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FÉCONDITÉ, CROISSANCE ET SURVIE DE DEUX POPULATIONS GÉNÉTIQUEMENT DISTINCTES DE *SEMIBALANUS BALANOIDES* AU VOISINAGE DE LEUR INTERFACE GÉOGRAPHIQUE

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Résumé

Fécondité, croissance et survie de deux populations génétiquement distinctes de *Semibalanus balanoides* au voisinage de leur interface géographique

Selon la littérature, le cirripède sessile, *Semibalanus balanoides*, retrouvé sur la côte est canadienne est constitué de deux populations génétiquement distinctes dont l'interface se situe à proximité de l'estuaire de la Miramichi au Nouveau-Brunswick. De part et d'autre de cette interface, les populations sont caractérisées par des différences significatives de fréquences alléliques au loci mannose phosphate isomérase (*Mpi*) et glucose phosphate isomérase (*Gpi*). L'étude effectuée à l'interface de ces populations a pour but de vérifier l'influence de la sélection naturelle et quelques facteurs environnementaux sur quelques indicateurs biotiques et les fréquences alléliques dans les populations. Des expériences de transplantations réciproques et des mesures de croissance, de survie et de fécondité sont menées. La croissance de même que la fécondité sont comparables entre les deux populations à chaque site étudié, alors que la survie diffère. L'analyse génétique sur les allozymes (*Mpi* et *Gpi*) effectuée sur les balanes transplantées survivantes et sur les témoins montre des fréquences alléliques modifiées après transplantation d'un côté à l'autre de l'interface. Nos résultats et ceux d'études antérieures, suggèrent le maintient de l'interface par une sélection naturelle sur les larves nouvellement fixées. Les facteurs de sélection nous éludent toujours cependant.

Remerciements

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Introduction générale

Pendant des millénaires, le livre de la Genèse de la Bible alimente la croyance populaire à l'effet que chaque espèce est une création unique. Au milieu du XVIII^e siècle, les preuves que les espèces changent au cours des âges commencent à s'accumuler cependant (Fontaine & Morin 1989). L'idée que l'évolution se produit par sélection naturelle est acceptée depuis le début du XX^e siècle, alors que les processus et l'importance relative entre les différentes forces évolutives restent à ce jour des sujets importants d'étude.

L'importance de la caractérisation de la structure génétique des populations est reconnue dans plusieurs domaines, notamment en gestion, en systématique et en évolution. Ainsi, la distinction génétique entre les populations s'avère un outil essentiel en tant qu'indicateur de repeuplement dans l'élaboration de plans de gestion de récolte des espèces économiquement importantes (Utter 1991) ainsi que dans la recherche fondamentale, afin de comprendre et de déterminer l'évolution des populations et des espèces. De plus, l'utilisation de la structure génétique des populations d'organismes marins en tant que bioindicateur du degré de pollution marine a déjà été suggérée (Nevo *et al.* 1983).

En dépit de l'apparente uniformité de l'habitat marin, les organismes de ce milieu ne sont pas uniformément distribués dans l'espace. En fait, ils forment plutôt des populations locales, isolées et plus ou moins denses selon les habitats favorables à leur survie (Burton 1983). La dispersion géographique des organismes benthiques marins est souvent assurée par les larves méroplanctoniques, qui représentent un moyen de dissémination prévilégié pour les espèces tempérées (Crisp 1978). Le potentiel de dispersion de plusieurs espèces selon les conditions hydrographiques, la durée des stades larvaires et le comportement alimentaire a été évalué (Crisp 1964, Schetelma 1975). Par exemple, pour les larves planctotrophes (qui se nourrissent à tous les stades larvaires), qui atteignent le stade de fixation vers l'âge de deux ou trois semaines, le séjour planctonique pourrait, selon la vitesse des courants, leur permettre de parcourir une distance annuelle se situant entre 50 et 100 kilomètres. Par comparaison, les larves téléplaniques (qui demeurent dans le plancton des mois), peuvent se disperser sur des distances de l'ordre de milliers de kilomètres, alors que les larves lécithotrophes (qui ne se nourrissent pas mais utilisent leurs réserves alimentaires), sont limitées en énergie et possèdent une période de dispersion plus courte (Schetelma 1975).

À titre d'exemple, Bourget *et al.* (1989) ont évalué la distance maximale potentiellement parcourue par les larves de *Semibalanus balanoides*, lorsqu'elles pénètrent le détroit de Cabot. Considérant la vitesse moyenne des courants (4 cm s^{-1}) dans cette région, de même que la durée larvaire maximale de six semaines, ces auteurs estiment que les larves pourraient franchir jusqu'à 145 km par année. Par conséquent, pour des espèces à durée de vie planctonique comparable ou plus grande, on s'attendrait à ce que la différentiation génétique entre populations voisines soit réduite, compte tenu du flux génique important entre populations géographiquement rapprochées. Alors que pour certaines espèces cette relation semble se vérifier (étoiles de mer: Williams & Benzie 1993 et Nishida & Lucas 1988), pour d'autres cela ne semble pas être le cas (moules: Koehn *et al.* 1980, Hedgecock 1986, Johannesson *et al.* 1990 et Quesada *et al.* 1995, crabes: Bert & Harrison 1988, pétoncles: Parsons, 1996).

Outre la dérive génétique, définie comme un changement dans les proportions des allèles du pool génique d'une population dû à des événements survenant au hasard dans les petites populations (Lafontaine & Morin 1989), et considérée comme un mécanisme naturellement présent, la restriction du flux génique et la sélection naturelle peuvent expliquer l'hétérogénéité génétique observée entre populations rapprochées.

Alors que la dispersion larvaire permet l'introduction de nouveaux arrivants, l'infertilité de ceux-ci (Burton 1983), les accouplements non aléatoires (Johannesson *et* *al.* 1993) ainsi que le comportement larvaire (Burton & Feldman 1982), peuvent causer une barrière au flux génique. Hedgecock (1986), définit le flux génique comme une migration effective des gamètes reproductrices entre les populations séparées ou une migration d'individus survivant jusqu'à la reproduction. Ainsi, la restriction du flux génique par l'entremise de mécanismes de rétention larvaire causée par certains courants océaniques, tourbillons et courants de surface (Dando & Southward 1981, Mitton *et al.* 1989, Parsons 1996), peuvent diminuer les capacités de dispersion des larves et par conséquent représenter une barrière hydrographique au flux génique.

En présence d'un flux génique important, la divergence génétique observée entre populations rapprochées peut être attribuée aux pressions de sélection locales (Johannesson *et al.* 1990, McDonald 1991; Brown & Chapman 1991, Duggins *et al.* 1995). Autrefois, l'approche typique était d'observer des changements graduels de fréquences alléliques et de les corréler avec les changements biotiques ou physiques d'un facteur présumé causal (O'Gower & Nichol 1968, Schopf & Gooch 1971). Plus récemment, c'est plutôt l'observation de patrons clinaux et l'étude de l'activité enzymatique sous différentes conditions environnementales qui permettent d'élucider les principaux mécanismes en cause (Levinton & Lassen 1978).

Semibalanus balanoides est une espèce boréo-arctique communément retrouvée dans l'étage intertidal. Sa distribution géographique s'étend le long des côtes de l'Atlantique nord et du Pacifique nord (Bourget *et al.* 1989). Dans l'Atlantique, elle colonise ainsi les côtes ouest et est, le sud du Groenland, une partie de l'Arctique canadien jusqu'en Caroline du nord (Barnes & Barnes 1976). *Semibalanus balanoides* est une espèce hermaphrodite dont l'autofertilisation est présumément impossible (Barnes 1957). La période de fertilisation a lieu à la fin octobre sur les côtes du Nouveau-Brunswick. Les balanes fécondées incubent leurs oeufs dans la cavité palléale pendant l'hiver jusqu'à la ponte qui, dans le sud du Golfe, a généralement lieu vers la fin avril. *Semibalanus balanoides* possède sept stades planctoniques, dont six stades nauplii et un stade cypris lécithotrophe (Bousfield 1954).

L'ensemble des connaissances actuelles concernant la morphologie, la croissance, le comportement, l'habitat et la génétique de *Semibalanus balanoides* dans l'est du Canada, atteste de la présence de deux populations distinctes (Bourget *et al.* 1989). Les cirripèdes du golfe du Saint-Laurent sont de plus grande taille et leur taux de croissance est plus élevé que celui des cirripèdes de l'Atlantique. De plus, les larves du nord-ouest du Golfe se fixent préférentiellement dans les crevasses (>95%; voir Bergeron & Bourget 1986; Chabot & Bourget 1988) alors que celles de l'Atlantique se fixent davantage sur les surfaces exposées. Holm et Bourget (1994) ont évalué la dispersion génétique de *S. balanoides* à partir de 19 sites s'étalant du sud-est de la Terre de Baffin jusqu'au sud-est de la Nouvelle-Écosse (Canada). Ils ont démontré l'existence de variations de fréquences alléliques régulières menant à une interface génétique (point de rupture) à proximité de l'estuaire de la Miramichi au Nouveau-Brunswick (Canada). En effet, la population au nord de la Miramichi affiche des fréquences élevées au locus manose-phosphate isomérase-B (*MpiB*) et de basses fréquences au locus glucose-phosphate isomérase-B (*GpiB*), alors que l'inverse s'observe pour la population située au sud de la Miramichi.

En comparant les fréquences alléliques des recrues et des adultes, Holm et Bourget (1994) ont suggéré le maintien de la discontinuité génétique entre les deux populations de balanes par une sélection naturelle possiblement associée avec des régimes de température différents. La présente étude a pour but (i) de vérifier l'hypothèse de la sélection post-fixation, à l'aide de transplantations réciproques entre les deux populations de *Semibalanus balanoides* à proximité de l'estuaire de la Miramichi (Nouveau-Brunswick), de même que (ii) de déterminer quels étaient les facteurs environnementaux susceptibles d'être impliqués. Nous avons étudié trois propriétés biologiques, la fécondité, la survie et le taux de croissance chez les balanes transplantées de part et d'autre de la Miramichi et les balanes témoins et nous avons également effectué des analyses sur les allozymes par gel d'électrophorèse afin de déterminer le génotype des balanes survivantes.

L'utilisation de transplantations réciproques afin de distinguer le caractère induit (variation non-génétique) du caractère hérité (variation génétique) de certains paramètres biologiques (croissance, fécondité, morphologie) entre différentes populations, a démontré son efficacité à plusieurs reprises (Levinton & Lassen 1978, Johannesson *et al.* 1990, Kautsky *et al.* 1990, Ciocco 1992). De même, l'emploi de transplantations pour l'étude de différentes populations de *Semibalanus balanoides* a précédemment été utilisé (Crisp 1964, 1968, Bertness *et al.* 1991).

Chapitre I

Fecundity, growth rate and survivorship of *Semibalanus balanoides* at the interface between two contiguous genetically distinct populations

Abstract

On the western coast of the Atlantic, according to the literature, two distinct populations of *Semibalanus balanoides* occur with a distinct interface near the Miramichi estuary (Northern N.B.). On each side of this interface, the populations are characterized by clinal variations for *Mpi* and *Gpi*. The present study was carried out to determine whether selection occurs at this interface and how early in the sessile life period it occurs. Reciprocal transplant experiments of newly settled individuals to both sides of the interface were carried out. No significant differences specifically linked to source or destination were observed in growth or fecundity for the two populations at the sites studied for either control or transplanted individuals. However, differences in survival were observed; individuals transplanted south of the estuary showed lower survival than local populations. An allozyme analysis of barnacle survivors for *Mpi* (mannose-6-phosphate isomerase) and *Gpi* (glucose-6-phosphate isomerase), the two enzymes whose frequencies are known to vary abruptly in this region, suggested a change of allele frequency in transplanted individuals. The latter came to ressemble that of the adults from target sites, while no change occurred in transplanted populations at the control sites. Taken together with previous results, our study suggests that selection occurs very early in the newly attached spat.

Introduction

In temperate and tropical benthic marine invertebrates, planktonic larvae represent the main means of dissemination. Given sufficient food and on absence of acute predation, the duration of the pelagic larval stage and the current speed are thought to define the potential distance of dispersion of those species and the gene flow (Scheltema 1986). Theoretically, there should be an inverse relationship between planktonic larval duration and dispersal and the likelihood of genetic differentiation between adjacent populations (Crisp 1978). Although for some groups of species this relationship seems to hold (ssouthars: Williams & Benzie 1993, Nishida & Lucas 1988), for others it doesn't (mussels: Koehn *et al.* 1980, Hedgecock 1986, Johannesson *et al.* 1990, Quesada *et al.* 1995; scallops: Parsons, 1996). Beside genetic drift, different causes could explain the latter situations: (i) restriction of gene flow, including immigrant infertility (Burton 1983), nonrandom mating (Johannesson *et al.* 1993), larval retention or directional dispersion mechanisms (Dando & Southward 1981, Mitton *et al.* 1989, Parsons 1996), larval behavior (Burton & Feldman 1982), or (ii) natural selection (Koehn *et al.* 1980, Johannesson *et al.* 1990, McDonald 1991, Brown & Chapman 1991, Duggins *et al.* 1995, Schmidt & Rand 1999).

Semibalanus balanoides, the common boreoarctic intertidal barnacle, is found on both sides of the Atlantic and on the western Pacific coast of America (Bourget *et al.* 1989). Along the western Atlantic coast, it extends from Greenland and the Canadian Arctic to North Carolina (Barnes & Barnes 1976). *Semibalanus balanoides* is presumed an obligate cross-fertilizing hermaphrodite (Barnes 1957) and in the eastern Gulf of St. Lawrence, fertilization occurs in October. Fertilized eggs are incubated in the mantle cavity over winter and are hatched the following spring. Planktonic development includes larval stages: six nauplii stages and a cyprid stage (Bousfield 1954).

Genetic studies of *S. balanoides* along the western Atlantic coast of North America and Gulf of St. Lawrence indicate there are two distinct populations (Bourget *et al.* 1989). From observations at a limited number of stations, Bourget *et al.* (1989) suggested that barnacles from the western Gulf were larger and their post-settlement growth rate was higher than barnacles from the Atlantic shores. Moreover, western Gulf cypris larvae (Capucins, Québec) behaved differently than Atlantic larvae (St. Andrews, New Brunswick), in such a way that the former settled preferentially (>95%) in crevices and the latter settled mainly on exposed surfaces (see Bergeron & Bourget 1986; Chabot & Bourget 1988). The allelic frequencies at two enzyme loci, mannose-phosphate isomerase-B (*Mpi* ^{B}) and glucose-phosphate isomerase-B (*Gpi* ^{B}) differed between the two populations, the western Gulf individuals showing higher frequencies for *Mpi* ^{B} and lower frequencies for *Gpi* ^{B} than the Atlantic population (Martel 1990). In a subsequent genetic study of *S. balanoides* at 19 sites along the Atlantic coast of North America from Greenland and Baffin Island, the Gulf of St. Lawrence, the Atlantic coast of Nova Scotia and New Brunswick (Canada), regular clinal variations at those same two loci (*Mpi* and *Gpi*) for these populations were observed with a distinct genetic interface located in the vicinity of the Miramichi estuary, New Brunswick (Holm & Bourget 1994).

In this study, we examine selection and the effect of geography on the newly settled individuals (spat) by means of reciprocal transplantations between the two populations of *S. balanoides* in the vicinity of Miramichi estuary. Specifically, we compare fecundity in local populations, survivorship and growth rate in reciprocally transplanted barnacles from north and south of the Miramichi Estuary and controls. Electrophoretic allozyme analyses of survivors were also carried out in order to determine genotype. This approach was privileged over others since reciprocal transplant experiments have been shown to be useful to highlight the causes of genetic differentiation among populations (Crisp 1964, 1968, Johannesson *et al.* 1990, Kautsky *et al.* 1990, Bertness *et al.* 1991). Larval dispersion and hydrographic patterns within the Miramichi region were simultanously examined in another study (Drouin & Bourget, in prep.).

Methods

Study site

The experiments were conducted in the southeastern part of the Gulf of St. Lawrence near the Miramichi Estuary (Fig. 1), during the spring through autumn of 1998. The Miramichi Estuary, is one of the largest estuaries in Atlantic Canada covering an area of 300 km^2 and a drainage basin area of 14 000 km^2. Tidal amplitudes in the study area range from approximately 0.5 to 1.4 m (Locke & Courtnenay 1996).

The shores in the region of study are dominated by sandy beaches over 200 km, at lsouth 100 km on either side of the Miramichi river mouth. Rocky outcrops are only sproradically present, and throughout the whole region hard substrata occurs primarily in the form of man-made jetties and quays. Indeed, hard substrata is so scarce that sampling sites for *S. balanoides* were difficult to find.

Transplant experiments

In order to examine the extent to which any barnacle population differences in fecundity, growth and survival might be environmentally induced (non-genetic variation) or inherited (genetic variation), we used reciprocal transplantations. Two series of transplantations were carried out based on published genetic results (Holm & Bourget 1994). A first set of transplantations (Experiment 1) started five days after settlement (29 May) and ended in mid-November 1998. Barnacles from Cap-Lumière, situated south of the Miramichi estuary (one origin), were transplanted to four different destinations, two of them located north of the estuary (Burnt Church and Val-Comeau) and two located south of the estuary (Pointe-Sapin and Cap-Lumière; Fig. 1). A second set of transplantations (Experiment 2) started 48 days (July 11) after settlement (mid-July 1998), and ended in mid-November 1998. Barnacles from Le Goulet (situated north of the Miramichi estuary), Cap-Lumière and Saint-Edouard (both situated south of the estuary) were transplanted to Burnt Church and Val-Comeau (both situated north

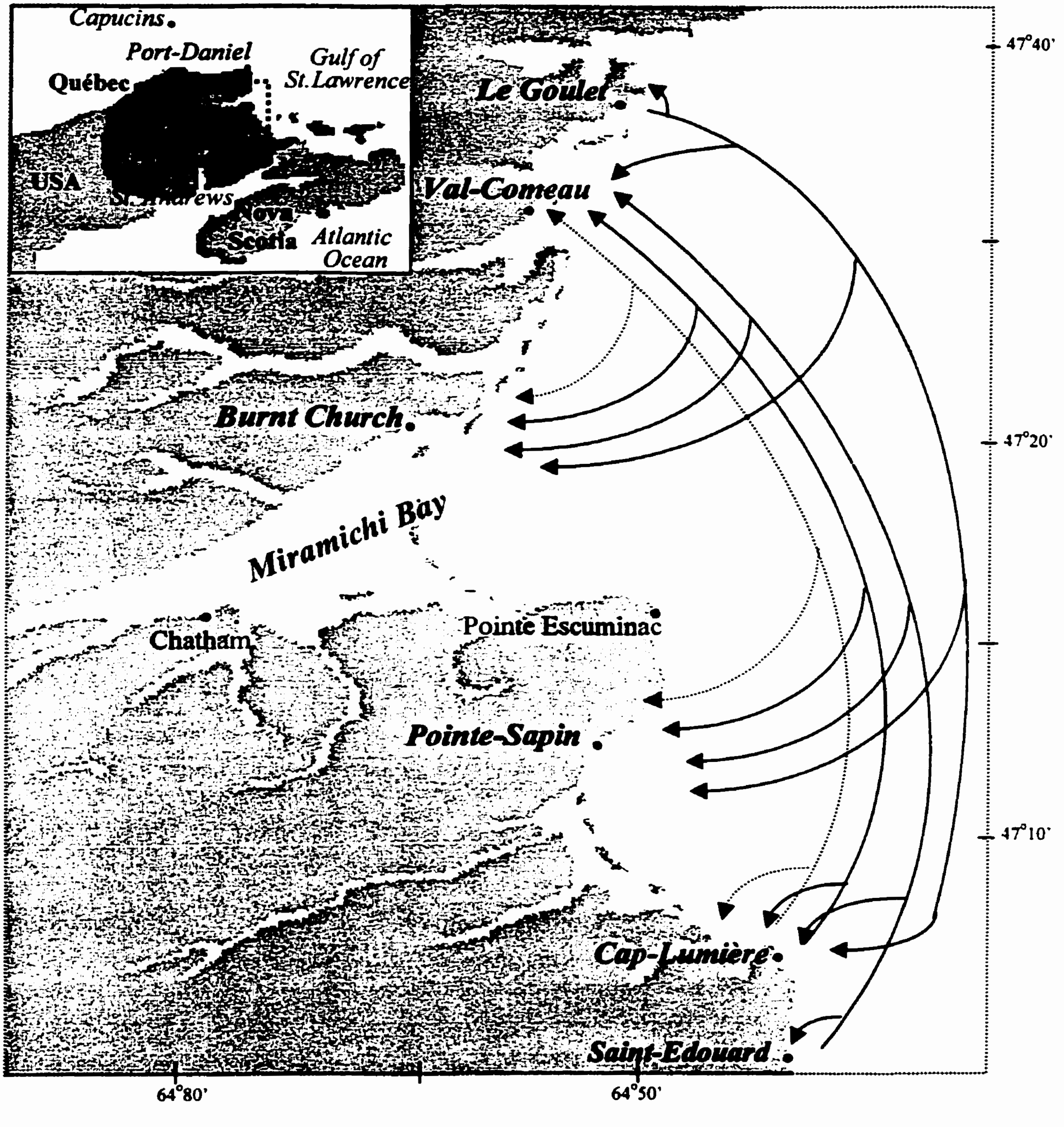

Figure 1. Sites from which *Semibalanus balanoides* recruits were obtained and to which they were transplanted. Dotted and full lines represent the sites used for the first and the second experiments respectively. Barnacles originated from Cap-Lumière (one origin) in the first experiment and from Le Goulet, Cap-Lumière and Saint-Edouard (three origins) in the second experiment. Arrows indicate transplant destinations and transplant controls.

of the estuary) and Pointe-Sapin and Cap-Lumière (both situated south of the estuary; Fig. 1). The reciprocal transplant experiments could not be carried out this time because initially settlement occurred only south of the Miramichi. There were no significant differences in initial size among destinations from any origins (Le Goulet: F = 2.371, df = 3, p> 0.112; Cap-Lumière: F = 2.389, df = 3, p > 0.074; Saint-Edouard: F = 2.079, df = 4, p> 0.091).

Experiment 1. For the first set of transplantations, recently metamorphosed *Semibalanus balanoides* recruits were collected on sixteen cobbles (approx. diam. = 18 cm) of similar heterogeneity (F = 1.71, df = 2, p > 0.2492), as measured using a carpenter's profiler (two measurements made at right angle to one another, precision ± 1mm, see Guichard & Bourget 1998). Settlement lasted about ten days. Recruits were haphazardly thinned to < 1 individual cm^{-2} to avoid competition. Five days after settlement had ceased (may 29), cobbles collected at Cap-Lumière, supporting on average 31.2 ± 13.9 newly settled individuals per cobble (max. age of spat = 15 days), were transplanted to the four destinations (Val-Comeau, Burnt Church, Pointe-Sapin and Cap-Lumière). Cobbles were secured to the breakwater rock using Kwik Plug® Lepage (Kingston, Ont.) cement according to their initial orientation and shore level. Transplanted cobbles remained solidly im place at least until day 220 , but some were lost late in autumn and therefore our statistical analyses did not include data from day 320.

Experiment 2. For the second set of transplantations, 42 cobbles (approx. diam. = 22 cm) of similar heterogeneity (F = 1.43, df = 1, p > 0.3540), colonized with *S. balanoides* (average 13.1 ± 8.8 individuals per cobble) spats were used with recruits thinned out to < 1 individual cm^{-2} 48 days after the beginning of settlement, 3 cobbles from each origin (Le Goulet, Cap-Lumière and Saint-Edouard) were transplanted to 4 destinations (Val-Comeau, Burnt Church, Pointe-Sapin and Cap-Lumière). Control transplantations were also done (three replicates per origin). Cobbles from different sources were interspersed, placed at same tidal height and secured to substratum as above.

Growth and survival. Experimental cobbles were photographed monthly between May and August and in November 1998. Mortality of recruits through November, basal area as well as rostro-carinal and lateral-lateral basal diameters (precision = ± 0.1 mm) were monitored from SigmaScan Pro (1995). Since the area and the two diameter measurements were highly correlated (Spearman $R^2 > 0.96$, $N = 1003$, $p < 0.0001$), only the rostro-carinal diameter was used in the analysis.

Fecundity. To estimate the fecundity of local (non-transplanted) populations north and south of the Miramichi estuary for 1997, we haphazardly collected fifty individuals immediately prior to larval release (15-19 April 1998) at each of the four localities (north: Val-Comeau, Burnt Church; south: Pointe-Sapin and Cap-Lumière). We measured the rostro-carinal basal diameter and height using vernier calipers (to 0.1 mm) and separated the egg masses from the soft tissue under the microscope. Masses of eggs were kept in 20% formaldehyde. Wet masses of eggs were washed in 3% ammonium formate and then passed through a 500 µm nylon filter prior to being weighed to ± 0.1 mg. The number of eggs/mg wet egg tissue was estimated by counting 2000 eggs and weighing these to the nearest 0.1 mg. On average, 2000 eggs were observed per 29 ± 3 mg of egg tissue. Thus total number of eggs/individual varied from 2455 to 6532. Results, however, will be presented as mass for simplification. Only this measurement was obtained in 1998. In 1998, individuals were collected (Val-Comeau: 10, Burnt Church: 14, Pointe-Sapin: 20 and Cap-Lumière: 13) and egg mass was again determined to the nearest 0.1 mg.

To determine if destination of transplanted individuals influenced fecundity, shell measurements and egg mass were determined as described above for transplanted individuals at all the study sites immediately after fall fertilization.

Electrophoresis. The somatic tissue of transplanted survivors on day 320 for both experiments, was collected for fecundity analysis and was kept at -80°C for genetic analysis. Saint-Edouard to Val-Comeau, Saint-Edouard to Pointe-Sapin and Le Goulet to Le Goulet were not included in the statistical analysis as the number of individuals was too low (< 10 ind. at the end of the experiment) to give reliable representation. Tissues were homogenized in 50-75 µl of an allozyme grinding buffer as described by Holm & Bourget (1994; 50 mM Tris-HCl pH 8.0, 1 mM $MgCl_2$, 1 mM DTT, 50% v/v glycerol). Mannose-phosphate isomerase (*Mpi*) enzyme locus was resolved using five microliters of homogenate, applied to cellulose acetate plates at the cathodal end of the gel and run at 200 V for 20-25 min. Glucose-phosphate isomerase (*Gpi*) enzyme locus was scored after migration on vertical discontinuous polyacrylamide slab gels (Ornstein 1964). Samples were all run with at lsouth one standard known genotype. Enzymes were stained according to Hebert & Beaton (1989).

Statistical analyses. All statistical analyses were carried out with SAS (SAS Institute Inc. 1998) using a significance threshold of 0.05. Assumptions of normality and homoscedasticity were respected, at times by transformation of the data. Heterogeneous variance was sometimes observed, but the analysis of variance is relatively robust to unequal variances (Milliken & Johnson 1992), provided that the larger sample sizes correspond to the populations with the larger variances, which was always the case. Normality was tested using the Shapiro-Wilks statistics (Zar 1984). Residual homoscedasticity was visually verified and confirmed (Montgomery 1991). When a source of variation was significant, *a posteriori* multiple comparisons (LS means; SAS 1998) were performed. Because of the lost of many cobbles during the study, the duration of the transplantations varied and the analysis of growth and survival were carried out on data until the day 220 in both experiments.

Growth. The analysis of growth rates of barnacles used in the two sets of transplant experiments were done using the Proc Mixed procedure for mixed linear models with a spatial power type and an autoregressive structure with unequal spacing in time (Littell *et al.* 1998). In order to compare the growth rates ($mm.d^{-1}$), simple contrasts were done (Montgomery 1991). The growth rates were examined as a function of origin and destination, comparing recruits sharing the same origin and transplanted to different destinations to control recruits (origin transplanted to origin). In the second experiment, growth data were log-transformed to meet the normality and heteroscedasticity assumptions. The analysis was carried out as for the first transplant experiment.

Survival. Survival analysis was carried out using Lifetest procedure (SAS 1998) based on Wilcoxon's Log-Rank statistics for the two experiments separately. Comparisons of the shape of the survival curves two by two were done taking into account origin and destination.

Fecundity. Natural fecundity of the two populations for each site for the years 1997 and 1998, was examined using an analysis of covariance. Basal diameter was used as covariable, since it was correlated ($R^2 = 0.34$, $N = 102$, $p < 0.0001$) with the egg mass. Data were log-transformed to respect normality and homoscedasticity assumptions.

To compare the fecundity of transplanted recruits, an analysis of covariance was done taking into account origin and destination. The two experiments were also analyzed separately. Because egg mass was correlated with the basal area of barnacles ($R^2 = 0.44$, $N = 79$, $p < 0.0001$), the basal area was used as a covariable in the analyses.

Genetic analysis. Allelic frequencies were calculated for each locus using the BIOSYS-1 program of Swofford & Selander (1989). Genotype frequencies were not presented as the sample size was too small and no reliale representation could be expected (see Annexe A). Comparisons of allelic frequencies for each locus within and among origins were carried out with χ^2 Monte-Carlo simulations (Roff & Bentzen 1989) of the REAP program (McElroy *et al.* 1991) using sequential Bonferroni corrections. Missing data on day 320 were primarly do to the incapacity of reaching the cobbles because of frozen substrata.

Results

Growth

Experiment 1. Recruits transplanted 5 days after settlement (from Cap-Lumière to Val-Comeau, Burnt Church, Pointe-Sapin and Cap-Lumière), differed in their growth rates according to local destination. Recruits transplanted north of the Miramichi showed slightly better growth than the recruits transplanted south of the Miramichi (Table 1a). Recruits transplanted to Val-Comeau grew slightly faster than the control recruits of Cap-Lumière and both Val-Comeau and Cap-Lumière individuals grew 3 to 4 times faster than the recruits transplanted to Pointe-Sapin (Fig. 2).

Experiment 2. July to November growth rates of recruits transplanted 48 days after settlement (from Le Goulet, Cap-Lumière and Saint- Edouard to Val-Comeau, Burnt Church, Pointe-Sapin and Cap-Lumière) differed significantly among destinations but the site to site variations suggest these variations are not linked to the regions north or south of the Miramichi (Table 1b). Recruits from Cap-Lumière transplanted to Burnt Church had a faster growth than the ones transplanted to Pointe-Sapin. No differences were found between recruits originating from Saint-Edouard and from Le Goulet transplanted to Val-Comeau, Burnt Church, Pointe-Sapin and Cap-Lumière (Fig. 3).

Survival

Transplanted individuals showed different survivals according to their destination. Recruits transplanted north of the Miramichi had a much higher survival than recruits transplanted south of the Miramichi.

Experiment 1. For the recruits transplanted from Cap-Lumière, survival curves (Fig. 4) varied significantly among destinations ($W = 80.67$, $df = 3$, $p < 0.0001$). At the end of the experiment, the survival varied from 60% (recruits transplanted to Val-Comeau) to 9% (control-transplant recruits at Cap-Lumière).

Table 1. Growth analysis using Mixed procedure (Little *et al.* 1998). Fixed factors and random factors are shown in the table. ***p<0.0001

Fixed factors				Random factors		
Source of variation	**NDF**	**DDF**	**F**	**Covariance parameter**	**Subjects**	**Estimates**
a) Barnacles transplanted 5 days after settlement						
Destination	3	203	474.88***	SP(POW)	Barnacle(Destination*Cobble)	0.9832
Date*Destination	3	690	479.72***	Residual		1.5354
b) Barnacles transplanted 48 days after settlement						
Origin*Destination	13	142	15.78***	SP(POW)	Barnacle(Origin*Destination*Cobble)	0.9959
Date*Origin*Destination	13	142	16.63***	Residual		0.0528

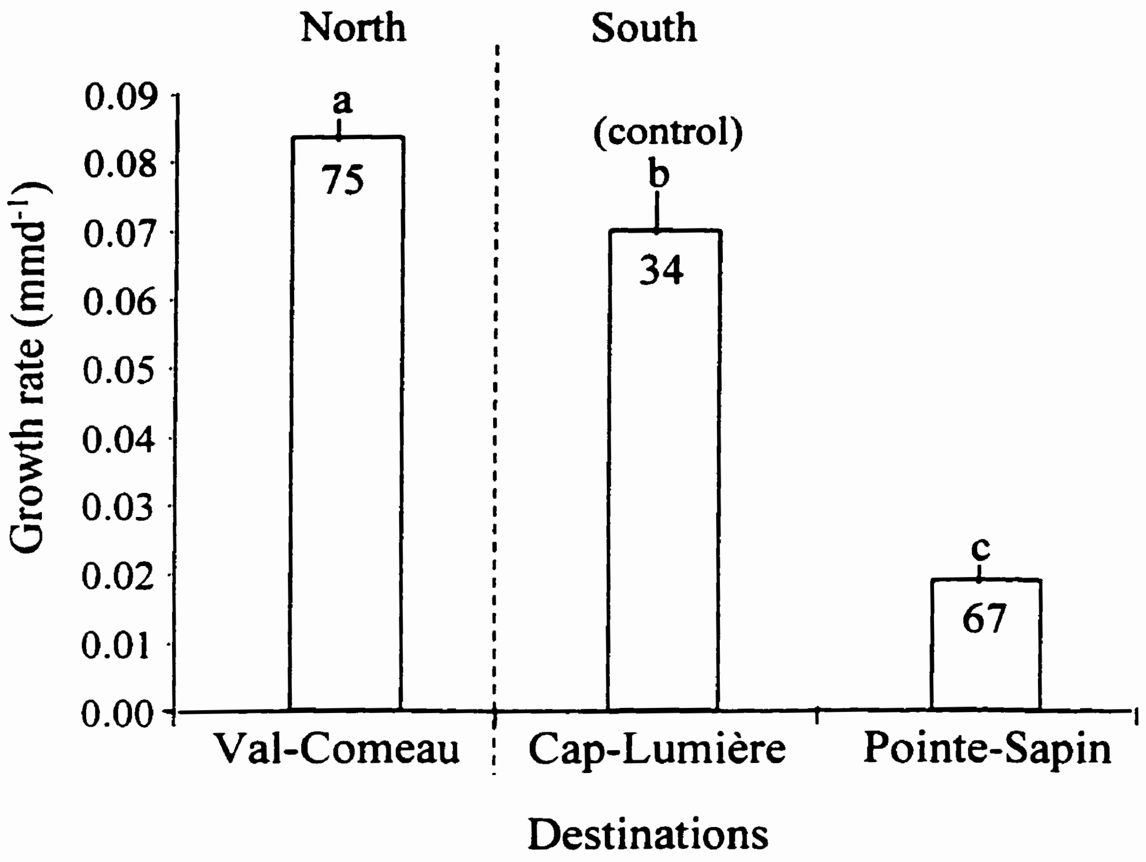

Figure 2. Growth rate (mm.d-1) of recruits transplanted from Cap-Lumière 5 days after settlement. Histogram bars represent the slopes of the growth curves, calculated using the procedure Proc Mixed (Littell 1998) on individuals from four cobble replicates that initially held an average of 31.2 ±13.9 solitary individuals (after thining). Results for Burnt Church destination are not shown, as only two sampling dates were obtained. These were not included in the statistical analysis. Numbers inside histogram bars represent sample size. Values with dissimilar letters differ significantly. Vertical bars indicate standard errors.

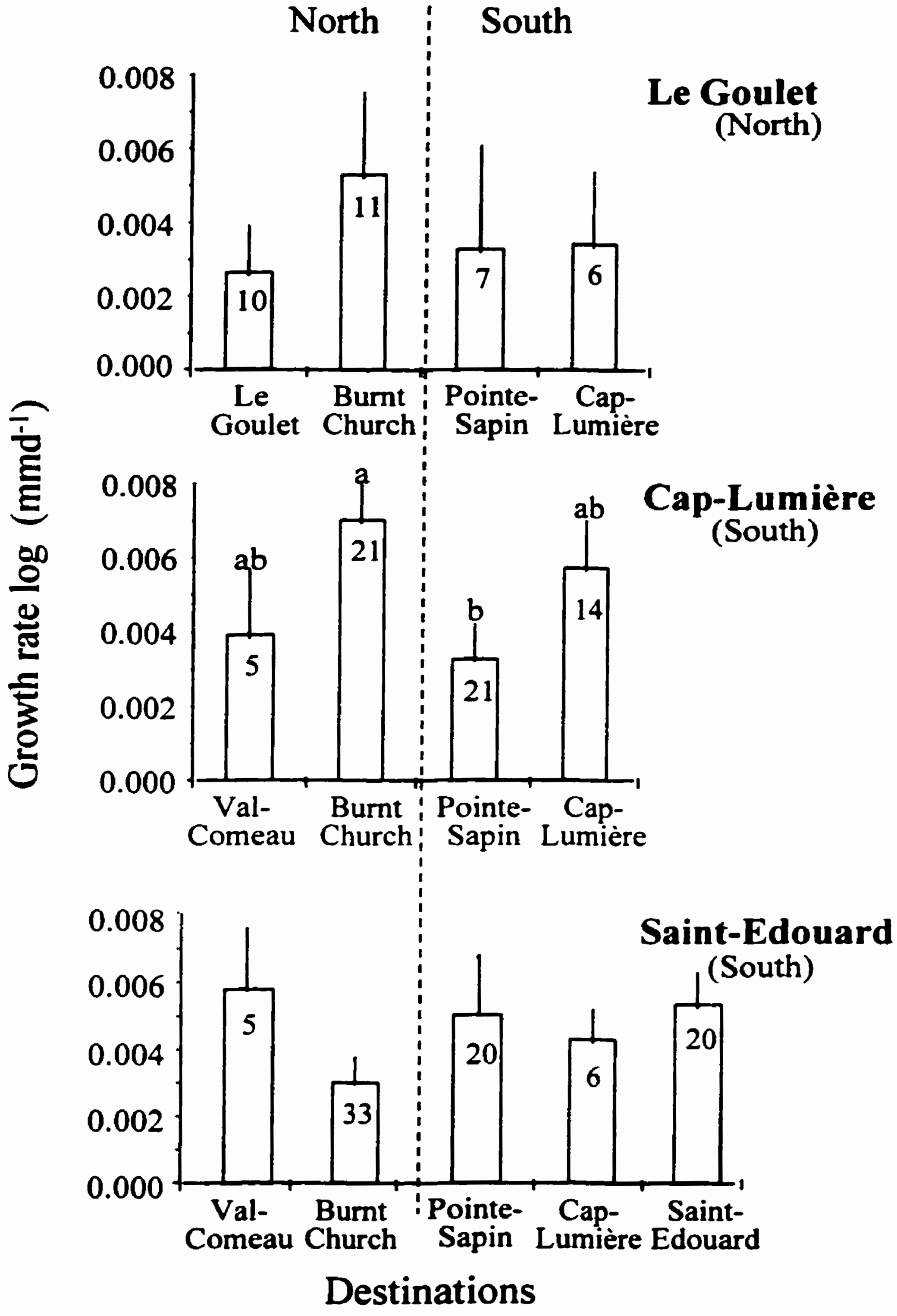

Figure 3. Growth rate (log) of recruits transplanted one month after settlement. The individuals transplanted from Le goulet to Val-Comeau were lost early in the experiment, no results for this transplantation are presented. The origin is indicated in bold character above each figure. Histogram bars represent the slopes of the growth curves calculated using the procedure Proc Mixed (Littell 1998) on individuals from three cobble replicates that initially held an average of 13.1 ± 8.8 solitary individuals (after thining). Vertical bars indicate standard errors. Significant differences are shown by dissimilar letters. Data were log-transformed to meet the normality and heteroscedasticity asumptions.

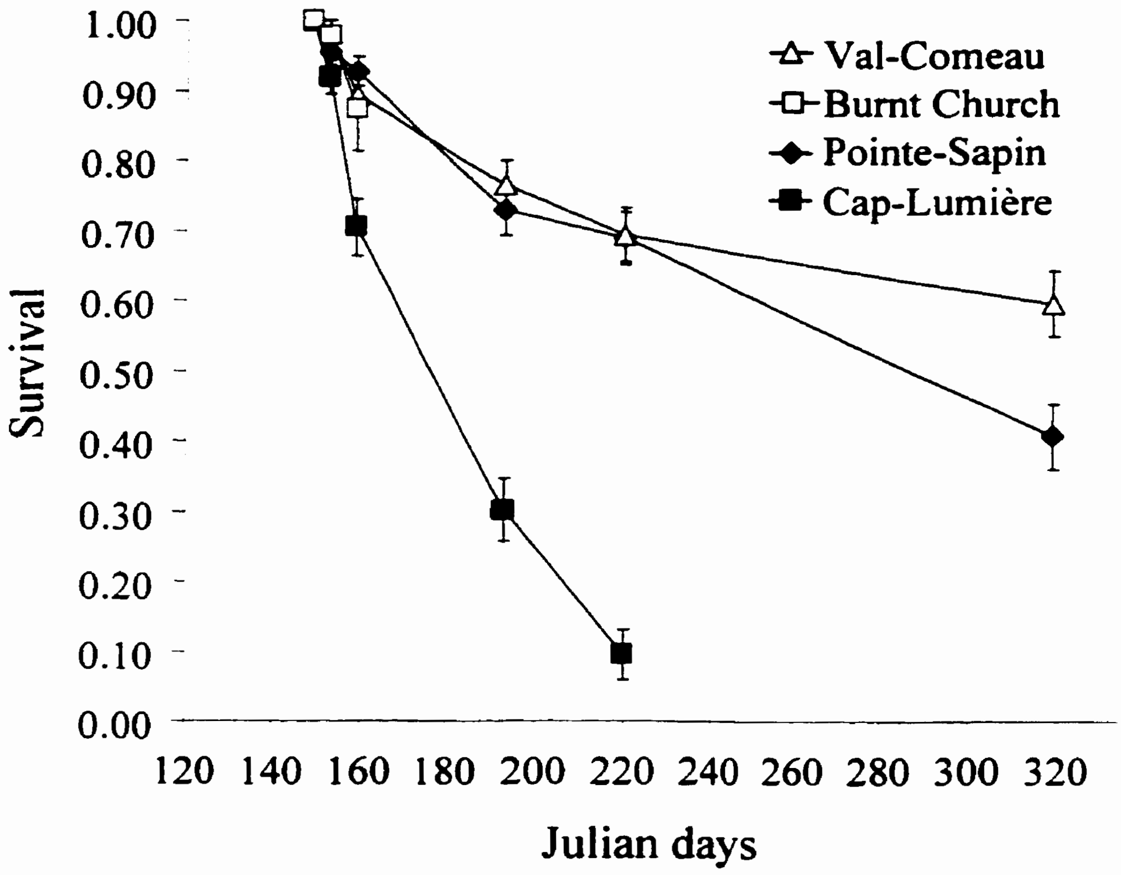

Figure 4. Survivorship of *Semibalanus balanoides* recruits transplanted from Cap-Lumière to different destinations 5 days after settlement. Data from each destination were collected on individuals located on four cobbles that initially supported on average 31.2 ± 13.9 solitary individuals each. Vertical bars indicate the standard errors.

Experiment 2. The slopes of the 13 survival curves (Fig. 5) for the recruits transplanted 48 days after settlement differed significantly ($W = 60.97$, $df = 12$, $p < 0.0001$). During the experiment, survival varied from 100% (recruits transplanted from Le Goulet to Pointe-Sapin) to 32% (recruits transplanted from Saint-Edouard to Cap-Lumière). The control recruits from Le Goulet and Cap-Lumière showed no survival differences with the recruits transplanted to other sites. However, survival of individuals transplanted from Saint-Edouard to Pointe-Sapin and Cap-Lumière was lower than the transplant controls (Saint-Edouard to Saint-edouard) and transplants to the northern sites (Val-Comeau and Burnt Church). While survival of the transplant controls was 20% lower than the transplants to the nothern sites, this difference was not statistically significant (see Fig. 5).

When survival is examined according to destination but independently of origin, recruits transplanted to the north destinations (Val-Comeau and Burnt Church) showed a much better survival than those transplanted to the south destinations (Cap-Lumière and Pointe-Sapin; $W = 23.28$, $df = 3$, $p < 0.0001$; Fig. 6).

Fecundity

Fecundity results reveal the brooding variability among years and sites. The analysis showed that barnacles fertilized in autumn 1997 (collected in April 1998) contained more eggs than barnacles fertilized in 1998, all sites pooled together (Table 2). No significant interactions (site*year) were observed. Barnacles located at Pointe-Sapin possessed significantly fewer eggs than barnacles located at Val-Comeau and Cap-Lumière.

No difference in fecundity could be linked to origin or destination (north or south the Miramichi; see Annexe B). In our study, nearly all (98%, N = 112) transplanted recruits sampled at the end of the experiment contained eggs. The egg wet mass of the transplanted recruits showed no significant difference between sites either

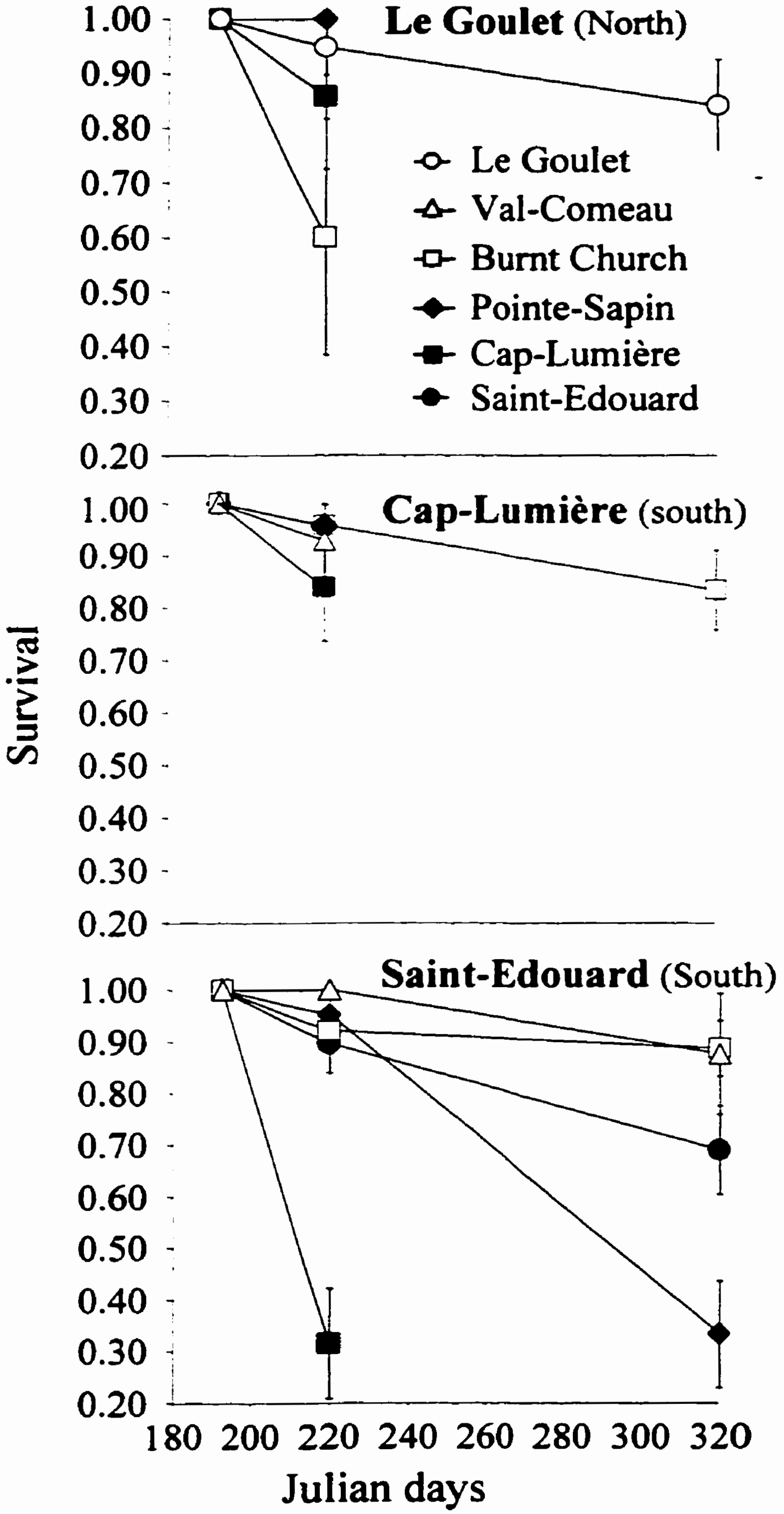

Figure 5. Survivoship of *Semibalanus balanoides* recruits transplanted from Le Goulet, Cap-Lumière and Saint-Edouard (in bold character) one month after settlement. Data from each destination were obtained from three cobble replicates that initially supported on average 13.1 ± 8.8 solitary recruits. Vertical bars indicate standard error. Empty symbols represent sites located west and full symbols represent sites situated east of the Miramichi estuary.

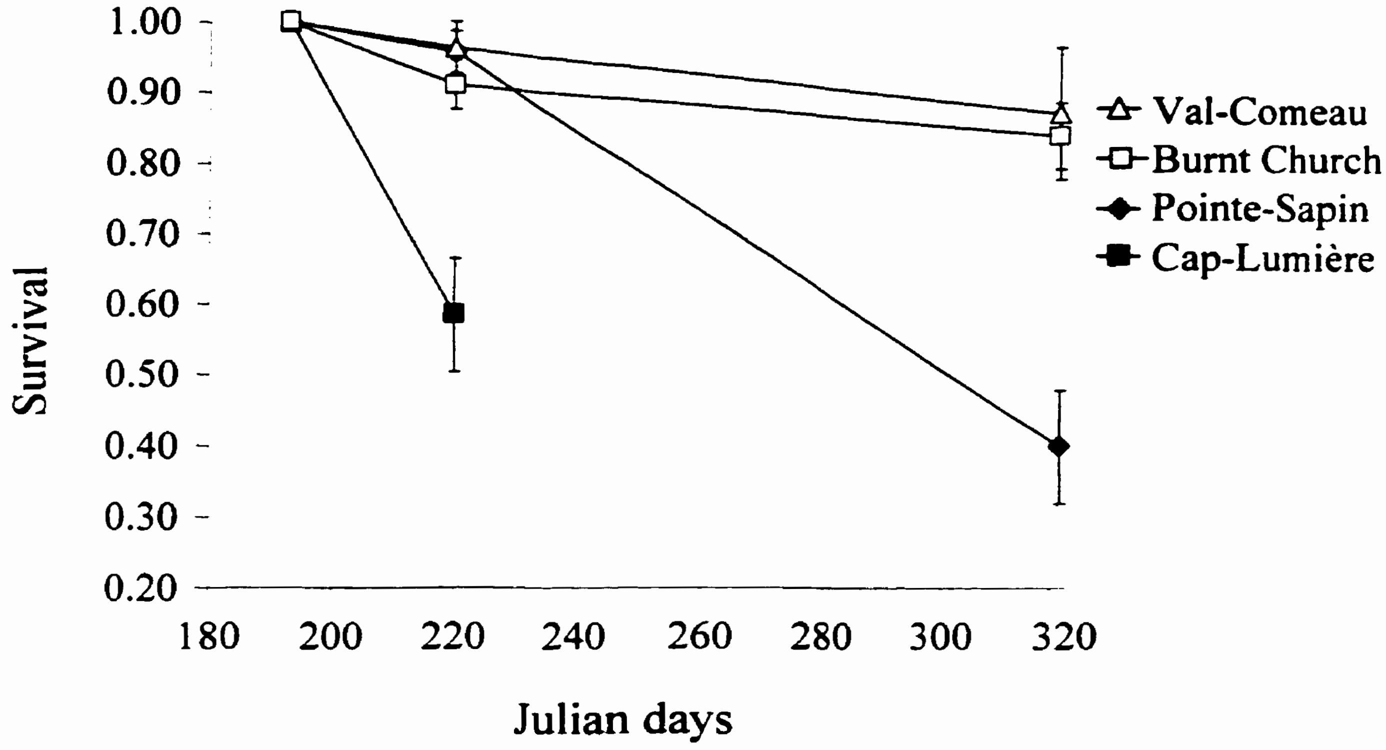

Figure 6. Survivorship of Semibalanus balanoides recruits transplanted one month after settlement (all origins combined) according to destination. Data from each destination were obtained from nine cobbles that initially supported on average 12.8 ± 9.2 solitary recruits. Vertical bars indicate standard errors. Survivorship at the west destinations (Val-Comeau and Burnt Church) differed significantly from that of the east destinations (Pointe-Sapin and Cap-Lumière).

Table 2. Analysis of variance showing the effect of site, year and their interaction on egg masses (µg). Natural logarithm was used to meet the ANOVA assumptions. *p<0.05, ***p<0.0001 and **ns** p>0.05.

Source of variation	**DF**	**MS**	**F**
Site	3	1.6381	3.02*
Year	1	9.8281	18.10***
Site*Year	3	0.9497	1.75 **ns**
Error	92	0.5430	
Corrected total	100		

for recruits that were transplanted 5 days after settlement ($F = 0.24$, $N = 35$, $df = 1$, $p > 0.6249$) or recruits transplanted 48 days after settlement ($F = 1.67$, $N = 75$, $df = 5$, $p > 0.1535$).

Genetic analysis

Data available for the genetic analysis came from barnacles originating south of the estuary, either from Cap-Lumière or Saint-Edouard and which were transplanted to the south (Saint-Edouard) or north (Burnt Church or Val-Comeau) of the estuary. Allelic frequencies are given in Table 3 and Table 4 show the coefficients for heterozygote deficiency or excess. Two common *Mpi* and *Gpi* alleles were observed (B and C) based on their distance from the origin on the gel. One additional rare allele was observed for each enzyme and was labeled A. All samples analysed, but one (Saint-Edouard to Burnt Church) were in Hardy-Weinberg equilibrium and no linkage desiquilibrium between loci was detected. Altough not significative, controls originating from the south and transplanted to the south (Saint-Edouard transplanted to Saint-Edouard), had higher Mpi^{B} frequencies and lower Gpi^{B} frequencies, recruits originating from the south (Saint-Edouard or Cap-Lumière) and transplanted to the north (Val-Comeau and Burnt Church) showed higher Gpi^{B} frequencies and lower Mpi^{B} frequencies than the barnacles from the control site (Saint-Edouard), suggesting a change in the gene frequency only a few months after transplantation. The new frequencies (after transplantation: exclusively for the Gpi^{B}) are consistent with the genotype frequencies of ***Semibalanus balanoides*** located on either side of the Miramichi estuary observed by Holm and Bourget (1994), either for the recruits or the adults (Fig. 7). In short, 4 months after transplantation to the north of the Miramichi the barnacles from the south of the Miramichi showed frequencies similar to those of natural populations. Estimates of $N_e m$ (effective number of migrants per generation) between north and south populations were calculated using the following formula: $\frac{1}{4}((1\text{-Fst})/\text{Fst})$. Results indicated an $N_e m$ of 15.38 for the *Mpi* and of 7.81 for the *Gpi*.

Table 3. Allelic frequencies at two loci for the survivors of Val-Comeau (V-C), Burnt Church (BC), Cap-Lumière (C-L) and Saint-Edouard (S-E). Numbers in parentheses represent sample size. Bold letters show the statistical results obtained from X^2 Monte-Carlo simulations adjusted with the Bonferroni correction. Significant differences are shown by different letters.
* Data from the first experiment.

	Destinations			
	North			**South**
Locus/ Allele	**C-L to V-C (33)***	**C-L to BC (20)**	**S-E to BC (26)**	**S-E to S-E (13)**
Mpi	**a**	**a**	**a**	**a**
A	0.000	0.000	0.000	0.038
B	0.561	0.550	0.462	0.615
C	0.439	0.450	0.538	0.346
Gpi	**a**	**a**	**a**	**a**
A	0.019	0.000	0.025	0.038
B	0.630	0.735	0.700	0.500
C	0.352	0.265	0.275	0.462

Table 4. Coefficients for heterozygote at two loci for the survivors of Val-Comeau (V-C), Burnt Church (BC), Cap-Lumière (C-L) and Saint-Edouard (S-E). Numbers in parentheses represent sample size. Ho: observed heterozygotes, He: expected heterozygotes, D: deficiency or excess. * Data from the first experiment.

	Destinations			
	North			**South**
Locus	**C-L to V-C (33)***	**C-L to BC (20)**	**S-E to BC (26)**	**S-E to S-E (13)**
Mpi				
Ho	15	6	4	5
He	16.508	10.154	13.176	6.760
D	-.091	-.409	-.696	-.260
Gpi				
Ho	15	5	6	7
He	13.189	6.818	8.897	7.240
D	.137	-.267	-.326	-.033

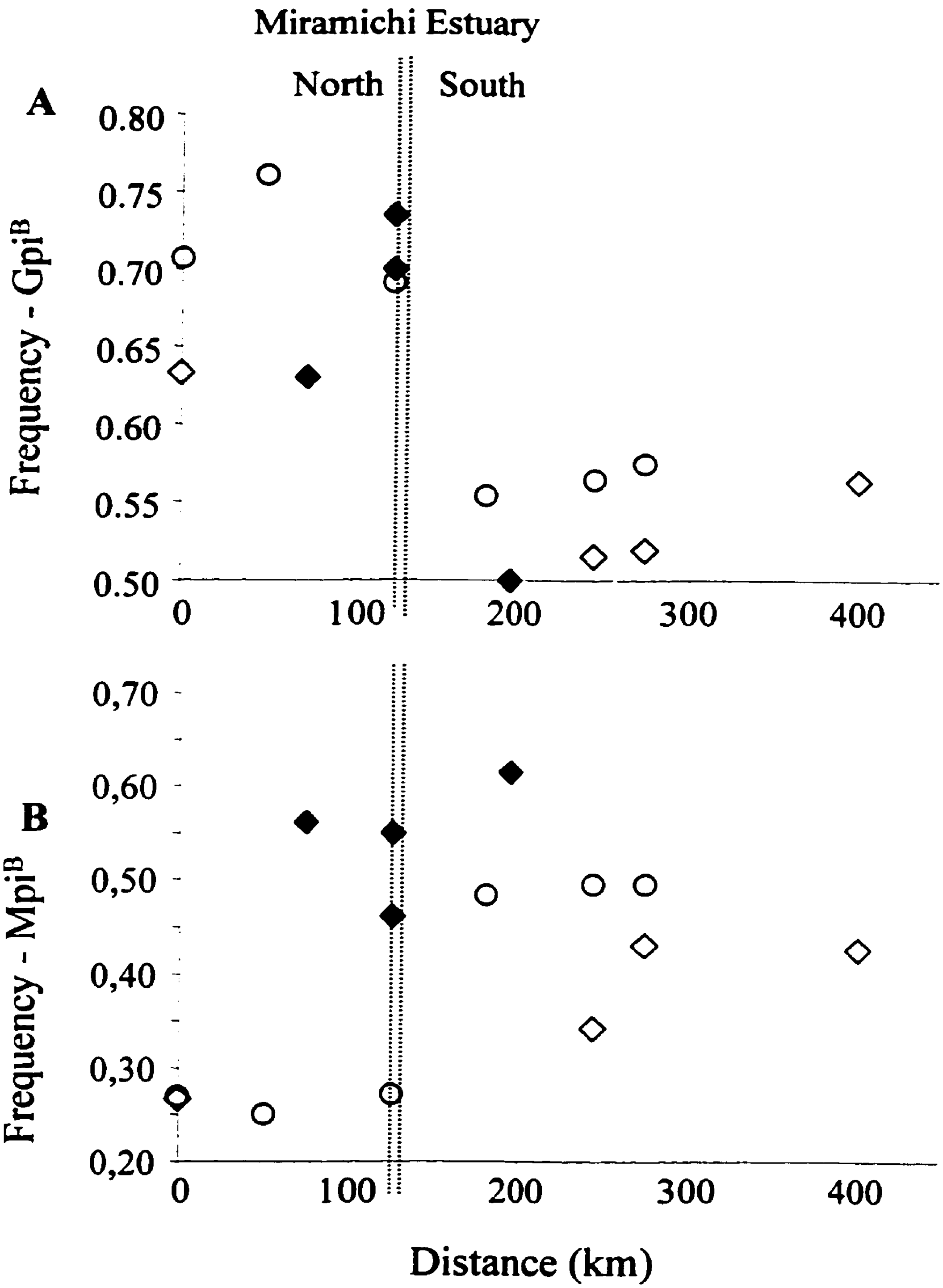

Figure 7. Change in the frequency of (A) *Gpi*^{B} and (B) *Mpi*^{B} with distance, starting Port-Daniel (Gaspé coast: Fig 1) at 0 km, for transplant barnacles from our study (filled symbols) and from Holm and Bourget (1994; empty symbols) for recruits (cirles) and adults (diamonds). Distances were estimated from 1:500 000 scale maps as straight line distance between sites.

Discussion

Our study proposed to determine whether selection occurred between the two populations of *Semibalanus balanoides* (south and north) of the Miramichi estuary. While the results show similarity in growth rate and fecundity among transplanted populations, there were significant survival differences according to destination and significant frequency variations after transplantation (*Mpi* and *Gpi*). The *Gpi* frequencies of transplanted populations came to resemble those reported for juvenile and adult populations by Holm & Bourget (1994) for the locality of transplantation.

Physical and biological barriers

Restriction of gene flow for species with high dispersal capacities could result either from physical (Quesada *et al.* 1995, Parsons 1996) or biological barriers (Benzie *et al.* 1992, Ford & Mitton 1993) to gene flow or from natural selection (Koehn *et al.* 1980, Schmidt & Rand 1999). Known circulation patterns in the southern Gulf of St. Lawrence suggest passive dispersion of the *Semibalanus balanoides* larvae from north to south (Lauzier 1965, Koutitonsky & Budgen 1991) and substantial gene flow between the two populations. A study conducted in our laboratory (Dufresne *et al.*, in prep.) on neutral mtDNA marker of adults of *Semibalanus balanoides*, confirms extensive gene flow between south and north populations of the Miramichi estuary. Furthermore, our estimates of $N_e m$ (effective number of migrants per generation between populations) between north and south populations for the two loci (*Mpi* and *Gpi*) studied indicate substantial gene flow, with values (*Mpi*: 15.38; *Gpi*: 7.81; both loci: 10.62) sufficiently high to infer larval mixing among barnacle populations in the vicinity of the Miramichi estuary.

For invertebrates with planktonic larvae, biological factors that may act on gene flow include food supply, high predation and larval behaviour (Burton 1983). The biological response variables measured in settled individuals (growth, survival and fecundity) have all been shown to be influenced by environmental factors in barnacles (see Bertness *et al.* 1991, Minchinton & Scheibling 1993). They can, however, also be significantly influenced by genetic make-up. Our experiment was aimed at determining the extent to which the genetic variations observed could be perceived as influencing other biological response variables. In our study, differences could be observed between growth rates at some destinations, but those differences could not be associated with one of the two regions studied (south or north of the Miramichi). Although differences were not statistically significant, young recruits seem to have a slightly better growth when transplanted north of the Miramichi (Fig. 2), however that difference seems to diminish in older barnacles (Fig. 3). These results suggest the presence of local factors that act on young recruits (spat) transplanted south of the Miramichi. Similarity of fecundity among populations suggest no influence of site or genetics on this response variable in the region of study. Interestingly, 98% of newly settled recruits from our study were able to reproduce within the first year of age, which is at odds with earlier observations who stated that breeding of *Semibalanus balanoides* in New Brunswick did not normally commence until the second year of life (Bousfield 1954).

Selection on newly attached spat

Low survival was observed at Cap-Lumière in both experiments. Three hypotheses could explain this result: i) intense local predation; ii) fresh water discharge from the Miramichi or, iii) selective mortality. The substantial differences in survival observed between the first (spat) and the second experiment (up to 48d old individuals) suggest that the crucial period for selection is the early phases shortly after settlement. Numerous studies have shown the high vulnerability of newly attached spat to local conditions (Connell 1961, Wethey 1986, Gosselin & Quian 1997, Hunt & Scheibling 1997 and Pechenik *et al.* 1998). For instance, specific local conditions such as rock type (Raimondi 1988), coastal heterogeneity, shore waves and consistent abundance of natural enemies (Connell 1985) are known to influence the survival within the first hours and days following settlement. Indeed, as in many other studies (Theisen 1978, Wethey 1984, Schmidt & Rand 1999) our's show that mortality occurs very early, within the first few days or weeks after settlement.

Given substantial gene flow, selection might act to modify the distribution of allele frequencies of barnacle recruits (Nevo *et al.* 1978, Patarnello *et al.* 1991, Raimondi 1992, Schmidt & Rand 1999). In all those studies, high genotype-dependent survival was detected. Our low sample sizes limited the statistical power of our tests. Nevertheless, we observed abrupt variations in allelic frequencies at both *Mpi* and *Gpi* loci. Moreover, the changes observed for the Gpi^B are consistent with the population genetic structure of adult barnacles reported by Holm & Bourget (1994). Indeed. barnacles transplanted from a site located south (Saint-Edouard) to a site located north (Burnt Church), showed frequencies that were more representative of northern adult barnacles. And, conversely, barnacles that remained at a site situated south showed frequencies more representative of barnacles originating south of the Miramichi.

The present isoenzyme results and survival values support the early post-settlement selection hypothesis. Indeed, in all transplanted populations in which we were able to follow survival for an extended period of time, survival values in populations south of the Miramichi were low ($\bar{x}$ = 36.7 ± 21.2%), much lower than north of the Miramichi ($\bar{x}$ = 80.1 ± 13.8%), and fully compatible with allele frequency measurements obtained. Indeed, on average a 10% change of frequency of *Gpi* is observed in newly attached individuals south of the Miramichi. While the same population experiences mortality of the order of 65% within a period of 5 mo, the duration of the experiment.

Based on a geographical scale, early studies (Bourget *et al.* 1989, Martel 1990, Holm & Bourget 1994) carried out on *S. balanoides* on the east coast of North america.

showed the presence of two contiguous populations. However, based on a regional scale, Dufresne *et al.* (in prep) proposed that barnacles from both sides of the Miramichi estuary would represent one population, in which local selection would occur. Although our study did not verify specifically this hypothesis, as our $N_e m$ for both loci (*Mpi* and *Gpi*) were very high, as barnacles from both sides brood at the same time and as both loci were in Hardy-Weinberg equilibrium, do not contradict this hypothesis.

Selection on *Gpi* and *Mpi* loci have been shown to occur in several species (barnacles: Wethey 1984, Bertness & Gaines 1993, Schmidt & Rand 1999; mussels: Levinton & Hassen 1978, Theisen 1978, Grant *et al.* 1992; sea anemones: Hoffmann 1981, Ayre 1995; amphipods: Patarnello & Battaglia 1992). The relationship between fitness and enzyme activity has been discussed in numerous studies (*Gpi:* Krause 1995, Zera 1987; *Mpi:* De La Fuente et al. 1986, Hernandez & De La Fuente 1988, see also Schmidt & Rand 1999), and many have related spatial variation in allele frequencies to environmental factors such as temperature (Grant *et al.* 1992), salinity (Theisen 1978), low oxygen concentration (Shihab & Heat 1987) and pollution (heavy metals: Lavie & Nevo 1982, Hvilsom 1983, Nevo et al. 1983, Patarnello *et al.* 1991; petrochemical agents: Lavie *et al.* 1984). In our experiment, there is no obvious relationship between temperature or pollution and the population structure at the *Gpi* or *Mpi* loci. However, spring outflow of the Miramichi estuary could have an impact on the barnacle spat population located south of the Miramichi by reducing salinity, since circulation patterns in this region favor water transportation north to south. Further work needs to be carried out to examine differential conditions, and while special attention must be placed on microscale factors (i.e. rock temperature, specific rock orientation as a function of waves and shades), as Schmidt & Rand (1999) recently observed, the regional factors (large scale factors) must be examined to explain regional differences in mortality.

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Conclusion générale

Avec la venue des techniques biochimiques en génétique, plusieurs études ont révélé une hétérogénéité génétique entre populations à différentes échelles spatiales (milliers de kilomètres: Flowerdew 1983, Ayre *et al.* 1991; centaines à dizaines de kilomètres: Theisen 1978, Koehn *et al.* 1980, Martel 1990, Holm & Bourget 1994, Hare & Avise 1996; mètres à centimètres: Rolan-Alvarez *et al.* 1997, Schmidt & Rand 1999). Alors que certaines d'entre elles ont associé cette divergence avec la restriction du flux génique (Dando & Southward 1981, Mitton *et al.* 1989, Parsons 1996), d'autres ont démontré la présence d'une mortalité sélective dépendante d'un génotype particulier en présence d'un important flux génique (Koehn *et al.* 1980, Grant *et al.* 1992, McMillen-Jackson *et al.* 1993).

Nos résultats suggèrent la présence d'un flux génique important entre les populations étudiées ($N_e m$: *Mpi*: 15.38; *Gpi*: 7.81; deux loci: 10.62) et des différences de fréquences alléliques significatives entre les populations transplantées au nord de l'estuaire de celles transplantées au sud. Les patrons de fréquence observés sont comparables à ceux obtenus par Holm & Bourget (1994), notamment pour le locus de la *Gpi*. En effet, ces derniers avaient observé pour les individus (adultes et recrues) récoltés au nord de l'estuaire, des fréquences alléliques de l'ordre de 0.70 pour la Gpi^B, alors que dans notre étude, elles sont de l'ordre de 0.68.

Bien que cette tendance ne soit pas significative, les juvéniles nouvellement fixés (de la première expérience) et transplantés au nord de la Miramichi, semblent afficher de meilleurs taux de croissance que ceux transplantés au sud de la Miramichi. Or, ces différences s'estompent avec le temps et elles ne sont plus guère observables lors de la deuxième expérience. Ces observations semblent suggérer l'existence de conditions environnementales particulières au sud de la Miramichi dans les premières semaines suivant la fixation. Comme les courants au voisinage de la Miramichi sont du nord vers le sud et que cette période (le printemps) coïncide grossièrement avec la crue printanière, ces différences pourraient être induites par des différences de salinité résultant de la décharge d'eau douce au sud de la Miramichi.

La reproduction chez *Semibalanus balanoides* est influencée par les conditions environnementales (Crisp 1964). Comme celles-ci fluctuent énormément à l'échelle locale, il n'est pas surprenant que nous n'ayons aucune différence de fécondité entre les individus transplantés de part et d'autre de la Miramichi.

La survie des individus transplantés affiche des différences régionales lorsque les observations sont réparties sur une longue période. En effet, les individus transplantés au nord de la Miramichi ont une meilleure survie que ceux transplantés au sud de la Miramichi. Ces différences sont encore plus notoires lorsque les origines sont regroupées (voir Fig. 6) et que l'effet de destination est examiné. Ces résultats suggèrent la présence de mortalité sélective aux sites situés au sud de la Miramichi. dans les premiers mois suivant la fixation.

Nos résultats portant sur les propriétés biologiques appuient les conclusions de Dickie *et al.* (1983) et de Mallet & Haley (1983) qui affirment que les conditions environnementales sont d'importants déterminants dans les variations de croissance entre populations, alors que les différences génétiques sont plutôt responsables des variations de la survie. Compte tenu de l'important flux génique entre les populations étudiées, de même que la différentiation génétique couplée à une mortalité élevée aux sites situés au sud de la Miramichi, nous suggérons qu'une sélection s'est vraisemblablement effectuée sur les individus transplantés au sud de la Miramichi.

Basées sur une échelle géographique, plusieurs études ont démontré l'existence de deux populations distinctes de *S. balanoides* dans l'est de l'Amérique du nord (Bourget *et al.* 1989, Martel 1990, Holm & Bourget 1994). Récemment, Dufresne *et* *al.* (en prép.) ont proposé l'hypothèse de l'existence d'une seule population, basée sur une échelle régionale. Bien que nous n'ayons pas testé cette hypothèse, nos résultats ne semblent pas la contredire.

Alors que la présence de mortalité sélective aux sites situés au sud de la Miramichi semble évidente, l'origine des larves reste un aspect non contrôlé dans la présente étude. En effet, puisque la fixation des larves s'est effectuée simultanément de part et d'autre de l'estuaire, il est difficile d'établir l'origine des individus transplantés. Selon les patrons de circulation orientés du nord vers le sud de la Miramichi, deux scénarios sont possibles. Le premier scénario étant que les larves originaires du sud (dans notre étude) et transplantées au nord sont en réalité des larves originaires du nord que les courants auraient transportées au sud de l'estuaire. Ainsi, toutes les transplantations effectuées comporteraient des larves originaires du nord. Le second scénario étant que les larves originaires du sud viennent réellement du sud.

Lorsque nous évaluons la mortalité nécessaire afin de compenser pour les changements alléliques observés, nous nous apercevons que seul le premier scénario est compatible. En effet, les individus transplantés à sud de la Miramichi montrent une mortalité de l'ordre de 64% alors que celle des individus transplantés au nord de la Miramichi est de 18%. Or, les changements de fréquences alléliques sont d'environ 10%. De plus, une étude menée simultanément a pu établir le génotype initial des larves récoltées au sud de la Miramichi et les conclusions suggèrent que les larves sont vraisemblablement originaires du nord de la Miramichi.

Les avantages physiologiques liés à certains loci ont été démontré par plusieurs auteurs (Koehn *et al.* 1980, Zera 1987, De La Fuente *et al.* 1986, Hernandez & De La Fuente 1988, Krause 1995, Schmidt & Rand 1999). Lors d'expériences conduites sur *Argopecten irradians,* Krause (1995) a mis en évidence au niveau biochimique, les avantages physiologiques associés au locus de la *Gpi.* Cette enzyme est située à l'embranchement de la voie glycolytique et du cycle du pentose. L'inhibition de cette dernière, perturbe la voie glycolytique et dirige une plus grande proportion du flux de carbone vers le cycle du pentose. Or, ce cycle est responsable de la production de grande quantité de nicotinamide adénine dinucléotide phosphate (NADPH), composé nécessaire à la biosynthèse des lipides. Les auteurs ont donc proposé un mécanisme par lequel l'inhibition différentielle génotypique de la *Gpi,* serait causé par un composé provenant du cycle du pentose, le 6-phosphogluconate. Par conséquent, certains génotypes de la *Gpi* , seraient associés à des teneurs lipidiques élevées.

Récemment, Schmidt & Rand (1999) ont également proposé un mécanisme physiologique par lequel la sélection au locus de la *Mpi* serait important dans la survie de *Semibalanus balanoides.* Dans le métabolisme des hydrates de carbone, le mannose, important composé retrouvé dans les algues, est converti en mannose-6-phosphate isomérase par l'hexokinase. À son tour, le mannose-6-phosphate est transformé par la *Mpi* en fructose-6-phosphate, utilisable dans la voie glycolique afin de générer des ATP. Or, lorsque l'activité de la *Mpi* est basse, un déficit en ATP est observé. Ce problème est amplifié lorsque l'organisme est émergé, puisque à ce moment c'est le mécanisme anaérobique qui gère son métabolisme. Les auteurs suggèrent donc, que si certains génotypes de la *Mpi* possédaient des différences biochimiques résultant en une meilleure performance sous certaines conditions environnementales, la combinaison d'une diète élevée en mannose et des conditions physiologiques stressantes, pourrait engendrer une mortalité différentielle.

Bien que ces mécanismes n'aient pas été vérifiés sur les populations de balanes à l'étude, ils démontrent toutefois l'existence potentielle d'avantages physiologiques associés aux loci sous sélection dans notre étude.

Les études antérieures portant sur l'espèce *Semibalanus balanoides,* ont démontré l'existence de deux populations génétiquement distinctes sur la côte est atlantique, de même que la présence d'une interface génétique à proximité de l'estuaire de la Miramichi. Notre étude s'inscrit à la suite de ces recherches, en proposant le maintien de cette interface par la sélection sur les juvéniles aux loci de la *Mpi* et de la *Gpi*, dès les premières semaines suivant la fixation. Bien que les facteurs impliqués lors de la sélection restent à élucider, cette étude donnent d'intéressantes pistes pour des études futures. Afin de bien cerner les facteurs impliqués, une attention particulière devrait portée aux micro-conditions environnementales telles; la température des roches et l'orientation de celles-ci en fonction des vagues et de l'ensoleillement.

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Annexe A

Table presenting the genotypes distribution. Statistical analysis were not done one those data du to small sample sizes.

	Destinations			
	North			**South**
Locus/ Genotype	**C-L to V-C (33)***	**C-L to BC (20)**	**S-E to BC (26)**	**S-E to S-E (13)**
Mpi				
BB	11	8	10	6
CC	7	6	12	2
BC	15	6	4	4
AC	-	-	-	1
Gpi				
AB	-	-	1	1
AC	1	-	-	-
BB	10	10	11	3
BC	14	5	5	6
CC	2	2	3	3

Annexe B

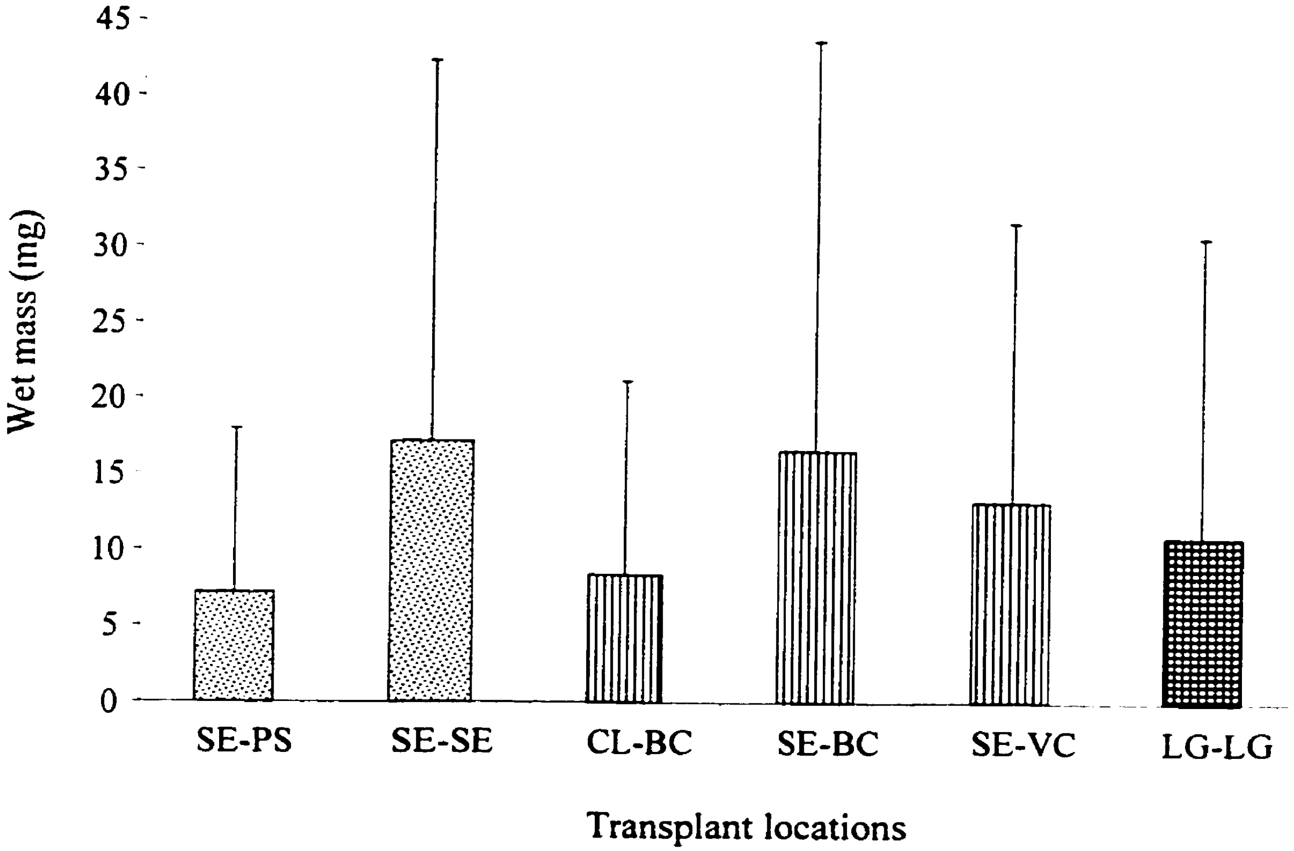

Figure representing fecundity (wet mass of eggs) for different transplant locations; Saint-Edouard (SE), Cap-Lumière (CL), Pointe-Sapin (PS), Burnt Church (BC), Val-Comeau (VC) and Le Goulet (LG) .