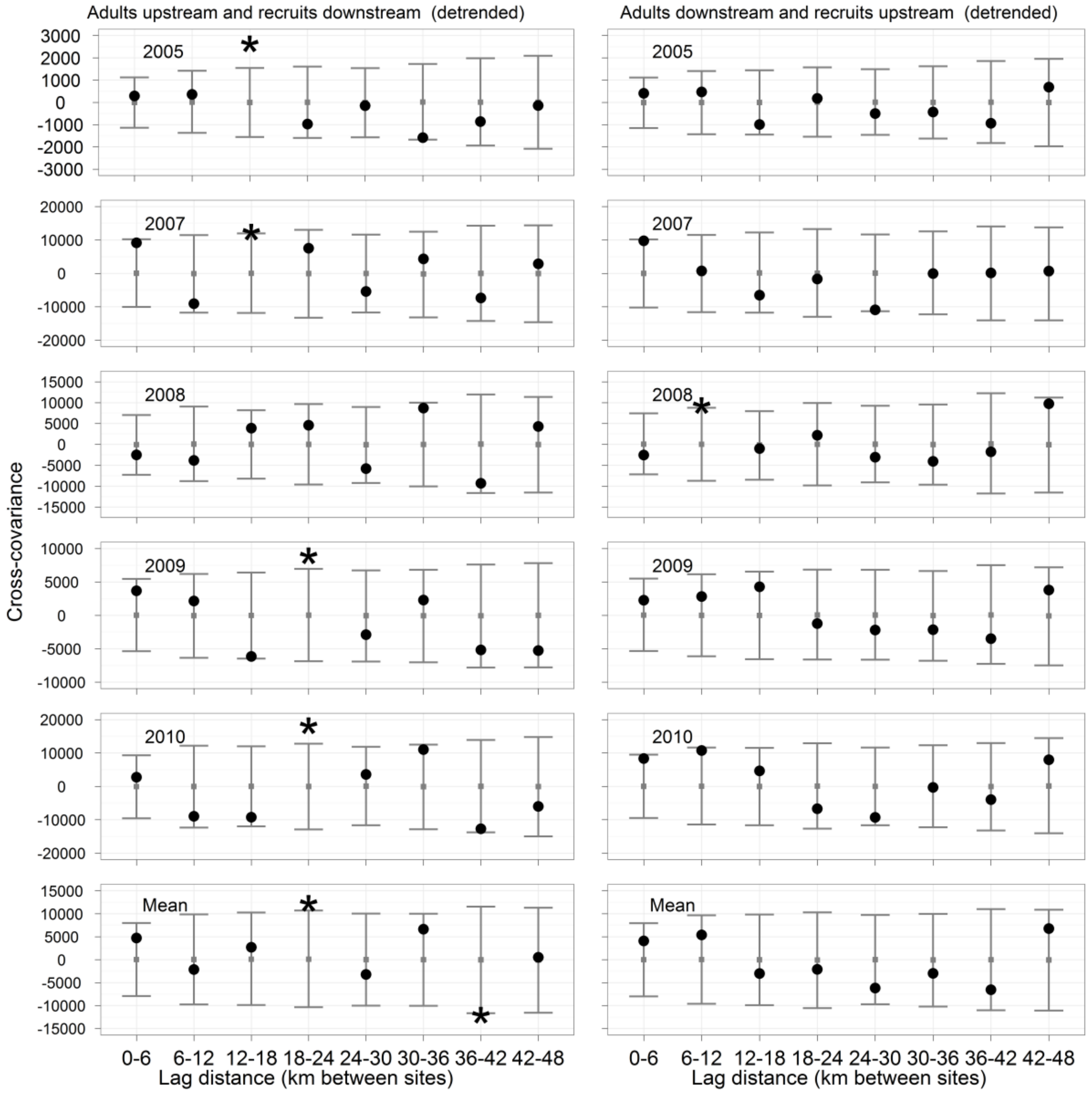

Figure 4.6 Cross-covariograms comparing annual (2005-2010) and averaged over all years (Mean) Mytilus spp. biomass with downstream recruitment (graphs on the left), and comparing recruitment with downstream mussel biomass (graphs on the right). Filled circles indicate cross-covariance values for original data, grey squares indicate mean values generated from 10,000 caterpillar randomized permutations, grey bars represent 95 % confidence intervals based on these randomizations, and significant cross-covariance values are noted with an asterisk. Sample sizes for each lag-distance class are 15+ pairwise comparisons

Chapitre 5. Conclusion générale

5.1 Rappel des principaux résultats

L'objectif principal de cette thèse était de caractériser les sources de variabilité du processus de connectivité démographique. Par ailleurs, les conséquences et implications d'une éventuelle variabilité de la connectivité ont également été considérées dans cette étude. Enfin, j'avais pour objectif d'examiner empiriquement la connectivité au sein d'une métapopulation marine sur plusieurs années, ainsi que les variations spatiotemporelles de la colonisation.

Ce travail a permis, en premier lieu, de réaliser une revue de l'état des connaissances actuelles et des avancements récents portant sur la connectivité démographique. Ce processus constitue un élément majeur en écologie, particulièrement dans le domaine marin où il reste très difficile à mesurer. Le nombre d'études dans ce domaine ayant considérablement augmenté dans les 15 dernières années, cette étude a permis de proposer différentes méthodes pour estimer les distances de dissémination larvaire et plus généralement la connectivité entre des populations à une échelle temporelle écologique (c.-à-d. une seule génération). Un nombre restreint de méthodes, très variées et impliquant divers domaines, permettent à ce jour d'estimer la connectivité et sa variabilité, dont celle utilisée dans le chapitre 4 de cette étude.

La décomposition du processus de connectivité a permis de révéler l'ensemble des sources de variabilité inhérentes à ce mécanisme, souvent considéré stable au cours du temps malgré des sources de variations multiples qui agissent à différentes échelles. Au regard des quelques études théoriques adressant cette problématique, une telle variabilité augmenterait la persistance à long terme, l'abondance, la dynamique et la variabilité génétique des métapopulations. Afin de mieux considérer la variabilité de la connectivité dans les stratégies de gestion des aires marines protégées et de la biodiversité, cette étude suggère de varier l'espacement entre les zones de protection et de privilégier un plus grand nombre de petites aires protégées pour « disperser les zones de risques ». En effet, les changements climatiques, dont l'ampleur demeure incertaine, font qu'il est important de proposer un large éventail d'habitats aux populations menacées. Cependant, l'applicabilité des recommandations émanant de ces études théoriques est complexe à mettre en œuvre et il n'existe encore que peu d'aires marines protégées de ce type permettant de valider les effets de telles mesures sur l'ensemble d'un écosystème (Jones et al. 2007).

Après avoir considéré le processus de connectivité pour l'ensemble des organismes marins ayant une phase bentho-pélagique dans le premier chapitre, il a été question par la suite d'approfondir l'étude de la variabilité de la connectivité de *Mytilus* spp. dans un système spécifique, l'EGSL, à différentes échelles spatiotemporelles. Cette thèse a ainsi permis de révéler le schéma temporel d'un processus clé de la connectivité, la colonisation, dans une zone boréale comme l'EGSL. La colonisation a lieu principalement au cours d'une ou deux périodes restreintes de l'été sous la forme de pics de recrutement primaire. Par ailleurs, cette étude a révélé la variabilité du schéma temporel et de l'intensité de la colonisation entre les deux années au cours desquelles cette étude s'est déroulée, l'année 2008 ayant montré un taux de colonisation nettement plus important et tardif qu'en 2009.

Cette thèse a aussi démontré qu'une grande partie de la colonisation observée au cours de la saison de reproduction de *Mytilus* spp. est constituée de recrues secondaires alors que le recrutement primaire s'effectue sur une période plus restreinte. Le recrutement primaire a lieu suite à la phase de dissémination larvaire alors que le recrutement secondaire est lié à des mouvements de post-larves à l'échelle locale, favorisés par les vagues. La différence entre les deux types de recrues s'avère donc importante lorsqu'on s'intéresse aux phénomènes de connectivité, car les échelles spatiales de dispersion vont de quelques dizaines ou, à la rigueur dans certaines conditions, centaines de mètres (recrues secondaires) à plusieurs dizaines de kilomètres (recrues primaires). Le transfert des recrues secondaires a donc lieu principalement au cours des tempêtes (déplacement forcé), particulièrement au cours des semaines suivant les évènements de recrutement primaire quand beaucoup d'individus sont en transfert vers un habitat propice à leur établissement (déplacement choisi). Les transferts de recrues peuvent donc être choisis par les individus ou forcés en fonction de différents facteurs environnementaux.

Cette thèse a également permis de révéler, grâce à une technique issue de la morphométrie des bivalves, que la durée de la phase larvaire pélagique est plus importante que dans les zones tempérées et dure de 27 jours à plus de 2 mois en fonction du taux de croissance considéré et du développement larvaire dans les eaux froides de l'EGSL. La taille de la coquille larvaire (Prodissoconch II - PII) affiche une grande variabilité au cours de la saison, mais surtout au sein d'une même cohorte de recrues. Par ailleurs, il a aussi été suggéré, suite aux résultats observés du chapitre 3, que l'augmentation de la taille de la coquille de la phase larvaire (PII) est principalement due au fait que les larves retardent leur fixation et atteignent donc une taille à la métamorphose plus importante.

En considérant une échelle spatiotemporelle plus importante dans le chapitre 4 (5 années, 100 km), ce projet a permis de mettre en évidence que la structure spatiale des populations benthiques montre une variabilité interannuelle, malgré une apparente stabilité des populations adultes sur chaque site. De façon moins surprenante, la structure spatiale du recrutement à l'échelle régionale a également montré des structures spatiales peu claires et variables entre les années quand elles ont pu être identifiées, malgré une concordance entre les années. De plus, les taux de recrutement ont montré, comme dans le chapitre 3, une importante variabilité d'une année à l'autre, l'année 2008 affichant le plus important taux de recrutement de la série temporelle. Ces variations des taux de recrutement montrent donc que certaines années ont un impact potentiellement plus important sur la dynamique des populations.

Finalement, cette étude a permis d'identifier, grâce à une méthode géostatistique robuste, le type de connectivité démographique et la distance à laquelle les populations adultes de *Mytilus* spp. ont un impact sur le recrutement à la suite de la dissémination larvaire dans l'EGSL. La distance de couplage démographique entre les populations adultes en amont et leur impact sur le recrutement en aval était de 12 à 24 km pour la majorité des années étudiées. Cependant, il a également été observé que des années exceptionnelles (ex. : 2008) peuvent afficher des taux de recrutement nettement plus élevés, ainsi que des schémas de connectivité différents. Bien que le couplage démographique semble être le schéma le plus observé dans ce système, il est intéressant de noter ces fluctuations de la connectivité et d'observer l'ampleur potentielle de cette variabilité.

5.2 **Contributions**

Cette thèse contribue à l'avancement des connaissances sur la connectivité démographique chez les organismes ayant un cycle vital bentho-pélagique, plus particulièrement la colonisation (fixation primaire), le recrutement et la phase de dissémination larvaire des invertébrés marins.

En premier lieu, cette thèse a permis de mieux décrire des étapes essentielles du processus de connectivité, la colonisation et le recrutement larvaire (chapitre 3 et 4), dans une région où les données étaient limitées (ex. : Hamdi H., données non publiées; Ardisson & Bourget 1991; Archambault & Bourget 1999; Bélanger 2009; Toupoint et al. 2012) concernant une des espèces clés (ex. : productivité secondaire, ingénieur écologique; Gutierrez et al. 2003) de l'EGSL. En effet, cette zone tampon entre les régions tempérées et subarctiques (zone boréale maritime) constitue un système où le comportement des espèces est sensiblement variable d'une région à l'autre en raison de la présence de divers gradients influant à grandes échelles (ex. : salinité, température; Bélanger 2009). Cette étude a permis de démontrer la similarité du comportement de *Mytilus* spp. dans l'EGSL avec celui des bivalves dans d'autres régions nordiques. La reproduction y est limitée à une ou deux courtes périodes au cours de l'été et montre des évènements de colonisation ponctuels. Ce comportement « nordique », probablement causé par des eaux plus froides, a également été remarqué au travers d'une durée estimée de la phase larvaire pélagique plus longue, liée notamment à un développement plus lent et menant à des tailles à la métamorphose (taille de la coquille PII) plus importantes qu'en région tempérée. Ces analyses ont aussi mis en évidence la variabilité du développement pendant la phase larvaire entre les individus issus d'une même cohorte. Une bonne connaissance du développement larvaire et de ces variations est en effet essentielle dans ce contexte de réchauffement global, car l'augmentation de la température de l'eau pourrait entraîner une accélération du développement larvaire, menant à des phases de dissémination plus courtes et causant ainsi des changements dans les schémas de connectivité.

Par ailleurs, l'analyse approfondie de la colonisation (chapitre 3) qui a été faite au cours de cette étude a permis de révéler l'importance du phénomène de recrutement secondaire tout au long de la saison de reproduction. Ce phénomène, ignoré dans de nombreuses études, constitue une importante partie de la colonisation en dehors des pics liés au recrutement primaire et peut mener à une surestimation de la colonisation primaire au cours de la saison de reproduction. Cette thèse a également révélé le rôle majeur de l'agitation du milieu environnant, à travers les vagues et le vent, dans le processus de recrutement secondaire. Bien que ces déplacements post-métamorphiques aient lieu sur de courtes distances le plus souvent, leur rôle dans la structure et la persistance des populations à l'échelle locale n'en demeure pas moins important et suggère qu'une meilleure compréhension de ces processus est nécessaire pour mieux identifier les périodes effectives de connectivité.

Cette thèse a également montré l'importance de l'échelle d'étude, d'un point de vue spatial et temporel, dans les études démographiques. Les études de colonisation à haute résolution (ex. : échelle temporelle hebdomadaire vs bimensuelle) ont permis de révéler des évènements importants (ex. : tempête, bimodalité du recrutement primaire en 2008) qui n'auraient pas été détectés et auraient donc entraîné des interprétations erronées ou incomplètes. D'un point de vue spatial, d'importantes variations du recrutement ont été relevées dans le chapitre 4 entre les différents sites, en plus des variations interannuelles et des variations au sein des sites. Cette variabilité du recrutement de *Mytilus* spp. a également été observée dans des études réalisées à grande échelle dans la zone infralittorale (< 80 km, Hamdi H., Le Corre N. et al., données non publiées) ou sur des bouées de navigation à l'échelle de l'EGSL (> 800 km, Ardisson & Bourget 1991; Bélanger 2009). De telles conclusions suggèrent l'existence de processus agissant à l'échelle locale, soit *précédent* la fixation larvaire (ex. : distribution différentielle des larves, comportement de fixation défavorisant la fixation dans les zones infralittorales), ou soit *suite* à la fixation ou colonisation (ex. : migration des post-larves, mortalité post-métamorphique). Le fait d'augmenter la résolution d'une étude représente un compromis entre d'une part l'investissement (budget, temps) et les données obtenues dont la quantité, la complexité et la structure doivent être en accord avec la variable étudiée.

En second lieu, cette thèse a permis de proposer deux méthodes visant à mesurer la phase larvaire d'un point de vue temporel (mesure de PII - chapitre 3), mais aussi d'un point de vue spatial (méthode géostatistique – chapitre 4). Bien que la dissémination au cours de la phase larvaire pélagique soit très difficile à étudier, particulièrement en raison de la petite taille des organismes, elle constitue une étape essentielle de la connectivité qui nécessite d'être mieux connue. Cette étude a contribué au développement de deux méthodes permettant, de façons indirectes, d'étudier la phase larvaire des organismes bentho-pélagiques.

Face à la difficulté de mesurer la durée de la phase larvaire, nous avons développé une technique indirecte, inspirée de Martel A. et al. (1993), afin d'obtenir une estimation de la durée de la phase larvaire de *Mytilus* spp. (chapitre 3). Cette donnée permet de renseigner un aspect essentiel afin d'affiner les mesures théoriques de la connectivité entre les populations (ex. : modèle hydrodynamique 3D). La mesure de la coquille PII, couplée à des valeurs précises de taux de croissance, permet donc d'estimer les variations de la durée de la phase larvaire dans des régions où l'environnement est relativement homogène. L'applicabilité de cette méthode est importante dans des systèmes très variés et pour divers types de bivalves à mode de développement larvaire de type planctotrophique, au cours de laquelle la véligère sécrète une coquille larvaire composée de deux régions, PI et PII. Chez ce type de bivalves, l'existence d'une démarcation notable entre la fin de la coquille larvaire (PII) et le début de la coquille juvénile (dissoconch), laquelle est conséquente à la métamorphose, permet en effet d'étudier la durée de la vie larvaire *a posteriori*, et ce à partir d'échantillons de post-larves bien préservés.

D’un point de vue spatial, l’estimation de la connectivité démographique demeure également complexe à mesurer en raison de la difficulté de suivre des larves de bivalves dans des masses d’eau en mouvement. Parmi les quelques méthodes mentionnées dans le chapitre 2 permettant d’estimer la connectivité démographique, la technique développée par Smith et al. (2009) a permis d’estimer le type de connectivité démographique et la distance réelle à laquelle une population a un impact sur le recrutement dans une autre population (chapitre 4). La répétition de cette méthode sur plusieurs années a permis de mettre en évidence sa capacité à détecter un processus de connectivité démographique malgré les variations dans la structure spatiale des données et la variabilité des processus écologiques impliqués.

En troisième lieu, cette thèse a permis de démontrer et soulever l’importance de la variabilité de la connectivité démographique à l’échelle écologique au sein d’une métapopulation marine. Il s’agit d’une des premières études évaluant empiriquement le processus démographique liant les populations entre elles, l’échelle spatiale des distances de connectivité et l’ampleur des variations de cette distance sur plusieurs années. De plus, l’impact potentiel d’une telle variabilité de la connectivité a également été traité de manière théorique.

Cette étude a permis de mettre en évidence l’existence d’un couplage clair entre les adultes et le recrutement dans des populations d’accueils à des distances caractéristiques de ce système (12-24 km), à une échelle semblable à celui observé par Smith et al. (2009) en 2003. Les distances de couplage démographique observées dans cette étude empirique, sur plusieurs années, ont montré que la dispersion larvaire était plus limitée que les simples estimations des modèles hydrodynamiques 3D qui ont tendance à surestimer les échelles de dispersion (Watson et al. 2010). Ces différences mettent en avant l’importance des processus côtiers agissant à faibles échelles (ex. : vagues, courant côtier, gyres locales, marées) qui sont difficiles à intégrer aux modèles hydrodynamiques en raison de leur résolution, mais qui pourraient créer, par exemple, la rétention de masses d’eau et ainsi mener à des schémas de dispersion larvaire plus limitée que les prédictions issues de simulations.

Cette étude de la connectivité sur 5 ans (chapitre 4) est la première montrant une connectivité stable au cours des années étudiées. Cependant, des légères variations (ex. : couplage à 12-18 ou 18-24 km) ont également été observées entre les différentes années d'étude et cette thèse est une des premières études (voir aussi : Carson 2010; Lopez-Duarte et al. 2012) présentant empiriquement une telle variabilité, bien que légère, de l'échelle spatiale de connectivité démographique. En effet, l'existence d'une année extraordinaire en 2008, où le schéma de connectivité est différent et montre un taux de recrutement exceptionnel, met en évidence une variabilité potentiellement importante de la connectivité. La compilation des études théoriques traitant des processus de dispersions (chapitre 2, ex. : Siegel et al. 2008; Watson et al. 2012) a permis de démontrer l'importance de la variabilité de la connectivité, à une échelle temporelle écologique, sur la dynamique des populations et ses applications dans de nombreux domaines (ex. : génétique, gestion des aires protégées).

5.3 **Perspectives et considérations futures**

Afin de poursuivre les travaux commencés dans cette thèse et palier à certaines limites évoquées dans cette étude, il serait intéressant de poursuivre les recherches dans quatre directions en particulier : (1) l'importance du recrutement secondaire chez les invertébrés marins, (2) l'importance de chaque espèce de *Mytilus* spp. dans les variations spatiotemporelles de la colonisation, (3) l'évaluation de la connectivité et de sa variabilité dans d'autres systèmes et (4) l'estimation de l'impact de la variabilité de la connectivité à une échelle plus vaste grâce à des modèles théoriques.

Cette thèse ayant mis en avant l'importance du recrutement secondaire, il serait intéressant d'approfondir les connaissances relatives à la dissémination post-métamorphose chez les invertébrés marins et plus particulièrement chez *Mytilus* spp.. En effet, l'importance du phénomène mériterait d'être quantifiée plus précisément afin de connaître la proportion des recrues primaires qui se déplacent, ainsi que l'âge de ces individus et les distances parcourues. Par ailleurs, cette étude se limitant à la période de reproduction de *Mytilus* spp., il serait intéressant de renseigner ce phénomène pendant le reste de l'année en élargissant la période d'étude. Aussi, il serait très intéressant d'évaluer la nature de ces déplacements et donc d'estimer l'importance des contraintes physiques ou des « choix » biologiques de l'animal. Les recherches dans ce domaine semblent montrer que les déplacements sont liés à un changement des besoins de l'animal au cours du temps (Newell et al. 2010), qui fait qu'il y a un changement volontaire d'habitat au cours des semaines suivant la métamorphose, favorisé par les courants locaux. Par exemple, des expériences dans un système avec des expositions aux vagues variables avec des « pièges » à recrues permettraient d'estimer plus sensiblement l'importance des vagues dans le délogement des individus par comparaison à la suspension « volontaire » dans des zones peu exposées. Aussi, des expériences sur les préférences de *Mytilus* spp. concernant les microhabitats à différents stades de vie, par exemple en estimant la taille des recrues dans différents types d'habitats naturels, permettraient de mettre en évidence les raisons des déplacements des recrues. Finalement, des expériences de marquage d'individus (ex. : calcéine, Moran & Marko 2005) pourraient révéler les échelles spatiotemporelles de dispersion impliquées, si elles ne sont pas trop importantes et permettent donc de récupérer un nombre relativement important d'individus.

Cette thèse a également montré des variations spatiotemporelles notables de la colonisation de *Mytilus* spp. dans l'estuaire du Saint-Laurent. Bien que les deux espèces présentes dans le système soient très proches (Thomas et al. 2004), il serait intéressant d'étudier la contribution de *Mytilus edulis* et *M. trossulus* à différents stades du développement afin de mieux définir les préférences des deux espèces et leurs hybrides. En effet, des comportements différents en fonction de l'environnement pourraient expliquer les distributions observées (Maloy et al. 2003; Toro et al. 2004; Dias et al. 2009) des différentes espèces et avoir d'importants impacts sur la stabilité de la métapopulation (Hogan et al. 2010). Dans un premier temps, il serait donc intéressant d'étudier la variabilité saisonnière du recrutement de chaque espèce et ainsi tenter d'expliquer les schémas de recrutement bimodaux ou multimodaux observés dans cette thèse. Par exemple, une variabilité du moment de ponte entre les espèces pourrait entraîner un recrutement plus hâtif qui favoriserait une des espèces. À plus grande échelle, il faudrait jauger la variabilité interannuelle du recrutement des deux espèces sur différents sites et analyser les corrélations entre la distribution des populations adultes et celle des recrues. Aussi, en raison des gradients spatiaux présents dans un estuaire tel que le Saint-Laurent (ex. : température, salinité, plancton), il s'agirait d'un système très intéressant pour étudier l'impact de différents facteurs environnementaux sur la présence et la persistance des deux espèces. Bien que la plupart des recherches évoquées dans ce paragraphe soient assez simples à mettre en œuvre, elles nécessitent cependant beaucoup d'analyses génétiques afin d'être représentatives des populations étudiées, et donc un financement conséquent.

Cette thèse a aussi participé au développement de méthodes indirectes afin d'estimer la durée (taille de la PII) et la distance parcourue (géostatistique) pendant la phase larvaire des organismes bentho-pélagiques. L'utilisation de ces méthodes dans des conditions différentes (ex. : espèce, région différente) permettrait de les optimiser et d'approfondir les connaissances de la phase larvaire, peu documentée, qui a un rôle essentiel dans la dissémination des invertébrés marins. Aussi, afin d'optimiser les estimations de la durée de la phase larvaire, il pourrait être intéressant de définir précisément le taux de croissance des larves in situ (plutôt que d'utiliser des données de laboratoire), en réalisant le suivi de plusieurs cohortes au cours de l'été parallèlement à la collecte de recrues primaires. Ces données permettraient de mieux évaluer la variabilité de la durée de la dissémination larvaire au cours de la saison et possiblement de relier ces variations à différents taux de succès du recrutement. Face à l'importante variabilité de la taille de la PII entre les individus, des expériences en environnement contrôlé sur une même cohorte permettraient de mesurer ce paramètre. Concernant la variabilité de la connectivité décrite dans cette étude grâce à la méthode géostatistique, il serait intéressant de poursuivre les mesures sur plusieurs années pour cerner l'ampleur de la variabilité potentielle de la connectivité. Par ailleurs, il serait possible d'effectuer une validation/comparaison des différentes méthodes applicables pour étudier la variabilité de la connectivité, évoquée dans le second chapitre, en comparant les résultats obtenus au sein d'un système (ex. : méthode géostatistique et modélisation hydrodynamique dans l'EGSL). On obtiendrait ainsi des fréquences de dispersion théoriques, que l'on pourrait comparer aux résultats réels de colonisation afin d'identifier l'impact des processus post-colonisation.

Cette étude ayant permis de mieux caractériser des processus essentiels à la dynamique des populations (ex. : échelle et variation de la connectivité, périodicité et stabilité des populations adultes), il serait donc approprié d'étudier leur rôle et leur impact sur la structure des populations à plus long terme. L'absence de corrélation entre le recrutement et l'abondance d'adultes (chapitre 4) suggère que l'impact du recrutement sur les populations déjà établies et leurs structures spatiales est complexe et s'intègre sur plusieurs générations. À l'aide de modèles théoriques de métapopulations, il serait possible de mieux comprendre la façon dont le recrutement et la dynamique des populations sont influencés par la structure spatiale des populations adultes (ex. : périodicité, gradient, « hot-spots »). Aussi, on pourrait examiner dans quelle mesure elles laissent des traces dans la structure spatiale des générations suivantes. Les modèles théoriques permettraient également d'étudier la dynamique d'une population en réponse à différents types de variation de la connectivité, tel que de la stochasticité, des évènements de recrutement exceptionnels ou des schémas de dispersion extraordinaires. Ultimement, dans un contexte de gestion d'aires marines protégées visant une espèce en particulier, le couplage d'un modèle théorique à un modèle physique hydrodynamique permettrait d'identifier les populations clés pour la persistance de la métapopulation. Par ailleurs, le rôle de la variabilité de la connectivité au sein de systèmes plus complexes demeure mal connu (voir section 2.5.2 et 2.6 de cette thèse). Il serait donc intéressant d'étudier l'impact de tels processus à plus larges échelles (ex. : biodiversité) à l'aide de modèles théoriques de métacommunautés ou métaécosystèmes.

Les idées de futures recherches évoquées ici constituent seulement quelques pistes afin de répondre aux questions générées lors de cette étude de doctorat. L'ampleur des domaines concernés est vaste, mais la compréhension de phénomènes complexes nécessite souvent l'intégration de plusieurs disciplines.

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Annexe 1. Coordonnées GPS des 29 sites d’étude du chapitre 4

Annexe 1: GPS coordinates of the 29 study sites (see figure 4.1), distance (km) from the western site, and sampling method for each year of study. “X” marks sites normally sampled, “-“ indicates sites which were not sampled, and “+” means that adults were sampled using percentage of mussel cover rather than biomass.

Site	Latitude	Longitude	Distance (km)	Year				
				2005	2007	2008	2009	2010
1	N 48°46.353'	W 67°45.352'	0.0	+	x	x	x	x
2	N 48°46.656'	W 67°44.63'	1.1	+	x	x	x	x
3	N 48°48.076'	W 67°40.169'	7.1	+	x	x	x	x
4	N 48°48.769'	W 67°37.988'	10.1	+	x	x	x	x
5	N 48°48.942'	W 67°37.135'	11.2	+	x	x	x	x
6	N 48°51.53'	W 67°28.427'	22.8	+	x	x	x	x
7	N 48°52.168'	W 67°26.918'	25.0	+	x	x	x	x
8	N 48°52.406'	W 67°25.959'	26.3	+	x	x	x	x
9	N 48°53.019'	W 67°23.758'	29.9	+	-	x	x	x
10	N 48°54.255'	W 67°19.308'	35.1	+	x	x	x	x
11	N 48°54.482'	W 67°17.964'	36.8	+	x	x	x	x
12	N 48°55'273'	W 67°15.782'	39.8	+	x	x	x	x
13	N 48°56.319'	W 67°11.289'	45.6	+	x	x	x	x
14	N 48°56.546'	W 67°09.944'	47.3	+	x	x	x	x
15	N 48°57.669'	W 67°06.303'	52.2	+	x	x	x	x
16	N 48°59.526'	W 67°00.973'	59.6	+	x	x	x	x
17	N 48°59.699'	W 67°00.399'	60.3	+	x	x	x	x
18	N 48°59.947'	W 66°59.661'	61.3	+	x	x	x	x
19	N 49°01.899'	W 66°54.938'	68.1	+	x	x	x	x
20	N 49°02.374'	W 66°53.216'	70.4	+	x	x	x	x
21	N 49°02.632'	W 66°52.446'	71.5	+	x	x	x	x
22	N 49°03.225'	W 66°50.346'	74.2	+	x	x	x	x
23	N 49°04.465'	W 66°45.935'	80.1	+	-	x	x	x
24	N 49°05.423'	W 66°44.229'	82.8	+	x	x	x	x
25	N 49°05.574'	W 66°42.54'	84.9	+	x	x	x	x
26	N 49°05.832'	W 66°41.704'	86.0	+	x	x	x	x
27	N 49°07.006'	W 66°35.521'	93.8	+	x	x	x	x
28	N 49°07.49'	W 66°34.34'	95.5	+	x	x	x	x
29	N 49°07.716'	W 66°33.569'	96.6	+	x	x	x	x