

UNIVERSITÉ DU QUÉBEC

VARIABLES ENVIRONNEMENTALES INFLUENÇANT LA DENSITÉ ET LA  
DIVERSITÉ DE LA MACROFAUNE ÉPIBENTHIQUE ET LA BIOTURBATION  
DANS L'ESTUAIRE ET LE GOLFE DU SAINT-LAURENT, CANADA

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## RÉSUMÉ

L'estuaire et le golfe du Saint-Laurent (EGSL), Canada, subit présentement un évènement hypoxique qui pourrait être causé par des changements dans la composition de la masse d'eau de fond et une augmentation de l'apport en matière organique. Le fond marin de l'EGSL a été photographié à 11 stations durant les étés 2006 et 2007. Les images ont ensuite été analysées afin d'identifier les traces de bioturbation (*Lebensspuren*) et les organismes macrobenthiques présents.

Les objectifs de cette étude sont : 1) d'identifier les variables environnementales qui influencent la densité et la diversité de la macrofaune épibenthique ainsi que les traces de bioturbation, et 2) de déterminer les différences entre les régions de l'EGSL avec des niveaux d'oxygène élevés, moyens et bas.

La concentration d'oxygène dans la couche de fond est la variable environnementale qui explique le mieux les densités de traces totales et de surface : les densités de ces traces augmentent alors que l'oxygène diminue. La densité de traces plus élevée dans la région hypoxique de l'EGSL est principalement due au déposivore de surface *Ophiura* sp., qui se retrouve en grande densité dans cette région. Les résultats indiquent que les conditions hypoxiques actuelles n'affectent pas négativement la densité et la diversité des traces de bioturbation ainsi que la richesse spécifique. Cependant, nous avons observé dans la zone hypoxique une augmentation des déposivores de surface (tolérants aux basses concentrations d'oxygène) et une diminution des suspensivores (intolérants aux basses concentrations d'oxygène). Nous émettons l'hypothèse que la diminution de la concentration d'oxygène des eaux de fond au cours des dernières années a causé un changement dans la structure de la communauté macro-épibenthique de l'estuaire maritime du Saint-Laurent (EMSL). Les espèces avec une plus faible tolérance aux basses concentrations d'oxygène, qui sont généralement responsables des traces en relief, sont remplacées par des espèces plus tolérantes, tels que les déposivores de surface *Ophiura* sp., qui sont responsables de la majorité des traces de surface.

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## INTRODUCTION GÉNÉRALE

Les océans recouvrent approximativement 70% de la surface terrestre, constituant ainsi le plus grand écosystème qu'on y retrouve. En raison d'une utilisation toujours grandissante de cet écosystème par l'Homme, plusieurs habitats marins subissent des pressions anthropogéniques importantes telles que la pêche, la pollution, le développement côtier et le réchauffement climatique. Prises individuellement ou agissant en synergie, ces pressions peuvent mener à une perte de biodiversité marine (Snelgrove, 1998; Snelgrove et al., 2000; Worm et al., 2006). Cette biodiversité marine est composée en majeure partie d'organismes benthiques habitant sur (épifaune) et dans (endofaune) les sédiments (Snelgrove, 1999). Plusieurs études ont démontré les effets importants qu'ont les organismes benthiques sur les sédiments marins tels que les processus biochimiques (Aller et al., 2001; Meysman et al., 2006; Middelburg & Levin, 2009), la géomorphologie (Murray et al., 2002), et la production primaire et secondaire (Snelgrove, 1998). La perte de biodiversité benthique marine aurait potentiellement des effets néfastes importants sur les fonctions et la santé des écosystèmes, ainsi que sur les processus marins (Snelgrove, 1998; Worm et al., 2006).

## **Influence des variables environnementales sur les communautés benthiques**

Les communautés benthiques sont aussi affectées par différentes variables environnementales de leur milieu. Les caractéristiques du substrat telles que la taille des sédiments (Warwick et al., 1991; Kostylev et al., 2001) et la teneur en matière organique (Pearson & Rosenberg, 1978; Rosenberg, 1995) sont reconnues comme étant des variables qui influencent la distribution et la structure des communautés benthiques. D'autres variables environnementales telles que la profondeur et la vitesse du courant (Kostylev et al., 2001), ainsi que la température et la salinité (Pearson & Rosenberg, 1978) sont aussi reconnues pour avoir un impact important sur la distribution et la structure des communautés benthiques. Cependant, parmi toutes les variables environnementales affectant les habitats marins, Diaz & Rosenberg (2008) rapportent que l'oxygène dissous est celle qui a changé le plus drastiquement depuis les années 1960. La diminution de l'oxygène dissous est un facteur bien étudié ayant des conséquences nuisibles pour les environnements marins. Cette diminution de l'oxygène dissous est très souvent due à une eutrophisation de nature anthropogénique, soit un apport accru de nutriments dans les eaux. Depuis les années 1960, les zones dépourvues de ressources de pêches en raison d'évènements hypoxiques dans les océans côtiers, appelées zones mortes, se sont propagées de façon exponentielle : aujourd'hui, des zones mortes sont répertoriées dans plus de 400 systèmes et couvrent une superficie

de plus de 245 000 km<sup>2</sup> (Diaz & Rosenberg, 2008). La diminution de l'oxygène dissous sous la valeur hypoxique généralement acceptée de 62,5 µmol L<sup>-1</sup> ou 2 mg L<sup>-1</sup> (Gilbert et al., 2005), cause une réduction de la croissance, de l'alimentation et de la valeur d'adaptation (ou « fitness » individuel) des animaux marins (Wu, 2002). Cependant, Vaquer-Sunyer & Duarte (2008) ont démontré que les organismes benthiques ont des seuils de tolérance variables à l'hypoxie et qu'une concentration de 2 mg L<sup>-1</sup> peut être létale pour plusieurs espèces. Néanmoins, l'hypoxie est reconnue pour forcer les organismes endobenthiques à migrer vers la surface des sédiments et, en conséquence, ces organismes deviennent plus vulnérables à la prédation (Llansó, 1992; Wu, 2002). En éliminant certaines espèces sensibles, l'hypoxie est aussi reconnue pour affecter la fonction et la structure des communautés en réduisant la diversité et la richesse spécifique (Diaz & Rosenberg, 1995; Wu, 2002). De plus, certaines études font mention que les suspensivores peuvent être remplacés par les dépositivores dans des conditions hypoxiques (Diaz & Rosenberg, 1995; Wu, 2002).

### **Le Saint-Laurent et le phénomène hypoxique**

Cette étude a été réalisée dans l'estuaire et le golfe du Saint-Laurent (EGSL), Canada. La présence du Chenal Laurentien, long de 1240 km et d'une profondeur variant entre 300 et 500 m, domine la morphologie de l'estuaire et du golfe du Saint-Laurent. La colonne d'eau du Chenal est stratifiée et est

composée de trois couches d'eau (Bugden, 1991). La couche de surface, d'environ 50 m, démontre de grandes variations de température et de salinité en réponse aux changements de flux de chaleur saisonniers et aux débits d'eau douce. La couche intermédiaire froide, qui s'étend de 50 à 150 m, démontre quant à elle de plus faibles variations saisonnières que la couche de surface. Il est reconnu que la couche de surface se fusionne avec la couche intermédiaire froide en hiver. La couche profonde, plus chaude, s'étend jusqu'au fond et subit des changements à long terme (Bugden, 1991). Cette couche profonde est formée du mélange, en proportion variable, d'eau froide bien oxygénée provenant du courant du Labrador ainsi que d'eau chaude moins oxygénée de la partie centrale de l'Atlantique nord transportée par le *Gulf Stream*. Le mélange de ces masses d'eau s'engage dans le Chenal Laurentien par son embouchure situé au rebord du plateau continental et se dirige lentement vers la tête des trois chenaux, un voyage de quelques années (Gilbert et al., 2005, 2007).

La concentration d'oxygène dans la couche profonde a diminué drastiquement depuis 1932 (Gilbert et al., 2005, 2007). Dans cette couche d'eau de l'estuaire maritime du Saint-Laurent (EMSL), Gilbert et al. (2005, 2007) ont découvert que la concentration d'oxygène dissous a diminué de près de 50% pour la période couvrant 1932 à 2003, passant de  $125 \mu\text{mol L}^{-1}$  de moyenne à  $65 \mu\text{mol L}^{-1}$ . En juillet 2003, environ 110 km de fond marin de la section longitudinale du Chenal Laurentien, situé dans l'EMSL, baignaient dans des eaux hypoxiques sous  $60 \mu\text{mol L}^{-1}$ . À cette même période, une concentration aussi

basse que  $51,2 \mu\text{mol L}^{-1}$  (16,2% de saturation) a été enregistrée à la station 23S (Fig. 1). De plus, la partie en amont du Chenal Laurentien, une aire couvrant  $1300 \text{ km}^2$ , était hypoxique en permanence avec des concentrations d'oxygène sous  $62,5 \mu\text{mol L}^{-1}$  ou  $2 \text{ mg L}^{-1}$  (Gilbert et al., 2005, 2007). Cette diminution d'oxygène serait principalement due à deux facteurs. Premièrement, une augmentation de  $1,65^\circ\text{C}$  de la température de la couche d'eau de fond pour la période de 1932 à 2003 suggère un changement de la proportion du mélange des masses d'eau formant la couche d'eau de fond du Chenal Laurentien. Ce changement contribuerait d'une demie à deux tiers de la diminution en oxygène. Deuxièmement, une augmentation de la demande en oxygène des eaux profondes et du sédiment due à une augmentation de l'apport en matière organique serait responsable de la partie restante de la diminution en oxygène (Gilbert et al., 2005; Thibodeau et al., 2006; Katsev et al., 2007). En effet, Thibodeau et al. (2006) rapportent une augmentation de la productivité marine dans l'EMSL depuis les années 1960. Cette augmentation de la productivité marine est reflétée par une augmentation du taux d'accumulation des kystes de dinoflagellés et des foraminifères benthiques. De plus, ils ont observé l'apparition de deux espèces de foraminifères benthiques tolérants à de basses concentrations d'oxygène et à des flux élevés de matière organique depuis les 40 dernières années.

Des études ont démontré que l'hypoxie (Diaz & Rosenberg, 1995; Ritter & Montagna, 1999) et l'enrichissement en matière organique (Pearson &



Rosenberg, 1978) peuvent mener à une diminution de la biomasse, de l'abondance et de la biodiversité. Ces deux facteurs pourraient ainsi avoir des effets néfastes sur la densité et la diversité des organismes benthiques ainsi que sur la bioturbation des sédiments de l'EGSL.

## **La bioturbation**

Au sens large, le terme bioturbation peut être défini comme étant le mélange et le transport de terre ou de particules de sédiment par différents organismes, incluant les microbes, les racines des plantes et les animaux fouisseurs (Rhoads, 1974; Meysman et al., 2006). L'importance de la bioturbation a été comprise en premier lieu par Charles Darwin, qui lui a dédié son dernier livre scientifique (Darwin, 1881). La bioturbation faite par les organismes fouisseurs, aussi appelés « ingénieurs de l'écosystème », a eu et continue d'avoir un rôle crucial à jouer dans l'évolution de la vie sur terre (Meysman et al., 2006). Ses organismes fournissent divers services clés aux écosystèmes. Ils sont en effet directement impliqués dans les cycles biogéochimiques du carbone et des nutriments (Solan et al., 2008), dont plus spécifiquement le processus de minéralisation de la matière organique à l'interface eau-sédiment (Gilbert et al., 2003; Maire et al., 2008). De plus, à travers leurs diverses activités, ils modifient les propriétés physiques (ex : le transport sédimentaire) et biologiques (ex : réseau trophique pélagique) du sédiment (Maire et al., 2008; Van Colen et al., 2008). La perte de telles espèces

ingénieuses pourrait avoir des impacts négatifs importants sur la biodiversité et les processus biochimiques à l'interface eau-sédiment (Coleman & Williams, 2002; Lohrer et al., 2004; Solan et al., 2004a).

Les traces de bioturbation sont aussi connues sous le nom de *Lebensspuren*, un mot allemand signifiant « trace de vie ». Elles peuvent être séparées en deux groupes principaux selon leur morphologie : les traces de surface et les traces en relief (Mauviel & Sibuet, 1985). Les traces de surface sont formées lorsque les organismes remanient uniquement les premiers centimètres du sédiment (ex : pistes, rides, sillons, etc.). Ces traces impliquent un mélange du sédiment qui peut être important en surface, mais qui n'affecte pas les particules situées profondément dans la colonne de sédiment. Quant aux traces en relief, elles sont formées lorsque les organismes mélangent le sédiment plus en profondeur lors de la formation ou de la maintenance de leurs diverses structures (ex : terriers en forme de fente, terriers simples, tumulus crevassés, etc.). Ce type de bioturbation, aussi appelé bioirrigation, implique le transport de l'eau interstitielle par des organismes benthiques lors de diverses activités telles que l'alimentation, l'enfouissement, la locomotion et la ventilation du terrier (Maire et al., 2008). Pour cette raison, il est présumé être plus important pour l'oxygénation et les processus biochimiques à l'intérieur de la colonne de sédiment « perforée ».

## La photographie benthique

Au cours des dernières décennies, la prise de photographies benthiques a prouvé son efficacité à identifier les organismes benthiques ainsi qu'à caractériser et à quantifier les traces de bioturbation (Heezen & Hollister, 1971; Kitchell, 1979; Mauviel & Sibuet, 1985; Solan et al., 2003; Jones et al., 2007). En particulier, cette technique est reconnue comme étant plus rapide que d'autres techniques d'échantillonnage benthique (benne, carottier, chalut, etc.) et a l'avantage de peu perturber l'environnement échantillonné (Kostylev et al., 2001). Cependant, les études des traces de bioturbation et de la macrofaune épibenthique qui y est associée, ayant été menées avec la technique de photographie benthique, ont principalement été réalisées pour décrire des environnements néritiques à moins de 200 m et des environnements abyssaux situés à plus de 2000 m de profondeur. En contrepartie, à notre connaissance aucune étude sur le même sujet dans des environnements bathyaux (entre 200 et 2000 m), tel que le Chenal Laurentien, n'a été publiée. Par contre, dans l'EMSL, Hutin et al. (2005) ont mené une étude en utilisant la photographie benthique afin de déterminer le lien entre le signal acoustique d'un sonar multi-faisceaux et un banc de pétoncle d'Islande (*Chlamys islandica*). Toutefois, aucune étude portant sur les traces de bioturbation faites à la surface du sédiment de l'EGSL n'a été publiée jusqu'à maintenant. Une étude menée à bord du submersible *Pisces IV* (Syvitski et al., 1983) a permis de recueillir des données sur le benthos de la zone bathyale du Chenal Laurentien. Cependant,

mis à part la mention de la présence plus ou moins importante des traces de bioturbation, aucune donnée quantitative n'a été fournie.

### **Communautés benthiques du Saint-Laurent**

Les organismes benthiques du Chenal Laurentien sont encore peu connus. Les études pionnières de Préfontaine & Brunel (1962) et de Peer (1963) sur les organismes endobenthiques ont pavé la voie aux études de Robert (1979) sur les mollusques, de Massad (1975) et de Massad & Brunel (1979) sur les polychètes ainsi que de Ouellet (1982) sur la macrofaune endobenthique de l'EMSL. Récemment, des études ont été menées dans l'EGSL sur les relations entre les variables environnementales et la faune endobenthique (Desrosiers et al., 2000; Bourque, 2009) ainsi que la faune épibenthique (Lévesque et al., 2008; Lévesque, 2009).

En règle générale, il est reconnu que l'abondance et la diversité des espèces dans un estuaire diminuent de l'océan vers l'amont (Rapoport, 1994; Schaffner et al., 2001). Pour ce qui est de l'EGSL, l'étude de Bourque (2009) a également permis de démontrer que la structure des communautés endobenthiques est spécialement affectée par la diminution de l'oxygène. En effet, elle observe une réduction de la richesse spécifique et de la diversité de Shannon pour la période couvrant 1980 à 2005-2006. Elle observe aussi une augmentation des espèces opportunistes à la surface des sédiments, telles que

*Myriochele* sp., qui sont généralement présentes dans les environnements perturbés par l'hypoxie. Les études de Lévesque et al. (2008) et de Lévesque (2009) ont quant à elles démontré l'importance de l'oxygène dissous comme variable environnementale structurant les communautés épibenthiques de l'EGSL. En effet, ces études rapportent une plus grande densité de cnidaires et de mollusques (tolérants aux basses concentrations d'oxygène) et une moins grande densité de crustacés (intolérants aux basses concentrations d'oxygène) dans la zone hypoxique que partout ailleurs dans l'EGSL. En plus des connaissances que nous avons des communautés benthiques en général, ces études démontrent l'importance de l'oxygène dissous comme variable environnementale structurant les communautés benthiques de l'EGSL.

### **Objectifs et hypothèses**

Les objectifs de cette étude étaient de : 1) déterminer les variables environnementales qui influencent la densité et la diversité macrobenthiques ainsi que les traces de bioturbation, et 2) déterminer s'il y a une différence significative entre les régions du fond marin de l'EGSL avec des concentrations d'oxygène faibles, moyennes et élevées. Les hypothèses étaient que : 1) la concentration en oxygène dissous sera la variable environnementale qui influencera le plus la densité et la diversité macrobenthique ainsi que les traces de bioturbation, et 2) la région hypoxique de l'EGSL aura une richesse spécifique

plus basse que les régions normoxiques, ce qui engendrera une plus faible densité et diversité des traces de bioturbation.

Ce mémoire de maîtrise, sous forme d'article scientifique, est rédigé en anglais et contient un chapitre. Cet article sera soumis à la revue *Aquatic Biology* au mois de septembre 2009.

## CHAPITRE 1

ENVIRONMENTAL VARIABLES INFLUENCING  
MACROBENTHIC AND BIOTURBATION DENSITY  
AND DIVERSITY IN THE ESTUARY AND GULF OF  
ST. LAWRENCE, CANADA

## 1.1 Introduction

Many marine habitats are presently under pressure by multiple anthropogenic threats such as fishing, pollution, coastal development, and global warming. Any one of these threats can lead to a loss of marine biodiversity (Snelgrove, 1998; Worm et al., 2006). Marine benthic organisms have important effects on sedimentary biogeochemical processes (Aller et al., 2001; Meysman et al., 2006; Middelburg & Levin, 2009), geomorphology (Murray et al., 2002), and primary and secondary productivity (Snelgrove, 1998). The loss of marine macrobenthic biodiversity would likely have negative effects on ecosystem functions, processes and health (Snelgrove, 1998; Worm et al., 2006).

Benthic communities are also affected by different environmental variables. Characteristics of the substratum such as the sediment grain size (Kostylev et al., 2001) and the organic matter content (Pearson & Rosenberg, 1978; Rosenberg, 1995) are known to influence benthic community distribution and structure. The decrease of dissolved oxygen, more often due to anthropogenic eutrophication, is a well-known deleterious factor for marine environments (Diaz & Rosenberg, 2008). The decrease of dissolved oxygen below the generally accepted hypoxic value of  $62.5 \mu\text{mol L}^{-1}$  or  $2 \text{mg L}^{-1}$  (Gilbert et al., 2005) is known to reduce growth, feeding and individual fitness of marine animals (Wu, 2002). However, Vaquer-Sunyer & Duarte (2008) demonstrated that marine benthic organisms have varying thresholds to hypoxia and that a



concentration of dissolved oxygen of  $2 \text{ mg L}^{-1}$  is lethal for many species. Nonetheless, hypoxia is known to force infaunal organisms to move closer to the sediment surface and, in consequence, become more vulnerable to predation (Llansó, 1992; Wu, 2002). By eliminating sensitive species, hypoxia is also known to affect community structure and function by reducing species diversity and species richness (Diaz & Rosenberg, 1995; Wu, 2002). Moreover, it is reported that under hypoxic conditions suspension feeders can be replaced by deposit feeders (Diaz & Rosenberg, 1995; Wu, 2002).

The present study was carried out in the Estuary and Gulf of St. Lawrence (EGSL), Canada. This environment is dominated by the 1240 km long, 300 to 500 m deep, Laurentian Channel. The water column in the Channel is stratified, with a surface layer (upper 50 m), a cold intermediate layer (50 to 150 m) and a deep warmer layer (below 150 m) (Bugden, 1991). In the Lower St. Lawrence estuary (LSLE), Gilbert et al. (2005) found that the oxygen concentration in the deep layer of water decreased by 50%, from  $125 \text{ } \mu\text{mol L}^{-1}$  to  $65 \text{ } \mu\text{mol L}^{-1}$ , for the 1932-2003 period. In July 2003, the landward region of the Laurentian Channel, an area covering  $1300 \text{ km}^2$ , was hypoxic with concentrations of dissolved oxygen lower than  $62.5 \text{ } \mu\text{mol L}^{-1}$  (Gilbert et al., 2005). An increase in organic carbon loading and changes in water mass composition are the principal causes (Gilbert et al., 2005; Thibodeau et al., 2006; Katsev et al., 2007). Hypoxia (Diaz & Rosenberg, 1995; Ritter & Montagna, 1999) and organic enrichment (Pearson &

Rosenberg, 1978) can lead to decreasing biomass, abundance and biodiversity, with possible negative effects on sediment bioturbation.

Bioturbation can be broadly defined as the mixing and transport of particles and solutes within sediments and soil by various organisms, including microbes, rooting plants and burrowing animals (Rhoads, 1974; Meysman et al., 2006). Bioturbation created by burrowing organisms, sometimes called “ecosystem engineers”, had and still has a crucial role in the evolution of life on earth (Meysman et al., 2006). The loss of engineer species could have important negative effects on biodiversity and on biogeochemical processes at the water-sediment interface (Coleman & Williams, 2002; Lohrer et al., 2004; Solan et al., 2004a; Middelburg & Levin, 2009).

Bioturbation traces are also known as “*Lebensspuren*”, a German term meaning life traces. They can be separated in two main groups, surface-traces and relief-traces, according to their morphology (Mauviel & Sibuet, 1985). Surface-traces are formed when organisms rework only the first few centimetres of the sediment, which leaves traces in the form of ploughs, tracks, furrows, etc. These traces imply sediment mixing that can be important, but which does not affect particles located deep within the sediment. In contrast, relief-traces, in the shape of simple burrows, slit-shaped burrows, crevassed mounds, etc., are formed when organisms rework sediments to much greater depths. This kind of

bioturbation is thought to be more important for oxygenation and biogeochemical processes deeper within the “perforated” sediment.

Over the last decades, benthic photography has proven its reliability to identify organisms and to characterise and quantify bioturbation traces (Heezen & Hollister, 1971; Kitchell, 1979; Mauviel & Sibuet, 1985; Solan et al., 2003; Jones et al., 2007). In particular, the photographic technique is known to be less time consuming than other benthic sampling techniques (grab, box-core, trawl, etc.) and has the advantage of leaving the environment mostly undisturbed (Kostylev et al., 2001).

The objectives of this study were to determine the environmental variables influencing the density and diversity of macrobenthic epifauna and bioturbation traces, and to determine if there are significant differences among regions of the seafloor in the ESL with high, medium and low oxygen levels. This was accomplished using benthic photography and different environmental measurements. The hypotheses are that 1) the oxygen concentration will be the most important environmental variable influencing the density and diversity of macrobenthic epifauna and bioturbation traces, and 2) the hypoxic region of the EGSL will have lower species richness and consequently, lower bioturbation trace density and diversity than normoxic regions.

## 1.2 Materials and methods

### 1.2.1 Field sampling

The study was conducted in the Estuary and Gulf of St. Lawrence (EGSL) on board the RV *Coriolis II* in August 2006 and July 2007 (Fig. 1). Eight stations were sampled from August 8<sup>th</sup> to 21<sup>st</sup> 2006 and three from July 7<sup>th</sup> to 9<sup>th</sup> 2007. Thirty images were taken at each of the 11 stations. The photographs were taken with a bottom contact Benthos underwater camera system equipped with a Pentax Optio MX4 digital camera of a resolution of 4.0 Megapixels mounted perpendicular to the seafloor. The mean ( $\pm$  SE) area covered by each image was  $0.82 \pm 0.02$  m<sup>2</sup>.

At each station, the deep layer water temperature and salinity were recorded with a Seabird CTD. Water samples were collected from the deep layer using 12 L Niskin<sup>®</sup> bottles (General Oceanics<sup>®</sup>) to corroborate CTD values and measure oxygen concentration. Dissolved oxygen was determined by Winkler titration (Grasshoff et al., 1999).

Surface layer sediments were collected from the top 5 cm of a boxcore or a Van Veen grab sample, and granulometric characteristics were analysed using a LS 13320 Beckman-Coulter Particle Size Analyser (Blott et al., 2004). Also, the

total organic content in the sediments was determined by the loss-on-ignition method (Dean, 1974).

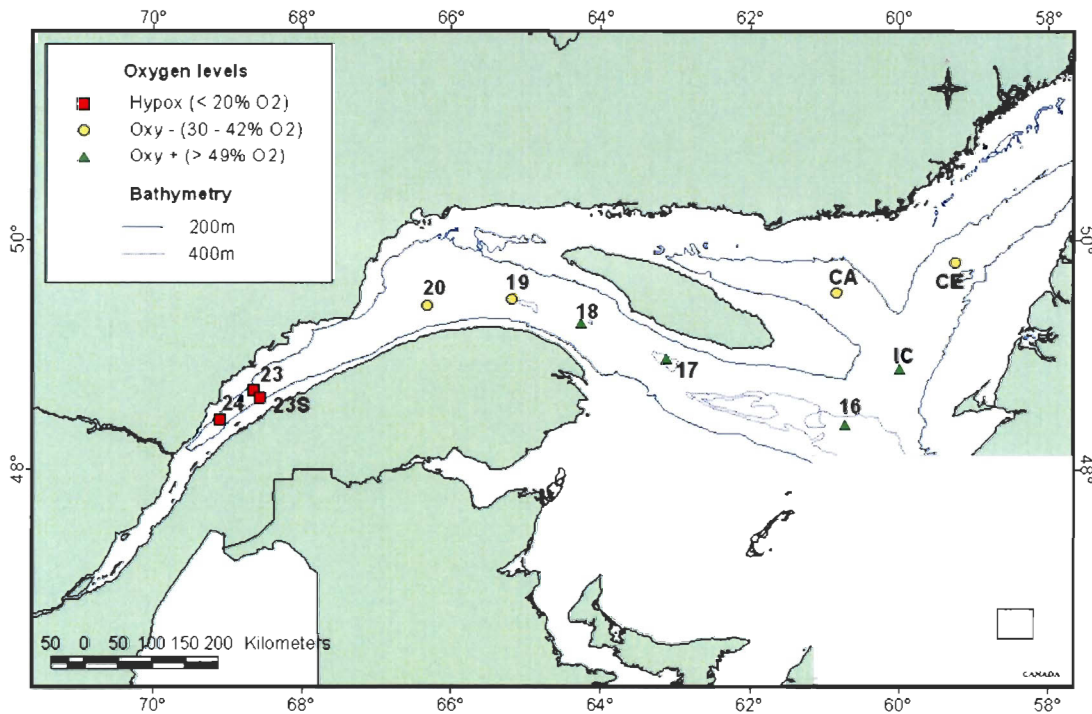


Figure 1: Stations sampled in the Estuary and Gulf of St. Lawrence, Canada, in August 2006 and July 2007. Oxy+ stations 16, 17, 18 and IC, and oxy- stations 19, 20, CA and CE were sampled in August 2006. The hypoxic stations 23, 23S and 24 were sampled in July 2007.

### 1.2.2 Image analysis

To determine the number of images to be analysed, we used the data from stations 20, 23 and IC to plot 1) a species and traces accumulation curve and 2) the mean and the variance of the accumulated species and traces. Both techniques lead to the conclusion that the analysis of fifteen images would give a

good estimate of the species and traces at a given station. Fifteen images were then randomly chosen for each station, except for station CA, where only 7 images were usable. A total of 157 images were analysed using the image analysis software "ImageJ" (<http://rsb.info.nih.gov/ij/index.html>). On each image, macrobenthic epifaunal organisms were identified to the lowest taxonomic level possible and counted. Identification was also confirmed with organisms collected with a Van Veen grab and an USNEL box core for a project on the infauna (Bourque, 2009). The abundances were converted to number per m<sup>2</sup>. Since only the arms of the Ophiuridae *Amphiura* sp. were visible, the total number of arms counted on a single image was divided by five to give the number of individuals. We recognize that this procedure could underestimate the number of individuals since not all five arms of each individual will always be extended to the sediment surface (Rosenberg, 1995). The area of each trace was manually encircled to determine the density of traces on each image. The area covered by surface-traces was measured and the number and the area of the relief-traces were determined. Due to the limited resolution of the images, only organisms and bioturbation traces  $\geq 5$  mm were identified.

Images were first examined to determine the types of bioturbation traces present. Based on the classification of Mauviel & Sibuet (1985) and Jones et al. (2007), an identification key was produced to represent the different traces found on the images (Appendix 1). These traces were classified based on their morphology. They were separated into two groups, surface-traces and relief-

traces, which were then separated into distinctive traces. The area covered by the different types of traces was determined and is hereafter referred as “trace density”. The area of small burrows was determined by approximating the burrow opening as a circle ( $A=\pi\cdot r^2$ ). A median burrow radius of 0.0075 m was used to calculate a median burrow area, which was then multiplied by the number of small burrows on the image to obtain an estimate of the total area of burrows openings. The area occupied by small slit-shaped burrows was determined by approximating their shape as a rectangle (Area=Width·Height) of median width 0.002 m and median length 0.0075 m. The total area occupied at the sediment surface by small slit-shaped burrows was then estimated from their number on an image. The area of seafloor occupied by macrobenthic epifauna was included in the total-traces density, surface-traces density and relief-traces density since organisms were presumably forming traces at the time the image was taken. The area of seafloor occupied by *Ophiura* sp., *Ctenodiscus crispatus*, *Pandalus* sp., *Sebastes* sp. and Rajidae was added to the surface-traces density while the area of the basal disc of Cnidarians was added to the relief-traces density.

### 1.2.3 Statistical analyses

Univariate indices of bioturbation traces and macrobenthic epifaunal diversity were calculated for each image. Univariate indices of bioturbation traces are: traces density (%), traces diversity (total number of different types of traces), Shannon-Wiener's diversity index ( $H'$ ,  $\log_e$ ) and Pielou's evenness index ( $J'$ ). The

univariate index of macrobenthic epifaunal diversity was species richness ( $S$ ) and corresponds to the number of species counted.

Stations were pooled based on their oxygen concentration. Groups were composed of stations with: i)  $> 49\%$   $O_2$  saturation (oxy+: stations 16, 17, 18 and IC), ii) between 30 and 42%  $O_2$  saturation (oxy-: stations 19, 20, CA and CE), and iii)  $< 20\%$   $O_2$  saturation (hypoxic: stations 23, 23S and 24).

Nested analyses of variance (ANOVA) were performed to determine if there was a significant difference between the oxygen levels ( $> 49\%$   $O_2$ , 30-42%  $O_2$  and  $< 20\%$   $O_2$ ) and the stations within these oxygen levels. This was followed by post-hoc Tukey tests for multiple comparisons when significant differences were observed. Normality of residuals was verified with the Shapiro-Wilk test and their homogeneity was verified visually (Quinn & Keough, 2002). Variables that did not satisfy these criteria were transformed (fourth root ( $\sqrt[4]{x}$ ),  $\log_{10}$  or  $\log_{(x+1)}$  when data contained zero values) and are indicated in the tables.

Multiple linear regressions were also performed using the stepwise procedure (probability to enter of 0.25 and 0.10 to leave) to determine environmental factors influencing traces density, traces diversity, species richness ( $S$ ), Shannon-Wiener diversity index ( $H'$ ) and Pielou's evenness index ( $J$ ). The VIF (variance inflation factor) multicollinearity test was performed to



select environmental factors with value lower than 10, a threshold indicating a strong collinearity between variables (Quinn & Keough, 2002). The six environmental factors retained were depth (D), mean sediment grain size (MGS), percent oxygen saturation ( $O_2$ ), percent total organic matter (TOM), temperature (T) and salinity (S). Dependent variables used were total-traces density (%), surface-traces density (%), relief-traces density (%), grey-coloured sediment density (%), total-traces diversity, surface-traces diversity, relief-traces diversity, species richness (S), Shannon-Wiener diversity ( $H'$ ) and Pielou's evenness ( $J$ ). Adjusted  $r^2$  was the criterion used to determine the environmental variables best explaining the indices. The normality was verified on residuals with the Shapiro-Wilk test and their homogeneity was verified visually (Quinn & Keough, 2002). Variables that did not satisfy these criteria were transformed ( $\sqrt{\cdot}$  or  $\log_{10}$ ).

Multivariate analyses were based on Bray-Curtis similarity matrices performed on untransformed and transformed presence\absence data. Taxa that appeared only once were excluded from these analyses (Clarke & Warwick, 1994). Variations in traces densities and macrobenthic epifaunal densities were studied using a permutational multivariate analysis of variance (PERMANOVA) performed with 4999 random permutations of appropriate units (Anderson, 2001; McArdle & Anderson, 2001). When there were too few possible permutations to obtain a reasonable test, a p-value was calculated using 4999 Monte Carlo random draws from the asymptotic permutation distribution (Terlizzi et al., 2005). Significant terms within the full models were analysed using appropriate pair-wise

comparisons. Non-metric multidimensional scaling (nMDS) ordinations of similarity matrices were performed to visualize multivariate patterns. Similarity percentage analyses (SIMPER) were used to determine bioturbation traces that contributed the most to the dissimilarity between oxygen levels (Clarke, 1993).

### 1.3 Results

Eighteen types of surface-traces and nine types of relief-traces were identified (Table 1). A total of 2654 organisms were identified, representing 22 different macrobenthic taxa (Table 2). Some representative images of organisms and traces found in the EGSL are presented in Fig. 2. The organisms with the highest density were two brittlestars *Ophiura* sp., followed by *Amphiura* sp. Other organisms found in high densities were the anemones *Edwardsia* sp. and the stalked tunicate *Boltenia ovifera* (Table 2).

In general, surface-traces covered a greater seafloor area than relief-traces, with the exception of stations 18 and 19 (Table 1). Imprints-depressions were the only type of surface-traces found at all stations in the EGSL. Simple ploughs were found at all stations except station 24. The *Ophiura* trace was the surface-trace with the highest density for a single station; this trace covered 7% of the seafloor at station 24. This trace was only found at the hypoxic stations 23

and 24. Shrimp trails were found at each oxy+ and oxy- stations where, except at station 16, *Pandalus* sp. was also recorded (Table 2).

Small burrows were found at all stations (Table 1). They were the most abundant relief-trace in numbers. Although they covered a small area of the seafloor, they were the relief-trace with the highest density except at station CA where large burrows had the highest density. Medium burrows and medium slit-shaped burrows were also found at all stations. Large burrows were found at all stations except at stations 17 and CE. Although small slit-shaped burrows were the second most abundant relief-trace in number, their density was low.

The highest density of organisms was found at the hypoxic station 24 (64.84 ind. m<sup>-2</sup>), which was dominated by *Ophiura* sp. (61.32 ind. m<sup>-2</sup>; Fig. 3 and Table 2). The lowest densities of organisms were found at the hypoxic station 23S and the oxy+ station 16 (5.14 ind. m<sup>-2</sup> and 5.87 ind. m<sup>-2</sup> respectively; Fig. 3 and Table 2). *Pandalus* sp. and unknown crustaceans were only found at oxy+ and oxy- stations, as was the case for *B. ovifera* and unknown bryozoans. *Actinauge* sp. and *Cerianthus* sp. were only found at hypoxic stations.

Table 1: List of surface and relief-traces identified on benthic images from the EGSL (based on Mauviel & Sibuet (1985) and Jones et al. (2007)), mean density (area of seafloor covered by traces (%)) and overall density per station (%).

	Hypoxic			Oxy-				Oxy+			
	23	23S	24	19	20	CA	CE	16	17	18	IC
<b>Surface-traces</b>											
<b>Imprints</b>											
Fish imprints	0	0	0	0	0	0	0.15	0	0.03	0	0
Ophiroid imprints	0.05	0	0	0	0	0	0	0	0	0	0
<b>Ploughs</b>											
Simple ploughs	1.73	2.71	0	0.22	1.05	0.89	1.33	0.66	1.87	0.21	0.18
Double ploughs	1.25	1.23	0	0	2.99	0	0	0.34	0	0	0
Discontinuous ploughs	0	0	0	0	0.11	0	0	0	0	0	0.10
<b>Ridges</b>											
Double ridges	0.11	0.39	0	0	0	0	0	0	0	0	0
<b>Trails</b>											
Asteroid trails	0	0.17	0	0	0	0	0	0	0	0	0
Double trails	0	0.03	0	0	0	0	0	0.14	0	0	0.13
Ophiroid trails	0.54	0	0	0	0	0	0	0	0	0	0
Shrimp trails	0	0	0	0.08	0.68	2.59	0.82	1.28	0.51	0.06	0.38
<b>Others</b>											
Feces	0	0	0	0	0	0	0.01	0	0	0	0.01
Imprints-depressions	0.47	2.00	0.15	0.92	0.68	0.63	0.67	0.53	0.94	0.87	1.19
Indeterminate surface-traces	0	0.54	0	0	0.21	0.27	0	0.13	0.04	0	0.04
<b>Organisms</b>											
Asteroidea	0	0.04	0	0	0	0	0	0	0	0	0
<i>Ophiura</i> sp.	1.16	0	7.00	0	0	0	0	0	0	0	0
<i>Sebastes</i> sp.	0	0	0	0	0	0	0.09	0	0	0	0
Shrimp	0	0	0	0.15	0.02	0.02	0.11	0	0.01	0.01	0.23
Rajidae	0	0.95	0	0	0	0	0	0	0	0	0
<b>Total surface-traces</b>	<b>5.32</b>	<b>8.05</b>	<b>7.15</b>	<b>1.37</b>	<b>5.73</b>	<b>4.40</b>	<b>3.20</b>	<b>3.07</b>	<b>3.41</b>	<b>1.15</b>	<b>2.25</b>
<b>Relief-traces</b>	<b>23</b>	<b>23S</b>	<b>24</b>	<b>19</b>	<b>20</b>	<b>CA</b>	<b>CE</b>	<b>16</b>	<b>17</b>	<b>18</b>	<b>IC</b>
<b>Burrows</b>											
Small burrows (0.5-1 cm)	0.41	0.30	0.08	0.54	0.82	0.12	0.27	0.27	0.09	0.36	0.17
Medium burrows (> 1-5 cm)	0.11	0.15	0.07	0.41	0.28	0.09	0.01	0.06	0.03	0.35	0.15
Large burrows (> 5 cm)	0.11	0.04	0.03	0.40	0.46	0.45	0	0.06	0	0.31	0.17
Small slit-shaped burrows (0.5-1 cm)	0	0.01	0	0.01	0	0.01	0.01	0.05	0.01	0.01	0.01
Medium slit-shaped burrows (> 1-5 cm)	0.01	0.03	0.02	0.02	0.03	0.05	0.02	0.09	0.02	0.06	0.03
<b>Mounds</b>											
Crevasse mounds	0	0	0	0	0.01	0	0	0.01	0	0	0.01
<b>Organisms</b>											
<i>Pennatula aculeata</i> basal disc	0.02	0.07	0	0.05	0.12	0.09	0.03	0	0.02	0.02	0
<i>Pennatula borealis</i> basal disc	0	0	0	0.08	0	0	0	0.12	0.06	0.05	0
<i>Actinauge</i> sp. basal disc	0.22	0.20	0	0	0	0	0	0	0	0	0
<b>Total relief-traces</b>	<b>0.89</b>	<b>0.79</b>	<b>0.20</b>	<b>1.51</b>	<b>1.71</b>	<b>0.80</b>	<b>0.35</b>	<b>0.65</b>	<b>0.23</b>	<b>1.17</b>	<b>0.54</b>
<b>Total-traces</b>	<b>6.22</b>	<b>8.84</b>	<b>7.36</b>	<b>2.88</b>	<b>7.44</b>	<b>5.20</b>	<b>3.54</b>	<b>3.72</b>	<b>3.63</b>	<b>2.32</b>	<b>2.79</b>

Table 2: Mean macrobenthic epifaunal density (ind. m<sup>-2</sup>) per taxa and per station for the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007.

Taxa	Stations										
	Hypoxic			Oxy-				Oxy+			
	23	23S	24	19	20	CA	CE	16	17	18	IC
<b><u>Ascidacea</u></b>											
<i>Boltenia ovifera</i>	0	0	0	0.12	0	12.54	13.07	0	0	0	1.99
<b><u>Bryozoa</u></b>											
Unknown bryozoans	0	0	0	0	0	7.29	12.98	3.85	6.62	0	1.00
<b><u>Cnidaria</u></b>											
<i>Actinauge</i> sp.	0.95	0.86	0	0	0	0	0	0	0	0	0
<i>Cerianthus</i> sp.	0.09	0.11	0	0	0	0	0	0	0	0	0
<i>Edwardsia</i> sp.	0	0	0	0	0	0	0	0.71	26.90	0	0.70
<i>Pennatula aculeata</i>	1.04	2.94	0	2.17	5.00	3.97	1.37	0	0.74	0.81	0
<i>Pennatula borealis</i>	0	0	0	0.83	0	0	0	1.21	0.57	0.49	0
<b><u>Crustacea</u></b>											
<i>Pandalus</i> sp.	0	0	0	1.23	0.31	0.19	0.94	0	0.10	0.08	1.92
Unknown crustaceans	0	0	0	0.35	1.27	0	0	0.10	0.09	0.34	0.09
<b><u>Echinodermata</u></b>											
<i>Amphiura</i> sp.	5.94	0.38	3.25	32.63	6.93	0.23	0	0	0.26	10.34	0.28
<i>Brisaster fragilis</i>	0	0.18	0	0	0	0	0	0	0	0	0
<i>Ctenodiscus crispatus</i>	0	0.28	0	0	0	0	0	0	0	0	0
<i>Ophiura</i> sp.	10.20	0	61.32	0	0	0	0	0	0	0	0
<b><u>Gastropoda</u></b>											
Buccinidae sp.1	0	0	0	0	0	0	0	0	0.10	0	0
Buccinidae sp.2	0	0.09	0	0	0	0	0	0	0	0	0
<b><u>Polychaeta</u></b>											
<i>Chaetopterus</i> sp. tubes	0	0	0	0	0.31	0	0	0	0	1.44	0
Sabellidae	0	0	0	0	0	0	0.08	0	2.89	0	3.80
Terebellidae	0.76	0	0	0	0	0	0	0	0	0	0
Unknown polychaete tubes	0.73	0.09	0.27	0.09	0	0	0	0	0.09	0.08	0.15
<b><u>Vertebrata (fishes)</u></b>											
<i>Lycodes</i> sp.	0.09	0	0	0	0	0	0	0	0	0	0.08
Rajidae	0	0.21	0	0	0	0	0	0	0	0	0
<i>Sebastes</i> sp.	0	0	0	0	0	0	0.52	0	0	0	0
<b>Total density</b>	<b>19.80</b>	<b>5.14</b>	<b>64.84</b>	<b>37.42</b>	<b>13.82</b>	<b>24.22</b>	<b>28.96</b>	<b>5.87</b>	<b>38.36</b>	<b>13.58</b>	<b>10.01</b>

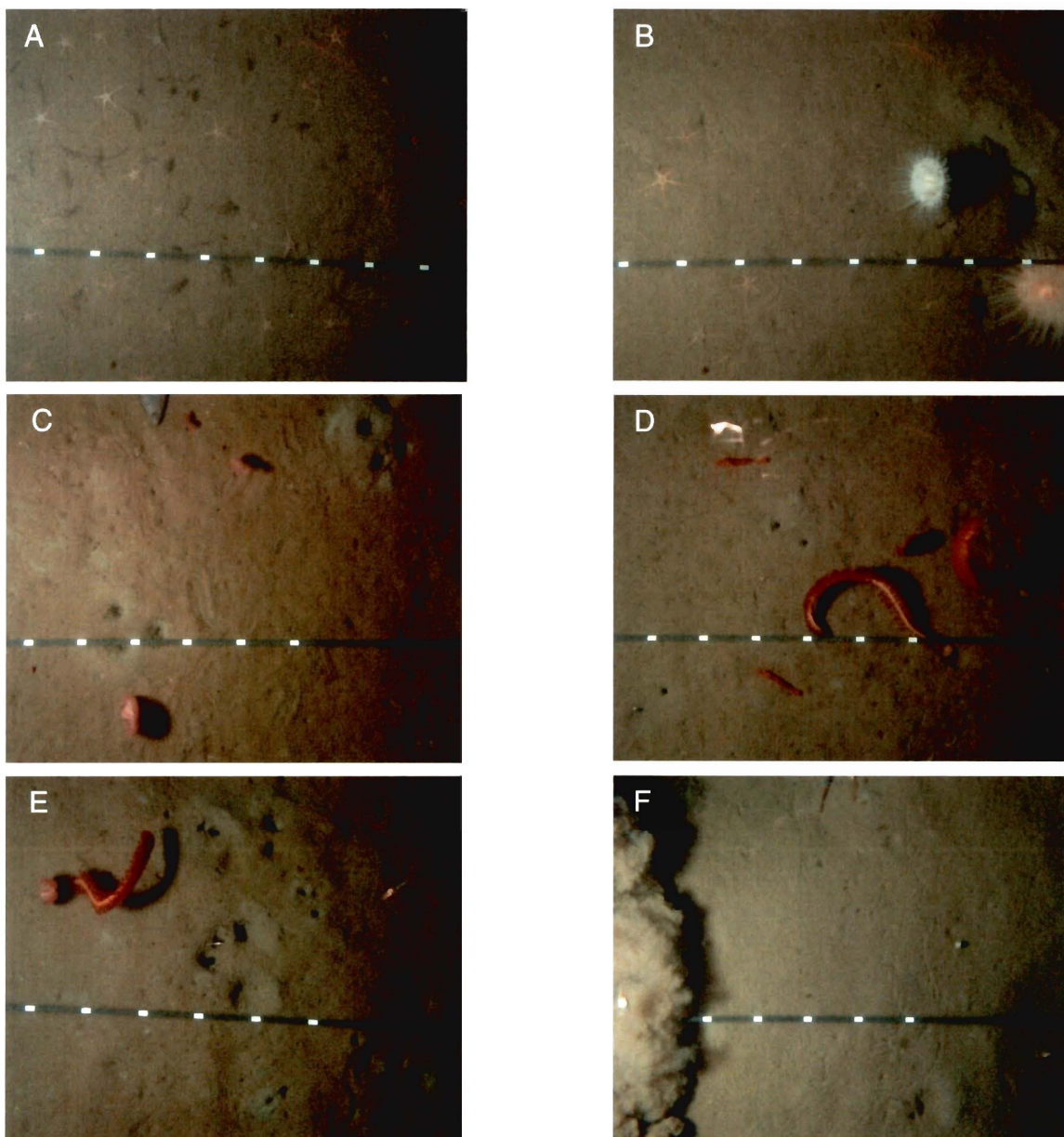


Figure 2: Representative photographs taken in the Estuary and Gulf of St. Lawrence in 2006 and 2007. A) Station 24: *Ophiura* sp. and detritus, B) Station 23: *Ophiura* sp., *Actinauge* sp. (right), *Lycodes* sp. (center right) in an imprint-depression and close to a medium burrow, C) Station 20: Small burrows, medium burrows with grey sediment (top right), double ploughs (from top left to down center), *Pennatula aculeata* (top center and down left), *Amphiura* sp. arms (top left) and flatfish (top center) D) Station 19: Small and medium burrows, *Pandalus* sp., *Pennatula borealis*, *P. aculeata* and *Amphiura* sp. arms, E) Station 18: Small, medium and large burrows, imprints-depressions (top right), simple ploughs (down right and down left), *P. aculeata*, *P. borealis* and unknown crustaceans, and F) Station IC: Sediment cloud (left), shrimp trail (down center to top right), imprints-depressions and *Pandalus* sp. Scale: 10 cm between two white lines.

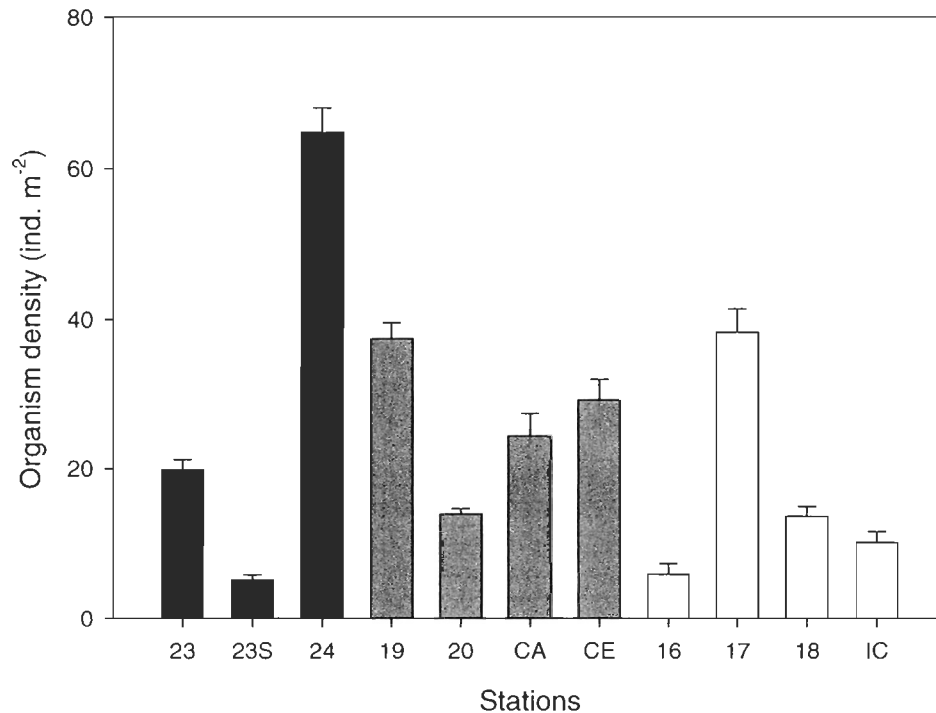


Figure 3: Mean total organism density (ind. m<sup>-2</sup> ± SE) for the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007. Oxygen levels: hypoxic stations (<20% O<sub>2</sub>) (black); oxy- stations (32-40% O<sub>2</sub>) (grey); oxy+ stations (>49% O<sub>2</sub>) (white).

### 1.3.1 Univariate analyses

The total-traces density (shown below as Mean ± SE) increased as the oxygen levels decreased; lower values were found at the oxy+ stations (3.12% ± 0.28), intermediate values at the oxy- stations (4.70% ± 0.46) and higher values at the hypoxic stations (7.47% ± 0.49) (Fig. 4A). The same pattern was observed for the surface-traces density (Fig. 4B). Nested ANOVAs showed a significant difference of total and surface-traces densities for the different oxygen levels (both  $p < 0.01$ ; Table 3). For the total traces density, Tukey's test showed that

oxy+ stations were significantly lower than hypoxic stations, and that oxy- stations were not significantly different from oxy+ and hypoxic stations (Fig. 4A). For the surface-traces density, Tukey's test showed that oxy+ and oxy- stations were significantly lower than hypoxic stations, and that oxy+ and oxy- stations were not significantly different from each other (Fig. 4B).

The relief-traces density (Fig. 4C) was higher at the oxy- stations ( $1.14\% \pm 0.12$ ), with high values for stations 19 and 20 ( $1.51\% \pm 0.17$  and  $1.71\% \pm 0.18$ , respectively) and low values for stations CA and CE ( $0.80\% \pm 0.35$  and  $0.35\% \pm 0.03$ , respectively). This was followed by oxy+ stations ( $0.65\% \pm 0.08$ ), with a low value for station 17 ( $0.23\% \pm 0.03$ ). The lowest relief-traces densities were found at the hypoxic stations ( $0.63\% \pm 0.08$ ), with the lowest value at station 24 ( $0.20\% \pm 0.05$ ). Nested ANOVAs indicated no significant difference between the oxygen levels for relief-traces density ( $p > 0.05$ , Table 3).

The density of grey-coloured sediment areas on the images (Fig. 4D) was higher at the oxy- stations ( $2.26\% \pm 0.43$ ), with the highest values at stations 19 and 20 ( $3.21\% \pm 0.81$  and  $4.41\% \pm 0.87$ , respectively). However, oxy- stations CA and CE had much lower values ( $0.23\% \pm 0.17$  and  $0.11\% \pm 0.06$ , respectively). Tukey HSD test within the oxy- group effectively revealed that the density of grey-coloured sediment areas at stations 19 and 20 were significantly higher than at stations CA and CE (Fig 4D). The oxy+ stations had intermediate



values ( $0.78 \% \pm 0.15$ ) while the hypoxic stations had the lowest values ( $0.14\% \pm 0.08$ ), with 0% for station 24. Nested ANOVAs indicated no significant difference between the oxygen levels for the density of grey-coloured sediment areas ( $p > 0.05$ , Fig. 4D and Table 3).

The difference in means between stations within each oxygen level did not show a clear pattern for either surface, relief and total-traces diversities, nor for species richness, Pielou's evenness and Shannon-Wiener diversity (Fig. 4E-J). Nested ANOVAs indicated that oxygen levels were not significantly different for those indices ( $p > 0.05$ , Table 3). However, nested ANOVAs indicated that stations within oxygen level were significantly different from each other for all those indices (all  $p < 0.001$ ; Table 3).

Table 3: Summary of nested ANOVAs for total-traces density ( $\log_{(x+1)}$ ), surface-traces density ( $\log_{(x+1)}$ ), relief-traces density ( $\log_{10}$ ), grey-coloured sediment density ( $\sqrt{V}$ ), total-traces diversity, surface-traces diversity, relief-traces diversity, species richness ( $S$ ), Pielou's evenness ( $J'$ ) and Shannon-Wiener diversity ( $H'$ ) to test the effect of oxygen level and station within oxygen level. Legend: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , NS.

Source of variation	Total-traces density ( $\log_{(x+1)}$ )			Surface-traces density ( $\log_{(x+1)}$ )		Relief-traces density ( $\log_{10}$ )		Grey-coloured sediment density ( $\sqrt{V}$ )	
	df	MS	$F$	MS	$F$	MS	$F$	MS	$F$
O <sub>2</sub> level	2	1.479	12.37**	2.081	8.74**	0.963	0.59	5.805	2.71
Station (O <sub>2</sub> level)	8	0.121	3.21**	0.242	4.74***	1.659	24.79***	2.182	19.61***
Error	146	0.038		0.051		0.067		0.111	
Total	156								

Source of variation	Total-traces diversity			Surface-traces diversity		Relief-traces diversity		Species richness ( $S$ )	
	df	MS	$F$	MS	$F$	MS	$F$	MS	$F$
O <sub>2</sub> level	2	46.822	2.59	7.058	0.54	12.260	2.64	2.465	0.24
Station (O <sub>2</sub> level)	8	18.414	6.00***	13.435	17.67***	4.729	5.25***	10.337	10.65***
Error	146	3.068		0.761		0.901		0.971	
Total	156								

Source of variation	Pielou's evenness ( $J'$ )			Shannon-Wiener diversity ( $H'$ )	
	df	MS	$F$	MS	$F$
O <sub>2</sub> level	2	0.524	1.39	2.086	1.25
Station (O <sub>2</sub> level)	8	0.385	24.18***	1.709	20.50***
Error	146	0.016		0.083	
Total	156				

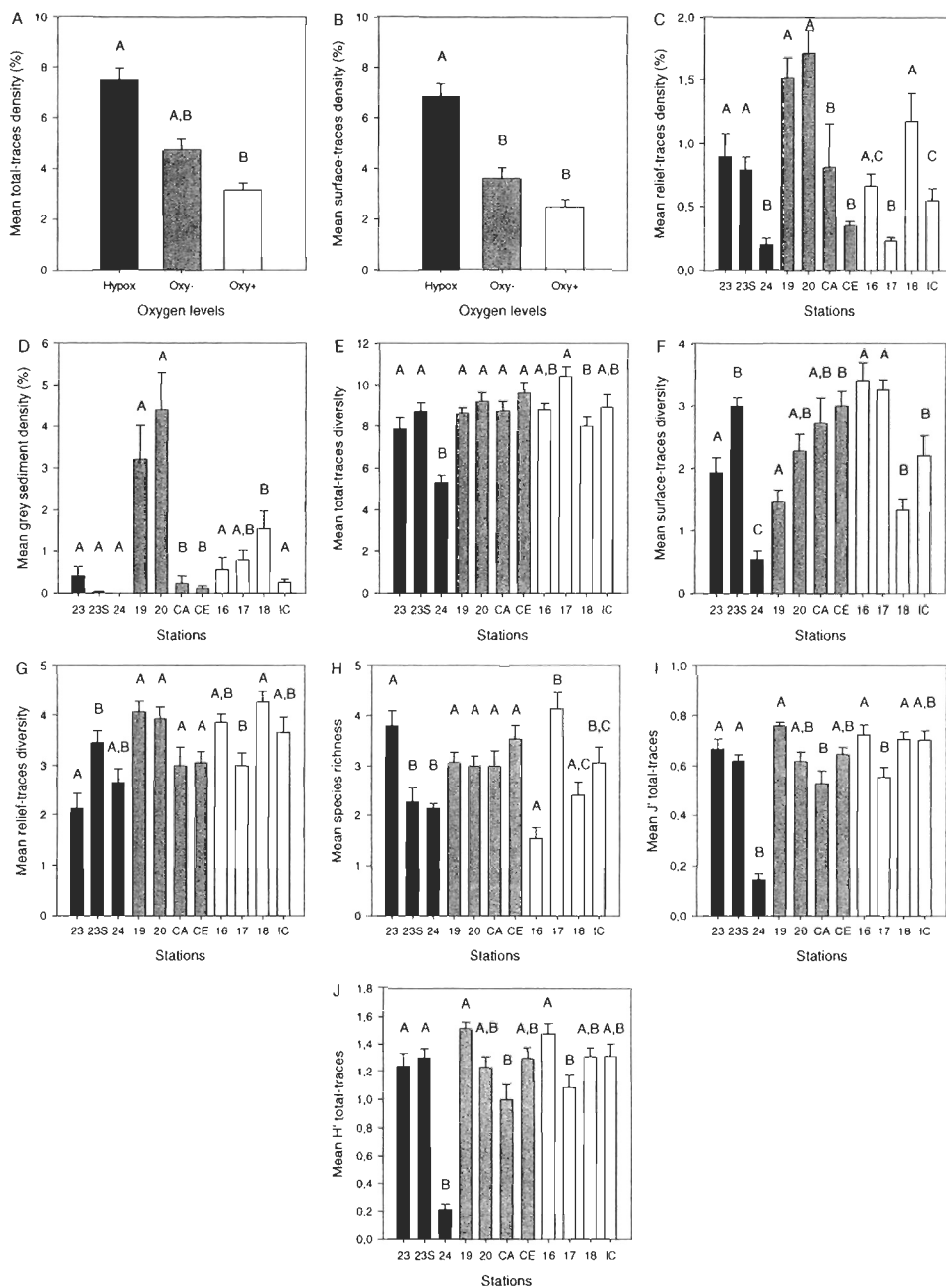


Figure 4: Mean ( $\pm$  SE) of: A) total-traces density (%) and B) surface-traces density (%) for three different oxygen levels, and C) relief-traces density (%), D) grey-coloured sediment density (%), E) total-traces diversity, F) surface-traces diversity, G) relief-traces diversity, H) species richness, I) Pielou's evenness ( $J'$ ) of total-traces and J) Shannon-Wiener's diversity index ( $H'$ ) of total-traces for stations within oxygen level. Letters above columns indicate the results of Tukey HSD test between (A-B) and within (C-J) oxygen levels, where categories with the same letter did not differ significantly. Oxygen levels: hypoxic stations (<20% O<sub>2</sub>) (black); oxy- stations (32-40% O<sub>2</sub>) (grey); oxy+ stations (>49% O<sub>2</sub>) (white).

Relationships between environmental variables and univariate indices of bioturbation traces, and macrobenthic epifauna were examined using multiple linear regression models. The oxygen saturation is the variable that best explains the total and surface-traces densities (Table 4). The variability of total and surface-traces was explained by the oxygen saturation at 62% and 55%, respectively (Table 4). We observed a decrease in total and surface-traces densities as the oxygen level increased (Fig. 5A and B). Environmental variables alone or combined never explained more than 53% of the other studied indices (Table 4). However, total organic matter and mean sediment grain size were often present as environmental variables explaining the regression models of the other indices. No multiple linear regression models could explain the species richness.

Table 4: Results of the multiple linear regression models (stepwise procedure) used to estimate total-traces density (%), surface-traces density (%), relief-traces density (%), grey-coloured sediment density ( $\sqrt{\sqrt{}}$ ) (%), total-traces diversity ( $\log_{10}$ ), surface-traces diversity, relief-traces diversity, species richness, Pielou's evenness ( $J'$ ) and Shannon-Wiener diversity ( $\log_e$ ) ( $H'$ ) among the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006-2007. Species richness is not included in the table since no variables could explain these data. Environmental variables in the regression models were depth (D, m), bottom salinity (S, psu), bottom temperature (T, °C), bottom oxygen saturation (O<sub>2</sub>, %), total organic matter (TOM, %) and mean sediment grain size (MGS,  $\mu\text{m}$ ). Note: Underlined total organic matter was  $\log_{10}$  transformed for grey-coloured sediment density ( $\sqrt{\sqrt{}}$ ) and total-traces diversity ( $\log_{10}$ ) models. Partial  $r^2$  below each regression coefficient; NS: not significant;  $r^2$ : Total  $r^2$ ; Adj  $r^2$ : Adjusted  $r^2$  and MSE: Mean squared errors.

	Intercept	D (m)	S (psu)	T (°C)	O <sub>2</sub> (%)	TOM (%)	MGS ( $\mu\text{m}$ )	$r^2$ (Adj $r^2$ )	MSE
<b>Total-traces density</b>	9.55	NS	NS	NS	-0.12	NS	NS	0.66 (0.62)	1.89
Partial $r^2$					0.66				
<b>Surface-traces density</b>	8.55	NS	NS	NS	-0.12	NS	NS	0.59 (0.55)	2.32
Partial $r^2$					0.59				
<b>Relief-traces density</b>	0.16	0.01	NS	NS	NS	NS	-0.13	0.44 (0.30)	0.17
Partial $r^2$		0.25					0.19		
<b>Grey sed density (<math>\sqrt{\sqrt{}}</math>)</b>	-9.95	NS	NS	NS	-0.02	<u>13.00</u>	-0.08	0.66 (0.51)	0.08
Partial $r^2$					0.19	0.34	0.13		
<b>Total-traces div (<math>\log_{10}</math>)</b>	0.40	NS	NS	NS	NS	<u>0.84</u>	NS	0.16 (0.07)	0.01
Partial $r^2$						0.16			
<b>Surface-traces div</b>	-305.79	-0.02	9.12	NS	NS	NS	NS	0.31 (0.14)	2.89
Partial $r^2$		0.15	0.16						
<b>Relief-traces diversity</b>	-95.33	NS	3.05	-0.78	NS	NS	-0.09	0.67 (0.53)	0.10
Partial $r^2$			0.39	0.11			0.17		
<b><math>J'</math> total-traces</b>	-0.21	NS	NS	NS	NS	0.12	-0.03	0.46 (0.32)	0.02
Partial $r^2$						0.22	0.24		
<b><math>H'</math> total-traces</b>	-0.59	NS	NS	NS	NS	0.27	-0.06	0.47 (0.34)	0.08
Partial $r^2$						0.24	0.23		

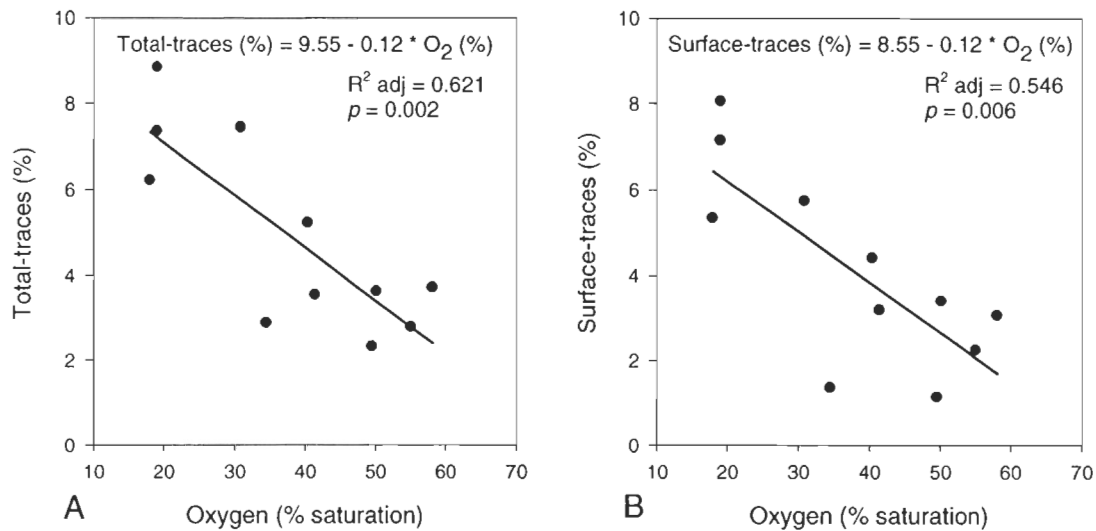


Figure 5: Relation between oxygen saturation (%) and A) total-traces density (%) and B) surface-traces density (%) at the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007.

### 1.3.2 Multivariate analyses

A clear difference between hypoxic and oxy+ stations was found with a non-metric multidimensional scaling (nMDS) plot of untransformed total-traces density data (Fig. 6A). The result was similar for nMDS plot of presence/absence-transformed total-traces density (Fig. 6B). PERMANOVA analysis revealed that untransformed total-traces density between oxygen levels were significantly different ( $P = 0.0314$ , Table 5). Similar results were obtained when total-traces density were presence/absence-transformed ( $P = 0.0346$ , Table 5). Pair-wise comparison test indicated that untransformed density data between hypoxic and oxy+ stations were significantly different ( $P = 0.0292$ ). However, pair-wise comparison revealed no significant difference on

presence\absence-transformed density data between the hypoxic and oxy+ stations ( $P = 0.056$ ). SIMPER analysis revealed that the *Ophiura* trace was contributing the most to the dissimilarity between the two oxygen levels at 33.69%, followed by the simple ploughs at 19.03% (Table 6).

On the other hand, pair-wise comparison test on untransformed total-trace density revealed no significant difference neither between hypoxic and oxy- stations, nor between oxy+ and oxy- stations. PERMANOVA analysis also shows no significant difference in organism density between the oxygen levels, both for untransformed and presence\absence-transformed data (Table 5).

Table 5: Permutational analysis of variance (PERMANOVA) (Anderson, 2001; McArdle & Anderson, 2001) results testing the effect of oxygen level and its interaction with total-traces and organism densities based on Bray-Curtis similarity matrices performed on untransformed and presence\absence transformed data.

<b>Source of variation</b>	<b>df</b>	<b>MS</b>	<b>Pseudo-<i>F</i></b>	<b><i>P</i> (perm)</b>
<b>Total-traces density</b>				
O <sub>2</sub> level	2	33669.0	1.92	0.0314
Station (O <sub>2</sub> level)	8	17900.0	10.61	0.0002
Residuals	146	1687.7		
<b>Total-traces density (presence/absence)</b>				
O <sub>2</sub> level	2	16157.0	2.42	0.0346
Station (O <sub>2</sub> level)	8	6814.7	15.65	0.0002
Residuals	146	435.6		
<b>Organism density</b>				
O <sub>2</sub> level	2	57002.0	1.41	0.1644
Station (O <sub>2</sub> level)	8	41344.0	41.74	0.0002
Residuals	146	990.6		
<b>Organism density (presence/absence)</b>				
O <sub>2</sub> level	2	58653.0	2.08	0.0710
Station (O <sub>2</sub> level)	8	28799.0	36.78	0.0002
Residuals	146	783.1		



Table 6: Results of similarity percentage analyses (SIMPER) showing the contribution (%) of the types of traces to the average Bray-Curtis dissimilarity of compared oxy+, oxy- and hypoxic groups as well as the average dissimilarity (%) among groups.

<b>Trace</b>	<b>Contr. (%)</b>	<b>Trace</b>	<b>Contr. (%)</b>
<b>Oxy+ &amp; Hypox (Avg. dissim. = 82.86)</b>		<b>Oxy- &amp; Hypox (Avg. dissim. = 81.77)</b>	
<i>Ophiura</i> traces (%)	33.69	<i>Ophiura</i> traces (%)	30.21
Simple ploughs (%)	19.03	Simple ploughs (%)	17.01
		Double ploughs (%)	11.56
<b>Oxy+ &amp; Oxy- (Avg. dissim. = 69.65)</b>			
Simple ploughs (%)	20.42		
Shrimp trails (%)	17.86		
Imprints-depressions (%)	17.51		

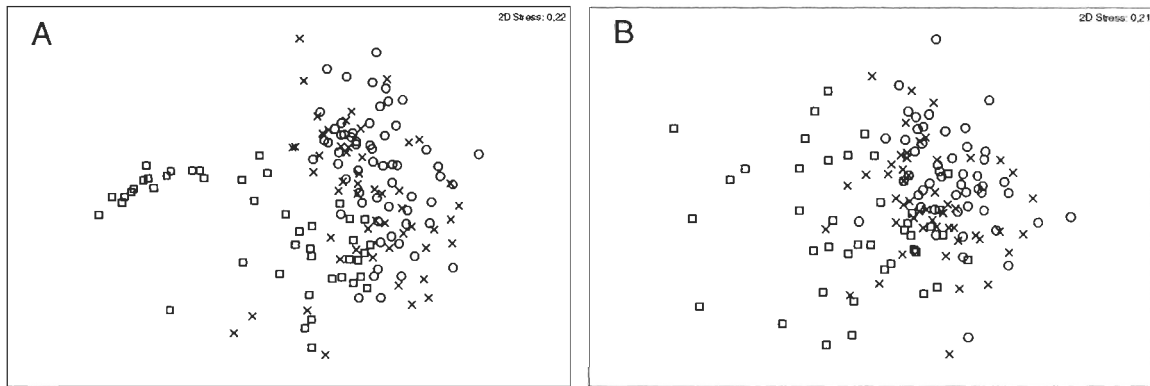


Figure 6: Non-metric multi-dimensional scaling (nMDS) plots of total-traces density per oxygen level based on A) untransformed data and B) presence/absence transformed data. Oxygen levels: hypoxic stations (□); oxy-stations (x); oxy+ stations (○).

## 1.4 Discussion

### 1.4.1 Macrobenthic epifauna

The results of this study indicate that the decreasing oxygen concentrations in the EGSL bottom waters has not yet lead to a decrease in macrobenthic species richness, which is contrary to our expectations. This observation does not appear to support previous studies conducted on the effects of hypoxia in other parts of the world (Diaz & Rosenberg, 1995; Wu, 2002; Diaz & Rosenberg, 2008). However, it has been reported that, under hypoxic conditions, suspension feeders are generally replaced by deposit feeders (Diaz & Rosenberg, 1995; Wu, 2002). Even if the statistical analyses presented here do not show significant differences in species richness between the different oxygen levels, our results could indicate recent changes of the macrobenthic epifauna community structure in the hypoxic zone of the EGSL, where suspension feeders and low-oxygen intolerant species have been replaced by deposit feeders and low-oxygen tolerant species. First, the species with the highest density and abundance, the deposit feeding, low-oxygen tolerant *Ophiura* sp. (Vistisen & Vismann, 1997), was only found at the hypoxic stations 23 and 24. Second, SIMPER analyses showed that the *Ophiura* trace contributed most to the difference between the hypoxic and the oxy+ stations. Third, the highest density of the suspension feeder *P. aculeata* at oxy- stations 20 and CA and the limited

presence of the suspension feeder *P. borealis* at the oxy+ and oxy- stations also support the indication of changes in community structure.

A recent study conducted in the deep waters of the EGSL (Bourque, 2009) found changes in the infaunal community structure due to oxygen depletion. In the deep hypoxic waters of the Lower St. Lawrence Estuary (LSLE), where stations 23, 23S and 24 are located, they found that the infaunal community structure had changed from 1980 to 2006. These changes were reflected by an increase of small opportunistic deposit feeders and a decrease of species richness and Shannon diversity (Bourque, 2009). In a review of the literature on hypoxia, Vaquer-Sunyer & Duarte (2008) demonstrated that cnidarians and molluscs are more tolerant to hypoxia while crustaceans are more sensitive. Lévesque (2009) effectively found a higher density of molluscs and cnidarians and a lower density of crustaceans in the hypoxic waters of the LSE. We found no crustaceans on the images from the hypoxic stations, but we did find them at the oxy+ and oxy- stations. We found cnidarians and molluscs, which are reported to be tolerant to low-oxygen concentrations, at stations covering all oxygen levels. Moreover, the habitat suitability model (using generalized linear model) developed by Lévesque (2009) and Lévesque et al. (2008) suggested the oxygen saturation as one of the explanatory variables influencing the biodiversity of the macrobenthic community collected with a Campelen bottom trawl in the EGSL. Our results and those of previous studies all suggest a change in the

community structure of the LSLE towards species more tolerant to the prevailing hypoxic conditions.

Studies on macrobenthic succession in relation to organic enrichment (Pearson & Rosenberg, 1978) and decreasing dissolved oxygen (Diaz & Rosenberg, 1995) demonstrated that benthic communities undergo transitional stages, from mature to short-lived opportunistic communities, during an event of organic enrichment or decreasing dissolved oxygen. Pearson & Rosenberg (1978) pointed out that benthic communities can, at one point, have low species richness and biomass, but high abundance of these few species. The low species richness but high density found at the hypoxic station 24 may suggest that this station is actually at this transition stage, situated between a mature community and a community composed of small, opportunistic and short-lived species.

While our study and others in the EGSL support the observation of community structure changes in the LSLE, the difference between the hypoxic and the oxy+ stations may also be explained by other factors such as the different biogeographic regions found in the EGSL. Brunel et al. (1998) divided the EGSL in 20 distinct zones based on bathymetric, biogeographic, oceanographic and physiographic criteria. Each region is known to be composed of particular species assemblages due to the specific characteristics of the region. In consequence, one can expect some differences in the species found in

two distinct biogeographic regions. However, we opted for the community structure change hypothesis due the recent findings of the importance of dissolved oxygen for structuring benthic communities in the EGSL and the large amount of literature found on the deleterious effects of hypoxia on benthic communities around the world. To support our hypothesis, we would require pre-hypoxia images at the same stations, which were not available at the time of this study. However, the infaunal historical data comparison from 1980 to 2006 performed by Bourque (2009) and Bourque & Archambault (unpubl.) support the community structure change hypothesis. In the LSLE, they found increasing abundance of polychaetes tolerant to low-oxygen concentrations and high organic carbon loadings, a decreasing abundance of molluscs and crustaceans, an increasing dominance in density of small surface deposit feeding species and a decreasing dominance of mobile omnivorous species.

#### 1.4.2 Bioturbation traces

The results of this study indicate the oxygen saturation as the environmental variable that best explains the densities of total and surface-traces in the EGSL, in agreement with our expectations. However, we also observed a strong relationship between the oxygen concentration and the densities of total and surface-traces, where the latter increase with decreasing oxygen. This last observation is contrary to our expectations and contradicts reports that hypoxic areas have reduced bioturbation (Diaz & Rosenberg, 2008). Our results may in part be explained by the fact that we added the area occupied by organisms to

the area covered by traces. Since the density of *Ophiura* trace was 7% at station 24, it increased the densities of total and surface-traces at this station. However, this cannot be the only explanation since the density of *Ophiura* trace was low at the two other hypoxic stations.

The density of macrobenthic organisms tended to increase with decreasing oxygen saturation (16.8 ind. m<sup>-2</sup> at oxy+ stations, 26.1 ind. m<sup>-2</sup> at oxy-stations and 29.9 ind. m<sup>-2</sup> at hypoxic stations), as did the densities of total and surface-traces; however the increase in macrobenthic organisms was not significant. SIMPER analyses indicated two types of surface-traces that explain most of the dissimilarity between the hypoxic and the oxy+ stations. These are *Ophiura* trace (only found in hypoxic stations) and simple ploughs (more abundant in hypoxic stations). Our results suggest that an increasing density of individuals, mostly *Ophiura* sp., is responsible for the increasing densities of total and surface-traces as the oxygen decreases. Since mobile deposit feeders such as *Ophiura* sp. move on the seafloor to find food, the density of their traces would be higher than sedentary species. The active mode of feeding and high density of *Ophiura* sp. at hypoxic stations could be the primary explanation for the highest density of total and surface-traces at the hypoxic stations.

Diversity of traces, species richness (*S*), Pielou's evenness (*J'*) and Shannon-Wiener diversity (*H'*) were not found to be significantly different for different oxygen saturation levels. However, significant differences were found

among stations with similar levels of oxygen saturation, indicating some spatial heterogeneity in the characteristics of bioturbation traces and the diversity of the macrobenthic epifaunal community.

Within the hypoxic group, certain particularities distinguished station 24 from station 23 and 23S; it had the highest organism density, but the lowest species richness, and the relief-traces density, the total and surface-traces diversities,  $J$  and  $H'$  were significantly lower than at the two other hypoxic stations. The low relief-traces density at the hypoxic station 24 can be explained by the persistent cloud of suspended matter obstructing the field of view on the benthic images (see Fig. 2A). This suspended matter in the water column close to the sediment made the identification of relief-traces difficult and may have lowered the counts for this station. There may also be a higher sedimentation rate at station 24, so that total and surface-traces are more rapidly erased. However, for the other indices, it is difficult to explain why this station is different from the two others, besides the fact that it is the most upstream station sampled in this study.

Total-traces densities in the Laurentian Channel were much smaller than abyssal depth traces densities reported by Kitchell et al. (1978) and Young et al. (1985). However, due to low sedimentation rates and lower hydrodynamic energy, traces on abyssal seafloor have more favourable conditions for conservation than traces in shallower water (Mauviel & Sibuet, 1985; Gage &



Tyler, 1991). Conversely, Diaz & Cutter (2001) showed that shallow-water surface burrows in muddy sediments had an average life span of 24 hours, with a range of 0.5 to > 264 hours. The hydrodynamic energy near the seabed in the Laurentian Channel, higher than at abyssal depths while lower than in shallow water, could explain the low traces densities found in this study. Furthermore, Young et al. (1985) suggested that mobile deposit-feeding organisms tend to “smooth out” microrelief characteristics of the seafloor. The hydrodynamic energy and the high abundance of deposit-feeding *Ophiura* sp. at station 24 could explain the low relief-traces density at this station.

Total-traces covered 3.1%, 4.7% and 7.4% of the sediment surface at the oxy+, oxy- and hypoxic stations, respectively. This degree of coverage is similar to values (about 7%) reported for continental slope sediments (Gage & Tyler, 1991). The rates of formation and destruction of traces depend on multiple factors, such as sedimentation rate, hydrodynamic energy, and the types of species that inhabit the seafloor. Even if the present study was carried out in shallower water and that traces have been found to be somewhat depth related (Kitchell & Clark, 1979; Gage & Tyler, 1991), these factors could explain the similar densities of total-traces in these different environments.

The seabed area analysed was similar at every stations (between 10.07 m<sup>2</sup> and 12.63 m<sup>2</sup>) except for station CA, where 4.87 m<sup>2</sup> were analysed. This could have resulted in an underestimation of the density and diversity of traces

and organisms at station CA. However, macrobenthic epifaunal and bioturbation traces indices used in this study did not show any distinctive discrepancy between this station and the others of the oxy- group. Moreover, in all indices, stations CA and CE were never significantly different. Consequently, we do not expect any particular impact of the difference in area of seafloor studied on the overall results and conclusion of this study.

#### 1.4.3 The origins of bioturbation traces

It is difficult to determine without direct observation which organism is responsible for the formation of a specific bioturbation trace. However, literature data and photographic evidence can help. Organisms crawling on the sediment surface create most surface-traces. When the organism responsible for the formation of a trace is known, the name of the trace reflects the name of the organism. Imprints-depressions are a large group of traces that includes small and large depressions created by feeding and resting organisms. However, it is not possible to determine their exact provenance. Studies mentioned that some depressions in the EGSL could be related to the release of gases from the sediments (Syvitski et al., 1983; Pinet et al., 2008). Thus, it is possible that some imprints-depressions traces are related to sediment gas and not the result of bioturbation.

Small burrows can be formed by polychaete worms (Diaz & Rosenberg, 1995). However, on some of our images, they were obviously formed by the

arms of *Amphiura* sp.. Medium and large burrows (or “fist-sized holes”) have been previously associated with the burrowing shrimp *Calocaris templemani*, the sea pens *Pennatula* sp. (Silverberg et al., 1995) and eel-shaped fishes (Syvitski et al., 1983), such as *Lycodes* sp. and *Melanostigma atlanticum*.

#### 1.4.4 Recent bioturbation

To our knowledge, this is the first time that an area of seafloor covered by grey-coloured sediments has been quantified. During submersible dives in the EGSL, Syvitski et al. (1983) observed the presence of grey-coloured sediments but did not provide quantitative measures. The generally brown colour of the surface sediments we observe is due to the presence of diagenetically-produced high concentrations of manganese and iron oxides (Sundby et al., 1981). The grey-coloured sediments that exist underneath the brown surface layer is indicative of reducing conditions and dissolution of the brown-coloured metal oxides. When grey-coloured sediments are found on the seafloor surface, it means that reduced subsurface sediments has recently been excavated by burrowing organisms and deposited on the surface. In the presence of oxygen, grey-coloured sediments turn brown rapidly. Diaz & Cutter (2001) found in a shallow-water experiment with polychaetes that grey-coloured sediments turns brown in 0.5 – 3 hours. Thus, our observations of extensive areas of grey-coloured sediment reflect active and recent deep bioturbation and excavation. There was no significant difference in grey-coloured sediment density in relation to the oxygen level, but the stations with the highest density of relief-traces also

had the highest density of grey-coloured sediment, reflecting recent and/or ongoing deep bioturbation. An example of deep bioturbation with excavation is the formation of medium burrows, a relief-trace, by the burrowing shrimp *Calocaris templemani*. Exchange of water between the burrow and the overlying water column, known as bioirrigation, has been shown to contribute to the oxygenation and oxidization of deeper anoxic-reduced sediments (Diaz & Cutter, 2001) and to the stimulation of microbial activity and diagenesis (Aller & Aller, 1998).

The resolution of the benthic images limits the identification of traces and organisms to features  $\geq 5$  mm. However, organisms and traces smaller than 5 mm were always present, and sometimes in high abundance, especially small burrows. In consequence, this may have reduced the density of some organisms and traces. Benthic studies conducted with microscale photography (Gage & Tyler, 1991) and sediment profile cameras (Rhoads, 1974; Solan et al., 2003) have shown an almost continuous disturbance of the sediment. Most likely, these techniques, if applied in the EGSL, would show much higher microrelief features of the seafloor than the ones reported here. The use of another technique, the axial tomodesitometry (CT scan), could further help to visualize and quantify the microrelief structures of endobenthic organisms in the EGSL (Michaud et al., 2003; Dufour et al., 2005; Weissberger et al., 2009). Their use could lead to a better understanding of the bioturbation patterns in relation to the organisms inhabiting the EGSL. Furthermore, sediment profile cameras have proven their

effectiveness in determining the depth of the apparent Redox potential discontinuity (aRPD) layer, the zone between oxidized and reduced sediments (Rosenberg et al., 2001). The depth of the RPD depends on the burrowing depth of infaunal organisms (Nilsson & Rosenberg, 2000; Rosenberg et al., 2003; Weissberger et al., 2009) and the dissolved oxygen concentration (Weissberger et al., 2009). Since infaunal organisms move closer to the sediment surface under hypoxic conditions (Llansó, 1992; Nilsson & Rosenberg, 2000; Weissberger et al., 2009), sediment profile imagery could be used to study the RPD along an oxygen gradient in the Laurentian channel of the EGSL and give valuable information on the impact of hypoxia on the infaunal community.

## **1.5 Conclusion**

This study was the first to relate environmental variables to bioturbation traces and their associated macrobenthic species via bottom photography in the deep waters of the EGSL. It demonstrates a clear influence of the oxygen level on the area of seafloor covered by bioturbation traces in the EGSL. We observed an increasing total and surface-traces density with decreasing oxygen. Furthermore, results indicate that actual hypoxic conditions in the EGSL do not affect negatively traces density, traces diversity and species richness.

On the other hand, our results may also indicate that the hypoxic regions of the EGSL are in a transition phase, where suspension feeders with low tolerance to low oxygen concentrations and responsible for most relief-traces are being replaced by more tolerant deposit feeders responsible for most surface-traces. However, without comparative pre-hypoxia images, we cannot support the community structure change hypothesis due to hypoxia. Nevertheless, if the dissolved oxygen concentration in the EGSL deep-water environment continues to decrease at the present rate, one can expect reductions of diversity, abundance and biomass and presumably, profound changes in community structure and function, as reported in other parts of the world (Pihl, 1994; Diaz & Rosenberg, 1995; Wu, 2002; Diaz & Rosenberg, 2008; Long & Seitz, 2009).

The next step will be to characterize and measure bioturbation vertically in the sediments in order to link vertical and horizontal bioturbation patterns to the organisms that create them and to the environmental conditions.

## CONCLUSION GÉNÉRALE

Cette étude est la première à tenter de relier les facteurs environnementaux aux traces de bioturbation et à la macrofaune épibenthique qui y est associée à l'aide de la photographie benthique. Les résultats démontrent clairement l'influence de la concentration de l'oxygène dissous sur l'aire du fond marin couvert par les traces de bioturbation totales et de surface. En effet, la saturation d'oxygène explique à elle seule respectivement 62% et 55% de la variabilité des traces totales et de surface. Les densités de traces totales et de surface des stations hypoxiques sont significativement plus élevées que celles des stations avec de fortes concentrations d'oxygène. Plus particulièrement, nous avons observé une augmentation des densités de traces totales et de surface avec la diminution d'oxygène. Contrairement aux hypothèses de départ, les résultats indiquent que les conditions hypoxiques actuelles qui prévalent dans l'EGSL n'affectent pas négativement la densité et la diversité des traces de bioturbation ainsi que la richesse spécifique. Cependant, dans la zone hypoxique de l'EGSL, nous avons observé une augmentation des déposivores de surface tolérants aux basses concentrations d'oxygène dissous et responsables de la majorité des traces de surface, tel que *Ophiura* sp. Toujours dans la zone hypoxique, nous avons aussi observé une diminution des suspensivores intolérants aux basses concentrations d'oxygène dissous et responsables de la majorité des traces en relief. L'augmentation des déposivores de surface serait principalement responsable de l'augmentation des traces de

surface et, en conséquence, des traces totales. La raison est que ces organismes remanient une plus grande aire des sédiments de surface lorsqu'ils se déplacent à la recherche de nourriture que les suspensivores, qui sont en général sessiles, et qui remanient donc peu la surface des sédiments lorsqu'ils se nourrissent. Ces observations nous permettent d'émettre l'hypothèse que les conditions hypoxiques qui prévalent dans l'EMSL ont mené à un changement de la structure de la communauté benthique. Cependant, pour supporter cette hypothèse, une étude comparative avec des images pré-hypoxie prises aux mêmes stations serait nécessaire. Ces images n'étaient malheureusement pas disponibles lors de cette étude.

Cette étude a permis de mieux connaître les traces de bioturbation à la surface des sédiments de l'EGSL, cependant, elle ne permet pas de connaître l'étendue de la bioturbation à l'intérieur des sédiments. Une avenue intéressante pour faire suite à cette étude serait d'étudier la bioturbation à l'intérieur des sédiments selon un gradient d'oxygène à l'aide d'un appareil permettant l'imagerie de profils sédimentaires (SPI – Sediment Profile Imagery) (Cicchetti et al., 2006). Cet appareil est muni d'un support en acier inoxydable et d'un module d'imagerie en forme de prisme qui pénètre l'interface eau-sédiment. La plaque arrière du prisme contient un miroir monté à un angle de  $45^{\circ}$  qui reflète le profil sédimentaire à la caméra (Solan et al., 2004b). En plus de permettre de visualiser et de quantifier les traces de bioturbation et l'endofaune à l'intérieur des sédiments, cette technique s'est avérée efficace afin de déterminer la



couche apparente du front d'oxydoréduction (aRPD – apparent Redox Potential Discontinuity) ; zone visible entre les sédiments oxydés de couleur généralement brune et les sédiments réduits plutôt gris (Rosenberg et al., 2001), délimitant ainsi la profondeur de pénétration de l'oxygène dans la colonne de sédiment (Katsev et al., 2007). Puisque la profondeur de la couche du front d'oxydoréduction diminue avec l'appauvrissement en oxygène dissous et varie selon la composition de la faune endobenthique (Weissberger et al., 2009), cette technique permettrait d'approfondir nos connaissances de l'effet de l'hypoxie sur les flux géochimiques entre la colonne d'eau et la colonne de sédiment, en plus de permettre d'étudier la bioturbation à l'intérieur des sédiments et l'endofaune selon un gradient d'oxygène dans l'EGSL.

L'appareil SPI serait aussi un outil très utile qui nous permettrait de déterminer l'indice de qualité de l'habitat benthique (BHQ – Benthic Habitat Quality) développé par Nilsson & Rosenberg (1997). Cet indice permettrait de déterminer plus en profondeur l'effet de l'hypoxie sur la qualité de l'habitat benthique de l'EGSL. L'indice BHQ peut être calculé après avoir analysé les images à l'intérieur de la colonne de sédiment prises par l'appareil SPI. Cet indice permet de paramétriser les structures à la surface du sédiment, les structures subsurface (y compris l'endofaune) et la profondeur de l'aRPD. L'indice BHQ varie entre 0 et 15 et est relié aux stages de succession de la faune benthique du modèle de Pearson & Rosenberg (1978) (Rosenberg et al., 2002). Le long d'un gradient environnemental de sévèrement perturbé à non

perturbé, les stages de succession des communautés benthiques peuvent être classifiés en quatre différents stages : stage de succession (SS) 0 (grandement perturbé), I (communauté perturbée/pionnière), II (communauté intermédiaire) et III (communauté « climax »/non perturbée) (Rosenberg et al., 2002). Un BHQ < 2 correspond au SS 0, un BHQ entre 2 et 4 au SS I, un BHQ entre 5 et 10 au SS II, et un BHQ > 10 au SS III (Rosenberg et al., 2002). Cet indice de la qualité de l'habitat benthique nous permettrait de déterminer le stage de succession benthique auquel chaque station échantillonnée appartient et ainsi, déterminer l'impact de l'hypoxie sur la communauté benthique de l'EMSL. De plus, en calculant cet indice, ceci nous permettrait de confirmer ou d'infirmer une hypothèse de la présente étude. Cette hypothèse est que la communauté benthique de la station 24 est dans une phase de transition caractéristique du stage de succession II de Pearson & Rosenberg (1978), se situant entre une communauté mature (SS III) et une communauté composée de petites espèces opportunistes et de courte longévité (SS I). Nilsson & Rosenberg (1997) suggèrent que cette technique est valide pour plusieurs habitats boréaux et tempérés. De plus, dans une étude ultérieure, Nilsson & Rosenberg (2000) ont démontré une forte corrélation entre les données de l'indice BHQ et la richesse spécifique, l'abondance et la biomasse : les changements de la qualité de l'habitat benthique suivaient étroitement les changements de stage de succession des communautés benthiques. L'indice BHQ s'avérerait donc un outil rentable pour classifier les habitats benthiques et évaluer l'impact de l'hypoxie sur les communautés benthiques de l'EGSL.

Dans une autre étude, Katsev et al. (2007) ont appliqué un modèle diagénétique au sédiment du Chenal Laurentien de l'EMSL. Ce modèle prédit que si la concentration d'oxygène dissous continue de diminuer à un rythme constant de  $1 \mu\text{mol L}^{-1} \text{an}^{-1}$ , mesure moyenne calculée sur les 70 dernières années, des changements dans les flux géochimiques deviendront mesurables d'ici les 20 prochaines années. Ces changements prendraient la forme d'une augmentation des flux de substances réduites hors des sédiments: les phases réactives de fer et d'oxyde de manganèse deviendraient épuisées et le sédiment deviendrait progressivement enrichi de sulfure de fer. Ces changements, dus à la diminution de l'oxygène dissous, auraient des effets importants sur l'épifaune et l'endofaune de l'EMSL. Ces effets commencent même déjà à être répertoriés sur l'endofaune (Bourque, 2009) et sur l'épifaune (Lévesque et al., 2008; Lévesque, 2009). Cependant, le modèle s'avère spécialement sensible aux taux et aux modes de bioturbation et de bioirrigation. Une étude quantitative portant sur les taux de bioturbation et de bioirrigation actuels dans l'EGSL permettrait d'affiner ce modèle, et ainsi, il serait possible de prédire plus précisément l'effet à long terme de la diminution de l'oxygène dissous sur les flux géochimiques, la bioturbation, la bioirrigation et les organismes qui y vivent.

La présente étude a permis d'identifier, de classifier et de dénombrer pour la première fois les traces de bioturbation dans l'EGSL. Elle a également permis de déterminer que l'augmentation de la densité des traces de bioturbation était reliée à l'augmentation des *Ophiura* sp., des organismes résistants à l'hypoxie. Cette étude est importante, car elle permet d'approfondir nos connaissances de

l'impact du phénomène hypoxique dans l'EGSL sur les organismes bioturbateurs, des animaux d'une importance primordiale dans l'écosystème marin.

Dans son dernier livre scientifique, Charles Darwin (1881) mentionnait que la bioturbation était un sujet dont il avait probablement sous-estimé l'importance jusqu'ici (Meysman et al., 2006). Près de 130 ans après la parution de son dernier livre, les connaissances sur la bioturbation ont grandement évolué. Cependant, il s'agit toujours d'un sujet d'une importance sous-estimée. Les études proposées ici permettraient d'approfondir notre connaissance de la bioturbation dans l'EGSL et ainsi, mieux cerner son importance sur les processus biologiques, chimiques, géologiques et physiques de l'EGSL.

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**ANNEXE**

Annexe 1. Clé d'identification des traces de bioturbation (Lebensspuren) retrouvées sur le fond marin de l'estuaire et du golfe du Saint-Laurent

### Liste des codes : traces superficielles

#### Traces superficielles : S

##### ***Indéterminé S0***

S0 Trace superficielle indéterminée

##### ***Pistes, rides et sillons S1***

S11 Sillon simple  
 S12 Sillon discontinu  
 S13 Sillon double  
 S14 Piste d'ophiure  
 S15 Piste de crevette  
 S16 Piste d'astérie  
 S17 Piste double  
 S18 Ride double

##### ***Déjections (pelotes fécales) S2***

S21 Toutes formes de déjections

##### ***Empreintes S3***

S31 Empreinte d'ophiure  
 S32 Empreinte de poisson  
 S33 Empreinte-dépression

#### Surface-traces: S

##### ***Indeterminate S0***

Indeterminate surface-trace

##### ***Ploughs, ridges, and trails S1***

Simple plough  
 Discontinuous plough  
 Double plough  
 Ophiuroid trail  
 Shrimp trail  
 Asteroid trail  
 Double trail  
 Double ridge

##### ***Feces S2***

Feces

##### ***Imprints S3***

Ophiuroid imprint  
 Fish imprint  
 Imprint-depression

## Liste des codes : traces en relief

### Traces en relief : R

#### ***Indéterminé R0***

R0 Trace en relief indéterminée

#### ***Relief convexe R1***

Aucune\*

#### ***Relief concave R2***

R21 Terrier simple

R211 Terrier simple petit (0,5 à 1 cm)

R212 Terrier simple moyen (> 1 à 5 cm)

R213 Terrier simple grand (> 5 cm)

R22 Terrier en forme de fente

R221 Terrier en forme de fente petit (0,5 à 1 cm)

R222 Terrier en forme de fente moyen (> 1 cm)

#### ***Relief complexe R3***

R31 Tumulus crevassé

#### ***Autres***

X : Structure indéterminée, pas une trace

### Relief-traces: R

#### ***Indeterminate R0***

Indeterminate relief-trace

#### ***Relief convex R1***

None\*

#### ***Relief concave R2***

Simple burrow

Small simple burrow

Medium simple burrow

Large simple burrow

Slit-shaped burrow

Small slit-shaped burrow

Medium slit-shaped burrow

#### ***Relief complex R3***

Crevassed mound

#### ***Others***

Indeterminate structure

\* Catégorie non utilisée dans cette étude, car l'angle de 90° de l'appareil-photo par rapport au fond marin ne permettait pas de voir adéquatement les traces en relief convexes.



**Clé d'identification des traces de bioturbation (*Lebensspuren*) retrouvées sur le fond marin de l'estuaire et du golf du Saint-Laurent :**

1 a : Trace superficielle (déjection, empreinte, piste, sillon ou ride) ou trace en relief (relief convexe, concave ou complexe)...voir 2

1 b : Structure indéterminée, n'étant ni une trace, ni un animal...**X**

2 a : Trace superficielle engendrée par l'activité animale à la surface des sédiments...**S**...voir 3

2 b : Trace en relief occasionnée par un remaniement sédimentaire en profondeur...**R**...voir 14

3 a : Piste, sillon, ride ou déjection...voir 4

3 b : Empreinte...**S3**...voir 12

4 a : Piste, sillon ou ride...**S1**...voir 5

4 b : Déjection quelconque à la surface du sédiment : Toutes formes de déjection...**S21** (Fig. 1)

5 a : Sillon ou ride...voir 6

5 b : Piste d'animal connu ou piste double...voir 9

6 a : Sillon...voir 7

6 b : Rides sinueuses séparées entre elles par une distance approximative de 3 à 5 cm : Ride double...**S18** (Photo 5)

7 a : Sillon simple ou sillon discontinu...voir 8

7 b : Deux sillons parallèles séparés par une ride (largeur totale : 5 à 8 cm) : Sillon double...**S13** (Fig. 1)

8 a : Sillon droit ou sinueux, 1 à 2 cm de large (Mauviel & Sibuet, 1985) : Sillon simple...**S11** (Fig. 1)

8 b : Succession de petites perforations, laissées peut-être par un poisson (Heezen & Hollister, 1971, dans Mauviel & Sibuet, 1985) : Sillon discontinu...**S12** (Fig. 1)

9 a : Piste similaire à deux sillons simples (d'une largeur de 1-2 cm) séparés d'une distance de 2-4 cm : Piste double...**S17** (Photo 4)

9 b : Autre que piste double...voir 10

10 a : Sillon large et sinueux avec contour dentelé et irrégulier, possible piste d'astérie : Piste d'astérie...**S16** (Photo 3)

10 b : Autre que sillon large et sinueux avec contour « dentelé »... voir 11

11 a : Piste d'un côté similaire à un sillon simple et de l'autre côté similaire à un sillon discontinu, les deux sont séparés d'une distance d'environ 10 cm : Piste de crevette...**S15** (Photo 2)

11 b : Sédiment récemment remanié sans forme précise et d'une largeur d'environ 10 cm, possible à identifier lorsqu'une ophiure est à côté : Piste d'ophiure...**S14** (Photo 1)

12 a : Dépression ou empreinte quelconque sans ouverture en son centre : Empreinte-dépression...**S33** (Photo 8)

12 b : Autre que dépression ou empreinte quelconque sans ouverture en son centre...voir 13

13 a : Empreinte élançée en forme d'étoile, ou en forme de « X » souvent observée en présence d'ophiures : Empreinte d'ophiure... **S31** (Fig. 4 et photo 6)

13 b : Empreinte en forme de « V », triangle ou losange. Empreinte souvent observée en présence de sébaste (*Sebastes* sp.), poisson semi-pélagique fréquemment retrouvé se reposant sur le fond marin : Empreinte de poisson...**S32** (Photo 7)

14 a : Trace en relief convexe (bombement) ou en relief concave (dépression)...voir 15

14 b : Trace en relief complexe formée d'un bombement de taille variable et d'un terrier à son sommet. De plus, de petites fissures partent de son sommet jusqu'à sa base : Tumulus crevassé...**R31** (Fig. 3)

15 a : Trace en relief convexe (bombement) :...Catégorie non utilisée...voir 15b

15 b : Trace en relief concave (dépression) : **R2**...voir 16

16 a : Terrier de forme circulaire : Terrier simple...**R21**...voir 17

16 b : Terrier en forme de fente...**R22**...voir 19

17 a : Terrier de forme circulaire de plus de 5 cm : Terrier simple grand...**R213** (Fig. 2 et 4)

17 b : Terrier de forme circulaire d'un diamètre de 5 cm ou moins...voir 18

18 a : Terrier de forme circulaire d'un diamètre situé entre plus de 1 cm et 5 cm : Terrier simple moyen...**R212** (Fig. 2)

18 b : Terrier de forme circulaire d'un diamètre entre 0,5 et 1 cm : Terrier simple petit...**R211** (Fig. 2 et 4)

19 a : Terrier en forme de fente avec ouverture de 0,5 à 1 cm : Terrier en forme de fente petit...**R221** (Fig. 4)

19 b : Terrier en forme de fente avec ouverture plus grande que 1 cm : Terrier en forme de fente moyen...**R222** (Fig. 4)

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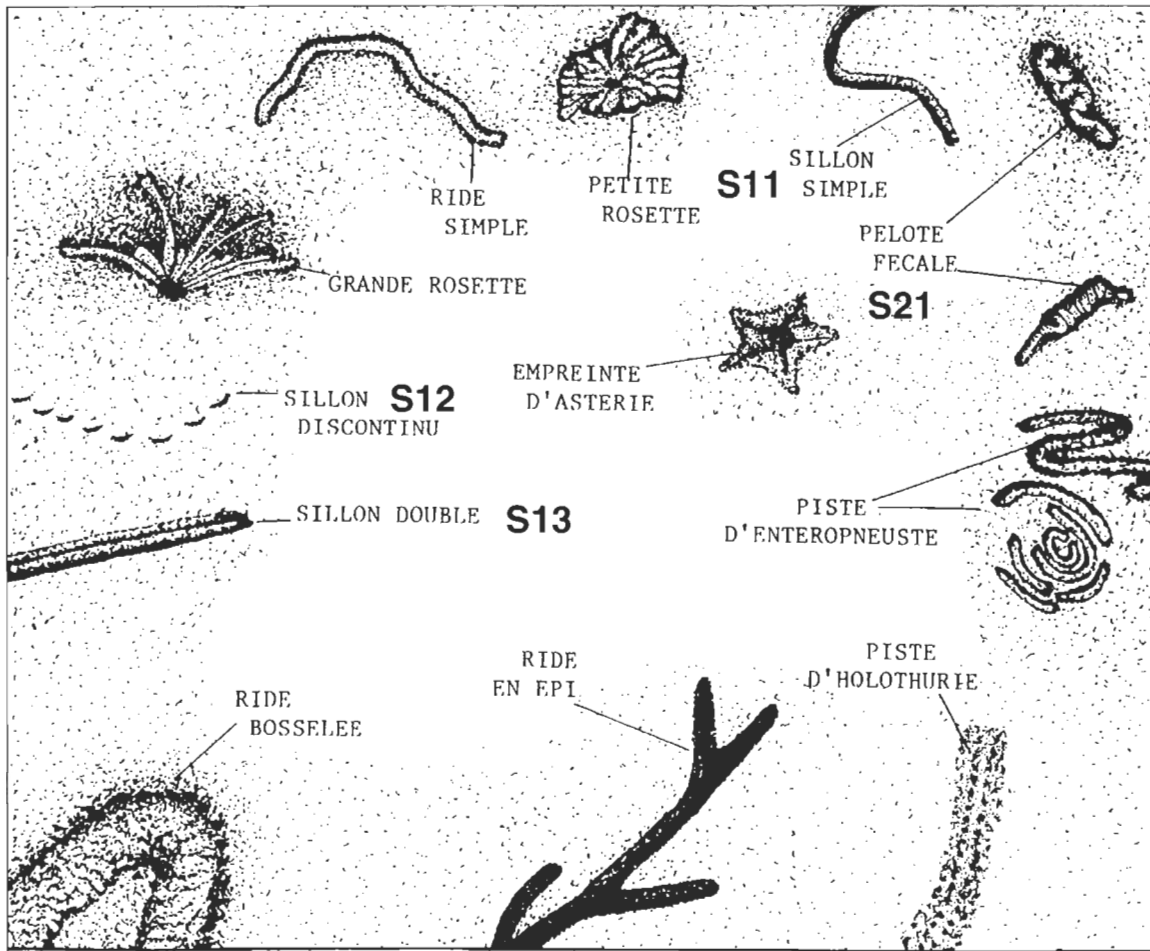


Figure 1 : Traces superficielles (tiré de Mauviel & Sibuet, 1985).

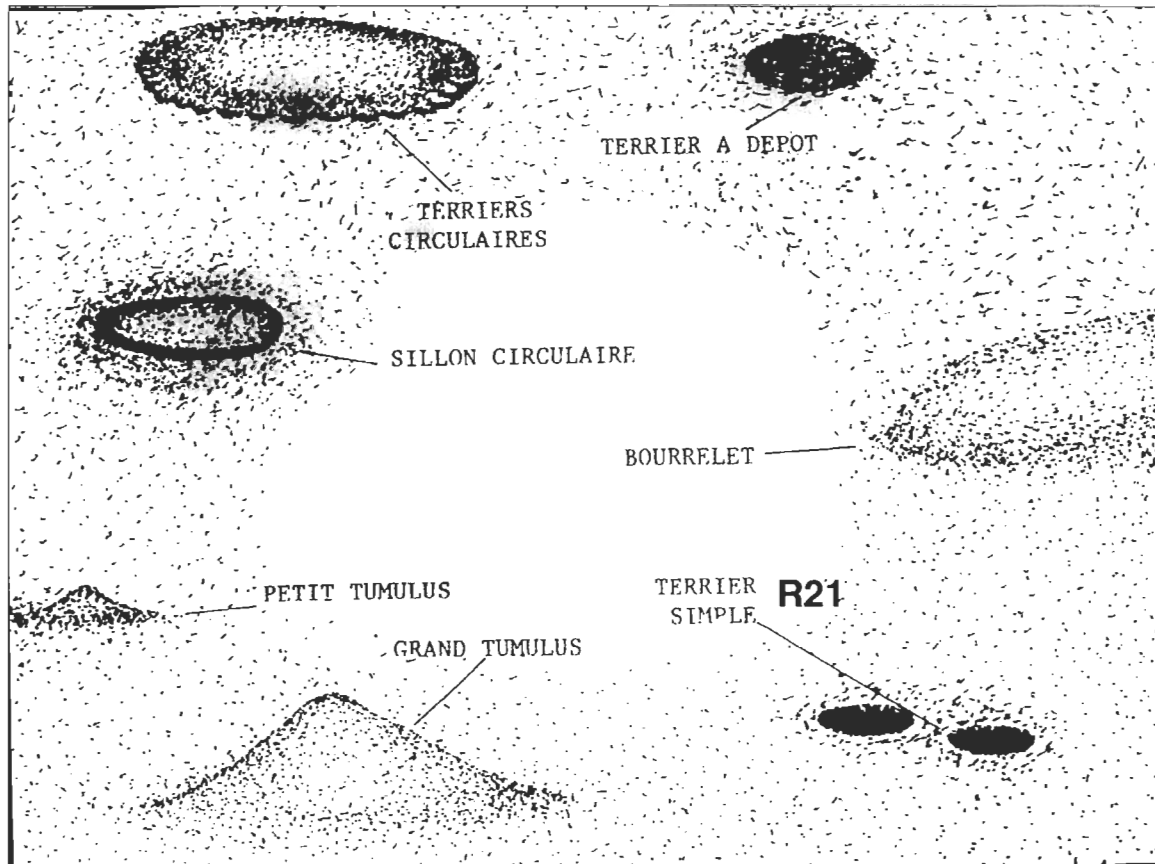


Figure 2 : Traces en relief convexes et concaves (tiré de Mauviel & Sibuet, 1985).

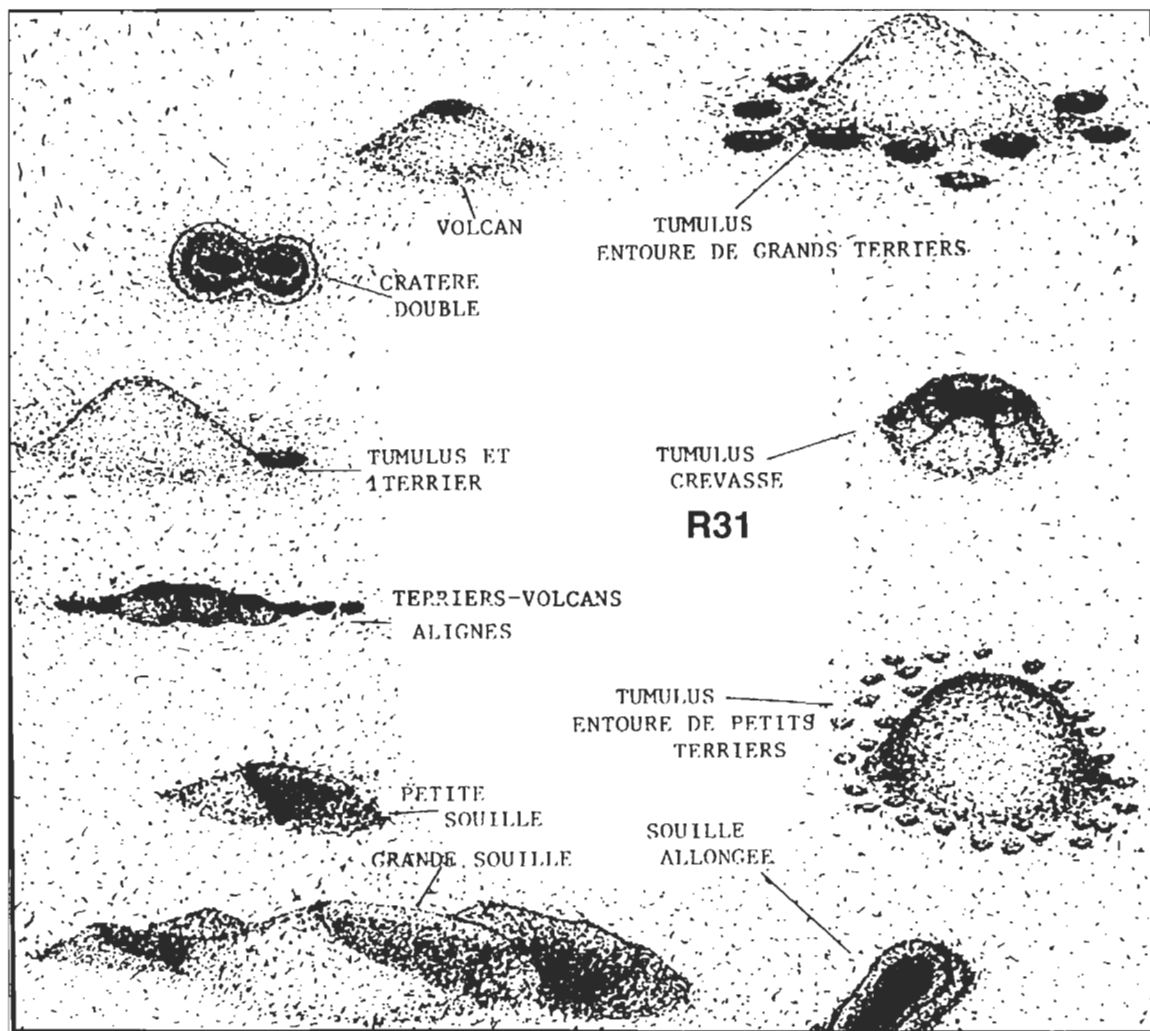


Figure 3 : Traces en relief complexes (tiré de Mauviel & Sibuet, 1985).

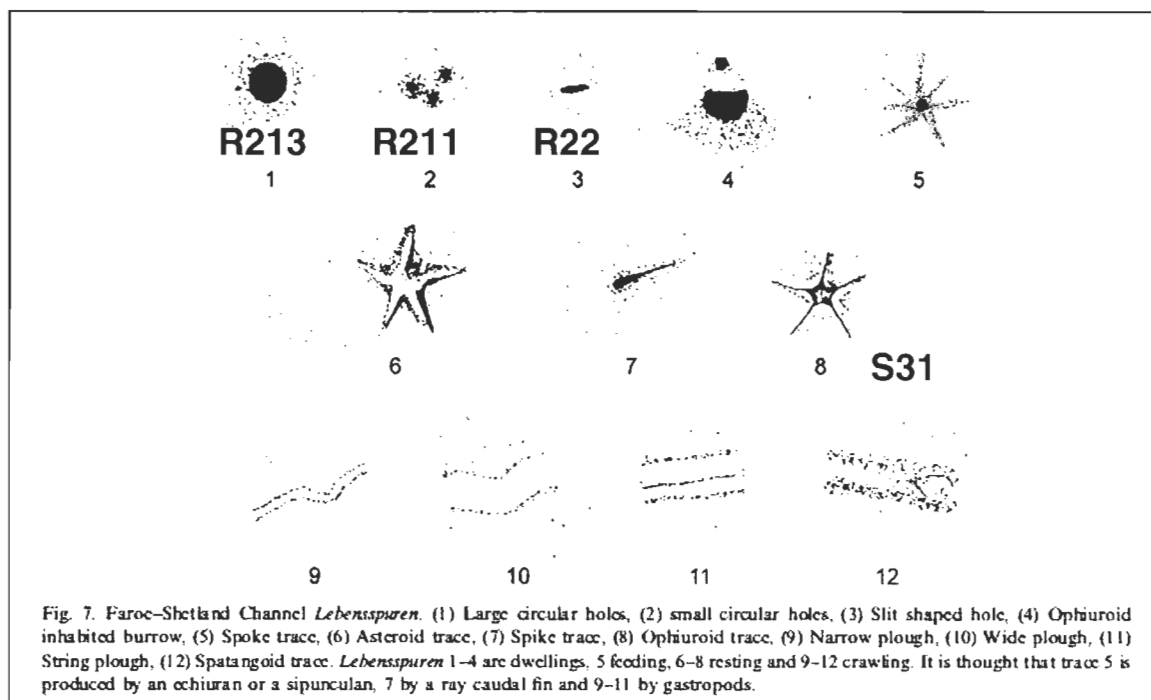


Figure 4 : Diverses traces superficielles et en relief (tiré de Jones et al., 1985).



Photo 1 : Photographie sous-marine provenant de l'estuaire maritime du Saint-Laurent (station 23) avec la présence d'une ophiure et une piste d'ophiure (S14).

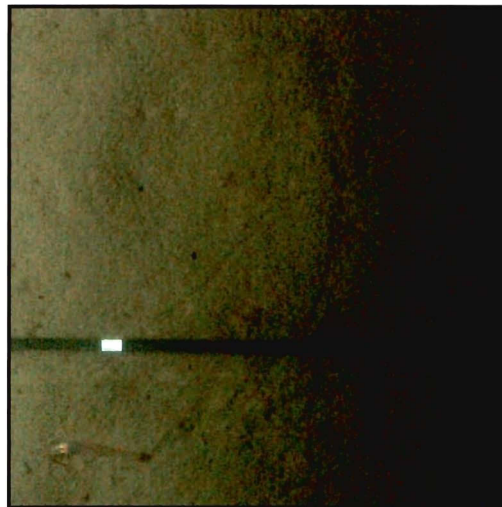


Photo 2 : Photographie sous-marine provenant de la tête du Chenal Anticosti (golfe du Saint-Laurent) avec la présence d'une crevette formant une piste de crevette (S15).



Photo 3 : Photographie sous-marine provenant de l'estuaire maritime du Saint-Laurent (station 23S) avec la présence d'une piste d'astérie (S16).



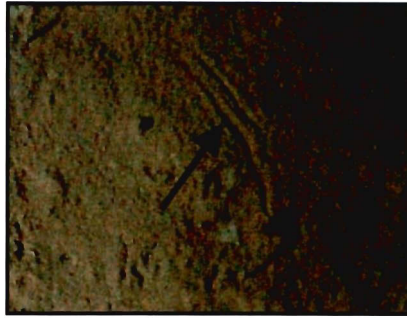


Photo 4 : Photographie sous-marine provenant du golfe du Saint-Laurent (station IC) avec la présence d'une piste double (S17).



Photo 5 : Photographie sous-marine provenant de l'estuaire maritime du Saint-Laurent (station 23) avec la présence d'une ophiure et d'une ride double (S18).



Photo 6 : Photographie sous-marine provenant de l'estuaire maritime du Saint-Laurent (station 23) avec la présence d'une empreinte d'ophiure (S31).



Photo 7 : Photographie sous-marine provenant du golfe du Saint-Laurent (station CE) avec la présence d'un *Sebastes* sp. et de plusieurs empreintes de poisson (S32).

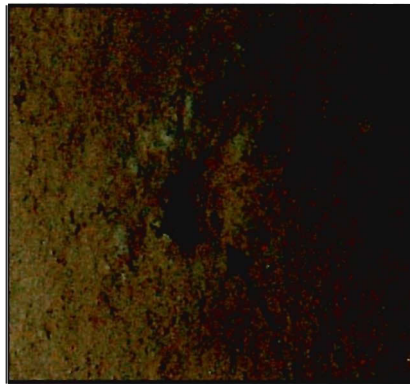


Photo 8 : Photographie sous-marine provenant du golfe du Saint-Laurent (station 17) avec la présence d'une empreinte-dépression (S33).

