Large-scale ecological patterns: discontinuous distribution of marine benthic epifauna*

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ABSTRACT: Spatial distribution patterns of benthic littoral fauna were studied over a 12 yr period in a large subarctic ecosystem, the Estuary and northwestern Gulf of St. Lawrence. Binary presence-absence data obtained from suspended collectors (navigation buoys) moored yearly, from May through November, were used to examine ecological affinities and spatial heterogeneity in species distribution. Analyses of species co-occurrence followed by arithmetic average clustering, conducted at large (whole system, Gulf, Estuary) and intermediate (North Shore plus Lower North Shore) spatial scales, revealed a recurrent species association (composed of 12 species including *Obelia longissima*, *Mytilus edulis*, *Balanus crenatus*, *Hiatella arctica*, and *Semibalanus balanoides*) characterizing the entire Estuary-Gulf area. Frequency analyses carried out along 3 potential pathways of larval dispersal made it possible to identify major spatial discontinuities in species distribution as well as the community members contributing most to them. The outstanding changes in composition and distribution of benthic species throughout the study area were highly coincident with well-defined physiographical (e.g. presence of straits, islands, contour of shoreline) and hydrographical (e.g. zones of freshwater inputs, upwellings, frontal zones) features of the system, particularly along the estuarine gradient.

INTRODUCTION

Littoral benthos distribution responds to 2 principal axes of variability, the vertical axis (e.g. influence of hydrological factors, water column stability, food supply, and behavioural patterns on zonation of species) and the horizontal axis (e.g. hydrodynamic control of larval migration and transport of adult individuals with horizontal distance), even though in nature, interactions of both axes are usually observed (Underwood & Denley 1984, Mann 1986a, b, Possingham & Roughgarden 1990). While distribution along the vertical axis has been thoroughly studied on shores (e.g. zonation studies), few studies have dealt with discontinuities along ecological gradients in highly variable environments such as estuaries and shelves, except in general terms (Southward 1967, Sanders

1968, Kinne 1970, Wolff 1983). The present study, which is concerned only with the horizontal axis of variability, examines the composition and distribution of the littoral epibenthic community of a large subarctic ecosystem, the Estuary and northwestern Gulf of St. Lawrence. Our main objectives were (1) to determine the spatial affinities (co-occurrence) of species colonizing this area, (2) to characterize their distributional discontinuities, and (3) to identify the most relevant environmental factors responsible for these discontinuities. The size and physical heterogeneity of this system (see below) and collecting methods used allowed us to study the changes in composition and distribution of species under a large range of environmental conditions, in the absence of any direct influence of the vertical axis caused by the tidal emersion-immersion cycle.

Our focus was on benthic littoral species possessing planktonic larval stages, sampled on suspended collectors moored in open coastal waters within the surface 0 to 2 m depth layer. Therefore, discontinuities, such as observed here, are more likely to be associated with hydrodynamic singularities and physico-chemical

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characteristics of the water mass, rather than with topographic features of the bottom and shoreline. Furthermore, the limits of species distributions observed in this study may differ from those observed on shores. Thus, our approach should be viewed as a means of highlighting potential dispersal ranges rather than absolute limits of species distribution. Indeed, on shores, the environmental factors are certainly more constraining for survival and growth than those observed in the water column offshore.

STUDY AREA

The Estuary and Gulf of St. Lawrence is a coastal system located on the eastern seaboard of Canada, extending from about 46 to 52° N and from 56 to 73° W (Fig. 1A). It receives a large input of freshwater from the St. Lawrence River and other tributaries, and exchanges water, heat, and salt with the North Atlantic Ocean through 2 main openings: Cabot Strait and the Strait of Belle-Isle. The former is 104 km wide with a maximum depth of 480 m, while the latter has a minimum width of 16 km and a sill depth of 60 m (Dickie & Trites 1983).

On the basis of morphological and hydrographical characteristics (e.g. Brunel 1970, Neu 1970), the Estuary-Gulf system can be divided into 4 distinct regions (Fig. 1): (1) The Fluvial Estuary, the well-mixed freshwater portion of the St. Lawrence River under tidal influence, from Île d'Orléans up to Lake Saint-Pierre some 180 km upstream. (2) The Upper Estuary, from Île d'Orléans to the mouth of the Saguenay. Mixing of the freshwater outflow of the river with the saltwater intrusion is largely carried out in this portion of the system. This 150 km long region exceeds 50 m in depth only in few places. It is characterized by a seaward surface salinity gradient ranging from 0 to 25 ‰ (Lavoie 1970, Neu 1970), and a maximum turbidity zone located between Île d'Orléans and Île aux Coudres (Kranck 1979, Lucotte & d'Anglejan 1986). Maximum summer surface temperatures (20 °C) are found near Île d'Orléans, decreasing to 8 °C downstream near the mouth of the Saguenay (Vigeant 1987). (3) The Lower Estuary from the Saguenay Fjord down to Pointe-des-Monts on the north shore and Les Méchins on the south shore. This 200 km long channel expands from a depth of less than 40 m and a width of 24 km at the western end to a depth of 340 m and a width of 46 km at the eastern end where it opens into the Gulf. This area is characterized by surface salinities varying from 24 to 30 ‰ and a pronounced stratification in summer. The summer temperatures of the surface layer vary from 4 to 12 °C with a more pronounced north–south than east–west gradient (El-

Sabh 1979, Vigeant 1987, Petrie 1990). (4) The Gulf, seaward from the Pointe-des-Monts–Les Méchins axis. One of the main bathymetric features of this region is the Laurentian Channel (with 2 branches, the Esquiman and the Anticosti Channels), with an average depth of 420 m and stretching over 1000 km from the Atlantic Ocean (through Cabot Strait) up to the head of the Lower Estuary. It is characterized by surface salinities varying from 27 to 32 ‰ and a 3-layered summer temperature structure. The surface layer ranges in thickness from 10 to 30 m depending on the location and the month (Lauzier et al. 1957, Banks 1966). In the northwestern sector of the Gulf, the highest temperature values are observed in the Gaspé Peninsula
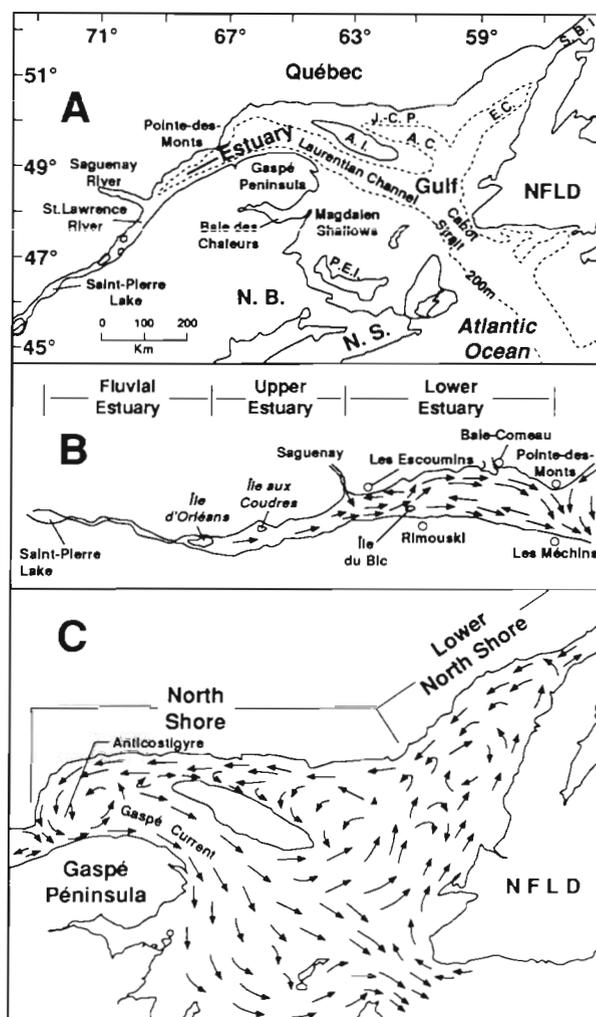

Fig. 1. The Estuary and Gulf of St. Lawrence. (A) Physiographic features; (B) summer surface circulation pattern in the Estuary (modified from El-Sabh 1977a); (C) summer surface circulation pattern in the Gulf (modified from El-Sabh 1976). S.B.I.: Strait of Belle-Isle; E.C.: Esquiman Channel; J.-C. P.: Jacques-Cartier Passage; A.C.: Anticosti Channel; A.I.: Anticosti Island

region (4 to 16 °C), intermediate values in both the western North Shore region (2 to 15 °C) and the Jacques-Cartier Passage (3 to 14 °C), and the lowest values in the Lower North Shore region (1 to 13 °C) (Vigeant 1987, Petrie 1990).

Water motion in the study area is maintained by runoff and other forcing factors such as tides, winds, heat fluxes, and geostrophy. In the Upper Estuary, the circulation pattern is based on a 2-layer flow system in which the lower more saline layer flows upstream while the upper fresher layer flows seaward. Under the influence of topography and geostrophy, the lower flow is deflected towards the north and the upper flow towards the south shore. The seaward flow is reinforced at the head of the Lower Estuary by the brackish outflow of the Saguenay Fjord and continues until it reaches the (Île du) Bic-Rimouski region. Here, the buoyant flow divides in 2 branches. One flows along the south shore and gives rise to the Gaspé Current, a strong coastal jet flowing seaward along the Gaspé Peninsula (Benoit et al. 1985, Mertz et al. 1988). The other flows northward across the Estuary and then divides in 2 further branches: one turns to the west and moves upstream off Les Escoumins, while the other moves seaward along the north shore. At the estuary-gulf boundary near Pointe-des-Monts, the influence of the cyclonic Anticosti gyre and the topography of the shoreline deflect this current towards the south coast where it mixes with the Gaspé Current (Neu 1970, El-Sabh 1979). This surface circulation pattern gives rise to 2 eddies: a large anti-cyclonic one centered between the mouth of the Estuary and Baie-Comeau, and a smaller cyclonic eddy between Rimouski and mouth of the Saguenay cross sections (El-Sabh et al. 1982, Mertz et al. 1989) (Fig. 1B). Another striking feature is the upwelling of cold waters from the deeper intermediate layer at the head of the Laurentian Channel. These waters have a strong impact both on the surface characteristics of this region and on the Gaspé Current transport (Ingram 1979, Bugden 1981).

In the Gulf the general surface circulation is counter-clockwise, with a 2-way flow in Cabot and Belle-Isle Straits (El-Sabh 1977a, Petrie et al. 1988). Several gyres, 20 to 100 km in diameter, occur in this area but their location and persistence vary appreciably, except for the Anticosti gyre which persists at all times. This cyclonic gyre, together with the density front formed at the entrance of the Gulf and the Gaspé Current, are the main features of the surface circulation in the western portion of the Gulf. The Gaspé Current remains a striking feature until it enters the open Gulf. It then spreads out in a general southeasterly direction and becomes weaker over the Magdalen Shallows. Part of this water is recirculated around the Gulf and

part exits to the Atlantic Ocean through Cabot Strait (El-Sabh 1976, Dickie & Trites 1983) (Fig. 1C). The northern portion of the Gulf receives considerable freshwater input from surrounding rivers and experiences episodic upwellings of cold waters, presumably induced by winds and tidal mixing (Lauzier et al. 1957, Steven 1974, Lacroix et al. 1985).

MATERIALS AND METHODS

Sampling of fauna. Navigation buoys, moored by Transport Canada from May through November of each year along shores of the Estuary and northwestern Gulf of St. Lawrence (Fig. 2), were used as collectors. The Estuary includes here the Lower and Upper Estuary as well as the lower hundred kilometres of the Fluvial Estuary. Sampling was carried out from 1974 to 1985 (except in 1978 and 1979), on up to 239 collectors per year. During winter the buoys were scraped and painted. The paint used contained no antifouling agents and, as a result, the buoys moored each spring had clean surfaces offering apparently little or no resistance to larval settlement. Throughout the annual 7 mo immersion period, the buoys were colonized by sessile organisms, presumably according to the relative abundance of their planktonic larvae. Since the buoys were moored and retrieved each year over short periods of time (about 2 wk), little or no seasonal differences in abundance among regions were introduced. The attached invertebrate fauna was sampled following the methods described in Fradette & Bourget (1980, 1981), Ardisson et al. (1990), and Ardisson & Bourget (1991). First, all macroscopic species observed on the buoys were collected and identified. Second, the species composition on each buoy was corroborated by examining a 0.01 m² quantitative sample obtained from the area of maximum abundance of each one of the following dominant species: the hydroid *Obelia longissima*; the bivalves *Hiatella arctica* and *Mytilus edulis*; and the cirripedes *Semibalanus balanoides*, and *Balanus crenatus*. The areas of maximum abundance were determined by visual inspection. Since the species distributions on the buoys were most often patchy, sampling the community in the areas of maximum abundance was the most practical way to obtain comparable data among buoys. The only alternative would have been to randomly select a large number of quadrats on each buoy, which would have generated an unmanageable number of samples.

Data analysis and underlying ecological models. The yearly presence-absence species data were used to identify the invertebrate associations in the area under study. Each year's binary data were assembled
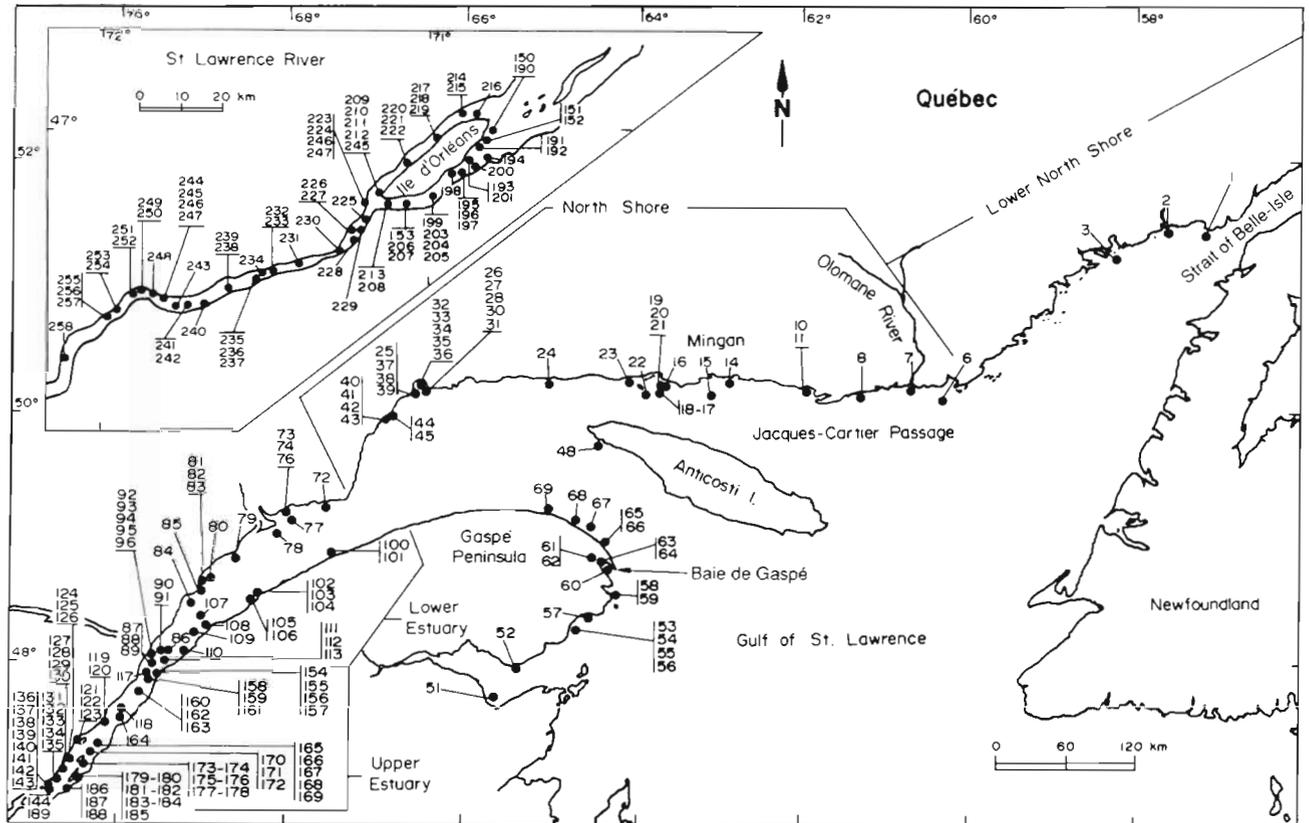
Fig. 2. Position of the sampling stations in the Estuary and northwestern Gulf of St. Lawrence

into a matrix of species × stations. The Fager &
McGowan (1963) coefficient of association S_{ab} (S_{24} in
Legendre & Legendre 1984) was then used to compute
pairwise similarities among all species. This coefficient
consists of the geometric mean of the proportion of
joint occurrences, corrected for sample size:

$$S_{ab} = \left[J_{ab}/(N_a N_b)^{1/2} \right] - \left[1/2 \, (N_b)^{1/2} \right]$$

where J_{ab} is the number of joint occurrences, N_a and N_b
are the total number of occurrences of species 'a' and
'b', and $N_b \geq N_a$. Pairs of species for which S_{ab} was
greater than 0.50 were considered to show positive
affinity for each other. The unweighted pair group
method of cluster analysis using arithmetic averages
(UPGMA; Rohlf 1963) was used to form groups within
which all species pairs showed positive affinity.
UPGMA was preferred to other agglomerative hierar-
chical methods because it gave the highest correlation
between the original similarities and the cophenetic
matrix (similarities implied by the dendrogram). Only
the independent groups of at least 3 related species
were considered as associations of species (Krylov
1968). In accordance with Venrick (1971), the species
not clustered but showing affinities with other species

within one or more groups were considered satellites
of those groups. In order to reduce the error of
perspective imposed by the spatial scale used in deter-
mining the invertebrate associations of species, 5 dif-
ferent geographic scales, from coarse to fine, were
examined: the whole system (Estuary and Gulf), the
Estuary and the Gulf regions taken separately, the
Gaspé Peninsula area, and the North Shore/Lower
North Shore area.

The presence-absence data were then used to show
the overall heterogeneity in species distribution at the
Estuary-Gulf system scale. Here, the yearly binary
data were assembled into 3 data matrices of species
× stations. Stations in the matrices were ordered to
form 3 one-dimensional spatial series of contiguous
collectors, parallel to the coast, representing 3 very
schematic potential pathways for dispersing species
(Fig 3). The first pathway (Model 1) corresponds to a
dispersal route following the counter-clockwise sur-
face water circulation bordering the Lower North
Shore, the North Shore and the Gaspé Peninsula. The
second pathway (Model 2) corresponds to a dispersal
route following the same circulation pattern along the
Lower North Shore and the North Shore, and then the
possible penetration of part of this water mass into the

intermediate layer flowing along the north coast of the Estuary. Finally, the third pathway (Model 3) corresponds to a route following the surface water outflow along the River, the south coast of the Estuary, and the Gaspé Peninsula. These potential pathways of dispersal for marine and freshwater species are based on the general circulation patterns of the surface and intermediate water layers of the Estuary-Gulf system (see section 'Study area' above). Since the sampling stations were spatially ordered along virtual lines (Fig. 2), the sequences of buoys along a series were of interest at large and intermediate spatial scales but irrelevant at a scale of tens of kilometres.

The spatial discontinuities in species distribution were determined by analyzing the 'optimal' locations where limits may be placed separating groups of contiguous stations along these virtual lines, in accordance with the method of Godron (1966). Thus, on a line composed of N stations and P presences of a species E, the number of combinations C of the N stations taken P at a time, assuming that each combination is equally probable, is computed as:

$$C_N^P = \frac{N!}{P!\,(N-P)!}$$

The uncertainty represented by the number of combinations gives a direct measure of the heterogeneity of the line with respect to the species E. Therefore, the amount of information H_t (measured in binons or bits), corresponding to knowing the exact position of each of the stations where the species occurs, is:

$$H_t = \log_2 C_N^P$$

Heterogeneity is nil when $P = 0$ or N, and maximum when $P = N/2$. From this, the limit value V for a particular station L situated on a line is given by:

$$V(L) = H_t - (H_g + H_d)$$

Here, H_g and H_d represent, respectively, the residual heterogeneity for the line fraction on the left and the right sides of the limit. After testing in this way for the limits of all the stations of the line, the average information for all species contained in the matrix was computed as Vm. The unbiased limit values of Vm (termed here Vr) were obtained by dividing each value of Vm by its individual mathematic expectancy (Ve). The sites of higher Vr values corresponded to the sites of higher overall heterogeneity and, consequently, to the 'optimal' limits between groups of stations along the considered line (Godron & Bacou 1975, Gauthier & Godron 1976).

Then we searched for the species whose first and last presence on the lines were statistically significant. According to Forman & Godron (1986), the information
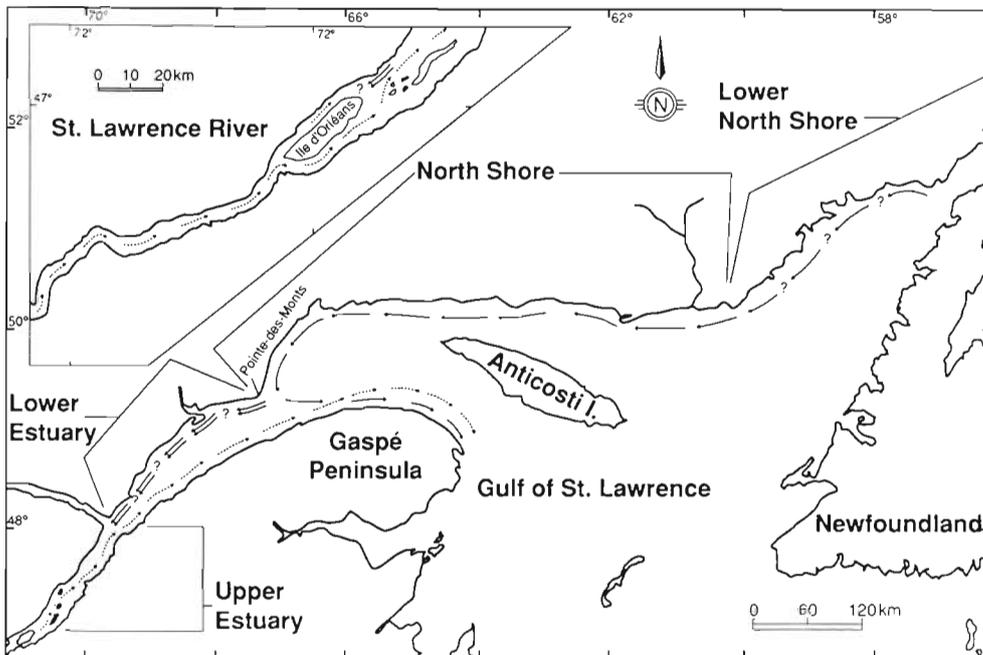

Fig. 3. Potential pathways for larval dispersal of marine and freshwater species, based on the general circulation patterns of the surface and intermediate water layers of the Estuary and northwestern Gulf of St. Lawrence. Model 1: continuous arrows; Model 2: continuous arrows up to Point-des-Monts plus double arrows up to the head of the Lower Estuary; Model 3: dotted arrows

I_d gained when observing a species first appearing in the Dth station along a line (the beginning) is obtained by computing:

$$I_d = H_t - \log_2 \frac{(N-D)!}{(P-1)!\,(N-D-P+1)!}$$

In the same way, the information I_f gained when observing that the end of a species is in station F along the line is:

$$I_f = H_t - \log_2 \frac{(F-1)!}{(P-1)!\,(F-P)!}$$

These calculations, computed for each of the species, allowed us to identify the species contributing most to the discontinuities observed on each line.

RESULTS

Frequency and species composition by subregion

Sampling of epibenthos on buoys yielded 68 invertebrate species (Table 1). Among these, there were 42 motile species from the taxa Gastropoda (10 species), Polychaeta (10), Isopoda (2), Amphipoda (12), Echinodermata (3), Pycnogonida (1), Decapoda (2) and Insecta (2), as well as 26 sessile species from the taxa Bryozoa (1), Hydroida (15), Bivalvia (5), and Cirripedia (5). Not all these species were continuously observed during the entire period of study. The number of species over all buoys fluctuated between 20 and 40 from year to year, with an average value of 31 species per year.

Among the species observed, only 13 (19 %, 6 motile and 7 sessile) were always present and more than half (57 %) were occasional or infrequent (present during 3 yr or less over a sampling period of 10 yr). Results given in Table 2 show that the more frequent a species was, the larger its geographic range of distribution.

Of the total number of species, 91 % were present in the Gulf whereas only 57 % were observed in the Estuary. At a smaller spatial scale, the largest number of species (51/68) was observed along the North Shore (Anticosti Island included), then along the Gaspé Peninsula (47/68). It should be stressed that the species observed in Anticosti Island waters (17/68) were also observed in the North Shore area and, excluding *Clytia hemisphaerica*, in the Gaspé Peninsula area as well. The Lower North Shore included less than half the species observed on the North Shore (22/68). Similarly, the Upper Estuary had half the species (16/68) observed in the Lower Estuary (32/68). Species richness on the north shore of the Estuary was about one third higher than that observed on the south shore. Finally, the number of species dropped to 6/68 in the Fluvial Estuary. The ranking of regions changed, however, when the average of the number of species present per buoy and region were estimated. From 2 to 13 species per buoy were observed in the Gulf, and from 0 to 10 in the Estuary. The largest average values were observed on the Gaspé Peninsula (8.0), the North Shore (7.2), Anticosti Island (7.0) and the Lower North Shore (6.9). The values dropped to 2.9 in the Lower Estuary, 0.9 in the Upper Estuary, and 0.2 in the River (Table 3).

The motile fauna represented 62 % of the total number of epibenthic species on the buoys. The number of species in the Gulf (38) was higher than that observed in the Estuary (23). Species richness by subregion closely followed the pattern outlined above for the total fauna. Three groups of organisms – Gastropoda, Polychaeta and Amphipoda – dominated the motile fauna (frequency between 79 and 95 %, depending on years). The gastropod *Lacuna vincta*, the polychaetes *Lepidonotus squamatus*, *Nereis pelagica* and *Phyllodoce maculata*, and the amphipods *Calliopius laeviusculus*, *Caprella septentrionalis*, *Ischyrocerus anguipes* and *Pontogeneia inermis* were the most frequent species both in the Gulf and in the Estuary. On the other hand, the gastropod *Acmaea testudinalis*, the amphipods *Gammarus oceanicus*, *Gammarus tigrinus* and *I. anguipes*, and the larvae of the insects *Ephemerella* sp. and *Hydropsyche recurvata* were the only species observed in the Fluvial Estuary. Whereas *Ephemerella* sp. was confined to the River, *H. recurvata* was observed in the Upper Estuary as well. No more than 20 % of the buoys moored in the River (n = 75) were colonized by motile fauna each year.

As for the motile fauna, the largest number of sessile species was observed in the Gulf (24), then in the Estuary (16). From these, the North Shore (Anticosti Island included) held the largest number of species (20), followed by the Gaspé Peninsula (18). Numbers dropped to 14 species in the Lower Estuary, and 11 species in the Lower North Shore region. Only 8 species were observed in the Upper Estuary and none in the River.

Limits of distribution of the recurrent sessile fauna

The recurrent sessile fauna (the sessile fauna present on buoys during the entire period of study) was largely distributed in the Gulf and to a lesser degree in the Estuary. However, distribution ranges differed among species (Fig 4). *Mytilus edulis* and *Balanus crenatus* were observed on all buoys moored in the Gulf and on about one third of those moored in the Upper and Lower Estuary. The frequency of observation of *Semibalanus balanoides*, *Obelia longissima* and *Hiatella arctica* on buoys ranged between 90 and 97 % for the

Table 1 Species composition of the Estuary and Gulf of St. Lawrence epibenthic fauna observed on the buoys during the period 1974 to 1985

Motile species
Mollusca: Gastropoda
  Acmaea testudinalis (O. F. Müller, 1776)
  Dendronotus frondosus (Ascanius, 1774)
  Doto coronata (Gmelin, 1791)
  Lacuna pallidula neritoidea Gould, 1840
  Lacuna vincta (Montagu, 1803)
  Littorina littorea (Linnaeus, 1758)
  Littorina obtusata (Linnaeus, 1758)
  Margarites helicinus (Phipps, 1774)
  Mitrella rosacea (Gould, 1841)
  Nudibranchiata[a]

Annelida: Polychaeta
  Autolytus cornutus Agassiz, 1863
  Harmothoe extenuata (Grube, 1840)
  Harmothoe imbricata (Linnaeus, 1767)
  Lepidonotus squamatus (Linnaeus, 1766)
  Nereis pelagica (Linnaeus, 1758)
  Paranaites speciosa (Webster, 1880)
  Pholoe sp.
  Phyllodoce maculata (Linnaeus, 1767)
  Spirorbis sp.
  Terebellidae[a]

Crustacea: Isopoda
  Idothea phosphorea (Harger, 1873)
  Jaera marina (Fabricius, 1780)

Crustacea: Amphipoda
  Aeginina longicornis (Kröyer, 1842)
  Calliopius laeviusculus (Kröyer, 1838)
  Caprella linearis (Linnaeus, 1758)
  Caprella septentrionalis Kröyer, 1838
  Gammarellus angulosus (Rathke, 1843)
  Gammarellus homari (J. C. Fabricius, 1779)
  Gammarus oceanicus Segestrale, 1947
  Gammarus tigrinus Sexton, 1939
  Ischyrocerus anguipes Kröyer, 1838
  Jassa falcata (Montagu, 1808)
  Metopa sp.
  Pontogeneia inermis (Kröyer, 1838)

Echinodermata
  Asterias vulgaris Verril, 1866
  Ophiura robusta (Ayres, 1851)
  Strongylocentrotus droebachiensis (O. F. Müller, 1776)

Pycnogonida
  Phoxichilidium femoratum (Rathke)

Crustacea: Decapoda
  Cancer irroratus (Say, 1817)
  Hyas sp.

Insecta
  Ephemerella sp.
  Hydropsyche recurvata (Banks, 1914)

Sessile species
Bryozoa[a]

Hydroida
  Abietinaria abietina (Linnaeus, 1758)
  Bougainvillia sp.
  Callycella syringa (Linnaeus, 1767)
  Campanularia integra (Macgillivray, 1842)
  Clytia hemisphaerica (Linnaeus, 1767)
  Eulaomeda sp.
  Halecium sp.
  Hydrallmania falcata (Linnaeus, 1758)
  Obelia dichotoma (Linnaeus, 1758)
  Obelia geniculata (Linnaeus, 1758)
  Obelia longissima (Pallas, 1766)
  Opercularella lacerata (Johnston, 1847)
  Rhizocaulus verticillatus (Linnaeus, 1758)
  Sertularia cupressina (Linnaeus, 1758)
  Tubularia larynx (Ellis & Solander, 1786)

Mollusca: Bivalvia
  Anomia aculeata (O. F. Müller, 1776)
  Hiatella arctica (Linnaeus, 1767)
  Mesodesma arctatum (Conrad, 1831)
  Mya arenaria Linnaeus, 1758
  Mytilus edulis Linnaeus, 1758

Crustacea: Cirripedia
  Semibalanus balanoides (Linnaeus, 1766)
  Balanus balanus (Linnaeus, 1758)
  Balanus crenatus (Bruguière, 1789)
  Balanus improvisus (Darwin, 1854)
  Lepas anatifera (Linnaeus, 1758)

[a] One species only

Gulf and between 8 and 27 % for the Estuary. On the other hand, *Tubularia larynx* and *Obelia geniculata* were observed on about 50 % of the buoys in the Gulf and < 6 % of the buoys in the Estuary.

The northeastern distribution for all the species except *Tubularia larynx* extended up to the limit of the sampling area in the Strait of Belle-Isle (Figs. 2 & 4). While all species were well distributed in the Gaspé Peninsula waters, their inner limit within the Estuary varied depending on species. *Mytilus edulis* exhibited the largest distribution range. It extended upstream

as far as the eastern tip of Île d'Orléans (47° 01' N, 70° 46' W). In decreasing order, *Hiatella arctica* and *Obelia longissima* were, respectively, observed in the neighbouring areas of Sault-au-Cochon (47° 12' N, 70° 36' W) and Cap Maillard (47° 16' N, 70° 35' W) on the north shore of the Upper Estuary. *Balanus crenatus* was well represented in the area surrounding Île aux Coudres. Their inner position in the Estuary was 49° 20' N, 70° 17' W. The limit of *Obelia geniculata* in the Estuary was the mouth of the Saguenay Fjord (48° 08' N, 69° 36' W). Downstream, *Semibalanus balanoides* was

Table 2. Distribution of the Estuary and Gulf of St. Lawrence epibenthic fauna observed on buoys during the period 1975 to 1985. Species are ordered by class of frequency. WNS: Western North Shore; MR: Mingan region; ENS: Eastern North Shore; LNS: Lower North Shore; AI: Anticosti Island; NGP: Northern Gaspé Peninsula; SGP: Southern Gaspé Peninsula; ——: range of distribution of species

Yearly frequency for 10 yr	Taxa	Estuary					Gulf						
		River	Upper South	Upper North	Lower South	Lower North	WNS	MR	ENS	LNS	AI	NGP	SGP
1	Littorina littorea					—							
	Mitrella rosacea												—
	Pholoe sp.						—						
	Spirorbis sp.						—						
	Terebellidae						—						
	Jaera marina		—										
	Cancer irroratus												—
	Hyas sp.							—					
	Abietinaria abietina											—	
	Eulaomeda sp.					—							
	Halecium sp.						—						
	Hydrallmania falcata											—	
	Rhizocaulus verticillatus							—					
2	Dendronotus frondosus						———————			—			
	Doto coronata						————						—
	Lacuna pallidula							————					
	Littorina obtusata			—			—						
	Margarites helicinus								—				—
	Autolytus cornutus				————								
	Harmothoe extenuata						—						—
	Paranaites speciosa												—
	Aeginina longicornis											——	
	Caprella linearis											———	
	Gammarus tigrinus	————											
	Jassa falcata						—						—
	Ophiura robusta						—						
	Phoxichilidium femoratum											—	
	Ephemerella sp.	—											
	Hydropsyche recurvata	————											
	Bougainvillia sp.			——									
	Callycela syringa				—		—						
	Clytia hemisphaerica						———————						
	Obelia dichotoma	————					—		—			—	
	Sertularia cupressina											—	
	Mesodesma arctatum					————						—	
	Mya arenaria					————						—	
	Balanus balanus						———————						—
	Balanus improvisus									—			—
	Lepas anatifera						—						
4–5	Idothea phosphorea		—				—						
	Gammarellus angulosus		—				—		————			—	
	Gammarellus homari		—				—	—				————	
	Metopa sp.								—	—		—	
	Campanularia integra		—					—		—			
	Opercularella lacerata		———————						—				
	Anomia aculeata						———————						—

Table 2 (continued)

Yearly frequency for 10 yr	Taxa	Estuary					Gulf						
		River	Upper south	Upper north	Lower south	Lower north	WNS	MR	ENS	LNS	AI	NGP	SGP
6–9	Acmaea testudinalis												
	Harmothoe imbricata												
	Caprella septentrionalis												
	Gammarus oceanicus												
	Ischyrocerus anguipes												
	Pontogeneia inermis												
	Asterias vulgaris												
	Stronglylocentrotus droebachiensis												
	Bryozoa												
10	Lacuna vincta												
	Nudibranchiata												
	Lepidonotus squamatus												
	Nereis pelagica												
	Phyllodoce maculata												
	Calliopius laeviusculus												
	Obelia geniculata												
	Obelia longissima												
	Tubularia larynx												
	Hiatella arctica												
	Mytilus edulis												
	Semibalanus balanoides												
	Balanus crenatus												

Table 3. Species richness of the Estuary and Gulf of St. Lawrence epibenthic fauna observed on buoys during the period 1974 to 1985. Numbers in normal print represent numbers of species present in a given region. **Boldface** numbers indicate total numbers of different species present in the region indicated by a given bracket

Species	Estuary					Gulf			
	River	Upper South	Upper North	Lower South	Lower North	Gaspé Pen.	Anticosti Is.	North Shore	Lower North Shore
Motile	6	6	6	13	17	29	9	31	11
		8		**18**			**31**		
			23					**38**	
Sessile	0	4	8	9	12	18	8	20	11
		8		**14**			**20**		
			16					**24**	
Total	6	10	14	22	29	47	17	51	22
		16		**32**			**51**		
			39					**62**	
Average no. of species per buoy and region	0.2	1.0	0.9	2.8	3.0	8.0	7.0	7.2	6.9
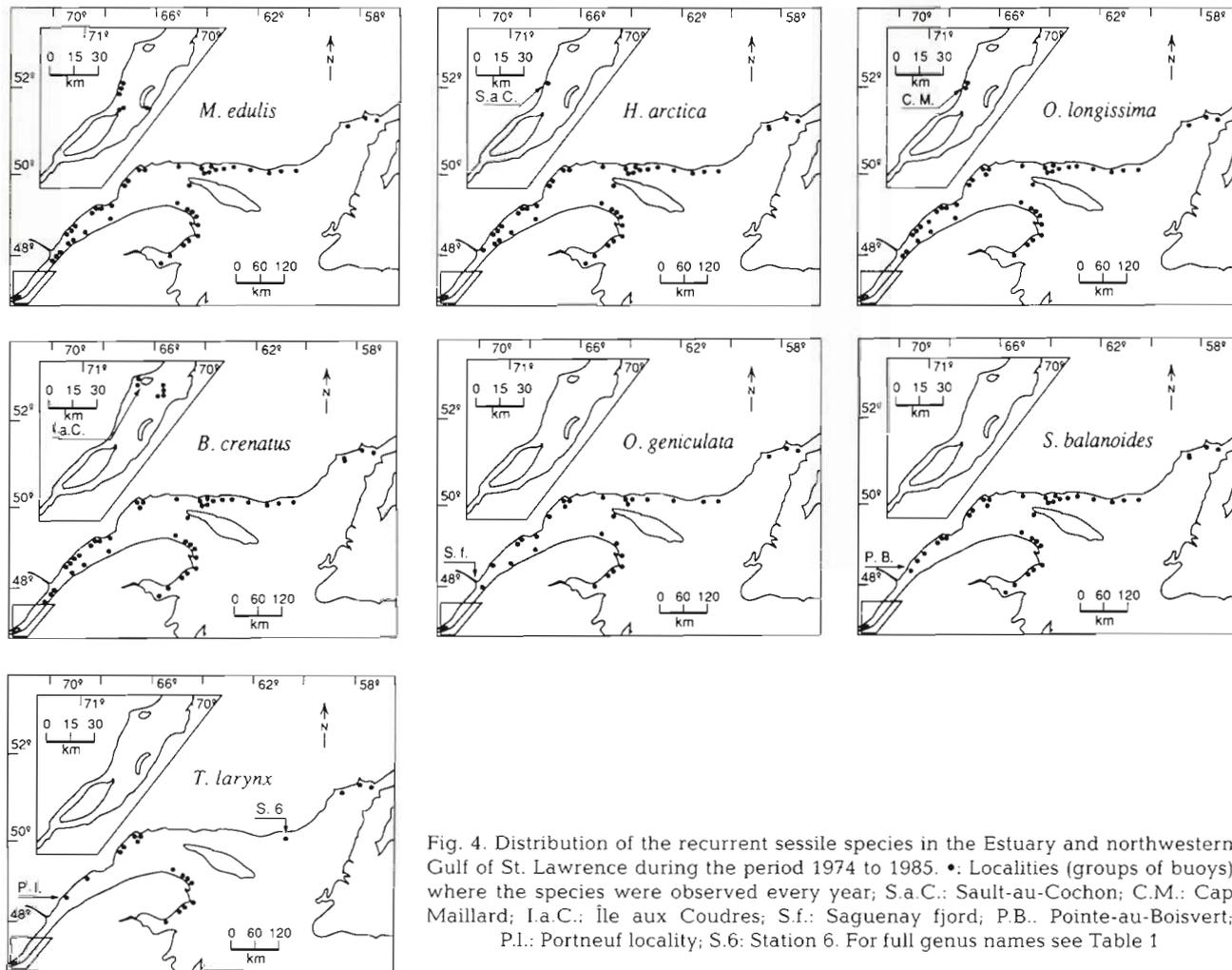
Fig. 4. Distribution of the recurrent sessile species in the Estuary and northwestern Gulf of St. Lawrence during the period 1974 to 1985. •: Localities (groups of buoys) where the species were observed every year; S.a.C.: Sault-au-Cochon; C.M.: Cap Maillard; I.a.C.: Île aux Coudres; S.f.: Saguenay fjord; P.B.: Pointe-au-Boisvert; P.l.: Portneuf locality; S.6: Station 6. For full genus names see Table 1

observed near Pointe-au-Boisvert, south of Portneuf (48° 33' N, 69° 07' W). *T. larynx* had the narrowest distributional range of all these species; it extended from Station 6 (50° 07' N, 60 °19' W), on the North Shore, to Portneuf (48° 44' N, 68 °58' W) in the Lower Estuary.

Species associations

At the whole system spatial scale, the major group of co-occurring species was composed of 17 species, among which 12 were grouped at $S > 0.50$ and 5 others were satellite species linked at lower similarity levels (Table 4). *Obelia longissima*, *Mytilus edulis*, *Balanus crenatus*, *Hiatella arctica*, *Semibalanus balanoides*, *Ischyrocerus anguipes* and *Lacuna vincta* frequently grouped together, whereas *Lepidonotus squamatus*, *Nereis pelagica*, *Calliopius laeviusculus*, *Phyllodoce maculata* and the nudibranch species either were not present or were satellite species during at least half of the 10 yr period. Although individual species were not

always present from year to year, the same basic species group persisted in time. Analyses carried out at the intermediate geographic scale (region) yielded about the same basic group, although some changes in species composition were observed (Table 5). At this spatial scale, the number of species tended to decrease due to reduced affinities of particular species with the other members of the group. For instance, *S. balanoides* became a satellite species only when it was viewed at the Gaspé Peninsula scale. Also, these analyses showed individual species joining the epibenthic association only in some particular regions of the study area, e.g. *Harmothoe imbricata* in the North Shore/Lower North Shore area, or *Acmaea testudinalis*, *Eulaomeda* sp., and *Autolytus cornutus* in the Estuary area (Table 5). A secondary group (association), observed only in 1981 at the large spatial scale (Table 4), was formed by *Obelia geniculata*. *Anomia aculeata* and *S. balanoides*, with *Tubularia larynx* as satellite species. Along the temporal axis, the yearly variation in species composition of the main epibenthic group at all but the Estuary scale,

Table 4. Yearly species composition of the main epibenthic group formed at $S > 0.50$ (Fager and McGowan's index of association), viewed at large (Estuary and Gulf) geographic scale. (+) Present; (−) not observed; (s) satellite species (linked at similarity levels ≤ 0.50); (&) secondary group (members of the second association)

Species	Year									
	1974	1975	1976	1977	1980	1981	1982	1983	1984	1985
Obelia longissima	+	+	+	+	+	+	+	+	+	+
Mytilus edulis	+	+	+	+	+	+	+	+	+	+
Balanus crenatus	+	+	+	+	+	+	+	+	+	+
Hiatella arctica	+	+	+	+	+	+	+	+	+	+
Semibalanus balanoides	+	+	+	+	+	&	+	+	−	+
Ischyrocerus anguipes	−	+	s	−	+	+	+	+	+	+
Lacuna vincta	s	−	+	+	+	+	+	+	+	+
Nudibranchiata	−	−	s	s	+	+	+	+	s	s
Lepidonotus squamatus	s	−	s	s	+	−	−	s	+	s
Nereis pelagica	−	s	s	s	−	−	+	+	−	s
Calliopius laeviusculus	s	s	s	−	s	s	+	+	s	+
Phyllodoce maculata	−	−	−	s	−	−	s	s	−	+
Caprella septentrionalis	−	−	−	−	−	−	−	s	−	s
Dendronotus frondosus	−	s	−	−	−	−	−	−	−	−
Tubularia larynx	−	−	−	s	−	&	s	s	s	−
Harmothoe imbricata	−	−	−	−	−	−	s	−	−	s
Obelia geniculata	−	−	−	−	−	&	−	s	−	−

Table 5. Changes in species composition of the main epibenthic group formed at $S > 0.50$ (Fager and McGowan's index of association) during the period 1974 to 1985, when viewed at different geographic scales. (+) Present; (−) not observed; (s) satellite species (linked at similarity levels ≤ 0.50)

Species	Geographic scale				
	Estuary and Gulf	Gulf	Estuary	Gaspé Peninsula	North Shore/ Lower North Shore
Obelia longissima	+	+	+	+	+
Mytilus edulis	+	+	+	+	+
Balanus crenatus	+	+	+	+	+
Hiatella arctica	+	+	+	+	+
Semibalanus balanoides	+	+	+	s	+
Ischyrocerus anguipes	+	+	+	+	+
Lacuna vincta	+	+	s	+	+
Nudibranchiata	+	+	+	s	+
Lepidonotus squamatus	+	+	−	+	+
Nereis pelagica	+	+	s	+	+
Calliopius laeviusculus	+	+	s	+	+
Phyllodoce maculata	+	+	s	+	s
Asterias vulgaris	−	−	−	+	−
Harmothoe imbricata	−	−	−	−	+
Caprella septentrionalis	s	s	−	s	s
Dendronotus frondosus	s	s	−	−	−
Tubularia larynx	s	s	−	s	s
Obelia geniculata	s	s	−	s	s
Anomia aculeata	−	s	−	−	s
Acmaea testudinalis	−	−	s	−	−
Eulaomeda sp.	−	−	s	−	−
Autolytus cornutus	−	−	s	−	−
Doto coronata	−	−	−	s	−
Bryozoa	−	−	−	s	−
Caprella linearis	−	−	−	s	−
Gammarellus homari	−	−	−	s	−
Gammarellus angulosus	−	−	−	−	s
Mya arenaria	−	−	−	−	s
Obelia dichotoma	−	−	−	−	s

followed closely the picture shown in Table 4. In the Estuary area (not shown), the number of species taking part in the species association for particular years was very low and no association between them was observed in 1977, 1981, and 1983.

Spatial heterogeneity in species distribution

During the period 1974 to 1985, the major breakpoints (Vr) along a given line (Models 1 to 3) did not always occur at the same locations. Further, the relative importance of these discontinuities was highly variable across years (Fig. 5). For instance, in 1977 (Fig. 5, Model 1) the most heterogeneous site corresponded to Station 42 (1.6 binons) whereas in 1983 (same model) the most heterogeneous one corresponded to Station 69 (2.2 binons). Indeed, the precise heterogeneity between each pair of stations depended on the heterogeneity of the entire line, the latter being in turn a function of the number of stations and species considered each year.

These discontinuities occurred at locations where several species appeared and disappeared abruptly each year (Table 6). Overall, results in Fig. 5 and Table

Model 1

Station number

1974   2 14 20 27 38 41 44 69 67 64 62 57 52 (↓1.4 ↓1.2)
       7 18 21 28 39 43 45 68 65 63 58 53

1975   1 7 10 19 21 26 28 38 40 42 45 68 64 62 54 (↓1.3 ↓1.6 ↓1.7 ↓1.5)
       2 8 15 20 23 27 34 39 41 43 69 66 63 58 53

1976   1 3 7 10 15 21 23 26 29 39 40 42 44 65 63 54 51 (↓1.3 ↓1.6 ↓1.7)
       2 6 8 14 20 22 25 27 30 39 41 43 68 64 57 53

1977   3 7 10 15 21 25 27 30 34 41 43 48 66 64 57 53 (↓1.4 ↓1.6)
       6 8 14 20 23 26 28 31 38 42 45 68 65 63 54 52

1980   1 3 7 10 15 21 23 25 27 30 36 38 42 44 48 66 63 54 52 (↓1.5 ↓1.7)
       2 6 8 14 20 22 24 26 28 31 37 39 43 45 68 64 57 53

1981   1 6 8 14 20 22 24 26 28 31 37 39 43 45 68 65 63 54 52 (↓1.5 ↓1.5 ↓1.6 ↓1.5)
       3 7 10 15 21 23 25 27 30 36 38 42 44 48 66 64 57 53

1982   1 6 8 15 18 21 23 26 28 31 36 38 42 44 (↓1.7)
       2 7 10 17 20 22 25 27 30 34 37 39 43 45

1983   1 3 7 10 14 16 20 22 24 26 28 31 33 35 38 42 44 48 68 66 64 61 57 55 53 (↓1.5 ↓1.5 ↓1.7 ↓2.2 ↓1.1)
       2 6 8 11 15 17 21 23 25 27 30 32 34 36 39 43 45 69 67 65 63 58 56 54 52

1984   16 18 21 24 26 28 31 36 39 43 45 69 67 65 63 60 58 56 54 52 (↓1.4 ↓1.4 ↓1.4 ↓1.4)
       17 21 23 25 27 30 35 37 42 44 48 68 66 64 61 59 57 55 53

1985   2 6 8 21 23 25 27 30 36 38 42 44 69 67 64 61 58 54 52 (↓1.9 ↓1.9 ↓1.5)
       3 7 20 22 24 26 28 31 37 39 43 48 68 66 63 60 57 53 51

Model 2

Station number

1974   2 14 20 27 38 41 44 77 79 84 (↓1.5 ↓1.2)
       7 18 21 28 39 43 45 78 82

1975   1 7 10 19 21 26 28 38 40 42 45 79 121 137 140 142 144 (↓1.6 ↓1.9 ↓3.3)
       2 8 15 20 23 27 34 39 41 43 77 93 131 138 141 143

1976   1 3 7 10 15 21 23 26 28 38 40 42 44 73 77 79 83 130 226 (↓1.5 ↓2.4)
       2 6 8 14 20 22 25 27 30 39 41 43 72 74 78 80 84 132

1977   3 7 10 15 21 25 27 30 34 41 43 74 129 (↓1.3)
       6 8 14 20 23 26 28 31 38 42 45 84

1980   1 3 7 10 15 21 23 25 27 30 36 38 42 44 74 78 80 90 88 212 257 (↓4.0 ↓3.3 ↓2.2)
       2 6 8 14 20 22 24 26 28 31 37 39 43 45 77 79 84 91 122 147

1981   1 6 8 14 20 22 24 26 28 31 37 39 43 45 77 79 84 95 90 (↓2.1 ↓2.1 ↓2.4 ↓2.7 ↓2.5)
       3 7 10 15 21 23 25 27 30 36 38 42 44 74 78 80 91 93 92

1982   1 6 8 15 18 21 23 26 28 31 36 38 42 44 73 77 79 81 83 90 96 126 128 132 136 140 (↓3.1 ↓3.7 ↓3.0)
       2 7 10 17 20 22 25 27 30 34 37 39 43 45 74 78 80 82 85 91 122 127 129 135 138 143

1983   1 3 7 10 14 16 20 22 24 26 28 31 33 35 38 42 44 72 74 78 80 91 121 126 128 P Y (↓1.6 ↓4.2 ↓4.4 ↓4.0 ↓3.7)
       2 6 8 11 15 17 21 23 25 27 30 32 34 36 39 43 45 73 77 79 84 118 122 127 129 W

1984   16 18 21 24 26 28 31 36 39 43 45 73 77 79 84 95 127 129 226 (↓1.6 ↓3.0 ↓2.4)
       17 21 23 25 27 30 35 37 42 44 72 74 76 80 91 88 126 226

1985   2 6 8 21 23 25 27 30 36 38 42 44 73 77 79 85 91 87 126 128 211 224 225 229 241 256 (↓1.6 ↓3.9 ↓4.5 ↓3.8 ↓3.0)
       3 7 20 22 24 26 28 31 37 39 43 72 74 78 80 80 95 122 127 129 210 223 226 243 248

Model 3

Station number

1974   150 163 157 68 64 62 54 (↓1.7 ↓1.8)
       181 160 69 66 63 58 53

1975   226 107 65 63 54 51 (↓1.9)
       166 68 64 57 53

1977   160 157 100 66 64 57 53 (↓2.7 ↓1.7)
       158 109 68 65 63 54 52

1980   257 152 160 105 105 66 63 54 52 (↓2.2)
       183 163 159 102 68 64 57 53

1981   160 157 109 107 66 64 57 53 (↓1.9)
       158 111 102 68 65 63 54 52

1983   183 177 172 171 167 165 163 159 157 105 104 102 69 67 65 63 58 56 54 52 (↓1.7 ↓4.2 ↓1.7)
       179 176 177 169 166 164 160 158 155 105 103 101 68 66 64 61 57 55 53

1984   225 187 182 177 175 135 155 104 102 69 67 65 62 60 58 56 54 52 (↓3.7 ↓3.3)
       226 184 179 176 173 158 154 103 101 68 66 64 61 59 57 55 53

1985   256 247 228 225 224 206 207 109 107 105 103 101 68 66 63 60 57 53 51 (↓3.2 ↓4.0)
       248 243 226 223 213 208 158 106 106 104 102 69 67 64 61 58 54 52

Fig. 5. Major yearly discontinuities along lines (models) 1, 2, and 3. Horizontal series of numbers represent contiguous stations (contiguous stations were arranged in top and bottom rows only to diminish the length of the lines); arrows point to stations where the optimal limits were found; values associated with the vertical arrows indicate the amount of information (binons or bits) corresponding to each major discontinuity. Number of buoys sampled varied from year to year

Table 6. Statistically significant cuts (beginnings and ends of species distributions) near areas of major heterogeneity. Significant beginnings and ends at a threshold of 0.05 (> 4.3 binons) are indicated by left and right brackets, respectively. For full genus names see Table 1

Station	Year	Species
Model 1		
6	1983	[L. anatifera], A. aculeata]
8	1975	[I. anguipes
	1981	[Hyas sp.]
	1985	[Nudibranchiata, [S. balanoides, [L. vincta, [B. crenatus, [H. arctica
14	1983	[N. pelagica
21	1975	[N. pelagica, G. oceanicus]
23	1984	[M. arenaria, [N. pelagica, [T. larynx
	1985	[M. arctatum, [S. droebachiensis, [H. imbricata, [L. squamatus, [N. pelagica, [T. larynx, C. hemisphaerica]
24	1983	[M. arenaria, [L. squamatus, [T. larynx
25	1976	[L. squamatus
	1977	[Nudibranchiata
	1980	[P. maculata, [G. angulosus, [T. larynx, [L. squamatus
	1981	[N. pelagica, [L. squamatus, [T larynx
	1982	[A. cornutus, [C. syringa, [H. imbricata, [T larynx, [N. pelagica, [P. maculata
42	1977	[S. droebachiensis], H. imbricata], Spirorbis sp.]
	1984	[Bryozoa], [S. droebachiensis, [O. lacerata, [G. angulosus, [P. maculata
68	1976	C. laeviuculus]
	1981	[C. linearis], G. homari]
	1985	[A. longicornis, [A. vulgaris, O. lacerata], P. inermis]
69	1974	[Nudibranchiata, [P. maculata, L. squamatus]
	1975	[G. homari, [L. squamatus, C. septentrionalis]
	1983	[C. linearis], [O. robusta], [S. cupressina], [P. femoratum], S. balanoides]
60	1984	C. septentrionalis], G. oceanicus], P. inermis], A. vulgaris], M. arenaria]
63	1975	[A. vulgaris, Bryozoa]
66	1980	G. angulosus], Metopa sp.], P. inermis]
54	1976	[H. extenuata
	1983	[S. droebachiensis], B. improvisus]
57	1974	[J. falcata
	1981	[H. imbricata], O. longissima]
	1984	[H. imbricata, C. laeviusculus], O. lacerata]
Model 2		
6	1983	[L. anatifera], A. aculeata]
8	1975	[L. palidulla]
	1981	[Hyas sp.]
14	1976	[D. coronata, [H. imbricata
18	1974	I. anguipes]
23	1975	[M. helicinus], [N. pelagica
	1984	[P. inermis]
	1985	[H. imbricata, [S. droebachiensis, [N. pelagica, [G. oceanicus, C. hemisphaerica]
25	1981	[N. pelagica, [L. squamatus, [T. larynx, P. maculata], C. septentrionalis], G. homari]
43	1981	I. anguipes], Bryozoa], L. squamatus]], L. vincta], Nudibranchiata], A. aculeata], S. balanoides]
73	1983	M. arenaria], L. vincta], O. geniculata]
74	1980	[A. testudinalis, [Eulaomeda sp., J. falcata], T. larynx], C. laviusculus], O. longissima], L. squamatus], L. vincta], M. edulis]
	1981	C. laeviuculus], O. geniculata]
	1982	[S. droebachiensis], L. squamatus], H. imbricata], L. vincta], O. geniculata]

Table 6 (continued)

Station	Year	Species
77	1974	*L. vincta*], *S. balanoides*]
78	1984	*O. lacerata*], *M. arenaria*], *H. arctica*]
	1985	[*A. cornutus*], *S. droebachiensis*], *L. vincta*], Nudibranchiata], *L. squamatus*]
83	1976	*H. arctica*], *S. balanoides*], *B. crenatus*]
	1982	*P. inermis*], *M. edulis*], *P. maculata*], *C. laeviusculus*], Nudibranchiata], *N. pelagica*], *I. anguipes*]
84	1981	*H. arctica*], *B. crenatus*]
90	1980	Nudibranchiata], *H. arctica*]
91	1983	Nudibranchiata], *O. longissima*], *M. edulis*]
	1985	*O. geniculata*], *C. septentrionalis*], *P. maculata*] , *I. anguipes*], *O. longissima*], *S. balanoides*]
93	1975	*C. septentrionalis*], *I. anguipes*], *H. arctica*]
121	1983	*C. laeviusculus*]
122	1980	*B. crenatus*]
	1985	[*C. integra*], *I. phosphorea*], *C. laviusculus*], *B. crenatus*]
126	1983	[*Bougainvillia* sp.
127	1982	[*Bougainvillia* sp., *O. longissima*]
	1984	*I. phosporea*], [*Bougainvillia* sp.
129	1985	*H. arctica*], *M. edulis*]
Model 3		
172	1983	[*B. crenatus, Bougainvillia* sp.]
158	1985	[*M. edulis*, [*B. crenatus*
100	1977	[*O. longissima*, [*H. arctica*, [*M. edulis*
101	1980	[*C. laeviusculus*, [*O. longissima*, [*I. anguipes*
	1981	[*L. squamatus*, [*P. inermis*, [*C. laeviusculus*, [*C. septentrionalis, A. testudinalis*], [*O. longissima*, [*H. arctica*, [*M. edulis*
	1983	[*O. geniculata*, [*O. lacerata*], [*H. imbricata*, [*H. arctica*
	1984	[*C. syringa*], [*O. lacerata*], [*O. geniculata*, [*M. edulis*,
	1985	[*N. pelagica*, [*P. maculata*, [*C. laeviusculus*
69	1975	[*L. squamatus*, [*I. anguipes*, [*H. arctica*
68	1976	[*S. balanoides*, [*H. arctica*, [*M. edulis*
63	1975	[*A. vulgaris*, [*S. balanoides*
	1977	[*P. maculata*, [*T. larynx*
66	1984	[*P. inermis*], [*S. droebachiensis*, [*S. balanoides*, [*T. larynx*, [*L. vincta, C. septentrionalis*]
54	1983	[*S. droebachiensis*

6 show a complex fluctuating pattern where the ranges of species distribution expand or shrink from one year to another, but where the major discontinuities at intermediate and large spatial scales are, however, distinctly defined. To better visualize these results, discontinuities observed at neighbouring stations (neighbours at a scale of tens of kilometres) were grouped so that only the stations or groups of stations where the major discontinuities occurred across the years were highlighted. These were: Model 1, Stns 6 to 8, 14 to 23, 25 to 43, 69 to 68, 66 to 60, 57 to 54; Model 2, Stns 6 to 8, 14 to 23, 25 to 43, 73 to 78, 83 to 84, 90 to 93, 121 to 129; Model 3, Stns 172, 158, 100 to 101, 69 to 68, 66 to 63, 54 (Fig. 6).

DISCUSSION

The invertebrate fauna observed on the buoys was mostly composed of intertidal and sublittoral marine and estuarine species. This fauna is characteristic of the northwestern Atlantic area and includes species whose distributions range from the Arctic Ocean to the Gulf of México. As in most typical estuarine environments (Remane & Schlieper 1971), the number of species diminished steadily following the decreasing salinity gradient. However, few freshwater species were found in the brackish portion of the system and no increase in richness of these forms was observed going up in the direction of the Fluvial Estuary.
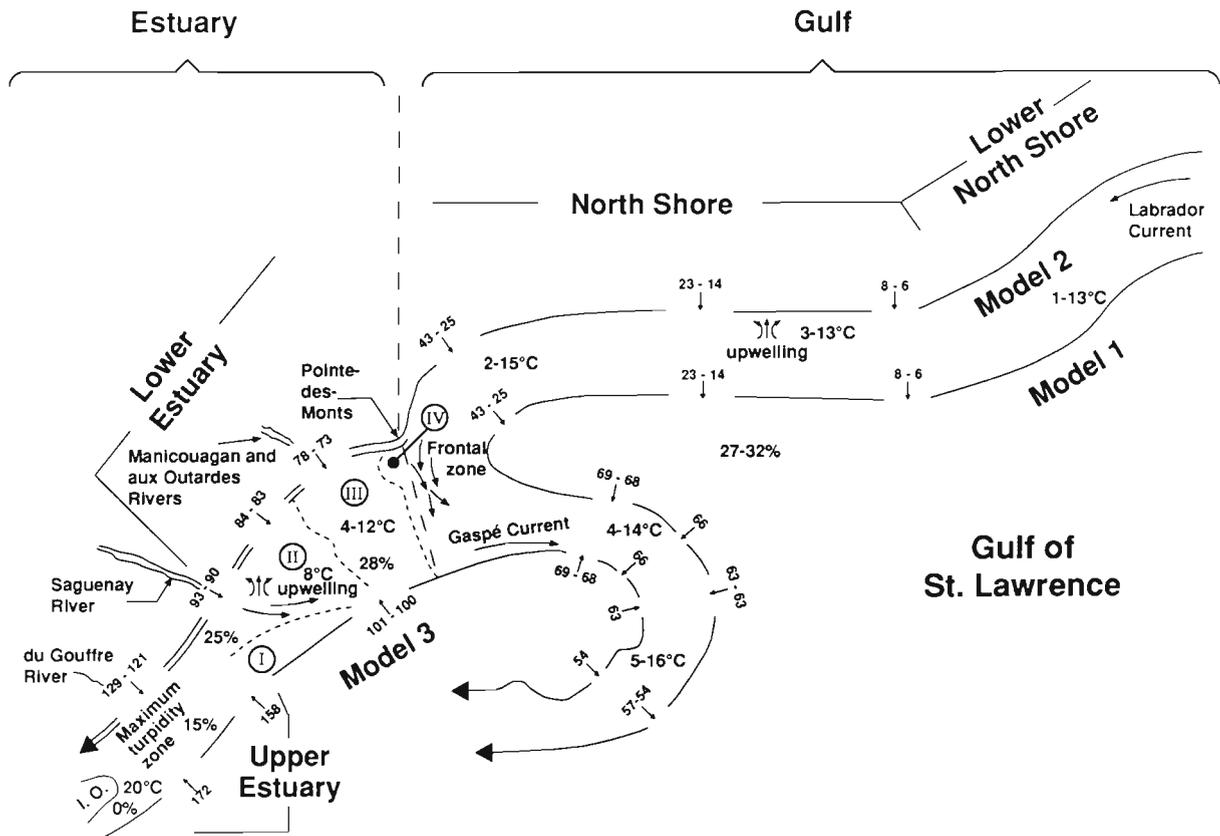
Fig. 6. Discontinuities in species distribution observed along the 3 lines (models) of larval dispersion considered. Arrows perpendicular to the paths of larval dispersal, and associated numbers (stations or groups of stations), summarize the regions of major discontinuities observed across the years; dashed lines and Areas I to IV indicate divisions of the Lower Estuary defined on the basis of hydrographic and primary production characteristics (modified from Therriault & Levasseur 1985)

Distributional relations of species

In spite of the large size and physical heterogeneity of the study area (Dickie & Trites 1983, El-Sabh & Silverberg 1990), the yearly analyses of species associations conducted at different spatial scales showed the same basic group of species throughout the overall Estuary-Gulf system. This group consisted of some 'foundation' species (Sutherland 1981, Dayton 1984) of hard-bottom substrata: the hydroid *Obelia longissima*, the bivalves *Hiatella arctica* and *Mytilus edulis*, and the cirripedes *Semibalanus balanoides* and *Balanus crenatus*. It also included some associated motile taxa, particularly *Lacuna vincta*, one unidentified nudibranch species, *Lepidonotus squamatus*, *Nereis pelagica*, *Phyllodoce maculata*, *Ischyrocerus anguipes*, and *Calliopius laeviusculus*.

The species grouping together on a recurrent basis are assumed to share common ecological traits and to respond in a related way to the properties of the environment (Fager & McGowan 1963, Legendre & Legendre 1978). Here, these species share (1) a planktotrophic pelagic development, (2) the ability to main-

tain themselves in the upper layer of the water column during the larval phase prior to settlement, and (3) the capacity to live continuously immersed during the adult phase. Furthermore, these species are under the direct influence of the environmental conditions prevailing in the surface water layer (e.g. temperature, salinity, turbidity, turbulence, water currents, and quality and quantity of food).

The occurrence of such a widespread and recurrent association does not imply that the overall epibenthic fauna behaves as an homogeneous entity. Only some species were highly coincident in their spatial distribution and were always members of the group. The boundaries of the association were diffuse and fluctuated from year to year, especially at the head of the estuary. When species distributions were mapped together (Table 2), it was apparent that the geographic ranges of the different species varied greatly. This variability probably reflects a spectrum of adaptive abilities allowing species to make use of different parts of the habitat and to adjust their range of distribution to the environmental changes.

Spatial discontinuities in distribution

Analytical approach

Patterns of species distribution may be described by defining ecological series of sampling sites along natural gradients of environmental change. In our study, the residual circulation patterns were assumed to reflect the major axes of species dispersion along the gulf and estuarine gradients. This is, however, a simplification since other dispersal patterns may also exist. No assumptions were made here regarding the swimming behaviour and vertical migration of larvae into the water column. Instead, it was inferred that larvae could be transported from one part of the system to another. For instance, the first model of species dispersal (Model 1) assumed that the larvae released along the Lower North Shore, the North Shore, and the Gaspé coast could be carried along by the dominant currents observed in the area. These dispersal models should not be interpreted as suggesting that larvae drift from the Strait of Belle-Isle to the Gaspé coast (Model 1) or to the Saguenay Fjord (Model 2) within a year, but rather as showing the potential corridors along which larvae could move in time to colonize favorable areas. In nature, the probability of long-distance larval transport is rather reduced. Indeed (1) for most species the duration of the larval development is too short, (2) the harsh and fluctuating environmental conditions may induce high larval mortality, and (3) the current patterns are variable both spatially and temporally (Scheltema 1982, Johannesson 1988). Accurate estimations of the distance travelled by larvae must be based on a comprehensive knowledge of the surface and subsurface circulation patterns. Published data on current variability in the study area are at best fragmentary when not contradictory (El-Sabh 1976, Gregory et al. 1989, Koutitonsky & Bugden 1991). Considering that the benthic fauna generally occur in discrete patches, the presence of migrants into the water mass was probably due to parent populations distributed at several points along the littoral. Thus, the larvae reaching the buoys could be released at any undetermined distance somewhere 'upstream' from the sites where they settled. In this context, the changes in species distribution observed across the years could be the result of demographic and environmental stochasticity affecting both the parent populations and the migrants carried by the currents.

The spatial discontinuities (Fig. 5) were the by-product of the heterogeneous distribution of all the species recorded along the lines of contiguous collectors. However, only the species whose first ('beginning') and last ('end') presence on the lines were statistically significant (Table 6) could be clearly asso-

ciated with each specific discontinuity. Given the high yearly variability in the distribution ranges of species, grouping together the neighbouring stations allowed us to better visualize the limits of distribution on an interannual basis. Thus, for example, the discontinuity formed by Stns 121 to 129, located in the Upper Estuary between Île d'Orléans and Île-aux-Coudres (Fig. 6), could be better associated with the distributional limits of *Idothea phosphorea, Calliopius laeviusculus, Obelia longissima, Hiatella arctica, Mytilus edulis,* and *Balanus crenatus.* In a similar way, the discontinuity represented by Stns 100 to 101, located on the south shore of the Lower Estuary, marked in a more perceptible way the limits of penetration of *Lepidonotus squamatus, Nereis pelagica,* and *Pontogeneia inermis* into the Estuary waters during the overall period of study.

Factors limiting species distribution

Regional differences in salinity, temperature, water column stability, larval advection, and food particle size spectrum could be expected to explain the observed patterns in species distribution. Such an explanation, to be satisfactory, should also include the behavioural patterns and ecological preferences of species at different stages of their life history. Thus, for instance, it has been shown that the feeding behaviour and the feeding effectiveness of hydroids vary with the species and the physical conditions of the environment (Marfenin 1981, Hunter 1989). However, in the absence of simultaneous field surveys of these factors and the dispersal dynamics of the benthic fauna, specific relationships between a factor or group of factors and the patterns of distribution of particular species remain speculative.

Even though, at this stage, definite causal relationships cannot be established, major discontinuities in species distribution (Fig. 6) were observed in areas where changes in well-defined physical features of the system do occur. The exact locations of discontinuities vary from year to year, presumably because local or regional hydrographical conditions also vary from year to year. The most outstanding are the following:

Discontinuities near Stns 6 to 8. This zone of discontinuities is located near the Strait of Belle-Isle, the coldest region of the system. Here, summer surface temperatures range from 1 to 13 °C (Vigeant 1987, Petrie 1990). This zone marks the transition between the North Shore region, under the influence of the Gulf conditions (Koutitonsky & Bugden 1991), and the region directly influenced by the Labrador Current. Steven (1974) described the latter as being the least

productive of the whole Estuary-Gulf system. Two species were observed exclusively in this zone: *Hyas* sp. and *Lepas anatifera*.

Discontinuities near Stns 14 to 23. The low temperatures observed all along the North Shore region in the summer suggest that upwelling occurs all along the coast (D. Lefaivre, Maurice Lamontagne Institute, pers. comm.). However, studies by Lauzier et al. (1957) suggest that the upwelling in the Mingan region is quasi-permanent during summer. We hypothesize that, in this area, the combined effects of local bathymetry on surface circulation as well as upwelling of cold (3 to 6 °C) waters, induced presumably by northwest winds and tidal mixing of cold intermediate waters with warmer surface waters (Lauzier et al. 1957), are responsible for the limits observed there. Hydrographically, this region is also unique on the North Shore in showing higher content of seston particles in the water column than surrounding areas (Nota & Loring 1964). *Doto coronata, Margarites helicinus, Lepidonotus squamatus,* and *Strongylocentrotus droebachiensis* began their distributional range on the buoys of the Lower North Shore/North Shore in the Mingan region, and *Clytia hemisphaerica*, present along the Strait of Belle-Isle, ended its distributional range there.

Discontinuities near Stns 25 to 43. This zone of discontinuities marks the limit between the Gulf and Estuary. It is physically characterized by a frontal zone formed by the cyclonic Anticosti gyre and the southerly transverse current at Pointe-des-Monts (10 to 40 cm s^{-1}; El-Sabh 1977b) which might constitute a physical barrier to the westward transport of surface-drifting larvae. Presumably, the latter could be advected by the surface-flushing circulation prevailing in this area. Another obstacle to the transport of larvae from the north shore of the Gulf to the Estuary is associated with salinity differences (as high as 6 ‰) from one side of the frontal zone to the other (Petrie 1990). The discontinuities also delimit a region of relatively high estuarine sestonic content from the lower sestonic load of the Gulf water (Nota & Loring 1964). Among the marine species whose distributional limits are located at the mouth of the Estuary are *Gammarellus angulosus, G. homari,* and *Anomia aculeata*.

Discontinuities near Stns 69 to 68. The zone where these discontinuities occur is strongly influenced by the Gaspé Current and also by the transverse current flowing from the north to the south shore of the Estuary where it merges with the Gaspé Current. Again, the transverse current may act as an hydrodynamical barrier to the larvae. Presumably, larvae entering the Gaspé Current are advected eastward to the open Gulf. As an example, the ophiuroid *Ophiura robusta* was present on the buoys moored along the western North Shore and northern Gaspé Peninsula, but was not observed on the buoys located within the Estuary.

Discontinuity near Stn 66. This discontinuity separates the stations north of the Baie de Gaspé from those of the Bay itself. Because of the topography of the Gaspé Peninsula, the former are directly influenced by the Gaspé Current while the latter are enclosed in a local estuarine system. *Metopa* sp. and *Sertularia cupressina* ended their distributional range along the North Shore and Gaspé Peninsula coast at Stn 66. *Gammarus oceanicus* and *Mya arenaria* extended their range to stations located inside the Baie de Gaspé.

Discontinuity near Stn 60. Stations situated south of Stn 60 down to Stn 54 are little influenced by the Gaspé Current, while at the same time not being quite under the physical influence of Baie des Chaleurs. These stations are located somewhat in a transitional region between these 2 areas.

Discontinuities near Stns 57 to 54. These discontinuities are located at the mouth of Baie des Chaleurs. They mark clearly the junction between the warm, semi-enclosed shallow system of Baie des Chaleurs and the more exposed stations located northwards. Three species – *Harmothoe extenuata, Jassa falcata,* and *Opercularella lacerata* – met their distributional limits along the Gaspé coast in this area.

Discontinuities near Stns 73 to 78. This zone coincides with the mouth of the Manicouagan and aux Outardes rivers, a system whose mean annual freshwater discharge is about 800 m^3 s^{-1}. These discontinuities mark the limit of penetration into the Estuary of *Lepidonotus squamatus, Jassa falcata, Strongylocentrotus droebachiensis, Tubularia larynx,* and *Mya arenaria*.

Discontinuities near Stns 83 and 84. The region delimited by Stns 83 and 84 up to the Saguenay River is directly influenced by the upwelling of cold intermediate waters (Ingram 1979, Therriault & Levasseur 1985). These discontinuities mark the limit of penetration along the north shore of the Estuary for *Nereis pelagica* and *Pontogeneia inermis*.

Discontinuities near Stns 90 to 93. These discontinuities correspond to the current outflow of the Saguenay River, the most important single tributary of the St. Lawrence Estuary (mean annual runoff of 1 800 m^3 s^{-1}). The strong (30 to 50 cm s^{-1}) transverse current associated with this hydrodynamical feature (El-Sabh 1977b) probably creates a barrier for the penetration of larvae and causes direct advection of particles eastward and towards the south shore. This zone marks the limit of penetration into the Estuary of *Caprella septentrionalis, Ischyrocerus anguipes, Obelia geniculata, Semibalanus balanoides,* and an unidentified nudibranch species.

Discontinuities near Stns 121 to 129. These disconti-
nuities correspond to the north shore limit of the zone
of maximum turbidity, as well as to the outer limit of
the maximum salinity gradient (0 to 18 ‰) of the Upper
Estuary (Kranck 1979, Lucotte & d'Anglejan 1986). The
area where these discontinuities occur is also under
the direct influence of the freshwater outflow of rivière
du Gouffre (mean annual runoff 21 m^3 s^{-1}), represent-
ing an additional source of osmotic stress for the or-
ganisms. It is also a region of upwelling of waters from
the Lower Estuary penetrating in the Upper Estuary.
These discontinuities mark the limit of penetration,
along the north shore of the Estuary, of the following
species: *Idothea phosphorea, Calliopius laeviusculus,
Obelia longissima, Hiatella arctica, Mytilus edulis,* and
Balanus crenatus.

Discontinuities at Stns 100 and 101. These disconti-
nuities are difficult to explain on the basis of local con-
ditions as no major apparent changes in physiographi-
cal or hydrographical features are distinguishable in
this area. According to Therriault & Levasseur (1985)
the area where these discontinuities occur is under the
influence of the Manicouagan and aux Outardes
plume, which influence, presumably, the physical con-
ditions even near the south shore of the Estuary.
Hydrographically, this area is more stable than adjoin-
ing ones due to the freshwater input and the mitigated
effects of tidal mixing. These discontinuities mark
the limit of penetration, along the south shore of the
Estuary, of *Lepidonotus squamatus, Nereis pelagica,*
and *Pontogeneia inermis.*

Discontinuity near Stn 158. Roughly, this discontinu-
ity corresponds to the limit between the Lower and
Upper Estuary on the south shore. These 2 bodies of
water differ obviously by their suspended seston load
and salinity gradient, abrupt in the Upper Estuary and
weak in the Lower Estuary. Presumably, the shallow
water on the south shore of the Estuary westward of
Stn 158, together with numerous small and medium-size
rivers, impose a fluctuating salinity regime detrimental
to the marine species.

Discontinuity near Stn 172. This discontinuity marks
the westward limit of saltwater penetrating along the
south shore. It also marks the limit of penetration into
the Upper Estuary of the hydroid *Bougainvillia* sp.

Thus, the epibenthic species discontinuities are
nearly always associated with major traits of the phys-
ical environment. These are either physiographical
features which induce major hydrographical changes
(e.g. entrance of Strait of Belle-Isle, Pointe-des-Monts
coastline, Cape Gaspé), hydrodynamic factors asso-
ciated with major localized freshwater inputs (e.g.
Manicouagan/aux Outardes rivers, Saguenay Fjord),
hydrodynamic singularities (e.g. Mingan and Lauren-
tian Channel head upwellings, density and turbidity

fronts), or surface circulation patterns (e.g. estuarine
transverse currents, Anticosti gyre, Gaspé Current).
Some of the species discontinuities shown in this
study correspond fairly well to ecological limits re-
ported in previous biogeographical studies. Thus, for
instance, discontinuities near Stns 121 to 129 and 158
correspond together to the limits separating the
medium and highly brackish subregions proposed by
Bousfield (1956) and Dunbar et al. (1980) for the
Upper Estuary. Similarly, discontinuities near Stns 93
to 90, 84 to 83, 78 to 73, and 101 to 100 (Fig. 6)
correspond to the ecological divisions proposed by
Therriault & Levasseur (1985) for the Lower Estuary
on the basis of phytoplankton biomass and produc-
tion. While the former investigators divided the study
area on the basis of ecological characteristics of the
littoral fauna, the latter ones divided it on the basis of
ecological characteristics of the phytoplankton com-
munity. Ardisson et al. (1990), by analysing the
spatio-temporal changes in the community structure
of biomass of the dominant epibenthic species of
the St. Lawrence system, distinguished 6 broad bio-
geographical zones whose limits closely reflect those
observed in this study, particularly within the Gulf
area.

The above discussion clearly shows that important
gaps exist in our knowledge of both physical coastal
processes and dispersal and survival of benthic larval
populations in this system. Our study identifies, how-
ever, a number of transitional areas where well-
defined changes in the physical or biological proper-
ties of the environment occur, pointing out several
critical regions where future work could be conducted
on larval dispersal and survival of newly settled spat.
The factors which determine the location and temporal
variation of the species discontinuities observed here
must be elucidated if the actual distribution patterns of
these species are to be understood. Particular attention
should be paid to the influence of different hydrody-
namical forces and behavioural mechanisms on drift
and larval dispersal, and this at intermediate and small
spatial scales.

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