UNIVERSITÉ DU QUÉBEC

VARIATION SPATIO-TEMPORELLE DE LA MACROFAUNE ENDOBENTHIQUE DANS LA ZONE PROFONDE DU SAINT-LAURENT (QUÉBEC, CANADA) EN RELATION AVEC LES CONDITIONS ENVIRONNEMENTALES

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MYLÈNE BOURQUE

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RÉSUMÉ

L'estuaire maritime et le golfe du Saint-Laurent forment un système complexe où la dynamique des conditions environnementales détermine les variations spatiales et temporelles au niveau des communautés benthiques. L'observation récente de zones hypoxiques profondes dans l'estuaire maritime du Saint-Laurent pourrait avoir une influence majeure sur la structure de ces communautés, étroitement liées aux conditions environnementales. Toutefois, la macrofaune benthique du Saint-Laurent reste encore méconnue. Afin de définir un éventuel impact sur l'aspect fonctionnel des communautés, la structure de la macrofaune benthique a été caractérisée dans le but de voir si les zones hypoxiques se traduisent par des modifications des communautés.

Notre objectif était de décrire les patrons de distribution des communautés endobenthiques dans deux régions du Saint-Laurent, l'estuaire maritime et le golfe du Saint-Laurent, et d'identifier les facteurs environnementaux influençant la structure des communautés. De plus, les variations temporelles au niveau des caractéristiques des communautés ont été décrites, afin de déterminer les effets potentiels de l'hypoxie. La macrofaune endobenthique a été échantillonnée en 2005 et 2006 à 20 stations, réparties le long de la zone profonde des deux régions étudiées. Les données ont été analysées selon une approche univariée et multivariée. Sept groupes de stations, basés sur l'abondance taxonomique, ont été identifiés dans la zone d'étude, selon une analyse par groupement. Les résultats ont montré une grande variabilité spatiale de la répartition des assemblages benthiques et des groupes fonctionnels, ainsi que des indices de diversité. La composition du sédiment (taille moyenne des grains et matière organique), la température et la salinité sont parmi les facteurs environnementaux influençant les assemblages d'espèces et les groupes fonctionnels. Les indices de diversité sont plutôt influencés par la profondeur, l'oxygène, la température et la taille du sédiment. L'analyse des données historiques démontre une diminution temporelle de la richesse spécifique et de la diversité de Shannon, attribuée possiblement au développement de l'hypoxie dans l'estuaire maritime du Saint-Laurent. Des changements au niveau des communautés benthiques ont été détectés, dont une augmentation de la densité de quelques espèces opportunistes vivant à la surface du sédiment, tels les polychètes du genre *Myriochele*, généralement présentes dans les premières étapes d'un milieu perturbé par l'hypoxie. Dans un contexte de changements climatiques, ces travaux permettront de mieux comprendre les causes et les impacts écologiques de l'hypoxie afin de déterminer les effets potentiels des modifications de la structure des communautés sur le fonctionnement global de l'écosystème.

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INTRODUCTION GÉNÉRALE

Les estuaires sont des environnements transitionnels complexes et dynamiques, caractérisés par des conditions hydrologiques, morphologiques et chimiques très variables (Day et al., 1989). De ce fait, les communautés benthiques vivant dans ces milieux varient à travers différentes échelles spatiales et temporelles, en raison de la grande variabilité des conditions environnementales (Ysebaert et Herman, 2002; Ellis et al., 2006). Les patrons de distribution des organismes benthiques dans de tels milieux sont souvent difficiles à prédire, étant donné la complexité des relations entre les paramètres physiques, les interactions biologiques (compétition et prédation) et le recrutement (Ellis et al., 2006). Un énorme défi pour les écologistes marins est d'identifier et de relier les processus physiques et biologiques responsables de ces patrons, en raison de la grande complexité de l'environnement benthique estuarien (Snelgrove et Butman, 1994). L'étude des habitats benthiques à grande échelle est essentielle dans la gestion des écosystèmes marins, car elle permet d'évaluer les changements environnementaux causés par les perturbations d'origines anthropiques qui surviennent dans les communautés, et plus récemment par les changements climatiques (Freeman et Rogers, 2003).

Rôle de la macrofaune

Le macrobenthos est une composante importante des écosystèmes estuariens et joue un rôle primordial dans la dynamique de ceux-ci. La macrofaune endobenthique forme un élément essentiel de la chaîne alimentaire estuarienne au niveau de la productivité secondaire. D'une part, elle est consommée par de nombreux poissons démersaux, oiseaux et crustacés épibenthiques, et d'autre part, elle est une source de nourriture importante pour les populations humaines (Snelgrove, 1998; Herman et al., 1999). De plus, par leurs activités d'alimentation et de bioturbation, les organismes endobenthiques participent activement au transport des particules et ont un impact sur l'oxygénation, le mouvement vertical et la stabilité du sédiment (Rhoads et Young, 1970; Rhoads, 1974). La macrofaune contribue également à la récupération des particules de matière organique qui sédimentent vers le fond marin tels les détritus, les pellettes fécales et les carcasses animales. En se nourrissant de ce matériel, ces organismes, qui servent de proies aux espèces s'alimentant sur les fonds, assurent le transfert trophique vers la colonne d'eau (Carlson et al., 1997; Snelgrove, 1998). Le macrobenthos est donc responsable d'une grande part du fonctionnement des écosystèmes estuariens, et, par conséquent, est très sensible aux gradients environnementaux estuariens.

Les communautés macrobenthiques sont souvent utilisées comme des indicateurs de la qualité et de l'état de santé du milieu marin et peuvent donc servir à détecter des changements de ce milieu. En raison de leurs spécificités écologiques, les organismes macrobenthiques jouent le rôle de bio-indicateurs de modifications de l'environnement et répondent rapidement aux stress de nature anthropique et naturelle (Dauvin, 2007). Leur relative immobilité les empêche d'échapper aux effets d'un stress ou d'une perturbation environnementale, reflétant ainsi les conditions locales. De plus, leur cycle de vie varié, leur grande diversité et leur tolérance variable à pollution et à la dégradation de l'habitat en font de bons indicateurs (Olsgard et al., 1997).

Influence des conditions environnementales sur les communautés benthiques

Les communautés benthiques des milieux estuariens sont directement exposées à la grande variabilité des conditions environnementales caractéristique de ces milieux. En raison de la variabilité dans la sélection des habitats chez les espèces benthiques, les relations entre la répartition des espèces et les variables environnementales se manifestent par des patrons de distribution (Hall, 1994; Glockzin et Zettler, 2008). De nombreuses études ont étudié la distribution spatiale des communautés macrobenthiques en fonction des changements des paramètres environnementaux.

L'hétérogénéité spatiale du macrobenthos le long d'un gradient estuarien est traditionnellement décrite en fonction de la salinité et de la composition du sédiment (Gray, 1981; Holland et al., 1987; Freeman et Rogers, 2003; Teixera et al., 2008). De nombreux travaux ont également décrit les relations entre la distribution et la diversité des espèces et le sédiment dans lequel elles vivent (Sanders, 1968; Rhoads, 1974; Snelgrove et Butman, 1994). Plusieurs études ont démontré l'importance des processus hydrodynamiques et du substrat (granulométrie et contenu en matière organique) sur la distribution des organismes benthiques dans un estuaire (Warwick et Uncles, 1980; Warwick et al., 1991; Rosenberg, 1995). D'autres travaux vont en ce sens, puisque la structure des communautés macrobenthiques serait fortement reliée à une interaction complexe entre l'hydrodynamisme, la dynamique sédimentaire et la biologie benthique (Hall, 1994; Paterson et Black, 1999; Herman et al., 2001). De plus, Rapoport (1994) et Schaffner et al. (2001) suggèrent que l'abondance et la richesse spécifique ont tendance à diminuer en amont de l'embouchure d'un estuaire. Malgré tout, il est difficile de décrire la distribution spatiale de la faune benthique en fonction des changements des facteurs environnementaux, car plusieurs de ces derniers covarient, d'autant plus que les animaux peuvent modifier leur environnement physique (Ellis et al., 2006).

Parmi toutes les variables environnementales influençant les communautés endobenthiques, l'oxygène dissous est un facteur limitant pour la macrofaune (Diaz et Rosenberg, 1995; Rabalais et al., 2001; Gray et al., 2002). Dans l'environnement marin, l'oxygène provenant de l'atmosphère ou du phytoplancton se dissous dans les eaux de surface et pénètre dans les eaux profondes, permettant ainsi aux organismes benthiques de respirer. Lorsque l'apport en oxygène dissous en profondeur s'affaiblit ou que le taux de consommation excède le taux d'approvisionnement, la concentration en oxygène diminue au point d'atteindre un niveau où l'impact sur la communauté benthique est important (Diaz, 2001). Cette condition de faible concentration en oxygène, appelée hypoxie, survient lorsque la concentration en oxygène du milieu est inférieure à 2 ml O_2 L^{-1} ou 62,5 µM, soit le seuil de tolérance de la plupart des organismes benthiques (Gray et al., 2002; Wu, 2002; Rabalais et al., 2001). Plusieurs scientifiques diffèrent à propos de la définition exacte de l'hypoxie, puisque les besoins en oxygène varient selon les espèces (Modig et Olafsson, 1998). Néanmoins, de nombreux auteurs retiennent la concentration précédente comme hypoxique, car c'est à partir de cette concentration que plusieurs impacts peuvent être observés sur la plupart des espèces marines (Diaz et Rosenberg, 1995; Rabalais et al., 2001).

L'hypoxie dans le Saint-Laurent

L'hypoxie est un phénomène qui peut survenir naturellement dans les milieux où la circulation d'eau est restreinte, tels les fjords et les zones d'upwelling. Le développement de l'hypoxie en eau profonde est principalement causé par la stratification de la colonne d'eau, empêchant ainsi les échanges d'oxygène entre les eaux profondes et celles de surface (Cloern, 2001). Cependant, depuis le siècle dernier, l'apport excessif de nutriments dans les écosystèmes marins côtiers et estuariens, tels les nitrates et phosphates, peut causer des phénomènes d'eutrophisation, contribuant ainsi à l'augmentation de la fréquence et de l'étendue des zones hypoxiques mondialement (Diaz et Rosenberg, 1995; Gray et al., 2002, Diaz et Rosenberg, 2008). Cette forte augmentation de la teneur en nutriments, associée à l'augmentation de la population humaine dans les zones côtières, notamment par l'utilisation de fertilisants pour l'agriculture et la déforestation, provoque une augmentation de la productivité primaire pélagique ou benthique. Celle-ci induit une augmentation de l'apport de matière organique de la surface vers le sédiment, la rendant directement disponible aux bactéries et aux organismes détritivores et brouteurs (Heip, 1995). Ce processus d'eutrophisation peut éventuellement conduire à des conditions hypoxiques. La forte augmentation de la quantité de matière organique vers le sédiment a comme effet d'augmenter le taux de respiration des organismes microbiens benthiques qui reminéralisent la matière organique. Ainsi, les processus de respiration contribuent à la diminution progressive de l'oxygène dissous dans le milieu et peuvent conduire à des conditions hypoxiques (Grall et Chauvaud, 2002; Gray et al., 2002).

Des données historiques provenant de l'estuaire maritime du Saint-Laurent (EMSL) démontrent que les concentrations en oxygène dissous à 300 m de profondeur ont diminué de plus de 50 % durant les 70 dernières années (Gilbert et al., 2005, 2007). En effet, l'oxygène dissous en profondeur a diminué de 125 μmol L^{-1} dans les années 1930 à une moyenne de 65 μmol L^{-1} pour la période 1984-2003. Des mesures effectuées en 2003, dans la partie profonde de l'EMSL située dans le Chenal Laurentien, ont révélé une concentration en oxygène dissous inférieure à 60 μmol L^{-1} sur une distance de 110 km, où la plus faible valeur mesurée était de 51,2 μmol L^{-1} (Gilbert et al., 2005, 2007). Au total, approximativement 1 300 km^2 des fonds de l'estuaire maritime seraient hypoxiques. Un réchauffement des eaux profondes de 1,65 °C de 1930 à 1980 suggère que les changements au niveau des proportions des masses d'eaux entrant dans le Chenal Laurentien jouent probablement un rôle dans la diminution de l'oxygène des eaux profondes. Il est estimé que la moitié à deux tiers de la diminution des concentrations en oxygène peut être expliquée par la diminution de la proportion des eaux froides, douces et oxygénées du courant du Labrador (Gilbert et al., 2005). Une augmentation des flux de carbone organique vers le fond, et conséquemment, de la demande en oxygène du sédiment, expliquerait le tiers manquant de la diminution de l'oxygène dissous en profondeur (Benoit et al., 2006 ; Thibodeau et al., 2006). En effet, une augmentation de la productivité biogénique marine dans l'estuaire maritime depuis les années 1960 a été observée, indiquée par la signature isotopique du carbone organique et de l'augmentation du taux d'accumulation des kystes de dinoflagellés (Thibodeau et al., 2006). De telles variations des indices sédimentaires sont souvent associées à l'eutrophisation des écosystèmes marins (Cloern, 2001). Toutefois, étant donné le manque actuel de connaissances, il est présentement impossible de prédire l'évolution du budget en oxygène de l'estuaire maritime et du golfe du Saint-Laurent et de préciser l'impact de la diminution de la concentration en oxygène dissous sur les communautés endobenthiques.

La déplétion de l'oxygène peut conduire à d'importants changements au niveau de l'abondance, la distribution, voire même la dynamique des communautés benthiques. L'hypoxie affecte directement ces communautés benthiques en diminuant le nombre d'espèces et en augmentant la densité et l'abondance totale de quelques espèces opportunistes qui survivent (Dauer et al., 1992; Llansó, 1992; Diaz et Rosenberg, 1995; Gray et al., 2002). La succession de la faune endobenthique et les effets d'une diminution de la saturation en oxygène à l'interface eau-sédiment ont été décrits par Gray (1992). Ce modèle montre que la distribution et le comportement de l'épifaune et de l'endofaune benthique en réponse à un gradient décroissant de saturation en oxygène est semblable au modèle de Pearson et Rosenberg (1978), décrivant la succession faunique le long d'un gradient croissant de matière organique (Fig. 1). Suivant un schéma similaire, le modèle de

Gray (1992) démontre qu'une déplétion de l'oxygène provoque une diminution du nombre d'espèces et de la diversité benthique dans le milieu. Ce modèle également aussi que des conditions de faible oxygénation favorisent quelques petites espèces opportunistes, tirant avantage d'un changement des conditions environnementales et augmentent en abondance, au détriment d'espèces plus grosses moins tolérantes. L'appauvrissement en oxygène conduit également à une réduction de la distribution de la faune en profondeur dans le sédiment, en plus d'une réduction de la diversité fonctionnelle de la communauté.

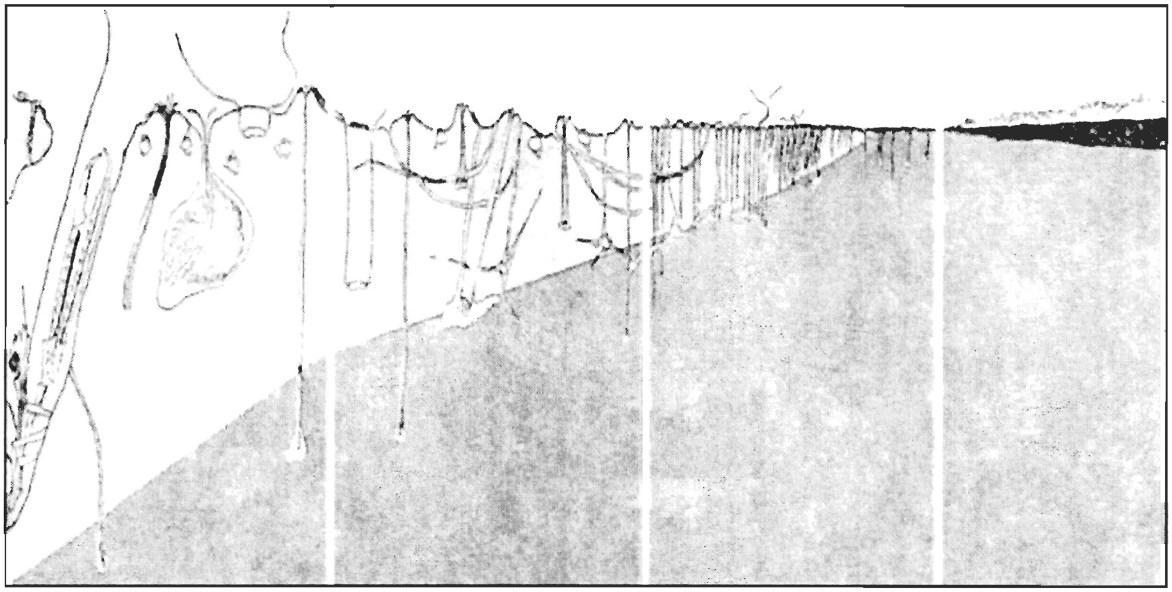

Figure 1. Schéma de la succession faunique et de la structure du sédiment le long d'un gradient d'enrichissement en matière organique (tiré de Pearson and Rosenberg, 1978).

Macrofaune du Saint-Laurent

Malgré son importance pour les pêcheries commerciales, la macrofaune endobenthique profonde dans le Saint-Laurent est encore méconnue, puisque seulement quelques études quantitatives ont été réalisées. Suite aux premiers travaux de Préfontaine et Brunel (1962) et Peer (1963), les plus récentes études sur la distribution et la diversité endobenthiques dans le Chenal profond de l'estuaire maritime sont celles de Robert (1979) sur les mollusques, Massad (1975) et Massad et Brunel (1979) sur les polychètes et Ouellet (1982) sur la distribution des invertébrés macrobenthiques. Dans le golfe du Saint-Laurent, la structure trophique du macrobenthos a été étudiée à trois stations dans la zone profonde par Desrosiers et al. (2000), alors que Long et Lewis (1987) ont échantillonné quelques stations à ces profondeurs. Cependant, très peu de ces études ont relié les communautés endobenthiques profondes aux conditions environnementales.

Objectifs et hypothèses de l'étude

L'objectif général de la présente étude était de décrire la structure des communautés endobenthiques profondes dans deux régions du Saint-Laurent, soit l'estuaire maritime et le golfe du Saint-Laurent, en termes d'assemblages, de diversité et de groupes fonctionnels. Plus spécifiquement, il s'agissait, d'une part, de décrire la variabilité spatiale des communautés endobenthiques et d'identifier les facteurs environnementaux contrôlant la distribution, la structure et les caractéristiques des communautés endobenthiques (abondance, diversité, assemblages d'espèces et composition trophique) dans ces deux régions. L'influence des facteurs géomorphologiques (bathymétrie, type de substrat et matière organique) et physico-chimiques (température, salinité et oxygène dissous) sur la structure des communautés a été considérée. Comme la répartition des communautés benthiques est étroitement liée aux conditions environnementales, la structure des communautés devraient être spatialement influencée par les changements au niveau des variables environnementales. Les conditions hypoxiques observées dans l'estuaire maritime devrait particulièrement influencer la composition des communautés benthiques présentes dans cette région. D'autre part, les caractéristiques et la structure des communautés endobenthiques, situées dans cette zone hypoxique, ont été comparés à des données historiques afin de déterminer les impacts causés par la diminution d'oxygène. Notre hypothèse est que la diminution temporelle de l'oxygène aura pour effet de modifier la composition des communautés benthiques et de diminuer l'abondance et la diversité des espèces.

Ce mémoire de maîtrise est présenté sous la forme d'un article scientifique, contenant un chapitre rédigé en anglais. Cet article sera soumis à la revue *Estuarine, Coastal and Shelf Science* à la suite du dépôt final du mémoire.

CHAPITRE 1

SPATIO-TEMPORAL VARIABILITY OF INFAUNAL COMMUNITY STRUCTURE IN THE DEEP ESTUARY AND GULF OF ST. LAWRENCE (QUEBEC, CANADA) IN RELATION TO ENVIRONMENTAL CONDITIONS

Mylène Bourque and Philippe Archambault

Institut des Sciences de la mer de Rimouski (ISMER), Université du Québec à Rimouski,
310 Allée des Ursulines, C. P. 3300, Rimouski, Québec, Canada, G5L 3A1

* Corresponding author: e-mail: philippe_archambault@uqar.qc.ca

1.1 Introduction

Estuaries are complex, dynamic, and highly productive ecosystems characterised by widely varying hydrological, geomorphological, and chemical conditions (Day et al., 1989). Estuarine benthic communities that inhabit these environments are exposed to a large range of spatial and temporal variations in environmental conditions, resulting in well-developed distribution patterns (Glockzin and Zettler, 2008). Due to the complexity of the estuarine benthic environment, the challenge for marine ecologists is to identify and link the physical and biological processes responsible for these patterns (Snelgrove and Butman, 1994). Understanding the broad-scale distribution of benthic habitats is essential to the management of marine ecosystems, as it helps to evaluate the natural and anthropogenic influences and effects on these ecological systems.

Many studies have investigated the distribution of soft-sediment macrofaunal communities in relation to environmental conditions. The spatial heterogeneity of macrobenthos along an estuarine gradient is traditionally described in relation to salinity and sediment composition (Mannino and Montagna, 1997; Ysebaert et al., 2002; Freeman and Rogers, 2003; Teixeira et al., 2008). Several authors have demonstrated the importance of both hydrodynamic processes and substratum (sediment grain size and organic matter content) in controlling physico-chemical conditions and therefore the benthic organism's distribution within an estuary (Warwick and Uncles, 1980; Warwick et al., 1991; Rosenberg, 1995). In addition, Rapoport (1994) suggested that total abundance and species richness tended to decrease with increasing distance from the sea. Thus, macrobenthic faunal patterns will depend on changes in environmental conditions, and small variations in the environment will generate detectable responses in the community (Olsgard et al., 1997). However, spatial distribution patterns of macrobenthic fauna are often hard to predict because the organisms modify their physical environment and many of the physical parameters will co-vary.

A number of univariate and multivariate biodiversity indices are commonly used to follow the changes in benthic communities in their environment and to help scientists and managers to evaluate the status of the ecosystems. However, univariate variables may remain constant even as the species composition changes (Clarke and Warwick, 2001a, Drouin et al., 2009, 2010). Species distribution and community changes should be taken into account, in addition to species richness, when measuring marine biodiversity (Ellingsen, 2001). Multivariate analyses have the potential to be more sensitive to relatively small changes in faunal composition than univariate methods (Downes et al., 2002; Drouin et al., 2009, 2010). The division of communities into groups or taxa that share similar functional attributes (functional-group) is a common means of simplifying the ecological analysis of community structure and function (Bondsdorff and Pearson, 1999). Hence, functional-group responses might be used for the assessment of pollution impacts on marine benthic communities (Clarke, 1993; Bonsdorff and Pearson, 1999). In this way, the AZTI Marine Biotic Index (AMBI) (Borja et al., 2000) and the multivariate approach M-AMBI (Muxica et al., 2007; Borja et al., 2007) have been used for monitoring purposes, to analyse the impacts on soft-bottom benthic communities resulting from various human pressures (Borja et al., 2003; Reiss and Kröncke, 2005 ; Labrune et al., 2006).

Oxygen depletion, seasonally common in many stratified marine ecosystems, may have strong effects on species abundance, distribution, and community dynamics (Dauer et al., 1992; Diaz and Rosenberg, 1995; Rabalais et al., 2001). The recent emergence of hypoxic areas in several estuaries seems to be associated with anthropogenic nutrient loading and coastal eutrophication (Nixon, 1995, Cloern, 2001; Gray et al., 2002; Diaz and Rosenberg, 2008). Severe hypoxia is defined as the threshold below which significant impacts on the biota can be observed and corresponds to dissolved oxygen concentrations of less than 2 ml O_2 L^{-1} or 62.5 μM (Diaz and Rosenberg, 1995; Rabalais et al., 2001). Recent measurements of dissolved oxygen along the Laurentian Channel of the Lower St. Lawrence Estuary (LSLE), Canada, revealed the presence of persistent, year-round, hypoxic bottom waters (Gilbert et al., 2005). Historical data from water samples taken between 300 and 355 m depth in the LSLE revealed that dissolved oxygen concentrations have decreased by more than 50% over the last 70 years, from 125 μmol L^{-1} in the 1930s to about 60 μmol L^{-1} in 2003. In July 2003, an area of approximately 1 300 km^2 of the Laurentian Trough was located in the hypoxic zone. One half to two thirds of the decline in oxygen concentration may be explained from a decreasing proportion of cold, fresh, oxygen-rich Labrador Current water entering the Gulf of St. Lawrence (GSL) (Gilbert et al., 2005). The remaining depletion in oxygen is possibly caused by increased fluxes of organic matter to the seafloor, which increase microbial respiration and mineralization (Benoit et al., 2006; Thibodeau et al., 2006). Faunal succession stages along an hypoxic gradient (Dauer et al., 1992 ; Llansó, 1992 ; Diaz et Rosenberg, 1995; Gray et al., 2002) suggest that benthic diversity decreases gradually with decreasing oxygen availability, but it is not clear how benthic communities respond to temporal changes in oxygen levels (Katsev et al., 2007).

The deep macrofauna of the LSLE and the GSL is still poorly known. Few quantitative studies have described the deep benthic infauna communities in the LSLE. Subsequent to the earlier investigations of Prefontaine and Brunel (1962) and Peer (1963), the most qualitative recent study on diversity and distribution of the benthic infauna in the estuary was realized by Robert (1979) on molluscs and Massad and Brunel (1979) on polychaetes. More recently, Ouellet (1982) performed a quantitative study of the general distribution of macrobenthic invertebrates, while the trophic structure of macrobenthos in the GSL was sampled and analysed by Desrosiers et al. (2000) and Long and Lewis (1987). However, none of these studies linked the environmental conditions to deep benthic infauna communities.

The main objective of the present study was to describe the macrobenthic infaunal communities from two distinct regions of the St. Lawrence, the Lower Estuary (LSLE) and the Gulf (GSL). Specifically, we examined spatial patterns of benthic community characteristics (e.g. abundance, diversity, functional groups) and the structure of benthic assemblages. The spatial distribution of macrofauna was evaluated with the environmental variables describing near-bottom physico-chemical conditions and sediment characteristics, in order to determine the role of such factors in structuring community structure. As the distribution of communities is linked to environmental conditions, we hypothesize that benthic communities should be strongly influenced by spatial changes in oxygen concentration. In particular, benthic assemblages located in the hypoxic zone should be different compared with those from locations not experiencing hypoxic conditions. We also quantified temporal variations among years in macrobenthic community structure in the hypoxic area of the LSLE using available historical data. Based on the outcomes of previous studies, we hypothesize that the temporal decrease in oxygen concentration should cause a shift in species composition, with an increase in opportunistic and tolerant species, and a decrease in diversity indices. Finally, we also want to establish the Ecological Quality Status of the deep channel of the Lower St. Lawrence Estuary and Gulf.

1.2 Material and methods

1.2.1 Study area

The Gulf of St. Lawrence (GSL) is a highly-stratified, semi-enclosed sea, connected to the North Atlantic Ocean through the Cabot Strait and the Strait of Belle-Isle. A major topographic feature of the system is the Laurentian Channel (LC), a deep submarine valley (250 - 500 m) that furrows the Gulf, extending from the margin of the North Atlantic Ocean to the Lower St. Lawrence Estuary (LSLE) (Fig. 2). The LC ends at Tadoussac where the bathymetry rises abruptly from 350 to 25 m over a distance of 16 km (Koutitonsky and

Bugden, 1991). Two other deep channels branch off from the LC between Newfoundland and Anticosti Island: the Esquiman Channel and the Anticosti Channel (Fig. 2). The circulation in the Laurentian Channel is estuarine, with water flowing seaward in the surface layer and landward in the deep layer (Saucier et al., 2003). The water column of the LC is stratified and can be divided vertically into three characteristic layers: 1) a low salinity (~ 25) surface layer, 2) an intermediate cold layer extending from 50 to 150 m depth, with saline water (32 to 34), and 3) a deep, warmer and saltier (> 34) layer, that is a mixture of Labrador current and North Atlantic waters (Dickie and Trites, 1983). A permanent pycnocline is located between 100 and 150 m that isolates deep waters from the atmosphere (Petrie et al., 1996). Under these conditions, oxygen concentration decreases gradually in the bottom waters, possibly because of changes in water temperature, respiration, and organic matter mineralization (Gilbert et al., 2005). Consequently, more oxygen is lost by vertical diffusion than can be replenished from the oxygen-rich surface waters, causing ever-decreasing oxygen levels from the mouth of the LC to the head of channels, where bottom waters are older (Coote and Yeats, 1979).

1.2.2 Field sampling methods and laboratory analyses

Sampling was conducted during two cruises, in summer 2005 (August 20-26) and 2006 (August 14-22), on-board the R/V *Coriolis II.* A total of 17 stations, extending 522 to 1049 km from the Laurentian Channel mouth, sampled deep waters of the LSLE and GSL, at depths varying from 257 to 434 m (Fig. 2a). In 2005, eight stations were sampled at the deeper part of the LSLE and at the northwestern end of Anticosti Island, along the longitudinal axis of the LC. Nine stations were sampled in 2006 in the GSL, along the Laurentian, Anticosti and Esquiman Channels. Station 23 (Fig. 2), which is located in the hypoxic zone of the LSLE offshore of Rimouski, was sampled during two consecutive years (2005 and 2006).

At each station, macrobenthic infauna samples in three replicates were collected with a van Veen grab (0.125 m^2) and sieved on-board through a 1 mm mesh, to enable quantitative comparisons with the historical faunal data from Ouellet (1982). The retained material was preserved in a buffered 5% formaldehyde-saline solution and macrofauna was stored in 70% ethanol after sorting. Macrobenthic organisms were counted and identified to the lowest taxonomic level possible. Macrofaunal species were classified into six functional groups by feeding type (surface deposit feeders, subsurface deposit feeders, filter feeders, carnivores, omnivores, and unclassified trophic group), according to the classification and observations of Fauchald and Jumars (1979), Desrosiers et al. (1986, 2000) and Gage and Tyler (1992). For each sample, total macrofaunal density (individual m^{-2}) was calculated for each functional group and species.

Surface sediment sub-samples were also collected from a box core, for later sediment property determination. Sediment composition was analyzed using a laser diffraction grain size analyzer (Beckman Coulter Counter LS 13 320), allowing the differentiation of particles ranging from 0.4 µm to 2000 µm in size, according to Blott et al.

(2004). Prior to its introduction into the instrument, the sub-sample of 1 g of sediment was disaggregated in 10 ml of a 1 g l^{-1} sodium hexametaphosphate solution (Calgon) and 40 ml of distilled water and shaked for 3h. An ultrasonic treatment was applied before and during the sample run in the instrument to improve the disaggregation of the sample (Blott et al., 2004). The frequency distribution of grain size diameter was analyzed using the GRADISTAT program (Blott and Pye, 2001). Grain size frequency per sample was expressed as percentage of sand, silt, and clay, and mean grain size (μm) was calculated. Total organic matter content (TOM) was measured as loss upon ignition at 500 °C for 12 h on 1 g of surface sediment and expressed as a percentage of total sample mass (Dean, 1974).

Physico-chemical data, such as depth, temperature, salinity and dissolved oxygen, were measured at each station with a Seabird® model SBE19 CTD instrument. The dissolved oxygen concentration was determined by the Winkler method (Carrit and Carpenter, 1966), for individual bottom water samples collected with Niskin bottles mounted on a rosette sampler at 5 m above the seafloor.

1.2.3 Temporal historical data

A literature review of historical data regarding the the deep-water macrobenthos of the LSLE and GSL (i.e. > 250 m) revealed only a few studies that contained quantitative data The macrobenthic faunal data from Ouellet (1982) were used to conduct temporal comparisons with 2005 and 2006 datasets. From these data, seven stations with the same position as those in the present study were selected for temporal analyses (Fig. 2b). These stations were sampled in 1980 along the longitudinal axis of the LC with a 0.125 m^{-2} van Veen grab (Ouellet, 1982). Each sampling station was represented by three pooled grabs, except at stations 23, 24 and 25, where five triplicated pooled grabs were sampled. All macrobenthic abundance data were transformed in density or numbers m^{-2} (ind. m^{-2}). For historical data, taxonomic names were verified and updated using the Integrated Taxonomic Information System on-line database (www.itis.gov).

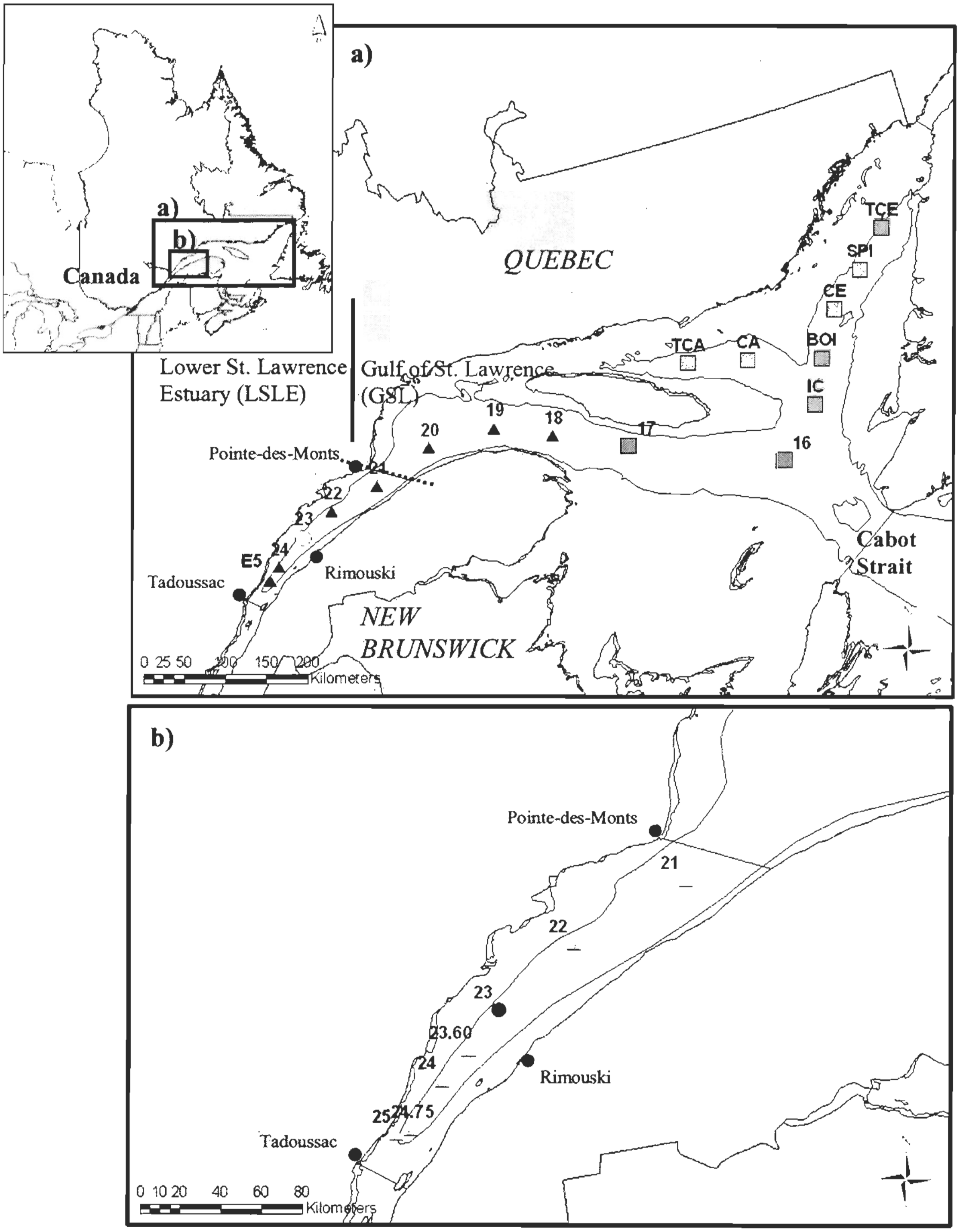

Figure 2. a) Study area showing the location of the 17 sampling stations in 2005 (▲) and 2006 (☐), with infauna and environmental data. Station 23 was sampled in both 2005 and 2006 (○). b) Map of the St. Lawrence estuary showing the location of the seven stations with infauna historical data, sampled in 1980 and 2005 (▲), except for station 23 which was also sampled in 2006 (●).

1.2.4 Statistical analyses

Spatial and temporal variability in macrobenthic community structure was analyzed with univariate and multivariate procedures. Methods of Clarke and Warwick (1994, 2001a) using the PRIMER software v. 6.0 (Clarke and Gorley, 2001), were used to detect spatial and temporal patterns in community structure. All multivariate analyses were based on the Bray-Curtis similarity (Bray and Curtis, 1957) calculated on square-root (√) transformed data. This transformation served to reduce the influence of very abundant species, so that the less-dominant, and even the rare species, would play some role in determining similarity between samples (Clarke, 1993; Clarke and Warwick, 1994). Before computing the similarity matrix, taxa that appeared once or in only one sample were removed from the dataset, as suggested by Clarke and Warwick (1994).

Spatial variability

Sampling stations with similar macrobenthic assemblages were regrouped using a hierarchical classification method (CLUSTER analysis) employing group-average linking. Taxa or species that were predominantly responsible for the similarity within clusters were identified by the similarity percentage procedure (SIMPER). This analysis ranked each species' percentage contribution, based on √ transformed densities, to the similarity within the cluster (Clarke and Warwick, 2001a).

Univariate indices of infaunal community diversity (total density (ind. m^{-2}), species richness (S), Shannon-Wiener diversity index (H', $\log_e$) and Pielou's evenness index (J': $H'/\log S$)) were calculated for all replicated samples. Species were assigned to one of the five ecological groups used by Borja et al. (2000) based on their sensitivity to organic enrichment, from very sensitive species (group I) to first-order opportunistic (group V). The organisms thus categorized were used to calculate a global index of community disturbance (AMBI – see Borja et al., 2000) using the software AMBI v 4.0 (http://www.azti.es). The M-AMBI index was also calculated, combining AMBI, richness, and Shannon diversity, to give a multivariate index (Muxika et al., 2007). In addition, average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) were calculated on macrofaunal densities (DIVERSE analysis, PRIMER). These indices are pertinent measures of biodiversity and provide important tools to compare meta-analyses over large spatial and temporal scales (Clarke and Warwick, 2001b).

The relationships between environmental variables and macrobenthic community structure were examined with a BIO-ENV analysis (Clarke and Warwick, 1994). This procedure was used to find the combination of abiotic factors which best accounted for species and functional groups community structure. Because of the dissimilarity in environmental conditions between the LSLE and the GSL, these two regions were analyzed separately. Multiple regression analyses were used to examine the relationships between univariate indices (total density, S, H', J', Δ^+, and Λ^+) and environmental parameters (depth, temperature, salinity, oxygen saturation, mean grain size, and total organic matter content). Two criteria, the adjusted r^2 and the Akaike Information Criterion (AIC), were used to select those environmental variables to be included in the model that best explained the univariate diversity indices. Collinearity was examined using a matrix of correlation coefficients between the different environmental variables, as recommended by Quinn and Keough (2002). For all univariate analysis, the assumptions of homogeneity of variances and normality were confirmed using the graphical examination of residuals (Quinn and Keough, 2002) and the Shapiro-Wilk's test, respectively. To respect the statistical assumptions, a logarithmic transformation was applied to the univariate indices when necessary and is indicated in the tables and figures.

Temporal variability

Temporal variability in the structure of macrobenthic infauna assemblages structure was identified using a permutational multivariate analysis of variance (PERMANOVA) with two sources of variation (Anderson, 2001; McArdle and Anderson, 2001) performed with 9999 random permutations of the appropriate units. Sources of variation were 1) year (fixed with 3 levels: 1980, 2005, and 2006), 2) station (fixed with 7 levels: E5, 24.75, 24, 23.60, 23, 22, 21), and 3) the interaction among these factors (3 years by 7 stations). When there were too few possible permutations to obtain a reasonable test, a p-value was calculated using 9999 Monte Carlo drawn from the appropriate asymptotic permutation distribution (Terlizzi et al., 2005). Significant terms in the full model were examined individually using appropriate pair-wise comparisons.

Multivariate patterns in macrobenthic assemblages were visualized using non-metric multidimensional scaling (MDS) ordination of dissimilarity matrices on √ transformed data. Discriminating species between years were recognized using the SIMPER procedure, based on √ transformed data. In order to detect temporal patterns in benthic infauna community characteristics in the LSLE, two-way analyses of variance (ANOVA) between stations and sampling years were used to compare univariate community characteristics (total density, S, H', J', Δ^+ and Λ^+), using the Tukey's test to calculate *a posteriori* comparisons (Underwood, 1997). The assumptions of homogeneity of variances and normality were verified using the graphical examination of residuals (Quinn and Keough, 2002) and the Shapiro-Wilk's test, respectively.

1.3 Results

1.3.1 Spatial structure of macrobenthic infaunal communities

A total of 80 species or taxa were identified in 2005 and 2006, within 52 different families, 23 orders, 14 classes and 9 phyla. Mean densities of macrobenthic organisms varied considerably in the study area, ranging from 69.3 to 754.7 ind. m^{-2} in the GSL, and 154.7 to 1091 ind. m^{-2} in the LSLE. Polychaeta were the dominant taxa in terms of density in the entire study area, varying from 55 % (station 17) to 94 % (station SPI) of the total macrofaunal composition. Polychaetes were more important in the LSLE than in the GSL, where they accounted for 82 % and 78 % of the total composition, respectively. Among the dominant species, the spionid *Spiophanes kroyeri* and the ampharetid *Ampharete lindstroemi* were more abundant in the LSLE, whereas the nereid *Ceratocephale loveni* and the lumbrinerid *Lumbrineris* sp. dominated in the GSL. Taxa such as Echinodermata, Arthropoda, and Mollusca were found in lower abundance in the study area, representing 6.3%, 5.3%, and 4.6% of the total composition, respectively. Regionally, the composition of molluscs was higher in the LSLE, due to the presence of the bivalve *Nucula delphinodonta*, while arthropod and echinoderm compositions were higher in the GSL, due mainly to important densities of the gammarid *Harpinia propinqua* and the ophiurid *Amphiura sundevalli*. Other taxa, from phyla Nematoda, Cnidaria, Nemertina, Sipuncula, and Chordata were also observed in both regions, representing 2.3% of the benthic composition in the LSLE and 4.9% in the GSL.

The CLUSTER analysis segregated the macrofauna from the study area into seven main groups (clusters) of stations: five groups at a 33% similarity level (I to V) and two groups at a 42% similarity level (VI and VII) (Fig. 3). Two clusters were located in the LSLE (II and III) and four in the GSL (I, IV, V, and VI), as shown in Figure 4. Cluster VI was located at the intersection between both regions. The five taxa predominantly responsible for the similarity within clusters are presented in Table 1a. Cluster II stations (E5 and 24) were found at the head of the LSLE and are characterized by high abundances of *A. lindstroemi*, *S. kroyeri* and *Trochochaeta multisetosa* (Table 2, Fig. 4). Most of the replicates of station 23, which is located across the shore from Rimouski and sampled in

2005 and 2006, belong to Cluster III (Table 2, Fig. 4). Polychaetes in high abundance, such as *A. lindstroemi*, *C. loveni,* and *Myriochele heeri,* contributed largely to the similarity within this group. Clusters VI and VII included most of the sampling stations and consisted predominantly of stations located in the GSL (Fig. 3). Cluster VI stations were found at the upper end of the LSLE (22 and 21) and at the northeastern end of Anticosti Island (20, 19 and 18), and were characterized by *C. loveni*, *Amphiura sundevalli,* and *Lumbrineris* sp. (Table 2, Fig. 4). Conversely, Cluster VII stations (TCA, CA, TCE, CE and SPI) were located in the Anticosti and Esquiman Channels, in the northeastern part of the GSL (Table 2, Fig. 4). According to the SIMPER analysis, species contributing principally to the differentiation from other clusters were *Lumbrineris* sp., *C. loveni,* and *Heteromastus filiformis* (Table 1a). Species such as *Tharyx* sp., *Lumbrineris* sp., and *Antalis occidentale* largely dominated Cluster V, which was composed of stations 17 and IC, located at the mouth of the Laurentian Channel and the Anticosti and Esquiman channels, respectively (Table 2, Fig. 4). Station BOI (Cluster I) was separated from the others by the presence of *Onuphis opalina*, *Axinopsida* sp., *Lumbrineris* sp., and *Pennatula aculeata* (Table 2, Fig. 4). Cluster IV (station 16), located in the GSL west of Cabot Strait, was characterized by high densities of *Tharyx* sp., *Lumbrineris* sp., and *Antalis occidentale* (Table 2, Fig. 4).

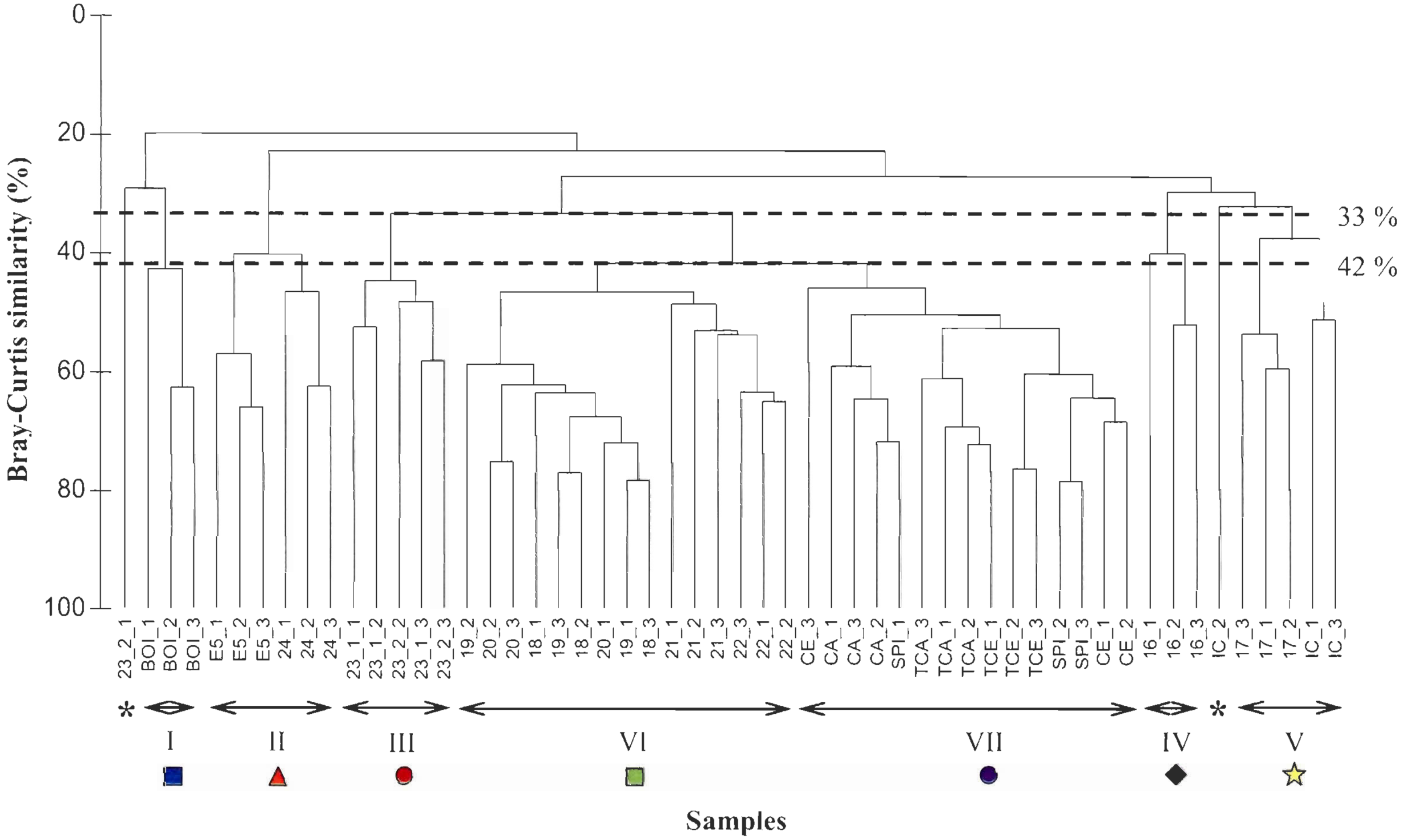

Figure 3. a) Hierarchical clustering with group average linking of √ transformed densities for each replicate, using Bray-Curtis similarity (%). The grouping of stations corresponded to the horizontal lines at 33 % similarity level (I to V) and 42 % similarity level (VI and VII). * represent an unclassified single replicate that were not included in further analyses.

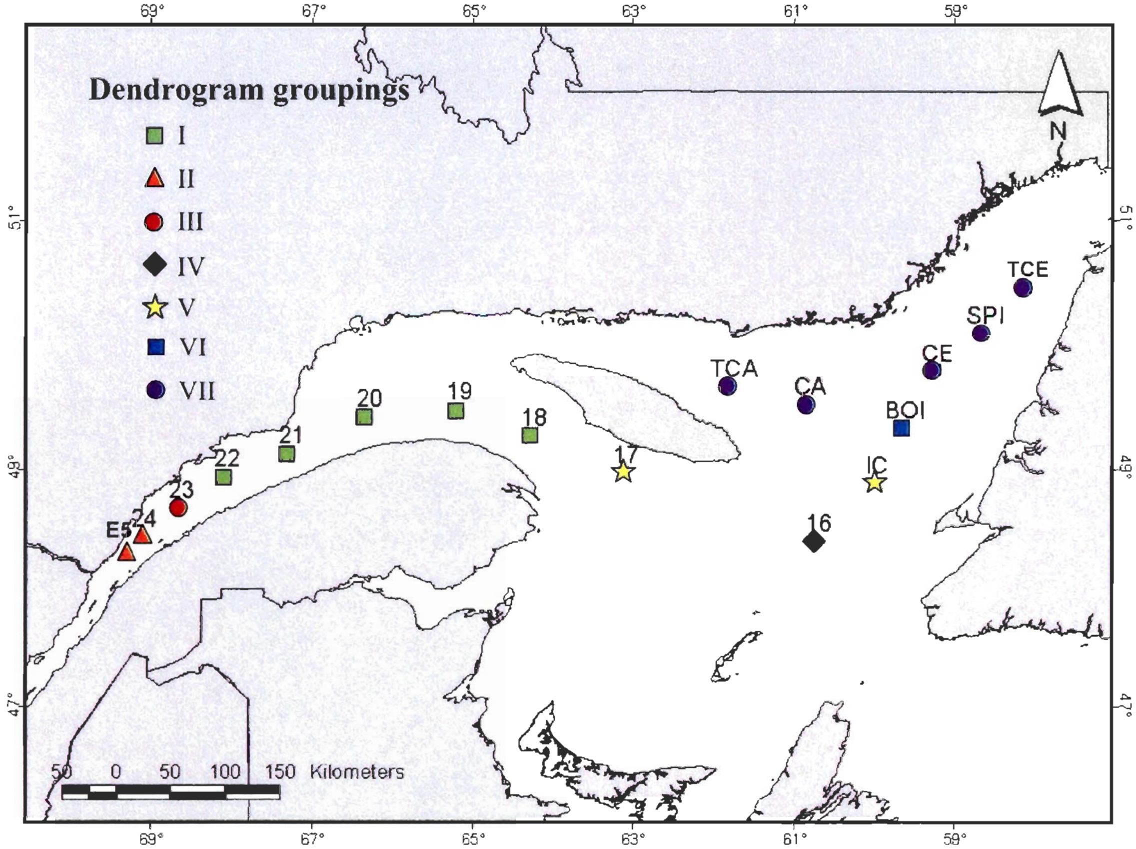

Figure 4. Map of the Lower St. Lawrence Estuary (LSLE) and Gulf of St. Lawrence (GSL) showing the locations of 17 sampling stations and their classification into 7 groups (I to VII), following a cluster analysis of species density data.

Table 1. Results of SIMPER analyses showing taxa with the greatest contribution (%) to the average Bray-Curtis similarity, based on √ transformed densities, of compared replicates within each cluster (I to VII) as well as the average similarity (%) for each group of samples.

Species	Contr. (%)	Species	Contr. (%)
Cluster I (Avg. similarity = 49.38)		**Cluster II** (Avg. similarity = 46.51)	
Onuphis opalina	37.46	*Ampharete lindstroemi*	17.40
Axinopsida sp.	31.44	*Spiophanes kroyeri*	16.07
Lumbrineris sp.	11.61	*Trochochaeta multisetosa*	11.80
Pennatula aculeata	11.27	*Terebellides stroemi*	10.20
		Maldanidae	9.57
Cluster III (Avg. similarity = 42.09)		**Cluster IV** (Avg. similarity = 44.05)	
Ampharete lindstroemi	31.12	*Lumbrineris* sp.	30.36
Ceratocephale loveni	18.84	*Amphiura* sp.	24.85
Myriochele heeri	15.08	*Tharyx* sp.	21.89
Axinopsida sp.	6.92	*Harpinia propinqua*	7.88
Tharyx sp.	4.63	Nemertea	7.88
Cluster V (Avg. similarity = 44.24)		**Cluster VI** (Avg. similarity = 53.71)	
Tharyx sp.	21.18	*Ceratocephale loveni*	25.83
Lumbrineris sp.	16.37	*Amphiura sundevalli*	17.34
Antalis occidentale	12.85	*Lumbrineris* sp.	14.91
Harpinia propinqua	8.23	*Heteromastus filiformis*	10.77
Amphiura sundevalli	7.95	*Ampharete lindstroemi*	10.39
Cluster VII (Avg. similarity = 53.92)			
Lumbrineris sp.	24.74		
Ceratocephale loveni	19.54		
Heteromastus filiformis	19.12		
Tharyx sp.	9.99		
Ampharete lindstroemi	4.19		

The changes in macrofaunal functional group distribution along a transect in the LSLE and the GSL are illustrated in Figure 5. The trophic structure of the LSLE was dominated by surface deposit feeders (SDF), contributing to 40-76% of total macrofaunal composition at stations E5 to 21. Surface deposit feeders, such as *S. kroyeri*, *A. lindstroemi,* and *T. multisetosa*, dominated at the head of the LSLE (stations E5 and 24), where subsurface deposit feeders (SBDF) like Maldanidae were also abundant. Continuing in this direction, species such as *A. lindstroemi*, *S. kroyeri,* and *M. heeri* were the most abundant SDF at upstream stations (stations 24 and 23). For example, near the boundary between the LSLE and the GSL (stations 22 and 21), SDF *M. heeri* and *A. lindstroemi* were once again dominant, but decreased gradually. A consequent increase in omnivores (O) was observed along the Laurentian Channel, mainly due to the increasing importance of *C. loveni*, *A. sundevalli,* and *Lumbrineris* sp. (stations 20, 19, and 18). Thereafter, a small decrease in omnivorous species was noted at the intersection of the Laurentian, Anticosti and Esquiman channels (stations 17, 16 and IC), whereas SDF species increased. Moreover, a high number of SBDF, such as Maldanidae, was observed at the intersection of Anticosti and Esquiman channels (station IC), and were more important in the GSL than in the LSLE. These organisms were also abundant at the head of Anticosti and Esquiman channels (stations TCA and TCE), counting for 38% and 27% of the total macrobenthic composition, respectively, even as omnivorous species like *Lumbrineris* sp. were dominant in this region of the GSL. A great number of SDF such as *Tharyx* sp., along with omnivores (i.e., *Lumbrineris* sp. and *H. filiformis*), were observed in the Anticosti Channel (station CA). However, only omnivores dominated stations in the Esquiman Channel (stations CE and

SPI), with high abundances of *C. loveni* and *Lumbrineris* sp. Omnivorous species, such as *O. Opalina* and *Lumbrineris* sp., also dominated the trophic structure at station BOI.

Among the other functional groups, Carnivores (C) and Filter feeders (FF) had only a minor presence in the study areas. A small increase in carnivore composition was observed in the LSLE, varying from 1 to 9.6 % from the head to the boundary of the GSL, whereas the highest abundance of FF was seen at station 23. In the gulf, both C and FF dominated at station BOI, representing respectively up to 11.5 and 15.3 % of the total benthic community. Sea pens (Pennatulacea, *P. aculeata*), were the most important carnivorous species, whereas bivalve species of Astartidae (*Astarte undata*) and Thyasiridae (*Axinopsida* sp.) were the most important filter feeders.

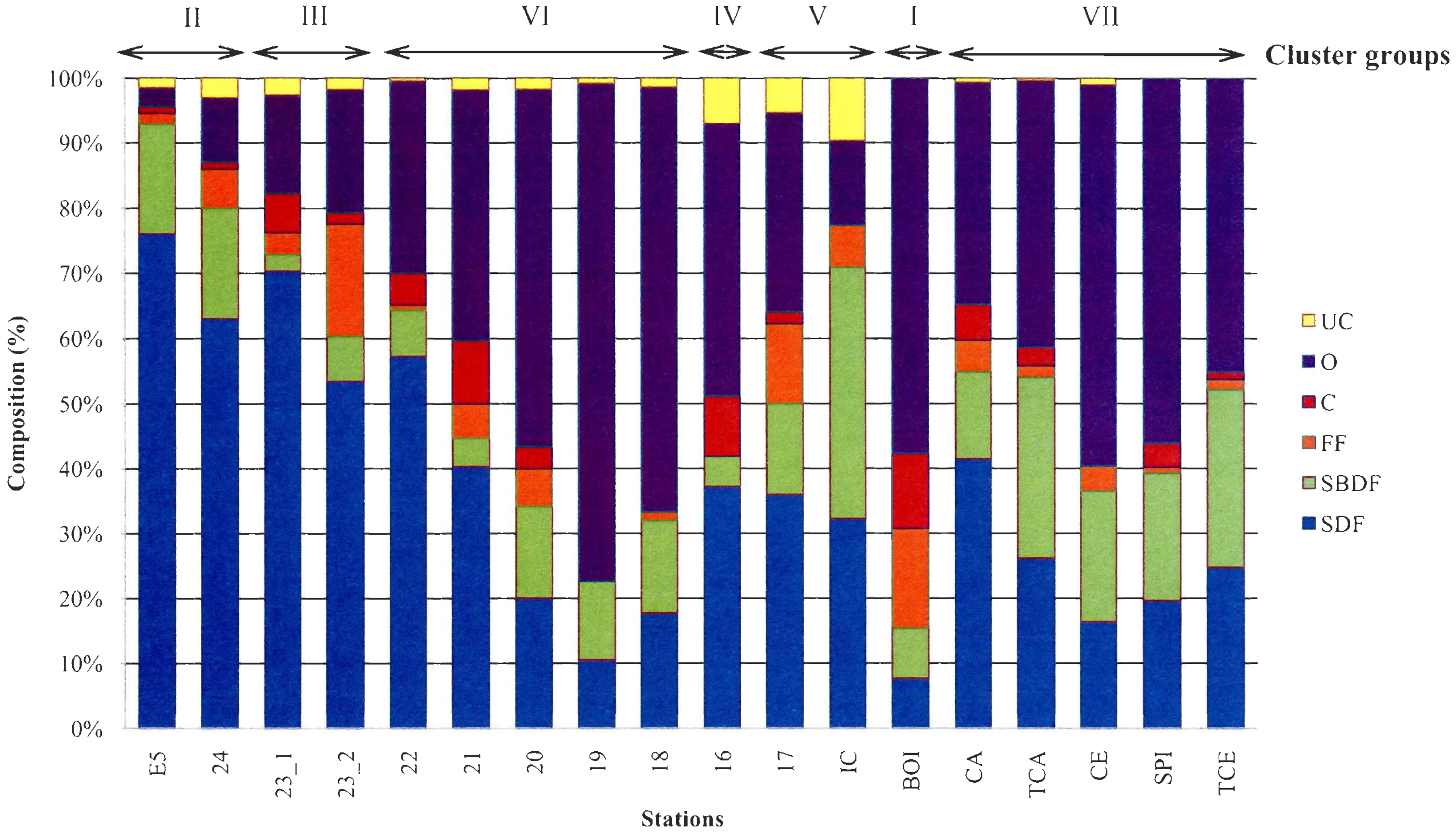

Figure 5. Composition (%) of the main macrofaunal functional groups sampled in the deep LSLE and GSL at the different stations in 2005 and 2006. SDF: Surface deposit feeders; SBDF: Subsurface deposit feeders; FF: Filter feeders; C: Carnivores; O: Omnivores; UC: Unclassified trophic groups. Clusters groups are identified on the top axis.

Univariate indices revealed differences among stations (Fig. 6). Total mean density of macrofauna species was highest at the head of the LSLE (E5), whereas station BOI exhibited the lowest value. This index was also high at station 22 and at the head of the Anticosti and Esquiman channels (TCA and TCE), while stations 16 and IC showed low densities of organisms. A similar spatial pattern was seen for AMBI and species richness (S), with the highest and lowest values observed at stations E5 and BOI, respectively. High values of Shannon-Wiener diversity (*H'*) were observed at stations 17 and CA, whereas lower diversities were found at stations BOI and 19. Conversely, station BOI exhibited the highest evenness (*J'*), followed by stations 17 and 16, while low values of *J'* were observed at stations E5, TCA and 22. Values of M-AMBI that are smaller than 0.62 are indicative of community moderately disturb to very disturb (<0.20). However none on the values calculated in the LSLE and in the GSL exhibited values smaller than 0.62 and many values were above 0.83, which means that the Ecological status are high (Fig. 6). This was the same pattern for the AMBI index.

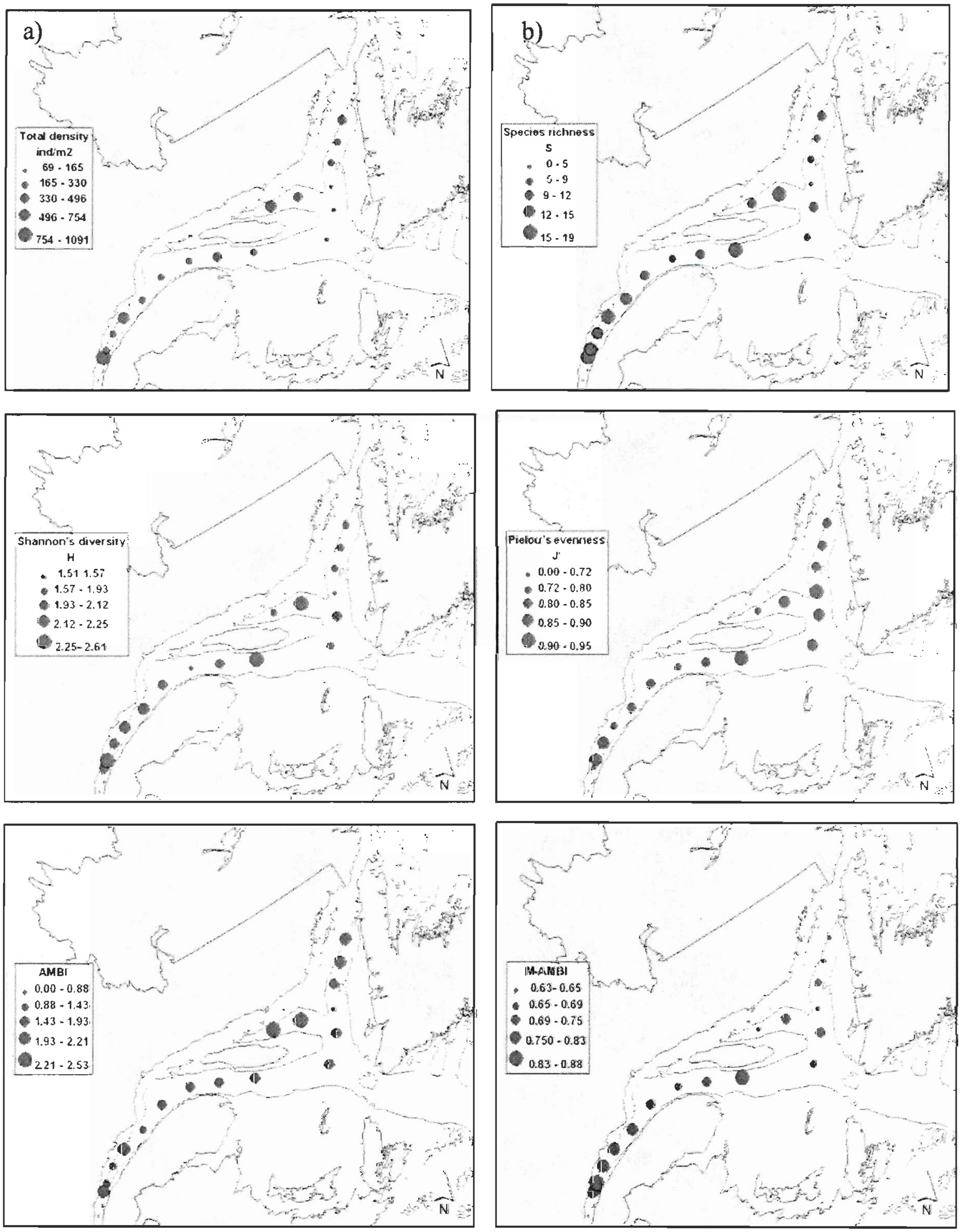

Figure 6. Total density (ind. m^{-2}), species richness (S), Shannon-Wienner diversity (H'), Pielou evenness (J'), AMBI, and M-AMBI at sampling stations in the study area.

1.3.2 Relationships between macrobenthic community structure and environmental factors

Stations sampled in 2005 and 2006 in the LSLE and GSL were distributed across a wide range of environmental conditions: depth (median: 323 m; range 257-434 m), bottom temperature (median: 5.40 °C; 4.87-5.79 °C), bottom salinity (median: 34.61 PSU; 34.38-34.86 PSU), oxygen saturation (median: 34.58%; 21.21-58.13%), mean grain size (median: 10.70 μm; 7.81-20.38 μm), and total organic matter content (median: 3.60%; 2.45 to 5.78%) (Table 1). Silt was the dominant grain size fraction in the LSLE and GSL, ranging from 65.6% to 88.5%. The clay fraction represented 10% to 32.6% of the sediment composition in the study area.

In the LSLE, mean grain size, salinity, and temperature best explained the pattern of species assemblages ($r_s = 0.432$) (Table 3a), with mean grain size as the single variable with the highest correlation ($r_s = 0.412$). In the GSL, temperature and salinity provided the best explanation of species composition ($r_s = 0.460$). The distribution pattern of functional groups in the LSLE was best correlated with temperature as a single variable ($r_s = 0.455$) and the combination of mean grain size, total organic matter, salinity, and temperature ($r_s = 0.465$). The highest correlation between functional assemblages and environmental parameters in the GSL was observed for temperature ($r_s = 0.282$), although the relation was relatively weak (Table 3b), due to several inter-correlations between environmental parameters. High correlations in the LSLE were observed for salinity and oxygen saturation (0.917), temperature and mean grain size (-0.819), and temperature and oxygen saturation

(0.794). In the GSL, mean grain size was highly correlated with organic matter content (0.837), whereas temperature was strongly negatively-correlated with depth (-0.809). These correlations could have a strong impact on analyses, as the effect of other important variables would not be detected. However, physical variables characteristic of estuaries, such as substrate type, salinity and temperature, are often strongly linked (Clarke and Green, 1988). As proposed by Callaway et al. (2002), it was decided to include all environmental variables in the analysis because the inter-correlations between environmental factors were not consistent for the entire study area.

In the LSLE, multiple linear regressions models explained up to 75% and 62% of total density and species richness (S) variances respectively, 20% of diversity (*H'*) variance and 57% of evenness (*J'*) variance (Table 4a). In addition, 31% of average taxonomic distinctness (Δ^+) variance and 26% of taxonomic distinctness (Λ^+) variance were explained in this analysis, whereas the models explained 65% and 90% of AMBI and M-AMBI variances, respectively. This analysis showed that depth and mean grain size best explained total density, S, *H'*, *J'*, AMBI, and M-AMBI. Also, oxygen saturation best explained total density, S, *J'* and Λ^+, whereas Δ^+, Λ^+, AMBI, and M-AMBI were best explained by total organic matter. Regression models calculated for the GSL explained up to 64% of total density, 23% of S, 15% of *H'*, and 35% of *J'* (Table 4b). Up to 47% and 17% of Δ^+ and Λ^+ variances, respectively, was explained by the models, whereas they explained up to 58% and 59% of AMBI and M-AMBI variances. Temperature was present in all regression models, except for *J'*, whereas mean grain size seemed to explain, in part, total density, S, *H'*, and Δ^+. Oxygen saturation best explained total density, *H'*, and *J'*, while Δ^+ and Λ^+ were best explained by total organic matter.

Table 2. Summary of results from BIO-ENV analyses for the Lower St. Lawrence Estuary and the Gulf of St. Lawrence, according to a) species and b) functional group. Spearman rank correlations (r_s) between biotic and abiotic similarity matrices, with highest correlations in bold. Biotic data were √ transformed; abiotic matrix was constructed using Euclidean distances. Environmental variables used in the analysis were depth (D, m), mean grain size (MS, μm), bottom oxygen saturation (%O_2, %), total organic matter content in the sediment (TOM, %), bottom temperature (T, °C), and bottom salinity (S, PSU).

a) Species

	Lower Estuary	Gulf
D	0.323	0.309
MS	**0.412**	0.161
%O_2	0.244	0.356
TOM	0.396	0.147
T	0.312	**0.414**
S	0.396	0.294
Best Correlation	MS, S, T (**0.432**)	T, S (**0.460**)

b) Functional groups

	Lower Estuary	Gulf
D	0.395	0.099
MS	0.441	0.006
%O_2	0.258	0.227
TOM	0.392	0.023
T	**0.455**	**0.282**
S	0.270	0.166
Best Correlation	MS, TOM, T, S (**0.465**)	T (**0.282**)

Table 3. Results of linear regression analyses estimating total density (Log_{10} ind. m^{-2}), species richness (S), diversity (*H'*, $\log_e$), evenness (*J'*: *H'*/log S^{-1}), average taxonomic distinctness (Δ^+), and variation in taxonomic distinctness (Λ^+) between stations in a) the LSLE and b) the GSL. Environmental variables used in regression models were depth (D, m), bottom temperature (T, °C), % of oxygen saturation (%O_2, %), mean grain size (MS, µm), and % of total organic matter in the sediment (TOM, %). Regression coefficients ± Standard Error; total R^2 (and adjusted R^2); MSE: Mean Squared Error.

a) LSLE

Diversity Index	**Intercept**	**Model**	**R^2 (Adj R^2)**	**MSE**
Log_{10} Total density	-51.97 ± 5.41	D (-0.06 ± 0.02) + MS (0.90 ± 0.33) + %O_2 (-0.49 ± 0.16) + T (13.59 ± 5.37)	0.75 (0.64)	0.20
S	-571.03 ± 395.22	D (-0.77 ± 0.42) + MS (9.5 ± 5.73) + % O_2 (-5.53 ± 2.83) + TOM (9.14 ± 7.90) + T (154.60 ± 92.44)	0.62 (0.46)	3.37
H' (Log_e)	5.72 ± 1.81	D (-0.009 ± 0.005) + MS (-0.07 ± 0.05)	0.20 (0.10)	0.27
J'	7.58 ± 2.18	D (0.005 ± 0.002) + MS (-0.12 ± 0.03) + %O_2 (0.09 ± 0.03) + T (-1.77 ± 0.52)	0.57 (0.44)	0.07
Δ+	-418.15 ± 371.23	TOM (4.26 ± 1.74) + S (13.69 ± 10.68)	0.31 (0.21)	4.55
Λ+	1336.24 ± 397.24	% O_2 (-20.62 ± 11.18) + TOM (-63.56 ± 31.57)	0.26 (0.16)	76.16
AMBI	-1527.36 ± 380.25	D (0.007 ± 0.03) + MS (0.44 ± 0.71) + TOM (0.73 ± 1.17) + S (7.53 ± 10.39)	0.65 (-0.73)	0.26
M-AMBI	31.88 ± 12.62	D (-0.003 ± 0.001) + MS (-0.06 ± 0.02) + TOM (-0.09 ± 0.04) + S (-0.84 ± 0.34)	0.90 (0.49)	0.00028

b) GSL

Diversity Index	**Intercept**	**Model**	**R^2 (Adj $R^{2)}$**	**MSE**
Total density (Log_{10})	8.26 ± 1.15	MS (-0.07 ± 0.02) + %O_2 (-0.008 ± 0.005) + T (-0.85 ± 0.20)	0.64 (0.60)	0.19
S	29.08 ± 33.72	D (0.03 ± 0.02) + MS (-0.78 ± 0.27) + T (-3.44 ± 5.16)	0.23 (0.15)	3.63
H' (Log_e)	6.06 ± 2.18	MS (-0.06 ± 0.03) + %O_2 (0.01 ± 0.009) + T (-0.73 ± 0.37)	0.15 (0.07)	0.36
J'	0.67 ± 0.04	%O_2 (0.004 ± 0.001)	0.35 (0.33)	0.06
Δ+	-42.63 ± 64.77	D (0.18 ± 0.04) + MS (-0.47 ± 0.45) + TOM (-4.10 ± 1.74) + T (20.44 ± 9.16)	0.47 (0.40)	6.09
Λ+	2433.01 ± 849.81	TOM (-41.57 ± 29.38) + T (-298.81 ± 115.51)	0.17 (0.12)	105.95
AMBI	-88.91 ± 71.54	D (-0.009 ± 0.006) + %O_2 (-0.05 ± 0.03) + TOM (-0.32 ± 0.21) + T (-2.66 ± 1.20) + S (3.22 ± 2.25)	0.58 (0.23)	0.14
M-AMBI	11.29 ±11.13	D (0.001 ± 0.0009) + %O_2 (0.007 ± 0.004) + TOM (0.06 ± 0.03) + T (0.20 ± 0.19) + S (-0.36 ± 0.35)	0.59 (0.25)	0.003

1.3.3 Temporal variability of macrobenthic communities structure

Significant temporal variability was observed in macrobenthic species assemblages within the LSLE, as indicated by the permutational multivariate analysis of variance (PERMANOVA) (Table 5). The global analysis showed a significant interaction between years and stations ($P = 0.0001$). Pairwise comparisons revealed significant differences in species assemblages between years 1980, 2005, and 2006 at stations 25, 24.75, 24, and 23. This relationship was revealed by the non-metric multidimensional scaling (MDS) ordination, which showed different clusters for each of the sampling years (Fig. 7a). Significant temporal changes were also observed for functional groups assemblages between years ($P = 0.0001$), whereas the interaction between years and stations was not significant ($P = 0.4836$) (Fig. 7b). However, even without significance, small variations over years were noted at stations 25, 23.60, and 23. No important changes were observed at station 23 between two consecutive years (2005 and 2006), and thus these samples were pooled together in subsequent analyses.

Results showed temporal changes between 1980 and 2005-2006 in the benthic composition of the LSLE. Annelida (polychaetes) increased from 66 to 78% over years, whereas a small decrease in the proportion of all other phyla was generally observed (Fig. 8a). Arthropoda and Mollusca decreased from 10% to 5% and from 13% to 7% respectively, while the variation in Echinodermata abundance was only 1%. Moreover, an important temporal change in functional groups composition was also observed (Fig. 8b).

Surface deposit feeders increased from 39% to 65%, whereas omnivores decreased from 39% to 15%. Small decreases in subsurface deposit feeders and filter feeders were noted, whereas the increase in carnivores was only 1 %.

The contributions of genus and functional groups to similarities within and between years, resulting from the SIMPER analysis, are presented in Table 6. The polychaetes of *Lumbrineris*, *Harpinia*, and *Melinna* spp. contributed most to the similarities in species assemblages, whereas for √ transformed densities, surface deposit feeders (SDF) and omnivores (O) dominated at the stations sampled in 1980 (Table 5a). Similarities among samples from 2005-2006 were due to the presence of the dominant polychaetes *Ampharete*, *Myriochele*, and *Ceratocephale*. Surface deposit feeders contributed for more than 50% in 2005-2006 samples. Benthic assemblages were 66% dissimilar between 1980 and 2005-2006, whereas functional groups were 30% dissimilar. From these results, the polychaetes, *Maldane* and *Melinna* along with the bivalve *Thyasira,* best explained the variability between sampling years for √ transformed densities (Table 6). Differences between years were mainly due to surface deposit feeders, whereas subsurface deposit feeders and omnivores contributed equally to the dissimilarity.

Table 4. Permutational analysis of variance (PERMANOVA) results testing the effect of year, station, and their interaction by species and functional group assemblage, based on the Bray-Curtis similarity matrices. Data were √ transformed prior to analysis.

Source of variation	df	MS	Pseudo-*F*	*P* (perm)
Species assemblages				
Year	2	7813.80	9.12	0.0001
Station	6	5394.20	6.30	0.0001
Year x Station	6	2039.40	2.38	0.0001
Residual	28	856.91		
Functional groups assemblages				
Year	2	1402.60	8.21	0.0001
Station	6	1707.10	10.00	0.0001
Year x Station	6	170.39	1.00	0.4836
Residual	28	170.79		

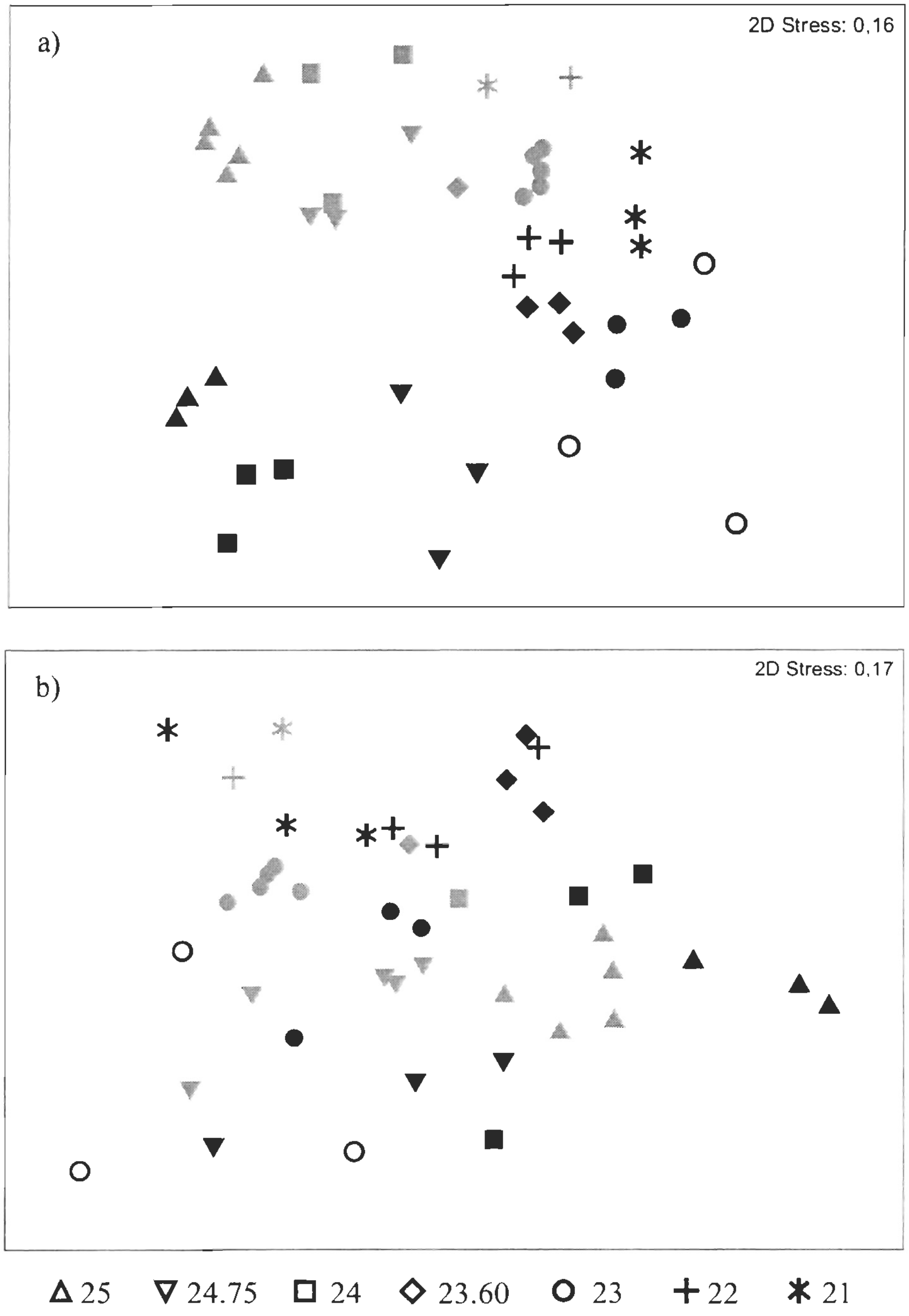

Figure 7. Two-dimensional nMDS ordination of a) macrofaunal species assemblages and b) functional groups from 1980 (grey), 2005 (black), and 2006 (white) at 7 stations in the LSLE, according to √ transformed densities (genus-level). Station 23 was only sampled in 2006.

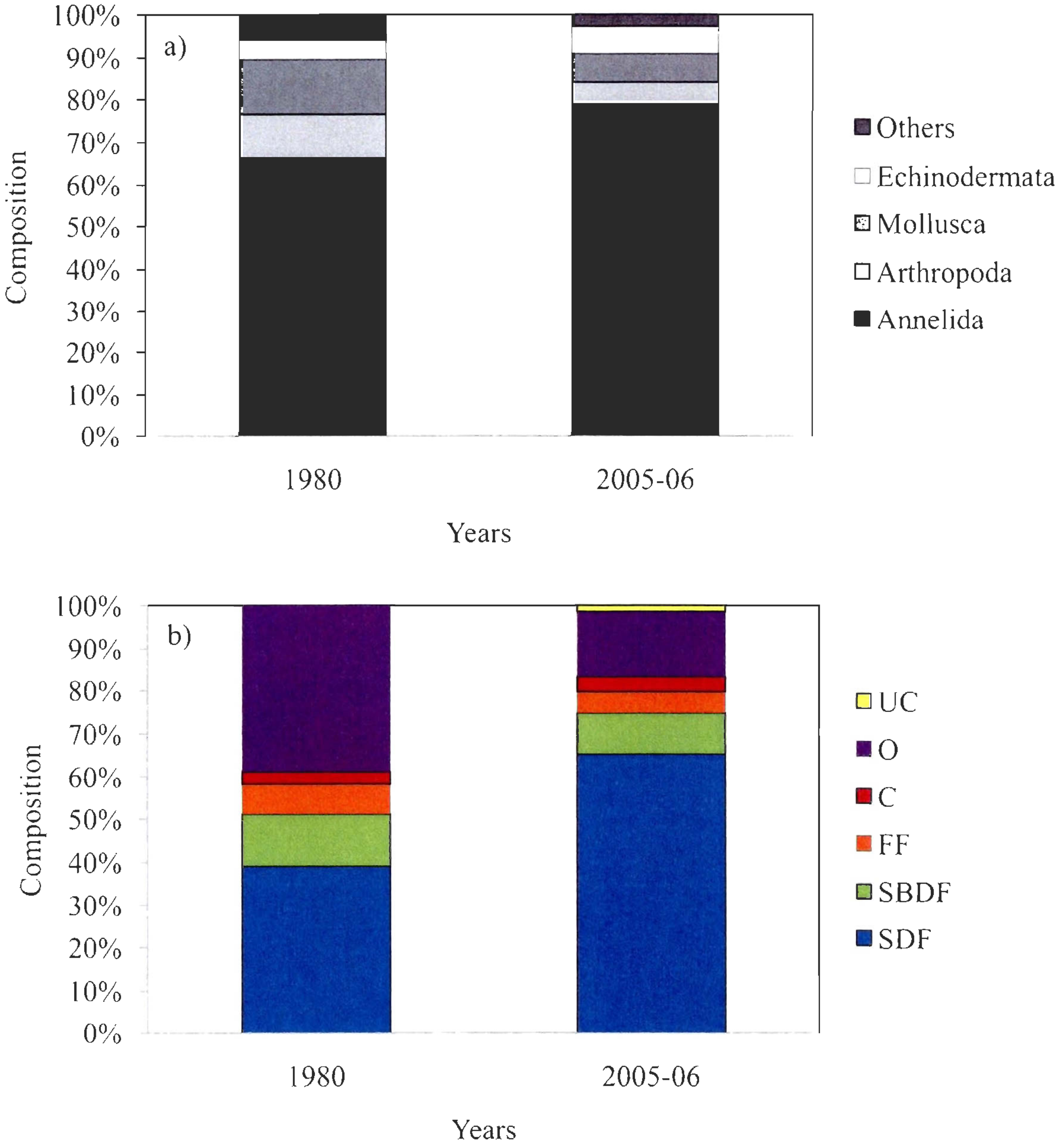

Figure 8. Composition of the main a) taxonomic and b) functional groups sampled in the LSLE, in 1980 and 2005-2006. Others: Chordata, Cnidaria, Nemata (Nematoda), Nemertea, Priapula, and Sipuncula. SDF: Surface deposit feeders; SBDF: Subsurface deposit feeders; FF: Filter feeders; C: Carnivores; O: Omnivores; UC: Unclassified trophic groups.

Table 5. Results of SIMPER analyses showing the greatest contribution (%) by taxa (Genus level) and functional group to a) the average Bray-Curtis similarity of compared replicates within a year (1980 and 2005-2006) as well as the average similarity (%) for each year and b) average Bray-Curtis dissimilarity of compared replicates between years (1980 and 2005-2006) as well as the average dissimilarity (%), based on √ transformed densities.

a)

Species		Functional groups	
Genus	**Contr. (%)**	**Genus**	**Contr. (%)**
1980 (Avg. similarity = 46.98)		**1980** (Avg. similarity = 75.87)	
Lumbrineris	12.87	SDF	38.00
Harpinia	10.02	O	28.90
Melinna	9.90	SBDF	15.75
Trochochaeta	8.01	FF	11.32
Onuphis	6.43		
2005-06 (Avg. similarity = 35.31)		**2005-06** (Avg. similarity = 68.09)	
Ampharete	19.38	SDF	52.32
Myriochele	10.42	O	17.98
Ceratocephale	8.92	SBDF	14.42
Trochochaeta	6.33	C	8.13
Lumbrineris	5.87		

b)

Species		Functional groups	
Species	**Contr. (%)**	**Species**	**Contr. (%)**
1980 & 2005-06 (Avg. dissim. = 69.96)		**1980 & 2005-06** (Avg. dissim. = 30.21)	
Spiophanes	5.89	SDF	30.89
Myriochele	5.25	SBDF	22.27
Ampharete	4.96	O	22.26
Ceratocephale	4.51	FF	14.18
Maldanidae	3.99	C	10.40

ANOVA results indicated that mean species richness (S) and Shannon-Wiener diversity (*H'*) were significantly higher in 1980, compared to 2005-2006 ($p = 0.0001$ and 0.0019 respectively) (Table 7). Inversely, AMBI was significantly higher in 2005-2006 ($p < 0.0001$). Nevertheless, a significant interaction between stations and years was observed for S ($p = 0.0019$) and AMBI ($p = 0.0002$) (Table 7). Total density and average taxonomic distinctness (Δ^+) was significantly different among stations. The number of species decreased from 1980 to 2005-2006, mainly at stations 25 and 24.75. Total density was higher in 2005-2006 whereas Pielou evenness was higher in 1980; unlike with M-AMBI, these variations were not significant (Table 7).

Table 6. Results of two-way ANOVAs, showing effects of sampling year (1980 and 2005-2006), station, and their interactions on total density (ind. m^{-2}), species richness (S), Shannon-Wiener diversity (H'), Pielou evenness (J'), average taxonomic distinctness (Δ^+), taxonomic distinctness variation (Λ^+), AMBI, and M-AMBI. Total density was $\log_{10}$ transformed.

Source of Variation	df	**Log_{10} Total density**			**S**			**H' (Log_e)**		
		MS	*F*	P	MS	*F*	P	MS	*F*	P
Year	1	0.027	0.88	0.357	345.24	43.84	< 0.0001	1.16	11.72	0.0019
Station	6	1.60	8.69	< 0.0001	88.33	11.22	< 0.0001	0.060	0.60	0.728
Station x Year	6	0.14	0.78	0.595	36.82	4.68	0.0019	0.18	1.80	0.134
Residual	28	0.031			7.88			0.099		

Source of Variation	df	**J'**			**Δ^+**			**Λ^+**		
		MS	*F*	P	MS	*F*	P	MS	*F*	P
Year	1	0.0092	1.03	0.320	6.00	0.35	0.561	1669.02	0.38	0.543
Station	6	0.018	2.07	0.0874	51.45	2.97	0.0228	5191.24	1.18	0.347
Station x Year	6	0.017	1.91	0.114	13.11	0.76	0.610	1597.00	0.36	0.897
Residual	28	0.0090			17.35			4411.08		

Source of Variation	df	**AMBI**			df	**M-AMBI**		
		MS	*F*	P		MS	*F*	P
Year	1	2.47	21.00	< 0.0001	1	0.024	13.51	0.169
Station	6	0.23	1.92	0.1199	6	0.011	2.85	0.425
Station x Year	6	0.79	6.69	0.0002	6	0.0051	6.30	0.296
Residual	28	0.33			14	0.0088		

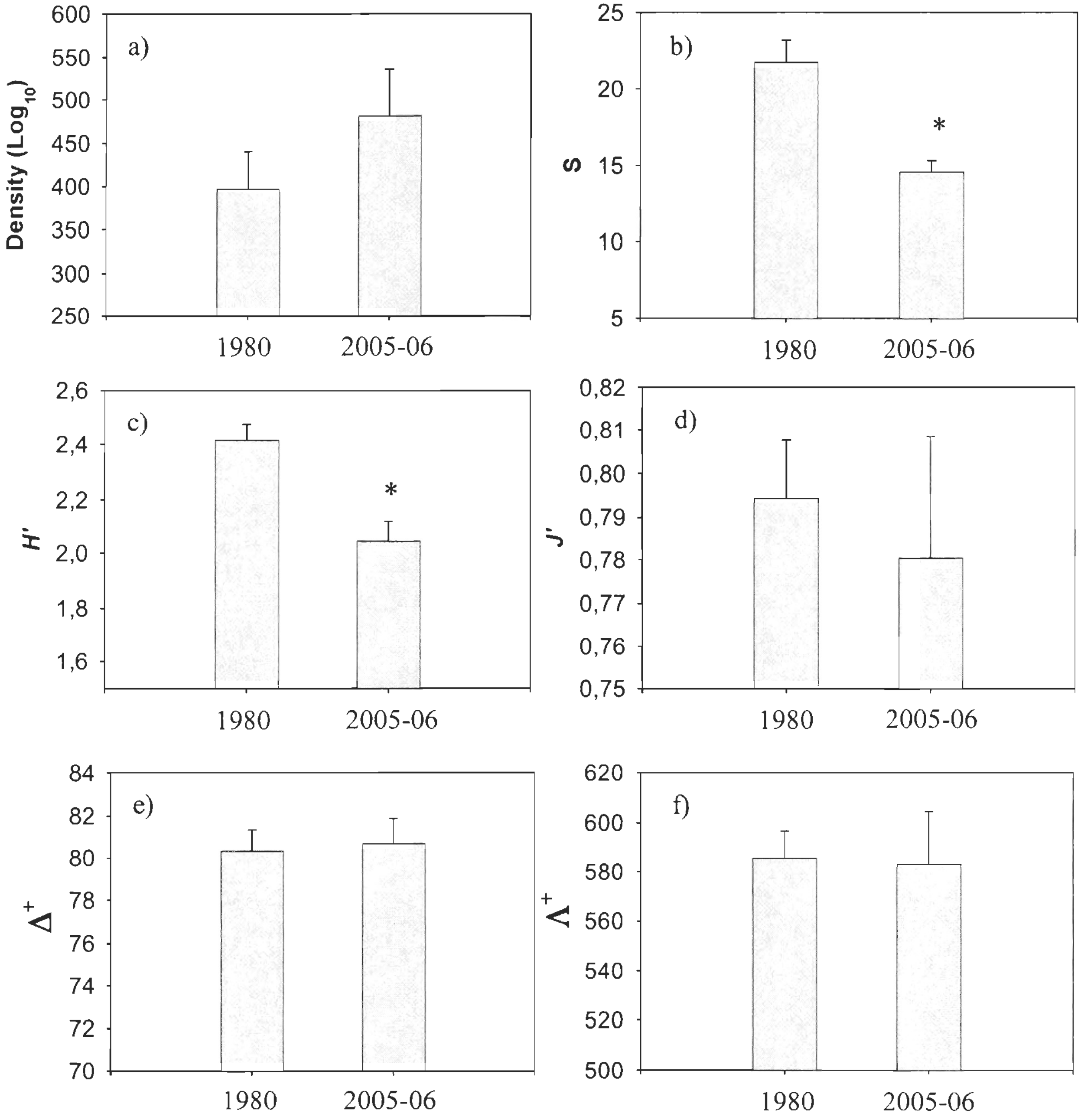

Figure 9. Mean a) total density (ind. m^{-2}); b) species richness (S); c) Shannon-Wiener's diversity index (*H'*); d) Pielou's evenness (*J'*); e) average taxonomic distinctness (Δ^+); and f) variation in taxonomic distinctness (Λ^+) in 1980 and 2005-06 in the LSLE. Error bars: ± Standard error; * above bars indicate significant differences ($p < 0.05$).

1.4 Discussion

The present study is the first attempt to relate spatial and temporal variations of macrobenthic infauna communities to environmental conditions and to establish the Ecological Quality Status condition in the deep waters of the Estuary and the Gulf of St. Lawrence (EGSL). Linking benthic communities to physical parameters of their environment is generally accepted as an important first step when describing distributional patterns (Flint and Holland, 1980; Freeman and Rogers, 2003). Establishing such relationships will allow for better predictions on how, and to what extent, natural or anthropogenic influences affect the distribution of communities.

1.4.1 Spatial distribution of macrobenthic assemblages

There appeared to be several, distinct boundaries between benthic communities in the study area, identified by changes in community structure and related to particular regions of the EGSL. The hierarchical clustering analysis divided the St. Lawrence into seven different benthic zones which corresponded to the biogeographic regions described by Brunel et al. (1998) that were separated on the basis of physiographic and bathymetric criteria.

The cluster analysis identified different infauna assemblages in the LSLE, corresponding to those described earlier by Ouellet (1982) and Massad (1975). Small annelids, molluscs, and crustaceans dominated the infauna composition at the head of the estuary, where most are surface deposit feeders such as ampharetid and spionid polychaetes, and subsurface deposit feeders (group II). This is in accordance with Belley et al. (2010) that observed only surface bioturbation activities in this area. Located at the confluence of the LSLE and the Saguenay Fjord, this area is characterized by abrupt changes in depth. This topographic feature, associated with tidal currents, induces persistent upwelling (Therriault and Lacroix, 1976; Koutitonsky and Bugden, 1991). The intense tidal mixing introduces high proportions of phytoplankton and zooplankton from the surface towards deep waters, constituting an important food supply for benthic organisms. As was noted by Ouellet (1982), we also observed a high number of biogenic structures, especially large burrows of head-down subsurface deposit-feeding maldanids, which are active bioturbators and bioirrigators, making food available for other deposit feeders. The benthic community at station 23 (group III) in the middle estuary differed from those in the upper and lower estuary, dominated principally by small surface deposit feeder polychaetes, such as *A. lindstroemi* and *M. heeri*, and some omnivorous species. Station 23 was also the deepest site sampled in the LSLE, located in the middle of a deep basin (Bugden, 1991). This topographic feature of the Laurentian Channel may influence the benthic community characteristics in this area. The small biogenic structures observed at this station suggested that deep-dwelling organisms did not dominate and that bioturbation, with the exception of the sediment interface, was less intense compared to the upper estuary, as a result of low oxygen concentration and food supply.

Along the estuarine gradient, towards the mouth of the Laurentian Channel, omnivores gradually dominated macrobenthic species assemblages. These findings were supported by previous observations in this region (Massad, 1975; Massad and Brunel, 1979; Ouellet, 1982; Desrosiers et al., 2000). In the transition zone between the Estuary and the Gulf, surface deposit feeders gradually decreased, whereas omnivores and subsurface deposit feeders increased simultaneously (group VI). The Anticosti Gyre, at the northwestern end of Anticosti Island, has a sloping bottom, which might receive occasional organic inputs arising from local phytoplankton blooms and horizontal advection of organic material from the near-shore zone (Desrosiers et al., 2000). Consequently, the decrease in food supply might favour the presence of mobile omnivores and subsurface deposit feeders (Fauchald and Jumars, 1979; Pearson and Rosenberg, 1978).

Macrobenthic assemblages in Anticosti and Esquiman channels were characterized by omnivores and deposit feeder species, whereas subsurface and surface deposit feeders were almost both equally abundant (group VII). As previously mentioned, the Anticosti Channel, similar to the Anticosti Gyre zone, might receive irregular inputs of organic matter which favour the subsurface deposit feeder and omnivore groups because of their greater mobility (Desrosiers et al., 2000). Moreover, the Anticosti Channel is characterized by low annual primary productivity (Steven, 1975; de Lafontaine et al., 1991), thus a benthic community comprised entirely of surface deposit feeders would not be sustainable (Desrosiers et al., 2000). It was not surprising to find a high proportion of subsurface deposit feeders in this area, with benthic assemblages similar to those found in the Anticosti Gyre. On the contrary, benthic assemblages in the Laurentian Channel mouth were dominated by deposit feeders and omnivores (group IV). According to Steven (1975) and de Lafontaine et al. (1991), the annual primary production in the Cabot Strait region is relatively low. However, due to topography, the Cabot Strait site is a relatively deep settling basin, which leads to an accumulation of organic matter as sediment on the seabed (Desrosiers et al., 2000). Thus, the deep macrobenthos may be receiving a regular flux of particulate matter from the water column, which could favour the surface deposit feeder group over the subsurface deposit feeders, as was observed in the present study.

Results showed that station BOI (group I) was very different relative to other stations in terms of benthic assemblages. This station was strongly dominated by the mobile omnivorous scavenger *Onuphis opalina* and the filter feeders *Axinopsida* sp. and *Pennatula aculeata*, with deposit feeders being poorly represented. Because of the seafloor topography, which is characterized by an undulating bottom (Brunel et al., 1998), environmental conditions were highly-variable at the mouth of the Esquiman Channel. Fluxes of organic matter sedimenting to the bottom in this area are relatively low, compared to the head of channels, which receive more food supply from the water column. In the same way, stations at the intersection of Anticosti and Esquiman Channels and south of Anticosti Island had similar benthic assemblages (group V). Surface and subsurface deposit feeders dominated in these benthic communities, but with different assemblages compared with other stations in the Gulf. The presence of the scaphopod *Antalis occidentale*, which feeds on microscopic detritus and organisms, largely contributed to this dissimilarity.

1.4.2 Spatial variability of benthic diversity

Univariate indices of diversity revealed high total density and species richness at the head of the LSLE, due to the high sedimentation rate prevailing in this area (Thibodeau et al., 2006). However, this region revealed low evenness and Shannon diversity values, because only a few of the dominant infaunal species were well-adapted to such conditions. In the middle section of the estuary, decreases in total abundance, species richness, and Shannon-Wiener diversity values were observed, compared to the upper and lower estuary. Located in the deepest portion of the Laurentian Channel, the middle estuary was characterized by a low sedimentation rate and a low oxygen level. This trend in diversity indices for the region was previously noted by Ouellet (1982). Many studies have demonstrated the importance of hydrological factors and sediment characteristics in structuring the soft-bottom communities of deep basins (Snelgrove and Butman, 1994; Rumohr et al., 1997; Bondsdorff and Pearson, 1999). The high evenness value at this station indicates that no one species was dominant, but rather that they were distributed equally in the benthic community.

In the gulf, at the northwestern end of Anticosti Island, a decrease in all diversity indices was observed, reflecting the irregular inputs of organic matter and the subsequent decrease in food supply (Desrosiers et al., 2000). In agreement with the increasing abundance of omnivorous species in the Anticosti Gyre, such environmental conditions favour the development of those few tolerant species adapted to low levels of organic matter, as demonstrated by the low evenness values. However, the area south of Anticosti Island revealed increasing values in species richness and Shannon diversity, indicative of changes in the environmental parameters for this area. This transition region between the estuary and the gulf favoured the increase of deposit feeders, with a consequent decrease in the proportion of omnivorous species. In the gulf, at the intersection of channels, total density, species richness, and Shannon diversity was very low. This station, which was the deepest site in the study area, may be receiving less organic matter than other stations, considering the low sedimentation rate. According to the accepted model of deepwater circulation in the gulf (Koutitonsky and Bugden, 1991), bottom waters entering the Laurentian Channel are well oxygenated, due to the weak respiration and organic matter mineralization of local sinks to the deep layers (Coote and Yeats, 1979).

In the northeastern part of the gulf, total density increased gradually while approaching the head of Anticosti and Esquiman Channels. These areas, similarly to the head of the Laurentian Channel, are characterized by sloping bottoms and intense mixing waters, which increases fluxes of organic matter to the seafloor as previously described. However, low Shannon diversity and evenness values were obtained in the Anticosti and

Esquiman channels, as observed by Long and Lewis (1987). This was largely due to the dominance in this area by a small number of opportunistic species such as capitellid, nereid, and lumbrinerid polychaetes.

1.4.3 Influence of environmental variables on macrobenthic communities structure

Results indicated that sediment composition (mean grain size and total organic matter) best explained the distribution of benthic communities in the LSLE. In the study area, deep sediments mainly consisted of fluid mud, composed of silt-clay, in agreement with Loring and Nota (1973). Under the energetic estuarine conditions prevailing at the head of the LSLE, sediment grain size and sand content were higher, with clay-sized sediment being deposited in the lower energetic portion of the estuary (Loring and Nota, 1973). The presence of the suspension feeder species, *Potamilla neglecta* and *Spiochaetopterus* sp., mostly at the head of the LSLE, was explained by high concentrations of sinking particles, resulting from intense mixing waters and high sedimentation rates, as suggested by Ouellet (1982). Massad and Brunel (1979) and Robert (1979) noted that species richness increased with sand content, as this provides a variety of microhabitats for the benthic infauna (Sanders, 1968). The linear multiple regression analyses confirmed the influence of sediment grain-size on the majority of diversity indices in the LSLE.

Our results showed that feeding strategies were influenced more by organic matter than species assemblages. Changes in functional groups that were observed when moving away from the head of the LSLE might be related to declining food resources. The amount and the quality of the organic material in the sediment play a key role in influencing the vertical distribution and trophic structure of macrofaunal communities (Snelgrove and Butman, 1994; Dauwe et al., 1998). Previous studies have demonstrated that sedimentation rates decrease exponentially with distance seaward along the Laurentian Trough (Silverberg et al., 1986; Smith and Schafer, 1999; Thibodeau et al., 2006). As the sedimentation rate decreases, the organic matter reaching the seafloor may also decrease, in agreement with the gradual increase of mobile omnivorous species along the estuary. Additionally, changes in taxonomic distinctness indices seem to be influenced by the organic matter content in the entire study area. In general, a lowering of the hierarchical level of taxonomic diversity with increasing level of perturbation should be observed in physically-stressed areas (Warwick and Clarke, 1995). As expected, a decrease in average taxonomic distinctness was observed at the head of the Laurentian, Anticosti and Esquiman channels, reflecting the environmental instability related to higher inputs in organic matter and lower oxygen concentration observed in the heads. Subsequently, the highest values of AMBI were associated with these most-perturbed sites, with their high organic matter contents and low oxygen saturations. However, these high values are largely under the level that could be considered critic for the Ecological Status (Borja et al. 2000). The AMBI values in our study for the Laurentian channel never reach 3.3 (lever for moderate quality Ecological

Status) suggesting that even with permanent hypoxic condition the St. Lawrence Estuary and Gulf are relatively in good and high quality status.

Despite their low variability, bottom temperature and salinity were among the factors that best described species assemblages and functional group distribution, as well as many diversity indices in the study area. Bugden (1991) showed that changes in along-channel bottom temperature appear to be compensated by changes in salinity. In this study, spatial gradients of bottom temperature and salinity were observed with decreasing values from the gulf towards the heads of the Laurentian, Anticosti, and Esquiman channels, ranging from 4.87 to 5.79 °C and from 34.38 to 34.86 PSU, respectively. Moreover, a number of studies have revealed that temperature and salinity were major factors affecting macrofauna species distribution and community structure within estuaries (Grebmeier et al., 1989; Ysebaert et al., 2002; Teixeira et al., 2008). Beuchel et al. (2006) noted that even small variations in temperature had significant impacts effects on benthic assemblages. Cusson et al. (2007) showed that bottom salinity and temperature were the most important environmental variables (among depth of site, bottom temperature, salinity, physical and chemical sediment characteristics) determining benthic assemblage patterns on the Canadian Arctic continental shelf. They also demonstrated, using multiple regression analyses, that variance in species richness and benthic community diversity was best explained by variance in salinity. Witman et al (2008) demonstrated that significant effects of chlorophyll *a* co-varied with the effects of salinity could explain benthic species diversity, which suggests that environmental stress as well as productivity influences diversity in the EGSL.

In the study area, our results showed that temperature and salinity were highly inter-correlated with other environmental parameters, such as oxygen, mean grain size, and depth. Clarke and Warwick (1994) have suggested substituting a single facter instead of several, correlated factors. However, studies have rarely been able to separate the physical variables that are characteristic of estuaries, such as substrate type, salinity, and temperature, because these variables are often tightly linked (Clarke and Green, 1988). The inter-correlation between environmental variables can strongly influence the results and then dissimulate the effect of other important factors. For example, dissolved oxygen concentration is a function of temperature, salinity, hydrodynamics, and organic matter content (Diaz and Rosenberg, 1995). Therefore, the acute oxygen gradient observed in the study area should strongly influence benthic community structure and diversity indices, especially in the hypoxic zone of the LSLE. Our results indicated an influence of oxygen saturation on diversity indices, but not on benthic assemblages as expected.

1.4.4 Temporal variability in benthic assemblages and diversity

The present study showed temporal variations in the benthic infauna community in the Lower St. Lawrence Estuary, which could be associated with the recent appearance of deep hypoxic waters (Benoit et al., 2006; Gilbert et al., 2005, 2007; Thibodeau et al., 2006).

Several proxies have provided consistent evidence of a significant change in environmental conditions in the Estuary over the recent decades. Thibodeau et al. (2006) suggested a recent increase in the rate of organic matter sedimentation and in marine biogenic productivity, which are responsible, in part, for the gradual depletion of dissolved oxygen concentration in bottom waters. Infaunal species were affected by hypoxic conditions, but hypoxia tolerance could vary among phyla and orders (Rosenberg et al., 1991). Our results indicated an increasing abundance of polychaetes, which were generally the most tolerant taxa to low oxygen levels and organic loading, and therefore indicative of hypoxia or organic pollution (Levin, 2000; Lim et al., 2006). Similar findings have been reported from other hypoxic events, as many taxonomic groups were more severely affected by hypoxic stresses, compared with polychaetes (Harper et al., 1981; Llansó, 1992; Diaz and Rosenberg, 1995; Gray et al., 2002). Indeed, the proportion of other taxa, principally molluscs and crustaceans, decreased in the hypoxic zone of the Lower St. Lawrence Estuary.

Under hypoxic conditions, species behaviour is modified and could result in reducing the burrowing depth of infaunal organisms, which are usually restricted to the upper few centimetres of the sediment (Llansó, 1992). This is supported by the increasing dominance in density by small surface deposit feeder species and the decreasing dominance of mobile omnivorous species in the Lower St. Lawrence Estuary. This pattern has been observed previously in studies that described hypoxia-disturbed, macrobenthic communities, which were dominated by shallow-dwelling, short-lived species, mainly annelids (Rhoads et al., 1978; Llansó, 1992; Rosenberg et al., 2001). Hypoxia causes the oxidative layer to migrate closer to the sediment surface by reducing the oxygen gradient to the sediment. This forces tube-dwelling and burrowing species to move closer to the sediment surface in an attempt to reach more-oxygenated waters (Rosenberg, 1977). According to Gray's benthic faunal succession model (Gray, 1992), changes in polychaete species may occur when the oxygen saturation level decreases to 25-10%. In the LSLE, bottom water dissolved oxygen has decreased from 33-41% saturation in the 1930s to 18-26% saturation in the 1990s. Despite considerable interannual variability since the mid-1980s, bottom oxygen levels at depths ≥ 300 m were below 20% of oxygen saturation in 2003, (Gilbert et al., 2005). Polychaetes, particularly the opportunistic spionids, dominated oxygen-stressed benthic communities in Chesapeake Bay on the US east coast (Llansó, 1992). In addition, Lee et al. (2006) stated that polychaetes such as *Myriochele* sp. might be an early indicator of organic enrichment, achieving high abundances during the early stages of such conditions. Similarly, benthic communities in the LSLE became dominated by a few small opportunistic species, such as the polychaetes *Sphiophanes kroyeri* (Family Spionidae), *Myriochele heeri* (Family Oweniidae), and *Ampharete lindstroemi* (Family Ampharetidae).

Macrobenthic communities in the LSLE exposed to low dissolved oxygen levels also exhibited lower species richness and species diversity. Hypoxia can modify the community structure by decreasing both of these diversity indices in benthic communities (Dauer et al., 1992; Llansó, 1992; Diaz and Rosenberg, 1995; Wu, 2002). As previously mentioned, large, long-lived dominant bioturbators such as maldanids are sensitive species that are likely to be eliminated by hypoxia. Species richness is also lower compared to unstressed areas, due to the smaller number of species possessing the physiological adaptations or behavioural characteristics to overcome the effects of stress (Dauer et al., 1992). The total density of individuals may be higher in stressed areas, due to adaptive strategies of opportunistic species, allowing rapid local recruitment (Dauer et al., 1992), whereas species evenness should decrease, resulting in increasing dominance by those few tolerant species (Levin, 2000). Nevertheless, even if the total abundance of benthic organisms and evenness was not significantly different between years, a small change was observed. According to the AMBI index, a significant change in the ecological status has occurred, despite all stations being classified as good and high Ecological Quality status. This suggests that the hypoxic zone in the estuary is actually in a transitional stage, as pointed out by Belley et al. (2010). However, temporal data is lacking that would enable us to confirm the potential relationship between changes in the macrobenthic structure and the development of hypoxia in the LSLE.

1.5 Conclusion

This study is one of the first to describe the spatial patterns in macrobenthic community structure in the Lower St. Lawrence Estuary and the Gulf of St. Lawrence and to establish the Ecological Status of the Laurentian Channel. Different benthic assemblages were identified within the study area, which appear to reflect the topographic and hydrological characteristics used to divide the St. Lawrence into biogeographical regions. Species assemblages, functional groups, and diversity indices varied greatly within the study area, reflecting the complexity of environmental factors in the St. Lawrence system. The Laurentian channel is in relatively good quality by our data suggested that the channel may be in a transition phase.

Also observed were temporal changes in community structure and diversity indices, including an increase in the density of small opportunistic surface deposit feeders and a small decrease in species richness and Shannon diversity. These modifications could be associated with the recent development of deep hypoxic waters in the Lower St. Lawrence Estuary. However, no profound changes in benthic communities were reported, which could indicate that this ecosystem is actually in a transition phase. Over the last decade, our knowledge of the spatial and temporal extent of hypoxia has advanced greatly. Nevertheless, several studies are currently underway in order to better understand the causes and potential impacts of oxygen depletion in deep waters. In a climate change context, the importance of benthic organisms on biological processes in the deep Lower St. Lawrence ecosystem will be important (bioturbation, organic matter degradation rate) in evaluating the potential impacts on ecosystem functioning. Understanding the processes controlling benthic communities will require further investigation, particularly on a broad scale where the variability encountered in environmental conditions is very high. The present study is an important first step towards developing a more complete understanding of the distribution of benthic communities in a deep-water estuarine ecosystem.

CONCLUSION GÉNÉRALE

La présente étude a permis de décrire la variabilité spatiale et temporelle de la structure des communautés endobenthiques dans la partie profonde de l'estuaire maritime et du golfe du Saint-Laurent. Les résultats obtenus dans ce mémoire au niveau de la structure spatiale des communautés supportent l'idée que le Saint-Laurent n'est pas une entité biologique homogène et peut être subdivisé en plusieurs régions comportant chacune une chaîne trophique caractéristique, tel que suggéré par de Lafontaine et al. (1991). En effet, le patron de distribution des assemblages macrobenthiques identifié dans la zone étudiée semble refléter les caractéristiques océanographiques et topographiques utilisées pour diviser le St-Laurent en grandes régions biogéographiques, telles que décrites par Brunel et al. (1998). Au total, sept groupes de stations différents en termes d'assemblages benthiques ont été identifiés dans la zone profonde du Saint-Laurent et correspondent généralement aux régions biogéographiques, principalement décrites en fonction de la bathymétrie, de la nature et de la texture des sédiments ainsi que de la dynamique des masses d'eau et des courants.

Tel que présumé, les conditions environnementales influencent grandement la répartition et la composition des communautés endobenthiques dans l'estuaire maritime et le golfe du Saint-Laurent. La composition du sédiment (granulométrie et contenu en matière organique) est un important paramètre qui semble expliquer la distribution des communautés benthiques et la variabilité des indices de diversité dans l'estuaire maritime et le golfe du Saint-Laurent. Cependant, les résultats ont révélé une influence des facteurs physico-chimiques, tels la température et la salinité, sur la composition des assemblages, les indices de diversité et le mode d'alimentation des organismes, et ce, malgré les très faibles variations de ces paramètres. Une étude sur la distribution des communautés épibenthiques dans l'estuaire maritime et le golfe du Saint-Laurent montre que la température affecterait également la répartition spatiale de ces assemblages d'espèces (M. Lévesque, comm. pers.). De plus, il est surprenant que l'oxygène dissous ne soit pas un des principaux facteurs expliquant la répartition spatiale des assemblages, notamment dans la zone hypoxique de l'estuaire maritime du Saint-Laurent. D'une part, la plus faible variabilité de la saturation en oxygène dans l'estuaire maritime comparativement au golfe pourrait justifier la diminution de l'influence de ce facteur. D'autre part, comme cette variable est fortement inter-corrélée avec d'autres facteurs environnementaux dans la zone d'étude, l'influence de l'oxygène sur les communautés benthiques peut paraître moindre qu'en réalité. Historiquement, il a été démontré que la composition du sédiment est un des plus importants facteurs contrôlant la composition et la répartition des communautés benthiques. Cette étude souligne toutefois l'importance de tenir compte de l'ensemble des paramètres physico-chimiques, comme la température et la salinité, dans l'étude des communautés benthiques des milieux profonds.

Suite aux analyses univariées et multivariées effectuées à partir des données historiques disponibles, une variation temporelle au niveau de la structure des communautés benthiques a été observée. Ces changements peuvent potentiellement être attribués au développement de l'hypoxie dans la zone profonde de l'estuaire maritime du Saint-Laurent. La diminution temporelle de l'oxygène expliquerait possiblement l'augmentation de la densité des petites espèces se nourrissant à la surface du sédiment, principalement des polychètes déposivores de surface, plus tolérants aux faibles niveaux d'oxygénation. Particulièrement, l'augmentation importante de la densité d'espèces opportunistes, telles que *Myriochele heeri*, *Ampharete lindstroemi* et *Spiophanes kroyeri*, semble corrélée avec la diminution de l'oxygène en profondeur. Ces espèces indicatrices dominent généralement les communautés benthiques soumises à des conditions hypoxiques et caractérisent les premières étapes d'un milieu perturbé par un fort enrichissement en matière organique.

Il est possible que les variations par rapport aux données historiques ne soient pas totalement attribuées au développement de l'hypoxie, mais à d'autres variables telles le pH ou la concentration en dioxyde de carbone (CO_2). Cependant, le manque de données temporelles au niveau des communautés benthiques et des conditions environnementales de la zone profonde de l'estuaire maritime ne permet pas de confirmer que l'hypoxie soit l'unique cause des changements observés. Il aurait été judicieux d'utiliser des données historiques réparties sur une plus longue période temporelle afin de voir l'impact réel de l'hypoxie sur les communautés. Toutefois, la complexité d'utiliser ce type de données est élevée, car la méthode d'échantillonnage et le type d'engin utilisés peut varier. Ainsi, il est difficile de comparer les données provenant de deux types d'engins d'échantillonnage différents.

Les tendances de la diminution de la concentration en oxygène dans différents écosystèmes suggèrent une constante augmentation des zones menaçant la dégradation des habitats. Depuis les dix dernières années, les connaissances sur l'expansion spatiale et temporelle de l'hypoxie dans l'estuaire maritime du Saint-Laurent ont grandement progressées. Toutefois, des études tentant de mieux comprendre les causes et les impacts biochimiques et écologiques de ces conditions sont actuellement en cours. Entre autres, des travaux tentent de déterminer l'importance de la bioturbation dans le fonctionnement de l'écosystème profond du Chenal Laurentien et du golfe du Saint-Laurent. Ceux-ci permettront de déterminer l'impact des changements observés au niveau de la structure de la communauté au niveau de l'écosystème. La modification de la communauté benthique peut avoir un impact important sur celui-ci. Par exemple, la diminution des espèces bioturbatrices, moins tolérantes à l'hypoxie, peut conduire à un débalancement au niveau de la dynamique de la communauté, modifiant non seulement le fonctionnement, mais aussi la composition faunique dans le milieu. En se déplaçant davantage vers la surface du sédiment pour gagner les eaux plus oxygénées, les organismes endobenthiques deviennent plus vulnérables face aux prédateurs. Conséquemment, la diminution progressive des proies benthiques aura pour effet de changer la diète des poissons démersaux dans les milieux affectés par l'hypoxie. Il serait donc important d'étudier l'influence des modifications dans la structure des communautés benthiques sur les communautés de poissons de fond dans le cas de futurs travaux.

La présente étude fourni un bon portrait de la variabilité spatiale de la structure des communautés endobenthiques dans la zone profonde de l'estuaire maritime et du golfe du Saint-Laurent. Elle contribue à la caractérisation de ce milieu particulier et à la compréhension de la relation entre les communautés benthiques et les conditions environnementales. Toutefois, comme la variabilité des conditions environnementales dans l'ensemble de la région étudiée est très grande, une approche considérant différentes échelles spatiales devrait être priorisée dans une étude future.

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ANNEXES

Annexe 1. Positions et variables environnementales mesurées aux différentes stations d'échantillonnage en 2005 et 2006.

No. Station	**Latitude**	**Longitude**	**Prof. (m)**	**Distance de l'embouchure du Chenal Laurentien (km)**	**Température (°C)**	**Salinité (psu)**	**Saturation en oxygène (%)**	**Matière organique totale (%)**	**Taille moyenne des grains (µm)**	**% Sable**	**% Silt**	**% Argile**
E5	48°18,171'	-69°16.889'	281	1048,95	4,90	34,38	21,212	6,356	13,887	5,61	67,34	27,05
25	48°13,970'	-69°27.033'	311	1058,53	4,87	34,39	21,045					
24.75	48°14,557'	-69°21.126'	332	1051,91								
24	48°25,880'	-69°06.050'	315	1040,72	5,10	34,50	21,559	6,962	10,174	0,00	70,88	29,12
23.60	48°32,680'	-68°53.600'	325	1030,71								
23_1	48°41,900'	-68°39.070'	350	1020,22	5,25	34,39	21,626	7.143	10,125	2,45	67,43	30,11
23_2	48°42,036'	-68°38.875'	347	1020,03	5,22	34,62	24,390	7,509	11,181	4,37	65,59	30,04
22	48°55,849'	-68°05.485'	321	992,40	5,33	34,60	24,717	6,030	9,900	0,80	66,60	32,60
21	49°07,210'	-67°16.930'	332	902,65	5,38	34,62	25,673	5,738	10,364	2,80	66,31	30,89
20	49°25,420'	-66°19.490'	331	905,02	5,47	34,68	28,923	9,305	9,752	3,11	65,68	31,22
19	49°29,020'	-65°11.940'	373	841,75	5,52	34,78	39,502	9,938	11,216	3,51	65,63	30,86
18	49°16,230'	-64°15.870'	378	773,39	5,27	34,56	49,535	9,610	11,037	2,34	71,19	26,47
17	48°57,966'	-63°06.871'	411	688,05	5,29	34,82	50,150	11,365	20,383	9,30	80,65	10,05
16	48°24,050'	-60°44.022'	434	521,66	5,01	34,86	58,130	10,854	13,019	3,00	84,68	12,33
IC	48°52,800'	-59°59.892'	330	549,10	5,60	34,78	55,068	9,349	9,198	0,00	85,99	14,01
BOI	49°20,459'	-59°40.789'	289	569,80	5,79	34,70	49,220	9,174	12,998	2,95	75,35	21,70
CA	49°32,157'	-60°51.026'	294	538,92	5,62	34,68	40,380	8,688	8,657	1,75	71,39	26,87
TCA	49°40,451'	-61°49.083'	282	695,51	5,55	34,59	35,640	9,039	9,043	0,00	72,05	27,95
CE	49°48,314'	-59°15.600'	257	605,41	5,64	34,56	41,400	9,383	7,808	0,00	73,98	26,02
SPI	50°07,252'	-58°40.033'	321	625,89	5,62	34,60	33,515	10,336	12,295	1,40	83,42	15,18
TCE	50°28,332'	-58°06.796'	281	655,21	5,43	34,49	29,217	10,688	14,275	3,56	80,72	15,72

Annexe 2. Liste des taxons d'invertébrés macrobenthiques récoltés aux différentes stations en 2005 et 2006.

Phylum/ Sous-Phylum	**Classe /Sous-Classe**	**Ordre/Sous-Ordre**	**Famille**	**Espèce**	**Densité tot (ind. m^{-2})**
Annelida	Polychaeta /Scolecida		Capitellidae	*Heteromastus filiformis*	1968
			Maldanidae	*Maldane sarsi*	88
			Maldanidae		544
			Opheliidae	*Ophelina cylindricaudata*	32
			Opheliidae	*Ophelina acuminata*	56
			Paraonidae		24
	/Palpata	Aciculata /Eunicida	Eunicidae	*Eunice pennata*	16
			Lumbrineridae	*Lumbrineris* sp.	2352
			Onuphidae	*Onuphis opalina*	480
		/Phyllodocida	Glyceridae	*Glycera capitata*	8
			Glyceridae	*Glycera* sp.	48
			Glyceridae		16
			Nereidae	*Ceratocephale loveni*	2968
			Pholoidae	*Pholoë minuta*	72
			Polynoidae	*Harmothoë imbricata*	8
			Sigalionidae	*Leanira tetragona*	112
		Canalipalpata /Sabellida	Oweniidae	*Myriochele heeri*	976
			Oweniidae	*Galathowenia oculata*	16
			Oweniidae		16
			Sabellidae	*Potamilla neglecta*	32
		/Spionida	Chaetopteridae	*Spiochaetopterus* sp.	32
			Spionidae	*Spiophanes kroyeri*	1088
			Trochochaetidae	*Trochochaeta multisetosa*	552
		/Terebellida	Ampharetidae	*Ampharete lindstroemi*	2192
			Ampharetidae	*Melinna* sp.	472
			Ampharetidae		72
			Cirratulidae	*Tharyx* sp.	1016
			Cirratulidae		40
			Flabelligeridae	*Diplocirrus longisetosus*	104
			Sternaspidae	*Sternaspis scutata*	64
			Trichobranchidae	*Terebellides stroemi*	416
Nematoda					192
Arthropoda /Crustacea	Malacostraca /Eumalacostraca	Amphipoda /Gammaridea	Ampeliscidae	*Ampelisca declivitatis*	184
			Ampeliscidae	*Ampelisca vadorum*	16

Phylum/ Sous-Phylum	**Classe /Sous-Classe**	**Ordre/Sous-Ordre**	**Famille**	**Espèce**	**Densité tot (ind. m^{-2})**
			Ampeliscidae	*Haploops laevis*	72
			Ampeliscidae	*Haploops tubicola*	24
			Ischyroceridae	*Ischyrocerus megacheir*	64
			Pardaliscidae	*Pardaliscella lavrovi*	8
			Phoxocephalidae	*Harpinia cabotensis*	104
			Phoxocephalidae	*Harpinia propinqua*	416
			Phoxocephalidae	*Harpinia* sp.	24
			Phoxocephalidae	*Phoxocephalus holbolli*	56
			Phoxocephalidae		56
		Cumacea	Diastylidae	*Diastylis goodsiri*	16
			Diastylidae	*Diastylis lucifera*	8
			Leuconidae	*Eudorella hispida*	16
		Decapoda /Pleocyemata	Calocarididae	*Calocaris templemani*	32
			Pandalidae	*Pandalus borealis*	8
		Isopoda /Anthuridea	Anthuridae	*Cyathura carinata*	24
		Calanoidea	Calanidae	*Calanus hyperboreus*	24
			Calanidae	*Calanus finmarchicus*	152
			Aetideidae	*Bradyidius similis*	16
Cnidaria					16
	Anthozoa /Alcyonaria	Pennatulacea /Subselliflorae	Pennatulidae	*Pennatula aculeata*	264
	/Hexacorallia	Actiniaria			16
	Hydrozoa	Hydroida /Leptomedusae	Sertulariidae		24
Nemertea					64
	Anopla	Heteronemertea			24
Mollusca	Bivalvia		Cuspidariidae	*Cuspidaria glacialis*	24
	Bivalvia /Heterodonta	Veneroida	Astartidae	*Astarte undata*	72
			Thyasiridae	*Axinopsida* sp.	288
	/Protobranchia	Nuculoida	Nuculanidae	*Nuculana pernula*	48
			Nuculidae	*Nucula delphinodonta*	280
			Nuculidae	*Nucula* sp.	24
			Yoldiidae	*Yoldia myalis*	40
	/Pteriomorphia	Arcoida	Arcidae	*Bathyarca* sp.	56
	Scaphopoda	Dentaliida	Dentaliidae	*Antalis occidentale*	96
		Gadilida	Pulsellidae	*Pulsellum lobatum*	40
Sipuncula					184
			Phascolosomatidae		8
Echinodermata /Eleutherozoa	Ophiuroidea				24

Phylum/ Sous-Phylum	**Classe /Sous-Classe**	**Ordre/Sous-Ordre**	**Famille**	**Espèce**	**Densité tot (ind. m^{-2})**
		Ophiurida /Chilophiurina	Ophiuridae	*Ophiura sarsi*	88
			Ophiuridae	*Ophiura robusta*	24
		/Gnathophiurina	Amphiuridae	*Amphiura sundevalli*	1000
			Amphiuridae	*Amphiura* sp.	48
	Echinoidea /Euechinoidea	Spatangoida /Hemiasterina	Schizasteridae	*Brisaster fragilis*	160
	Asterozoa /Asteroidea	Praxillosida	Goniopectinidae	*Ctenodiscus crispatus*	16
Chordata /Vertebra	Actinopterygii /Neopterygii	Perciformes /Zoarcoidei	Zoarcidae	*Lycode* sp.	8

Annexe 3. Densités moyennes (ind. m^{-2}) des espèces macrobenthiques de chaque groupe fonctionnel pour les stations échantillonnées en 2005 et 2006.

Espèces pour chacun des groupes fonctionnels	**E5**	**24**	**23_1**	**23_2**	**22**	**21**	**20**	**19**	**18**	**17**	**16**	**IC**	**BOI**	**CA**	**TCA**	**CE**	**SPI**	**TCE**
Déposivores de surface																		
Paraonidae	0	0	2.67	0	0	0	5.33	0	0	0	0	0	0	0	0	0	0	0
Glycera capitata	0	0	0	0	0	0	0	0	2.67	0	0	0	0	0	0	0	0	0
Glycera sp.	0	0	0	0	0	0	0	2.67	0	5.33	2.67	0	0	5.33	0	0	0	0
Glyceridae	0	0	0	0	0	0	0	0	0	5.33	0	0	0	0	0	0	0	0
Myriochele heeri	18.67	8.00	40.00	10.67	226.67	0	0	0	0	8.00	2.67	0	0	0	0	10.67	0	0
Galathowenia oculata	0	5.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oweniidae	0	2.67	0	0	0	2.67	0	0	0	0	0	0	0	0	0	0	0	0
Spiochaetopterus sp.	5.33	0	0	0	5.33	0	0	0	0	0	0	0	0	0	0	0	0	0
Spiophanes kroyeri	328.00	29.33	2.67	0	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0
Trochochaeta multisetosa	93.33	21.33	2.67	2.67	21.33	8.00	0	0	0	0	0	2.67	0	16.00	0	2.67	13.33	0
Ampharete lindstroemi	269.33	53.33	114.67	18.67	37.33	80.00	29.33	5.33	13.33	2.67	2.67	2.67	0	24.00	48.00	5.33	5.33	18.67
Melinna sp.	2.67	2.67	0	8.00	10.67	10.67	2.67	2.67	0	0	8.00	8.00	0	2.67	74.67	0	2.67	21.33
Ampharetidae	0	0	0	0	0	0	0	0	0	2.67	2.67	0	0	16.00	0	2.67	0	0
Tharyx sp.	80.00	0	18.67	21.33	2.67	5.33	0	2.67	2.67	24.00	10.67	24.00	0	72.00	21.33	8.00	24.00	21.33
Cirratulidae	2.67	0	5.33	0	2.67	2.67	0	0	0	0	0	0	0	0	0	0	0	0
Diplocirrus longisetosus	0	0	0	0	0	0	0	0	0	21.33	2.67	8.00	0	0	2.67	0	0	0
Terebellides stroemi	16.00	24.00	5.33	8.00	13.33	2.67	0	0	0	0	0	0	0	2.67	42.67	8.00	8.00	8.00
Harpinia cabotensis	0	0	13.33	2.67	2.67	0	0	5.33	10.67	0	0	0	0	0	0	0	0	0
Harpinia propinqua	2.67	5.33	10.67	8.00	10.67	5.33	13.33	8.00	21.33	13.33	8.00	8.00	0	13.33	0	8.00	2.67	0
Harpinia sp.	0	0	0	0	0	0	0	0	5.33	0	0	0	2.67	0	0	0	0	0
Diastylis goodsiri	0	0	0	0	2.67	0	0	0	0	2.67	0	0	0	0	0	0	0	0
Diastylis lucifera	0	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eudorella hispida	2.67	0	0	0	0	0	2.67	0	0	0	0	0	0	0	0	0	0	0
Cyathura carinata	2.67	0	0	0	0	0	0	0	0	0	0	0	0	5.33	0	0	0	0
Bathyarca sp.	0	0	0	0	0	0	0	0	0	2.67	0	0	2.67	10.67	2.67	0	0	0
Phascolosomatidae	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sipuncula	0	0	0	0	0	0	0	0	0	0	0	0	0	5.33	2.67	0	0	53.33

Ophiura robusta	0	0	0	0	0	0	0	0	0	5.33	0	0	0	0	2.67	0	0	0
Brisaster fragilis	2.67	0	5.33	2.67	5.33	2.67	10.67	5.33	8.00	8.00	2.67	0	0	0	0	0	0	0
Ctenodiscus crispatus	0	0	0	0	2.67	2.67	0	0	0	0	0	0	0	0	0	0	0	0
Phoxocephalus holbolli	0	13.33	0	0	0	0	0	2.67	2.67	0	0	0	0	0	0	0	0	0
Phoxocephalidae	0	0	0	0	0	0	0	0	2.67	8.00	0	0	0	8.00	0	0	0	0
Total SDF	829.33	168.00	221.33	82.67	346.67	122.67	64.00	34.67	69.33	109.33	42.67	53.33	5.33	181.33	197.33	45.33	56.00	122.67
Déposivores de subsurface																		
Heteromastus filiformis	13.33	5.33	0	0	32.00	10.67	42.67	40.00	42.67	18.67	2.67	0	2.67	50.67	205.33	32.00	40.00	117.33
Maldane sarsi	2.67	0	0	0	0	0	0	0	0	0	0	0	2.67	0	0	13.33	10.67	0
Maldanidae	90.67	13.33	2.67	0	10.67	2.67	0	0	0	0	2.67	32.00	0	8.00	2.67	8.00	2.67	5.33
Ophelina cylindricaudata	0	0	0	0	0	0	0	0	0	5.33	0	2.67	0	0	0	2.67	0	0
Ophelina acuminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.67	0	2.67	13.33
Sternaspis scutata	18.67	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana pernula	2.67	2.67	0	10.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucula delphinodonta	56.00	13.33	0	0	0	0	2.67	0	8.00	2.67	0	10.67	0	0	0	0	0	0
Nucula sp.	0	8.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yoldia myalis	0	0	5.33	0	0	0	0	0	5.33	0	0	2.67	0	0	0	0	0	0
Antalis occidentale	0	0	0	0	0	0	0	0	0	16.00	0	16.00	0	0	0	0	0	0
Total SBDF	184.00	45.33	8.00	10.67	42.67	13.33	45.33	40.00	56.00	42.67	5.33	64.00	5.33	58.67	210.67	56.00	56.00	136.00
Filtreurs																		
Potamilla neglecta	5.33	0	0	0	0	2.67	0	0	0	0	0	0	0	2.67	0	0	0	0
Ampelisca declivitatis	0	0	0	0	0	2.67	0	0	2.67	2.67	0	0	0	0	0	0	0	0
Ampelisca vadorum	0	0	0	0	0	0	0	0	0	0	0	0	0	2.67	0	0	0	0
Haploops laevis	0	0	0	0	0	0	0	0	0	18.67	0	0	0	0	2.67	0	0	0
Haploops tubicola	0	0	0	0	0	0	2.67	0	0	0	0	0	0	0	0	0	0	0
Calanus hyperboreus	2.67	0	0	2.67	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0
Calanus finmarchicus	0	2.67	2.67	0	0	10.67	16.00	0	2.67	2.67	0	5.33	0	2.67	5.33	0	0	0
Astarte undata	2.67	0	0	0	2.67	0	0	0	0	13.33	0	0	0	0	0	0	0	5.33
Axinopsida sp.	8.00	13.33	5.33	24.00	0	0	0	0	0	0	0	5.33	10.67	10.67	5.33	8.00	2.67	2.67
Pennatula aculeata	0	0	2.67	0	5.33	2.67	8.00	0	0	5.33	0	0	8.00	18.67	21.33	0	10.67	5.33
Cuspidaria glacialis	0	0	2.67	0	0	0	0	0	0	0	0	0	0	2.67	0	2.67	0	0
Molgula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total FF	18.67	16.00	10.67	26.67	5.33	16.00	18.67	0.00	5.33	37.33	0.00	10.67	10.67	21.33	13.33	10.67	2.67	8.00

Carnivores																		
Pholoë minuta	2.67	0	0	0	10.67	8.00	2.67	0	0	0	0	0	0	0	0	0	0	0
Harmothoë imbricata	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leanira tetragona	2.67	2.67	10.67	2.67	8.00	10.67	0	0	0	0	0	0	0	0	0	0	0	0
Actiniaria	0	0	2.67	0	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0
Heteronemertea	0	0	0	0	0	5.33	0	0	0	0	2.67	0	0	0	0	0	0	0
Nemertea	2.67	0	2.67	0	0	2.67	0	0	0	0	8.00	0	0	5.33	0	0	0	0
Trichotropis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycode sp.	0	0	0	0	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0
Total C	10.67	2.67	18.67	2.67	29.33	29.33	10.67	0	0	5.33	10.67	0	8.00	24.00	21.33	0	10.67	5.33
Omnivores																		
Eunice pennata	2.67	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineris sp.	10.67	0	13.33	10.67	18.67	21.33	34.67	50.67	69.33	48.00	32.00	8.00	13.33	90.67	160.00	72.00	64.00	66.67
Onuphis opalina	2.67	0	2.67	0	18.67	13.33	5.33	5.33	5.33	26.67	0	2.67	18.67	34.67	13.33	2.67	2.67	5.33
Ceratocephale loveni	0	2.67	26.67	10.67	66.67	53.33	109.33	117.33	101.33	0	0	5.33	8.00	18.67	136.00	88.00	93.33	152.00
Ophiura sarsi	16.00	2.67	2.67	5.33	2.67	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphiura sundevalli	0	18.67	2.67	2.67	69.33	29.33	26.67	80.00	80.00	18.67	0	5.33	0	0	0	0	0	0
Amphiura sp.	0	0	0	0	0	0	0	0	0	0	16.00	0	0	0	0	0	0	0
Ophiuroidae	0	0	0	0	2.67	0	0	0	0	0	0	0	0	5.33	0	0	0	0
Total O	32.00	26.67	48.00	29.33	178.67	117.33	176.00	253.33	256.00	93.33	48.00	21.33	40.00	149.33	309.33	162.67	160.00	224.00
Non-classées	16.00	8.00	8.00	2.67	2.67	5.33	5.33	2.67	5.33	16.00	8.00	16.00	0	2.67	2.67	2.67	0	0
Overall total	1090.67	266.67	314.67	154.67	605.33	304.00	320.00	330.67	392.00	304.00	114.67	165.33	69.33	437.33	754.67	277.33	285.33	496.00