

Larval transport processes of barnacle larvae in the vicinity of the interface between two genetically different populations of *Semibalanus balanoides*

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ABSTRACT: Previous studies have shown a genetic interface (*MPI*, *GPI* loci) between 2 populations of the barnacle *Semibalanus balanoides* in the vicinity of the Miramichi Estuary, New Brunswick, in the Gulf of St. Lawrence. We examined whether gene flow between these 2 adjacent populations was restricted by larval dispersal. We determined the distribution pattern of *Semibalanus balanoides* planktonic larvae. Current velocity and direction, larval settlement and genetic structure of recruits were measured. Physical results and genotype distribution for *MPI* support the larval exchange hypothesis (north to south). The presence of another allele, *GPI*4*, suggests a substantial contribution of another population, possibly from the subtidal zone, to the larval pool. In accordance with previous studies, our results suggest strong selection on newly settled spat in the intertidal zone.

KEY WORDS: Larval transport · *Semibalanus balanoides* · *MPI* · *GPI* · Gene flow · Hydrodynamic structure · Circulation patterns

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INTRODUCTION

Planktonic larvae are dispersed by a combination of currents at a variety of space and time scales. This dispersal of individuals has important population dynamic and genetic consequences (Gaines & McClenaghan 1980, Roughgarden et al. 1988, Ebenhard 1991, Gilpin 1991). In larval dispersion models, the major processes usually considered are diffusion, advection and mortality (Okubo 1980, Possingham & Roughgarden 1990, Hill 1991, Richards et al. 1995, Alexander & Roughgarden 1996). Both larval behavior (Burton & Feldman 1982) and oceanographic circulation patterns (Ketchum 1954, Ayers 1956, Hedgecock 1986, Mitton et al. 1989) may limit dispersal and thus

influence genetic differentiation (Bertness & Gaines 1993). Outside estuaries (see Bousfield 1955, Epifanio et al. 1984, 1989, Epifanio 1988a,b, Dame & Allen 1996), larval transport is poorly understood (LeFèvre & Bourget 1992) and despite the fact that coastal circulation is known to vary, the influence of oceanographic transport has received little consideration (Bertness & Gaines 1993).

Given the potential for long-range dispersal of planktotrophic larvae, it is not surprising that many studies have found large scale genetic homogeneity for such species (Berger 1973, Gooch et al. 1973, Janson & Ward 1984, Johnson & Black 1984, Hoagland 1985, Holborn et al. 1994). However, there is also evidence for differentiation of local populations in species with a planktonic larval stage (Hedgecock 1986).

The cirripede *Semibalanus balanoides* is the dominant intertidal barnacle in circumboreal waters. Its life cycle includes 7 different larval stages, 6 nauplii and 1 cypris (Bassindale 1936). In North America, it is pre-

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sent in the North Atlantic, from Baffin Island to Cape Hatteras (Wells et al. 1960, Barnes & Barnes 1976). Crisp (1964), Barnes (1965), Barnes & Barnes (1976) and Flowerdew (1983a,b) presented evidence for racial differences among American and European populations, and Holm & Bourget (1994) confirmed these variations, though they showed that regional variations were often larger than trans-Atlantic differences. Bourget et al. (1989) have shown that behavioral, morphological and genetic differences occur between the Gulf of St. Lawrence and North Atlantic populations of *Semibalanus balanoides*. The 2 populations had different allele frequency for 2 allozymes, MPI (mannose-6-phosphate isomerase) and GPI (glucose-6-phosphate isomerase). Holm & Bourget (1994) have subsequently described the genetic characteristics of 11 populations from different sites within the Gulf of St. Lawrence and found a discontinuity in allele frequency, for the same 2 loci (*MPI** and *GPI**) in the vicinity of the Miramichi Estuary, New Brunswick. The population north of the Miramichi Estuary is characterized by low *GPI*3* and *MPI*2* frequencies while the population south of the Miramichi Estuary is characterized by relatively high frequencies for these 2 allozymes.

In our study, we determined if gene flow between those 2 adjacent populations was restricted by larval dispersal. We sampled plankton to determine the dispersal pattern of *Semibalanus balanoides* larvae in the interface region over the dispersal period. In large scale dispersal studies, larval abundance needs to be

examined as a function of hydrodynamics (Gaines & Bertness 1993) and other physico-chemical processes both in time and space. Therefore, current velocity and direction, water salinity and temperature were also measured. Finally, we determined whether larval distribution corresponded to larval settlement by deploying settlement collectors and characterizing the genetic structure of recruits settled onto the collectors.

MATERIALS AND METHODS

Study area. The study area was situated in the southwestern Gulf of St. Lawrence, in the vicinity of the Miramichi Estuary, New Brunswick (Fig. 1). In this region, Lauzier (1965) described a cyclonic eddy in the northern entrance of the Northumberland Strait with a southerly drift along the New Brunswick coast and a northeasterly drift along the Prince Edward Island coast. Using a model, Trites & Drinkwater (1991) suggested an offshore transport of surface waters along the northeast coast of New Brunswick, under normal winds. The predictions agreed with the upwelling proposed by Lauzier (1967), although we suspect the model itself may have been strongly influenced by Lauzier's initial suggestion of a gyre in this region.

Mean sea surface salinity for the spring is about 28 to 30‰ and mean surface temperature reaches up to 12°C (Petrie 1990). The Miramichi Estuary is one of the largest estuaries in Atlantic Canada (surface area 300 km²; drainage basin area ~14 000 km²) (Locke & Courtenay 1996). At its mouth, it is about 20 km long and 20 km wide. The average annual flow at the mouth of the river is approximately 250 m³ s⁻¹, but daily peaks of 6300 m³ s⁻¹ can be reached during the spring freshet (Lavoie 1995). Predicted tidal amplitude for that region ranged from 0.1 to 1.4 m during the study period (Canadian Hydrographic Service 1998).

Larval sampling. Plankton samples were collected at 15 offshore stations located in the Gulf of St. Lawrence near the mouth of the Miramichi Estuary. The area covered by the stations (~10 × 100 km) was approximately 1000 km². The grid of sampling stations consisted of 5 transects of 3 stations perpendicular to the coast (Fig. 1). Stations were located at a distance of 2, 6 and 10 km from the coast. The latter corresponding to the maximum offshore distance *Semibalanus balanoides* larvae have been observed in other studies (Lefèvre & Bourget 1991). Two sections were located north of the Miramichi Estuary, a middle one in front of the mouth of the estuary and two to the south (Fig. 1). All stations (n = 15) were sampled on a weekly basis from 4 May to 2 July 1998. Sampling all the stations took 2 to 3 d, depending on weather conditions. Sampling was conducted regardless of the tidal stage and

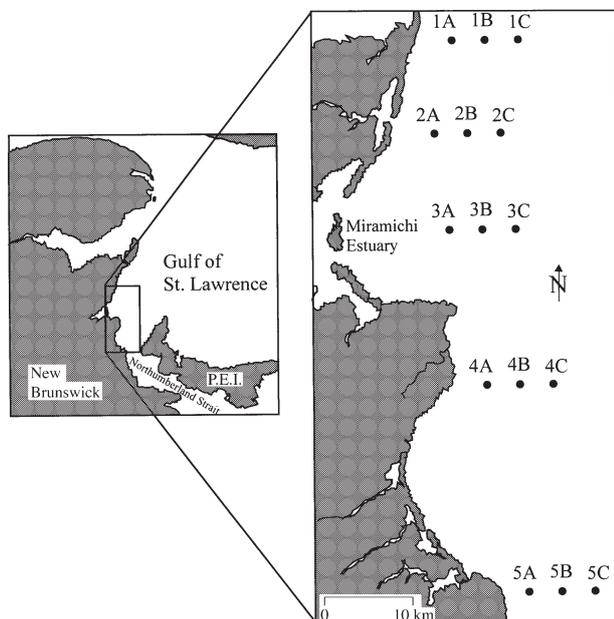


Fig. 1. Map of the study area situated in the southern Gulf of St. Lawrence and position of sampling stations near the mouth of the Miramichi Estuary

took place during daytime between 6:00 and 18:00 h. Local variability in larval density was estimated by using 2 samples (Omori & Hamner 1982) at each station throughout sampling. Samples were preserved in 4% formaldehyde in filtered seawater for later identification and enumeration.

We used a 150 μm plankton net of 0.25 m radius, as the first stage of *Semibalanus balanoides* larvae have a minimum size of about 220 μm (Bassindale 1936). The early nauplii stages of *S. balanoides* are located mainly near the surface, the later stages in midwater, while cypris larvae are mostly suprabenthic (Bousfield 1955, Gaines & Bertness 1993, Miron et al. 1995), so sampling integrated the whole water column. We sampled horizontally for 1 min close to the surface, obliquely for 30 s from the surface down to the bottom, horizontally 1 min near (~1 m) the bottom and finally 30 s obliquely from the bottom back to the surface, at throttle speed (~2.5 km h^{-1}). Because the sampling design integrates larvae over the whole water column, the likelihood of capturing all larval stages was the same at each station. Station depths varied between 6.8 and 25 m. For each sample, a calibrated flowmeter (General Oceanics, Model 2030) was attached at the mouth of the net to measure the quantity of water filtered. An average of 24.3 m^3 of seawater was filtered per tow.

Recruitment. At the 2 northern and the 2 southern sections close to the shore (Stns 1A, 2A, 4A and 5A), 9 grey Arborite® panels (10 \times 30 \times 0.1 cm; the rough surface of the back of panels were used as collectors) were moored vertically on 3 lines, 50 m apart, each supporting 3 panels which automatically oriented parallel to the water current direction. The panels were at 0.70, 0.90 and 1.10 m from the bottom. They were moored on 5 and 6 May 1998. At that period, no cypris larvae were present in the water column. The panels were retrieved on 3 June and settled barnacles were frozen at -80°C for genetic analysis.

Environmental data. At the 6 km station of each transect (Stns 1B, 2B, 3B, 4B and 5B), a currentmeter (Aanderaa, Model RCM 4, InterOcean) was moored at 1 m from the bottom. At Stn 3B, an additional currentmeter was also moored at 6 m from the surface. Current velocity ($\pm 1 \text{ cm s}^{-1}$), direction ($\pm 1^\circ$), seawater temperature ($\pm 0.15^\circ\text{C}$) and salinity (conductivity, $\pm 0.03 \text{ mmho s}^{-1}$) were monitored. All physical data were recorded every 15 min throughout the sampling period, from 25 to 28 April to between 1 and 2 June 1998. Also, on each visit at each station, a salinity-temperature profile using a CTD (Sea Bird Electronics, Sea Cat Profiler, Model SBE 19) was made in order to determine the degree and depth of stratification of the water column.

Laboratory procedures. *Semibalanus balanoides* larvae were identified to the larval stage according to

Bassindale (1936), Pyefinch (1948) and Crisp (1962). A bulb pipette method was used for subsampling. Samples were diluted to 200 ml, stirred until approximately homogeneous, and subsampled (with 5 ml aliquots) until either 300 *S. balanoides* larvae were obtained or 25% of the total sample volume had been subsampled (Van Guelphen et al. 1982). Results are expressed as number of larvae m^{-3} for analysis, and stages were grouped as nauplii (stages 1 to 3), metanauplii (stages 4 to 6) and cyprids.

Genetic analysis. Somatic tissues of each recruit collected on panels were homogenized in 50 μl of homogenization buffer (0.2 M Tris-HCl pH 8.0, with 30% sucrose, 1% polyvinylpyrrolidone, 0.1% Nicotinamide Adenine Dinucleotide [NAD], 5 mM dithiothreitol, and 1 mM 4-[2-aminoethyl]-benzenesulfonyl fluoride hydrochloride [Pefabloc Sc, Boehringer Mannheim]). The solution was applied to a horizontal cellulose acetate gel (Hebert & Beaton 1989). The polymorphic enzymes examined were glucose phosphate isomerase (GPI EC 5.3.1.9) and mannose phosphate isomerase (MPI EC 5.3.1.8). These have been shown to exhibit substantial variability and have been studied in the adult populations in the study area (Holm & Bourget 1994). A 'standard' was prepared by mixing homogenates of individuals of different genotypes. This 'standard' of all possible alleles for a given locus was applied on each gel to ensure exact allele identification. The gene nomenclature for protein-coding loci follows the recommendations of Shaklee et al. (1990).

Data analysis. Larval densities of different stages of *Semibalanus balanoides* through time and space were used to determine dispersal patterns. Allele frequencies, observed and expected heterozygosities under the assumption of Hardy-Weinberg equilibrium and heterozygote deficiency index (D), were calculated for each locus using the BIOSYS-1 program of Swofford & Selander (1989). Results in allele frequencies were compared with published results in adults (Holm & Bourget 1994) to determine the origin of recruits ('northern' or 'southern' populations; see 'Introduction').

RESULTS

Current, salinity and temperature

Mean current velocity averaged between 0.2 and 3.4 cm s^{-1} for all the transects over the 30 d of immersion. At Stn 4B, current was predominantly northeast while, at Stn 5B, the northwest direction predominated (Fig. 2). This hydrodynamic structure was stable over the sampling period and suggests an anticyclonic eddy at the northern end of the Northumberland Strait.

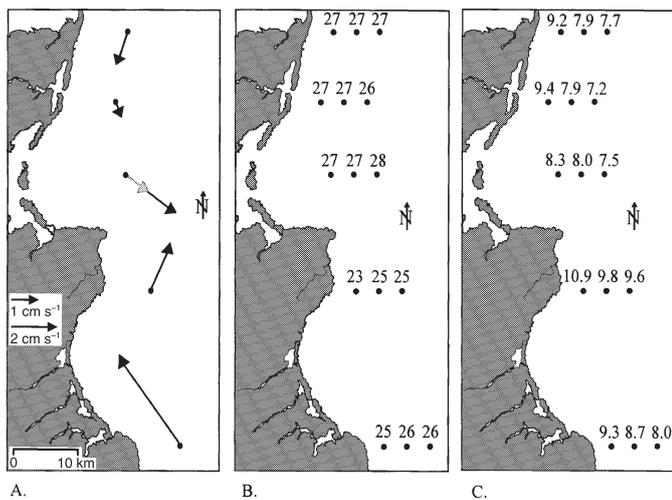


Fig. 2. (A) Mean current velocities and directions. Black arrows represent current vectors close to the bottom and gray arrow current vectors at 6 m from the surface. As will be seen from the figure, bottom and surface current directions were parallel. (B) Mean sea surface salinities (‰) and (C) mean sea surface temperatures (°C) from CTD casts in the southern Gulf of St. Lawrence near the mouth of the Miramichi Estuary, between 4 May and 2 July 1998.

See Fig. 1 for station identification

From the northern end of the sampling grid the transect closer to the mouth of the Miramichi Estuary, currents were predominantly southward. Mean surface salinities averaged between 23 and 28‰ and were lowest at Stn 4A, the station closest to the coast south of the Miramichi Estuary (Fig. 2). Mean surface temperatures averaged between 7.2 and 10.9°C and in general were higher at stations on the southern transects sampled (Fig. 2).

Larval sampling

In general, we observed very low larval densities at most of the stations through time (Fig. 3). Along the 2 northern transects (1 and 2), we observed a considerable number of larvae only at the 2 stations close to the shore for the first sampling date (138.7 and 49.6 larvae m^{-3} for Stns 1A and 2A, respectively). Otherwise, larval densities were always <10 larvae m^{-3} . Along the transect at the mouth of the Miramichi Estuary, densities were always <1 larvae m^{-3} except for the first sampling date when they reached 28.2, 28.6 and 20.7 larvae m^{-3} for Stns 3A, B and C, respectively. On all of these 3 transects, cypris larvae never reached densities >0.8 larvae m^{-3} , and most of the time none were observed.

On the transects south of the mouth of the Miramichi Estuary, larval densities were always higher than on the northern transects. This north-south asymmetry in

larval densities was especially evident for cyprids. Along Transect 4, highest larval densities for all stations were observed on the 2 first sampling dates. Few cyprids were observed at Stn 4A on the second week of sampling (9.6 cyprids m^{-3}), and after, very low larval densities were observed (7.9 to 0.4 larvae m^{-3}), except on the last sampling date at Stn 4A. Transect 5 was the only one in which substantial numbers of cyprids were found, reaching 87.1 cyprids m^{-3} at Stn 5C in wk 3 of sampling. Finally, on the last week of sampling, we observed a second pulse of early nauplii at Stns 4A and 5A, suggesting a second spawning period.

Recruitment

Probably due to the intense lobster fishing in the area, 2 of the settlement structures were lost (Transects 2 and 4). At Stn 1, no larvae or spat were observed on any of the 9 arborite panels. At Stn 5, we observed a total of 48 recruits (177 recruits m^{-2}). These recruits had a mean rostro-carinal diameter of 1.67 mm (± 0.22 mm, $n = 13$) which corresponds to an age of 1 to 2 wk (Bourget et al. 1989). Recruitment on current-

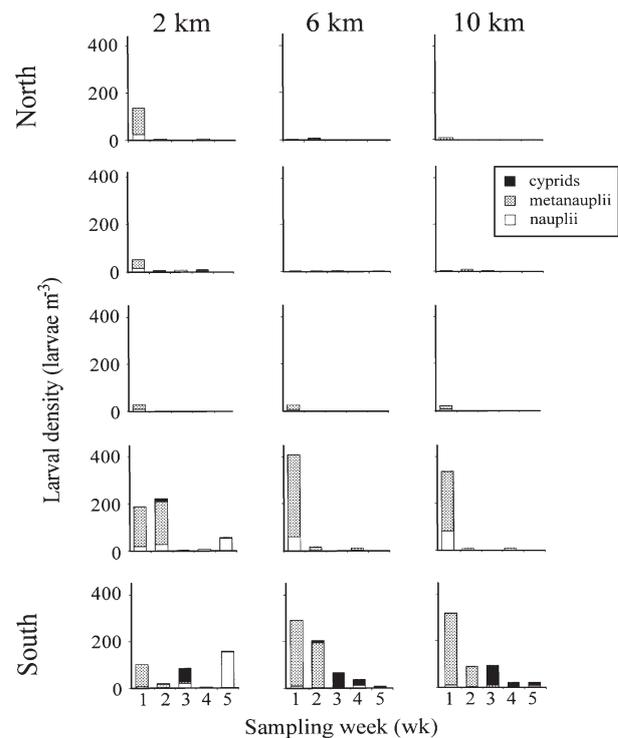


Fig. 3. *Semibalanus balanoides*. Density of planktonic larvae (larvae m^{-3}) for each sampling week (first, 4 May; last, 2 June 1998) near the mouth of the Miramichi Estuary, in the southern Gulf of St. Lawrence. Columns represent distances offshore and rows represent transects, from north to south (see Fig. 1)

Table 1. *Semibalanus balanoides*. Allelic frequencies for *MPI* and *GPI* for barnacles recruited onto panels (approx. 2 wk old). Lines 1 and 2 are results from Holm & Bourget (1994) for the same region. Line 4 represents the allele frequencies after we applied artificial selection of 100% against *GPI*4*

Source	n	<i>MPI*1</i>	<i>MPI*2</i>	<i>MPI*3</i>	n	<i>GPI*2</i>	<i>GPI*3</i>	<i>GPI*4</i>
North 1992	92	0.01	0.27	0.72	94	0.69	0.31	0.00
South 1992	91	0.00	0.48	0.52	94	0.55	0.45	0.00
Recruits 1998	46	0.03	0.36	0.61	48	0.53	0.24	0.23
After selection on <i>GPI*4</i>	28	0.02	0.38	0.61	28	0.71	0.29	0.00

meters moored at the middle stations of each transects reflected the above pattern since the currentmeter moored at Stn 5B was the only one to recruit barnacles.

Genetic analysis

We observed, for the *MPI** locus, 1 rare and 2 common alleles, labeled as 1, 2 and 3, based on their distance from the origin on the gel. For the *GPI** locus, 3 common alleles were found. They were labeled as 2, 3 and 4 as we did not find the rare allele 1 identified previously (Holm & Bourget 1994). Allelic frequencies on recruits are presented in Table 1 along with Holm & Bourget's (1994) results on adults for the closest north and south sampling stations. For *GPI*, we observed a third common allele, *GPI*4*. In Holm & Bourget (1994), this allele occurred only in newly settled individuals and at a very low frequency (0.019). Since this allele has never been reported on adults along the coast, we assumed strong selection against *GPI*4*. As a modeling exercise, we therefore applied artificial selection of 100% against *GPI*4* by excluding from analysis all individuals with this allele, and examined the other loci. Selection pressure did not affect allelic frequency for *MPI**, but for the *GPI** results were somewhat at odds with the expected values. Thus recruits had *GPI** frequencies comparable to the frequencies of the south population, and *MPI** frequencies intermediate between the north and south, which suggest recruitment from the 2 different populations. For *MPI**, the proportion of observed heterozygotes (H_o) were generally in a good agreement with values expected (H_e) under Hardy-Weinberg equilibrium before ($D = -0.096$, $p = 0.505$) and after selection ($D = -0.070$, $p = 0.623$). For *GPI**, we observed a significant deficit of heterozygosity both before ($D = -0.186$, $p = 0.038$) and after selection ($D = -0.484$, $p = 0.008$).

DISCUSSION

Our study examines whether larval exchange occurs between Gulf populations of *Semibalanus balanoides*

north and south of the Miramichi Estuary. Current directions suggested a north to south larval exchange. This hypothesis is also supported by larval distribution and genetic analysis.

Hydrodynamic structures

In the northern part of the study area, currents had a predominantly southward orientation. This pattern would favor unidirectional transport of larvae from the northern region to the southern region.

The orientation and stability of currents south of the Miramichi Estuary suggest the presence of an anticyclonic gyre at the entrance of the Northumberland Strait. Lauzier (1965) described a cyclonic gyre in the same region, but his results were based on drift bottles releases from fixed stations in the Strait and recoveries along the coast. The inferred circulation of the surface waters in the Northumberland Strait (as presented by Lauzier 1965) should be taken with care as the bottles may indicate surface circulation patterns under various weather conditions, a fact recognized by Lauzier (1965). Here, our results are based on *in situ* recordings of current directions and velocities over a long period. We observed higher surface temperature at the mouth of Northumberland Strait, which are also typical of an anticyclonic gyre.

Lower salinity observed at Stn 4A suggests that freshet from the Miramichi Estuary might flow south along the coast instead of directly offshore in the Gulf St. Lawrence.

Larval transport processes and recruitment

Larval densities are affected by the reproductive output of adults (Barnes 1956, 1962, Connell 1961, Geraci & Romairone 1982). In our study, low larval densities were observed through time. This is not too surprising since there is a lack of hard substrate available for colonization and consequently few adults are present, as a result therefore, a low number of larvae are spawned. An analogous situation was observed in

Portugal where the long sandy coast south of São Martinho do Porto proves a geographical barrier to marginal dispersion and thus limits the southern distribution of the barnacle *Elminius modestus* (Barnes & Barnes 1965).

The presence of larvae during the first sampling week on Transect 3, their disappearance from this and northern transects after, and their increase on southern transects with time suggests a north-south larval drift. Local current directions also support this hypothesis. High larval densities observed on southern transects suggest that larvae coming from the north are mixed with those originating from the south. The gyre occurring south of the Miramichi Estuary may cause larval retention and could help explain those higher densities observed in this region. In the past, gyres have often been associated with larval retention (Johnson 1960, 1971a,b, Knudsen 1960, Efford 1970, Alldredge & Hamner 1980, Kendall et al. 1982, Nichols et al. 1982, Yoshioka 1986).

For cypris, the observed densities were very low everywhere, but were found in greatest numbers along Transect 5, the only one where recruitment was observed on collectors (Stn 5A) and on current meters (Stn 5B).

Genetic origin of spat and selection on *GPI*4*

Genetic results obtained from the analysis of recruits at Stn 5A seem to support the hypothesis of larval mixing, as does larval densities and current analysis. For *MPI*2*, we observed an allele frequency intermediate between that observed in populations from the northern and southern Gulf of St. Lawrence (Holm & Bourget 1994) suggesting that larvae from both populations settled on our panels. The same results were obtained by Holm & Bourget (1994) with recruits from Shediac, approximately 100 km south of the Miramichi Estuary. However, the allelic frequency of *GPI*2* would suggest that recruits on panels originate mainly from the southern population. For *GPI** locus, the presence of a third relatively frequent allele (*GPI*4*, frequency of 0.23) is intriguing. This third allele was also observed by Holm & Bourget (1994) in recruits from Port Elgin (0.019) and Pictou (0.009), both situated south of Miramichi Estuary in the Northumberland Strait and was considered as a rare allele then. This allele was never observed in adults. In our study, *GPI*4* was not a rare allele. The recruits were obtained from panels which were continuously immersed. All other genetic analyses on *Semibalanus balanoides* in this region were obtained from adults or recruits sampled in the intertidal zone, thus exposed to emersion during low tides. Glucose-6-phosphate isomerase (GPI) is a catalyzing enzyme in the interconversion of glucose-6-phosphate and fructose-6-phosphate in

glucolysis and gluconeogenesis. The kinetic properties of different allele forms of *GPI** are well known to vary with temperature (Hoffmann 1981a, Hall 1985, Van Beneden & Powers 1989, Zamer & Hoffmann 1989). The latter factor also appears to be an important selective factor at the *GPI** locus in amphipods (Patarnello & Battaglia 1992), mussels (Hall 1985), sea anemones (Hoffmann 1981b), and fish (Van Beneden & Powers 1989). These results combined with those of our study suggest that temperatures experienced during emersion may be involved in the selection process. However, Schmidt & Rand (1999) found that GPI was neutral among thermal microhabitats for *S. balanoides*.

The *GPI*4* allele has never been found in adults of the intertidal. It is thus possible that selective pressure is exerted against that specific allele. Recruits studied by Holm & Bourget (1994) were collected about a month after settlement and had very low frequencies of *GPI*4*. In our study, recruits were collected 1 to 2 wk after settlement but were not submitted to desiccation and large temperature variations stress characteristic of the intertidal. *Semibalanus balanoides* is known to occur subtidally as well as tidally (Bousfield 1954, 1955, Bourget & Lacroix 1973). We hypothesize that the *GPI*4* allele will be present in a parental population that do not undergo those selective pressures from the intertidal zone, and we suggest that *GPI*4* must be frequent in barnacles from the subtidal zone. If this were the case, the former studies underestimated that recruitment source, which could explain the observed frequency of *GPI*4* over 20%.

It is not too difficult to determine what the frequency of *GPI*4* would have been if those barnacles settled on panels had been recruited to the intertidal zone, and had been subjected to a selective pressure of 100% on *GPI*4*. The allele frequency for *GPI*2*, which corresponded to the frequencies observed in the southern population before selection, was more characteristic of the northern population after the application of selective pressure (without *GPI*4*). These results need to be interpreted with caution, however, since the origin of larvae may be less clear than initially thought and there may be a substantial contribution to the larval pool of larvae of unknown genetic composition, from a subtidal population.

In the light of our results, gene flow from north to south appears to occur in the area studied. Our genetic results suggest that the divergence observed in the population must be maintained through strong selection. In addition, the presence of *GPI*4* suggests that an unknown adult source, possibly from the subtidal zone, could substantially contribute to the larval pool. Further work needs to establish (1) the contribution of subtidal barnacles to the larval pool and their importance in the larval exchange process, and (2) selective factors acting on newly settled recruits.

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