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A B S T R A C T

The bottom water in the > 300 m deep Lower St. Lawrence Estuary (LSLE) is persistently hypoxic in contrast to the normoxic bottom waters in the Gulf of St. Lawrence (GSL). We photographed the seabed at 11 stations in the Estuary and Gulf of St. Lawrence (EGSL) during the summers 2006 and 2007 and analysed the images to identify bioturbation traces (lebensspuren) and benthic macrofauna. The objective was to identify the environmental variables that influence the density and diversity of benthic macrofauna and bioturbation traces, and the differences that exist among regions with high, medium and low oxygen levels in the bottom water. The bottom water oxygen concentration is the variable that best explains the densities of total-traces as well as surface-traces. However, the density of these traces was higher in hypoxic regions than in well-oxygenated regions. The higher density of traces in the hypoxic region of the LSLE is mainly due to the activities of the surface deposit feeder *Ophiura* sp., which occurs in large numbers in this region. Possible explanations explored are stress behaviour of the organisms in response to hypoxia and different benthic macrofauna community structures between the hypoxic regions of the LSLE and the normoxic regions of the GSL. In the former, surface deposit feeders and low-oxygen tolerant species dominate over suspension feeders and low-oxygen intolerant species.

1. Introduction

Many marine habitats are under pressure from multiple anthropogenic threats such as fishing, pollution, coastal development, and global warming, all of which can lead to a loss of marine biodiversity (Snelgrove, 1998; Snelgrove et al., 2000; Worm et al., 2006). Benthic organisms influence sedimentary biogeochemical processes (Aller et al., 2001; Meysman et al., 2006; Middelburg and Levin, 2009), primary and secondary productivity (Snelgrove, 1998), and even geomorphology (Murray et al., 2002). Loss of macrobenthic biodiversity will likely have negative effects on the functions, processes, and health of ecosystems (Snelgrove, 1998; Worm et al., 2006).

Benthic community composition and structure are affected by the sediment grain size distribution (Warwick et al., 1991; Kostylev et al., 2001), the productivity (Witman et al., 2008), the organic matter content (Pearson and Rosenberg, 1978; Rosenberg, 1995), and the oxygen level in bottom waters (Rosenberg et al., 2001). Other environmental variables such as depth and current velocity (Kostylev et al., 2001), and temperature and salinity (Pearson and Rosenberg, 1978) are also important. In the coastal ocean, increased eutrophication is often accompanied by decreasing oxygen levels (Diaz and Rosenberg, 2008). Oxygen concentration less than 62.5 μmol L^{-1} or 2 mg L^{-1}, a value often referred to as the upper limit of hypoxic water (Gilbert et al., 2005), reduce feeding, growth and individual fitness of marine animals (Wu, 2002). Different taxa have different tolerance thresholds to hypoxia (Diaz and Rosenberg, 1995) and the 2 mg L^{-1} may not be an appropriate definition of hypoxia for all taxa (Vaquer-Sunyer and Duarte, 2008). Episodes of decreasing oxygen concentrations may force infaunal organisms to move closer to the sediment surface (Llansó, 1992; Wu, 2002) and cause deposit feeders to replace suspension feeders (Diaz and Rosenberg, 1995; Wu, 2002; Levin et al., 2009). Responses of organisms to hypoxia depend among other factors on the duration, periodicity and severity of low-oxygen concentrations (Levin et al., 2009). Hypoxia can be lethal to some organisms and eliminate sensitive species, thereby reducing species richness and altering both the function and structure of benthic communities (Diaz and Rosenberg, 1995; Wu, 2002; Diaz and Rosenberg, 2008; Levin et al., 2009).

Bioturbation is an important activity of benthic organisms that mixes and transports particles, water, and solutes within the

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sediment and across the sediment water interface (Rhoads, 1974; Aller, 1982; Meysman et al., 2006). Benthic organisms are thus directly involved in the biogeochemical cycles of carbon and nutrients, including organic matter mineralization (Mermillod-Blondin and Rosenberg, 2006). Through physical activities such as constructing, maintaining, and ventilating burrows, they modify the physical and biological properties of sediments (Van Colen et al., 2008; Middelburg and Levin, 2009). Bioturbation by burrowing organisms, which are sometimes called "ecosystem engineers", has played an important role in the evolution of life on earth (Meysman et al., 2006). The loss of engineer species can have important negative effects on benthic biodiversity and biogeochemical processes (Coleman and Williams, 2002; Lohrer et al., 2004; Solan et al., 2004; Middelburg and Levin, 2009).

Bioturbation often leaves visible traces on the seafloor that are known as "*Lebensspuren*", a German term meaning life traces. These traces fall under two main groups according to their morphology: surface-traces and relief-traces (Mauviel and Sibuet, 1985). Surface-traces are formed when organisms rework only the first top millimetres or centimetres of the sediment column, which leaves shallow traces in the form of ploughs, tracks, and furrows. These traces imply a sediment mixing that can be important, but that does not affect particles located deeper in the sediment. The relief-traces are surface manifestations of burrows, and come in the shape of circular or slit-shaped holes, crevassed mounds etc. They are formed when organisms excavate or maintain their burrows and reflect much deeper reworking of sediments than the other group. The burrows are irrigated through the process of bio-irrigation, which implies transport of sediment porewater and the solutes and gases they contain (Shull et al., 2009).

Benthic photography is a useful tool for identifying benthic macrofauna and characterise bioturbation traces (Heezen and Hollister, 1971; Kitchell, 1979; Mauviel and Sibuet, 1985; Solan et al., 2003; Jones et al., 2007). The technique is 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 disadvantage is that photography does not see below the sediment surface, obliging the observer to make inferences about subsurface life, structure, and processes from their surface manifestations.

The present study was carried out in the Laurentian Trough, a 300–500 m deep submarine valley that traverses the Estuary and Gulf of St. Lawrence (EGSL) and intersects the continental shelf (Fig. 1). The deep water in the Trough originates in the Northwest Atlantic, and as it flows slowly landward it looses oxygen through respiration and organic matter mineralization. This creates a negative dissolved oxygen gradient from east to west (Gilbert et al., 2005). However, the state of health of this vast ecosystem, measured by the availability of dissolved oxygen to organisms that live in and use the seafloor and adjacent bottom waters, has been declining for at least the last 70 years. In the 1930s, the oxygen levels at 300 m depth in the Lower St. Lawrence Estuary (LSLE) were 38% of saturation. In 2003, oxygen saturation had decreased to about 20% with some observations as low as 16%. Approximately 1300 km^2 of the LSLE bottom waters are now persistently hypoxic (Gilbert et al., 2005). The declining oxygen levels are attributed in part to changes in ocean circulation and mixing in the northwest Atlantic, possibly linked to climate variability through the North Atlantic Oscillation, and to an increased flux of organic matter to the seafloor (Gilbert et al., 2005; Thibodeau et al., 2006; Rabalais et al., 2010).

Our objective was to examine, using benthic photography, the density and diversity of benthic macrofauna and bioturbation traces and their relations to environmental variables in order to determine if there are significant differences among regions of the seafloor in the ESGL bathed in water with high, medium and low oxygen levels. We hypothesized that the oxygen concentration is the most important environmental variable influencing the density and diversity of benthic macrofauna and bioturbation traces, and that the hypoxic region of the LSLE would have lower species richness and consequently lower bioturbation trace density and diversity than normoxic regions situated in the Gulf of St. Lawrence (GSL).

2. Materials and methods

2.1. Field sampling

Photographs of the seafloor were collected at a series of stations along the axis of the 300–500 m deep Laurentian Trough in the EGSL in August 2006 and July 2007 (Fig. 1). Eight stations were sampled in 2006 and three in 2007. Thirty images were taken at each of the 11 stations using a bottom contact Benthos underwater camera system equipped with a Pentax Optio MX4 digital camera with 4.0 Megapixels resolution mounted perpendicular to the seafloor. The sediment was illuminated with a 382 Edgerton Deep Sea Standard Benthos flash mounted at a 30° angle to the seafloor. A scale was attached to the camera system to allow physical measurements. The area covered by each image was 0.82 ± 0.02 m^2.

Near-bottom temperature and salinity were recorded with a Seabird CTD, and bottom water samples were collected to determine dissolved oxygen concentration by Winkler titration (Grasshoff et al., 1999).

Samples of surface sediments were collected from the top 5 cm of a box core or a Van Veen grab sample and granulometric properties were analysed using a LS 13320 Beckman–Coulter Particle Size Analyser (Blott et al., 2004). The total organic matter content of the sediments was determined by loss-on-ignition (Dean, 1974).

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 a species and traces accumulation curve and calculate the mean and variance of the accumulated species and traces. Both approaches led to the conclusion that the analysis of a 15 images sub-sample would allow to evaluate the species and traces distribution without significantly affecting the result. Fifteen images were randomly chosen for each station, except for station CA, where only 7 images were usable. A total of 157 images were then analysed using the image analysis software "ImageJ" (http://rsb.info.nih.gov/ij/index.html). Benthic macrofaunal organisms were identified to the lowest taxonomic level possible and counted. Identification was also confirmed with organisms collected with a Van Veen grab and a USNEL box core for a parallel study of the infauna (Bourque, 2009). 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. This procedure may underestimate the number of individuals since not all five arms of each individual are always extended to the sediment surface (Rosenberg, 1995). The area covered by grey-coloured sediments (i.e. recently excavated subsurface sediments) and the area of each trace were manually encircled to determine their density 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

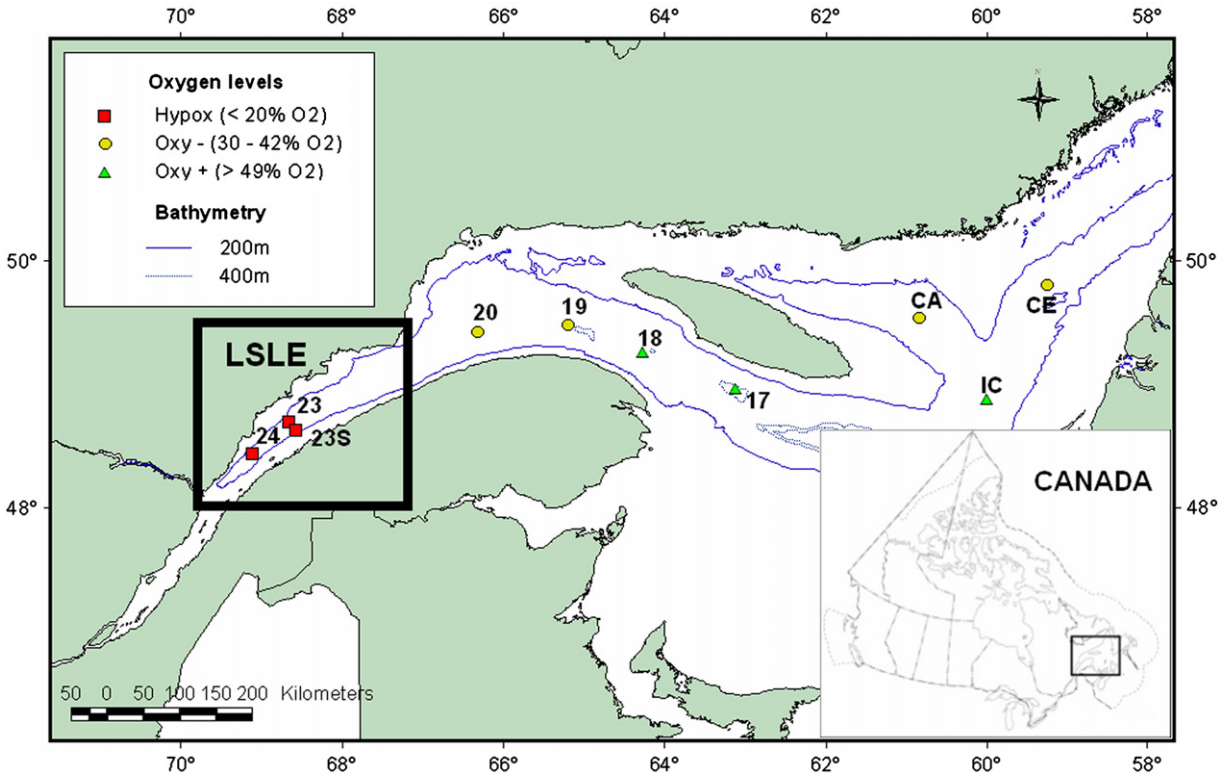

Fig. 1. Stations sampled in the Estuary and Gulf of St. Lawrence (EGSL), Canada, in August 2006 and July 2007. The thick square shows the hypoxic Lower St. Lawrence Estuary (LSLE) situated west of the Gulf of St. Lawrence (GSL). Oxy+ stations 16, 17, 18 and IC, and oxy− stations 19, 20, CA and CE were sampled in August 2006. The hypoxic stations 23, 23S and 24 were sampled in July 2007.

resolution of the images, only organisms and bioturbation traces ≥ 5 mm were identified.

Based on the classification of Mauviel and Sibuet (1985) and Jones et al. (2007), an identification key was produced to represent the different traces found on the images. The traces were separated into two groups – surface-traces and relief-traces – which were then separated further into distinctive sub-groups. The area covered by the different types of traces was determined and is hereafter referred as "trace density". The area of small burrow openings was determined by approximating the opening as a circle ($A=\pi r^2$). 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 burrow 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 benthic macrofauna 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.

2.3. Statistical analyses

Univariate indices were calculated for bioturbation traces (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')) and for benthic macrofaunal diversity (species richness).

Stations were pooled into three groups based on the oxygen concentration in the bottom water: (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).

The changes in the univariate indices over the different oxygen levels (> 49% O_2, 30–42% O_2 and < 20% O_2) were analysed by 2-factor nested analysis of variance (ANOVA). 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 and Keough, 2002). Variables that did not satisfy these criteria were transformed (fourth root ($\sqrt{\sqrt{}}$), $\log_{10}$ 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 the univariate indexes given above. The variance inflation factor (VIF) multi-collinearity test was performed to select environmental variables with values lower than 10, a threshold indicating a strong collinearity between variables (Quinn and Keough, 2002). The six environmental variables 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 and Keough, 2002). Variables that did not satisfy these criteria were transformed ($\sqrt{\sqrt{}}$ or $\log_{10}$).

Multivariate analyses were based on the Bray–Curtis similarity matrices performed on untransformed and transformed presence/absence data. Taxa that appeared only once were excluded from these analyses (Clarke and Warwick, 1994). Variations in traces densities and benthic macrofaunal densities were studied using a permutational multivariate analysis of variance (PERMANOVA) performed with 4999 random permutations of appropriate units (Anderson, 2001; McArdle and 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).

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). 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).

Table 1
List of surface and relief-traces identified on benthic images from the Estuary and Gulf of St. Lawrence (based on Mauviel and Sibuet (1985) and Jones et al. (2007)), mean density (area of seafloor covered by traces (%)) and overall density per station (%). $n=15$ except for CA, where $n=7$.

	Hypoxic			**Oxy−**				**Oxy+**			
Surface-traces	**23** 343 m	**23S** 308 m	**24** 321 m	**19** 374m	**20** 331m	**CA** 293m	**CE** 257m	**16** 435m	**17** 410m	**18** 390m	**IC** 330m
Imprints											
Fish imprints	0	0	0	0	0	0	0.15	0	0.03	0	0
Ophiuroid imprints	0.05	0	0	0	0	0	0	0	0	0	0
Ploughs											
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
Ridges											
Double ridges	0.11	0.39	0	0	0	0	0	0	0	0	0
Trails											
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
Ophiuroid 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
Others											
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
Organisms											
Asteroidea	0	0.04	0	0	0	0	0	0	0	0	0
Ophiura sp.	1.16	0	7.00	0	0	0	0	0	0	0	0
Sebastes 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
Total surface-traces	**5.32**	**8.05**	**7.15**	**1.37**	**5.73**	**4.40**	**3.20**	**3.07**	**3.41**	**1.15**	**2.25**
Relief-traces	**23**	**23S**	**24**	**19**	**20**	**CA**	**CE**	**16**	**17**	**18**	**IC**
Burrows											
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
Mounds											
Crevassed mounds	0	0	0	0	0.01	0	0	0.01	0	0	0.01
Organisms											
Pennatula aculeata basal disc	0.02	0.07	0	0.05	0.12	0.09	0.03	0	0.02	0.02	0
Pennatula borealis basal disc	0	0	0	0.08	0	0	0	0.12	0.06	0.05	0
Actinauge sp. basal disc	0.22	0.20	0	0	0	0	0	0	0	0	0
Total relief-traces	**0.89**	**0.79**	**0.20**	**1.51**	**1.71**	**0.80**	**0.35**	**0.65**	**0.23**	**1.17**	**0.54**
Total-traces	**6.22**	**8.84**	**7.36**	**2.88**	**7.44**	**5.20**	**3.54**	**3.72**	**3.63**	**2.32**	**2.79**

Table 2
Mean macrobenthic epifaunal density (ind. m^{-2}) per taxa and per station for the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007. $n=15$ except for CA, where $n=7$.

Taxa	Stations										
	Hypoxic			Oxy−				Oxy+			
	23 343 m	23S 308 m	24 321 m	19 374 m	20 331 m	CA 293 m	CE 257 m	16 435 m	17 410 m	18 390 m	IC 330 m
Ascidiacea											
Boltenia ovifera	0	0	0	0.12	0	12.54	13.07	0	0	0	1.99
Bryozoa											
Unknown bryozoans	0	0	0	0	0	7.29	12.98	3.85	6.62	0	1.00
Cnidaria											
Actinauge sp.	0.95	0.86	0	0	0	0	0	0	0	0	0
Cerianthus sp.	0.09	0.11	0	0	0	0	0	0	0	0	0
Edwardsia sp.	0	0	0	0	0	0	0	0.71	26.90	0	0.70
Pennatula aculeata	1.04	2.94	0	2.17	5.00	3.97	1.37	0	0.74	0.81	0
Pennatula borealis	0	0	0	0.83	0	0	0	1.21	0.57	0.49	0
Crustacea											
Pandalus 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
Echinodermata											
Amphiura sp.	5.94	0.38	3.25	32.63	6.93	0.23	0	0	0.26	10.34	0.28
Brisaster fragilis	0	0.18	0	0	0	0	0	0	0	0	0
Ctenodiscus crispatus	0	0.28	0	0	0	0	0	0	0	0	0
Ophiura sp.	10.20	0	61.32	0	0	0	0	0	0	0	0
Gastropoda											
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
Polycheata											
Chaetopterus 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
Vertebrata (fishes)											
Lycodes 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
Sebastes sp.	0	0	0	0	0	0	0.52	0	0	0	0
Total density	**19.80**	**5.14**	**64.84**	**37.42**	**13.82**	**24.22**	**28.96**	**5.87**	**38.36**	**13.58**	**10.01**

With the exception of stations 18 and 19, surface-traces covered a greater seafloor area than relief-traces (Table 1). Imprints-depressions were the only type of surface-traces found at all the stations in the EGSL. Simple plough furrows 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 the most abundant relief-trace in numbers and were found at all stations (Table 1). Although they covered a small area of the seafloor, they were the relief-trace with the highest density except at station CA where the highest density was of large burrows. 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 areal density was low.

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

3.1. Univariate analyses

The total-traces density (shown below as mean ± SE) was highest at low oxygen levels: 3.12% ± 0.28 at the oxy+ stations, 4.70% ± 0.46 at the oxy− stations, and 7.47% ± 0.49 at the hypoxic stations (Fig. 4A). The same pattern was observed for the surface-traces density (Fig. 4B). Nested ANOVAs showed a significant difference between total and surface-traces densities (both $p<0.01$) for the different oxygen levels (Table 3). Tukey's test showed significant lower total-traces density at the oxy+ stations than at the hypoxic stations (Fig. 4A). This test also showed significant lower surface-traces density at oxy+ and oxy− stations than at the hypoxic stations (Fig. 4B).

The difference in means between stations within each oxygen level did not show a clear pattern for the other indices measured (Fig. 4C–J). Nested ANOVAs indicated that oxygen levels were not significantly different for those indices ($p>0.05$, Table 3).

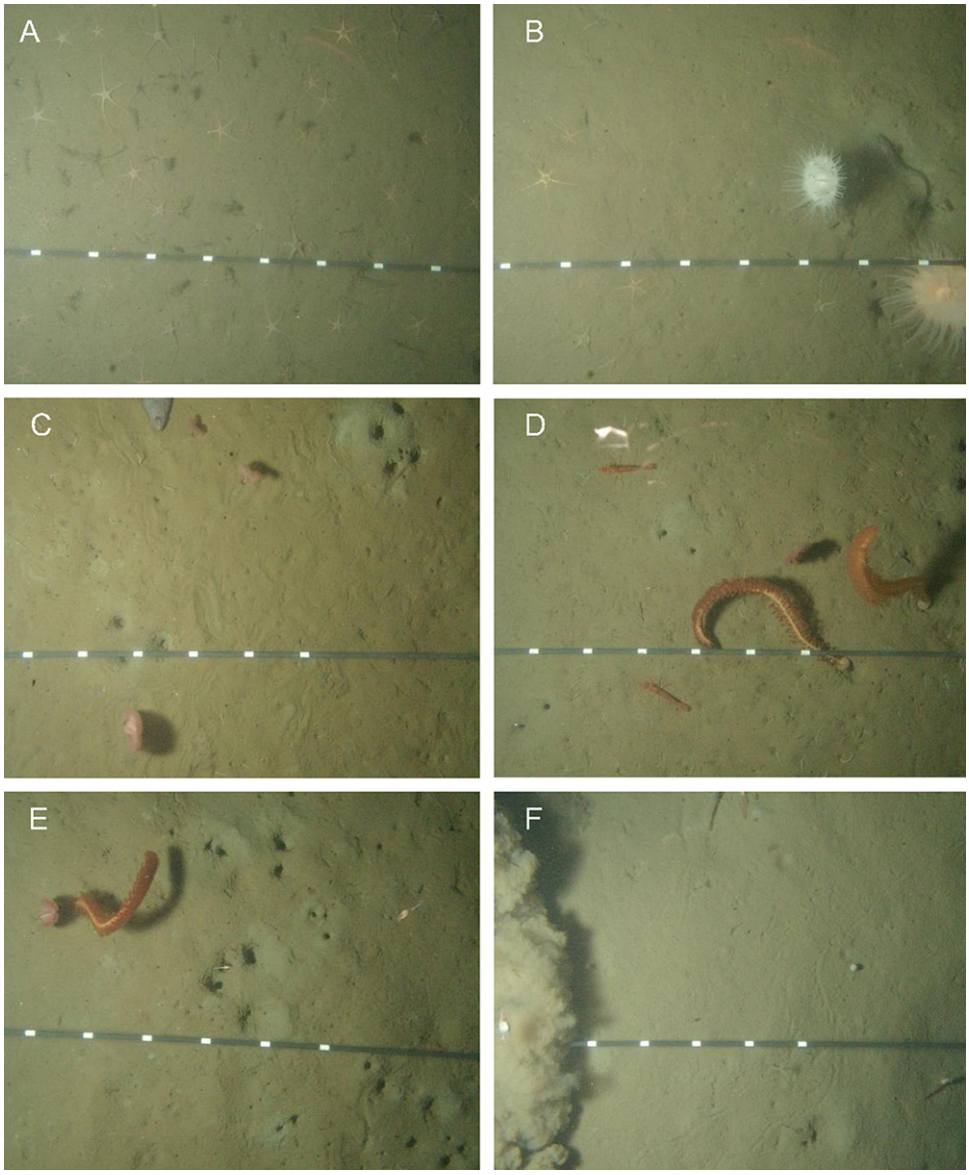

Fig. 2. Representative photographs taken in the Estuary and Gulf of St. Lawrence in 2006 and 2007. (A) Station 24: *Ophiura* sp. and detritus, (B) Station 23: *Ophiura* sp., *Actinauge* sp. (right), *Lycodes* sp. (center right) in an imprint-depression and close to a medium burrow, (C) Station 20: Small 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.

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).

Relationships between environmental variables and univariate indices of bioturbation traces, and benthic macrofauna 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 at 62% and 55%, respectively, by the oxygen saturation (Table 4). We observed higher total and surface-traces densities at lower oxygen levels (Fig. 5A and B). Environmental variables alone or combined never explained more than 53% of the other 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.

3.2. Multivariate analyses

A clear difference between hypoxic and oxy+ stations was found with a non-metric multidimensional scaling plot (nMDS) of untransformed total-traces density data (Fig. 6A). The result was similar for an nMDS plot of presence/absence-transformed total-traces density (Fig. 6B). PERMANOVA analysis revealed that untransformed total-traces density between oxygen levels was 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

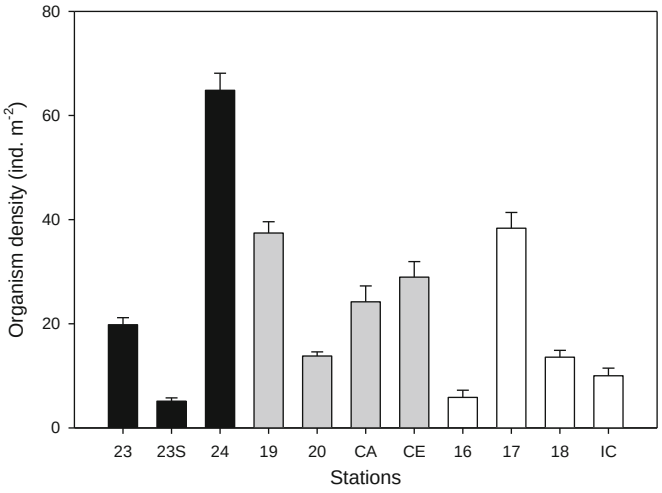

Fig. 3. Mean total organism density (ind. $m^{-2} \pm SE$) for the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007. Oxygen levels: hypoxic stations ($<20\%$ O_2) (black); oxy− stations (32–40% O_2) (grey); oxy+ stations ($>49\%$ O_2) (white).

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, a pair-wise comparison test on untransformed total-traces density revealed no significant difference neither between hypoxic and oxy− stations, nor between oxy+ and oxy− stations. PERMANOVA analysis also showed no significant difference in organism density between the oxygen levels, both for untransformed and presence/absence-transformed data (Table 5).

4. Discussion

Unlike shallower hypoxic environments, where vertical mixing can ventilate the bottom water on seasonal time scales, the permanent stratification in the EGSL prevents ventilation of the bottom water (Gilbert et al., 2005). Thus, the oxygen concentration in the EGSL bottom water does not fluctuate between low and high saturation levels but responds slowly to changes in organic carbon inputs, which control the oxygen concentration in the bottom water, and to changes in the oxygen concentration in the oceanic water mass that enters the Gulf of St. Lawrence and forms the deep landward-moving bottom water. During the past 70–80 years the oxygen concentration in the bottom waters in the LSLE has decreased at an average rate of 1 $\mu mol\ L^{-1}\ yr^{-1}$ (Gilbert et al., 2005; Katsev et al., 2007). Clearly, one expects a community of organisms that experiences slow change on long time scales, as we find it in the EGSL, to be significantly different from one that has to adapt to a seasonally changing oxygen regime. It might be fair to assume that, with a rate of change as slow as 1 $\mu mol\ O_2\ L^{-1}\ yr^{-1}$, local communities are adapted (but slowly changing) to nearly stable local oxygen concentrations. Thus we expect to find different benthic communities along the bottom water oxygen concentration gradient, each adapted to a local slowly changing oxygen regime. This should be kept in mind when interpreting our data.

4.1. Benthic macrofauna

The negative oxygen gradient from the well-oxygenated GSL to the hypoxic LSLE does not cause a significant difference in macrobenthic species richness between the hypoxic and normoxic stations. This observation is contrary to our expectations since previous studies on the effects of hypoxia conducted in other parts of the world report a decrease in macrobenthic species richness in environments affected by low-oxygen concentrations (Diaz and Rosenberg, 1995; Wu, 2002; Diaz and Rosenberg, 2008; Levin et al., 2009). Rabalais et al. (2001) found a correlation between benthic species richness and abundance and oxygen, salinity, temperature and sediment characteristics in a continental shelf with seasonal hypoxia. Yet, no variable could explain the variability of our observed species richness in the linear regression models. The lowest oxygen value found in our study was 18% saturation or 56.6 $\mu mol\ L^{-1}$ (station 23) which is not as close to anoxia as in many other hypoxic environments. It is possible that the oxygen concentrations in the LSLE bottom water are not low enough to cause a significant difference in macrobenthic species richness between the hypoxic stations of the LSLE and the normoxic stations of the GSL.

Two frequently reported effects of hypoxia on benthic macrofauna may help explain our results: the dominance of deposit feeders over suspension feeders in hypoxic environments (Diaz and Rosenberg, 1995; Wu, 2002; Levin et al., 2009) and the changing behaviour of organism in response to hypoxic stress (Baden et al., 1990; Rabalais et al., 2001). Even though the statistical analyses we applied did not reveal significant differences in macrobenthic species richness between the different oxygen levels, it is nevertheless possible that similar species richness were generated by different community compositions. Thus, the species with the highest density, the surface deposit feeding, low-oxygen tolerant *Ophiura* sp. (Vistisen and Vismann, 1997) was only found at the hypoxic stations 23 and 24. Moreover, as shown by the SIMPER analyses, the *Ophiura* traces contributed most of the difference between the hypoxic and the oxy+ stations. We also observed the highest density of the suspension feeder *P. aculeata* at oxy− stations 20 and CA, and the presence of the suspension feeder *P. borealis* was restricted to the oxy+ and oxy− stations. Therefore, our results may well indicate that the benthic macrofauna community structure is different in the hypoxic regions of the LSLE and the normoxic regions of the GSL. In the former region, surface deposit feeders and low-oxygen tolerant species dominate over suspension feeders and low-oxygen intolerant species.

A recent study conducted in the hypoxic region of the LSLE where stations 23, 23S and 24 are located found that the infaunal community structure had changed from 1980 to 2006 in response to oxygen depletion (Bourque, 2009). These changes were reflected by an increase of small surface deposit feeders, and by an increase abundance of polychaetes tolerant to low oxygen concentrations and high organic carbon loadings. The change was also reflected by a decrease of species richness, Shannon diversity, abundance of molluscs and crustaceans and mobile omnivorous species. In a review of the literature on hypoxia, Vaquer-Sunyer and Duarte (2008) demonstrated that cnidarians and molluscs are more tolerant to hypoxia whereas crustaceans are more sensitive. In another study conducted on the macrobenthic community in the EGSL collected with a Campelen bottom trawl, Lévesque (2009) found a higher density of molluscs and cnidarians and a lower density of crustaceans in the hypoxic region of the LSLE. We detected 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)

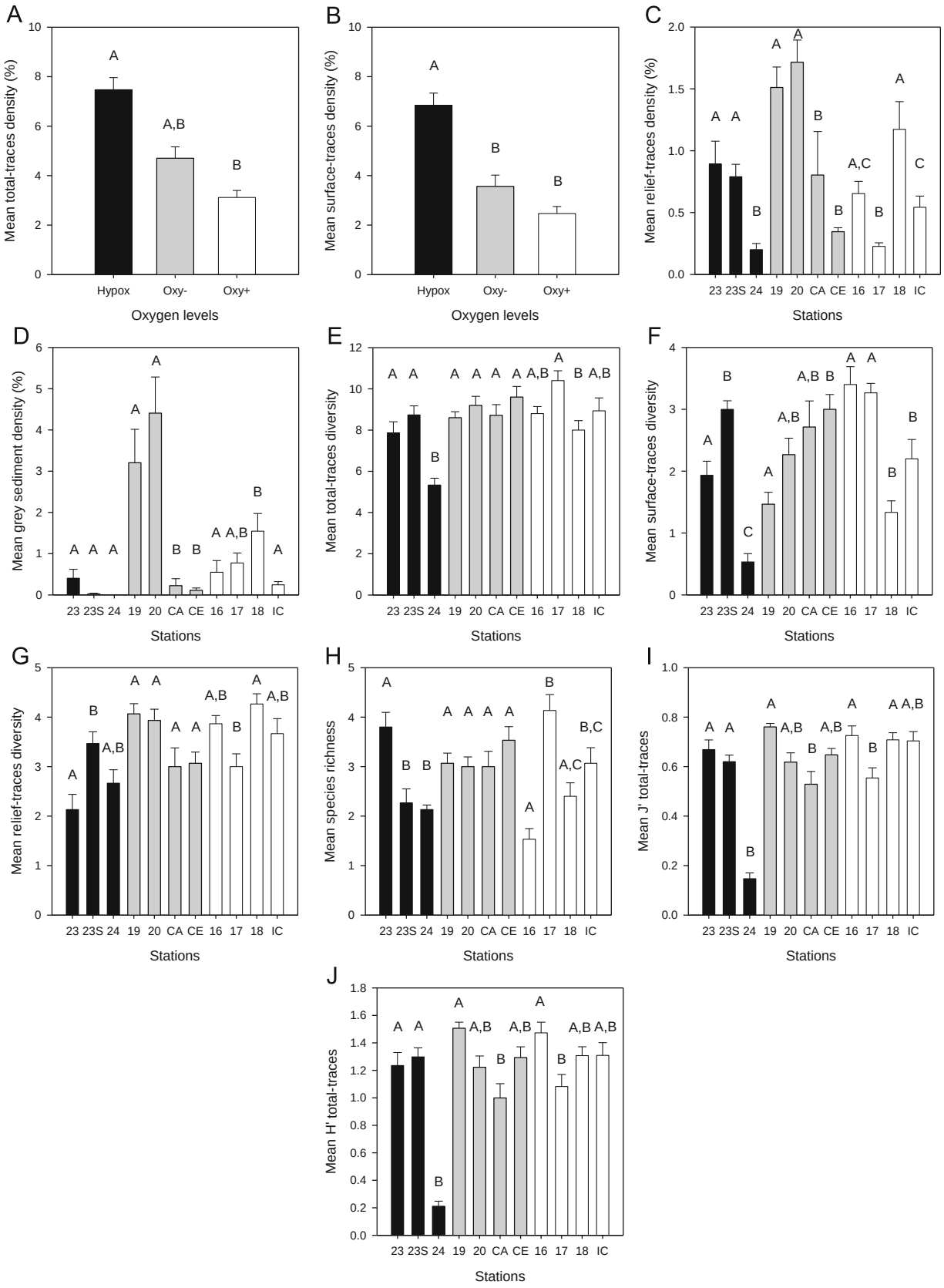

Fig. 4. Mean ($\pm$ SE) of: (A) total-traces density (%) and (B) surface-traces density (%) for three different oxygen levels, and (C) relief-traces density (%), (D) grey-coloured sediment density (%), (E) total-traces diversity, (F) surface-traces diversity, (G) relief-traces diversity, (H) species 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_2) (black); oxy$-$ stations (32–40% O_2) (grey); oxy+ stations ($>49\%$ O_2) (white).

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 ($\sqrt{\sqrt{}}$), total-traces diversity, surface-traces diversity, relief-traces diversity, species richness, Pielou's evenness (J') and Shannon–Wiener diversity (H') to test the effect of oxygen level and station within oxygen level.

Source of variation		Total-traces density ($\log_{(x+1)}$)		Surface-traces density ($\log_{(x+1)}$)		Relief-traces density ($\log_{10}$)		Grey-coloured sediment density ($\sqrt{\sqrt{}}$)	
	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*
O_2 level	2	1.479	12.37**	2.081	8.74**	0.963	0.59	5.805	2.71
Station (O_2 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								
		Total-traces diversity		**Surface-traces diversity**		**Relief-traces diversity**		**Species richness**	
	df	MS	*F*	MS	*F*	MS	*F*	MS	*F*
O_2 level	2	46.822	2.59	7.058	0.54	12.260	2.64	2.465	0.24
Station (O_2 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								
		Pielou's evenness (J')		**Shannon–Wiener diversity (H')**					
	df	MS	*F*	MS	*F*				
O_2 level	2	0.524	1.39	2.086	1.25				
Station (O_2 level)	8	0.385	24.18***	1.709	20.50***				
Error	146	0.016		0.083					
Total	156								

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS.

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), bottom temperature (T,°C), bottom oxygen saturation (O_2, %), total organic matter (TOM, %) and mean sediment grain size (MGS, μm). 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*	*T* (°C)	O_2 (%)	TOM (%)	MGS (μm)	r^2 (Adj r^2)	MSE
Total-traces density	9.55	NS	NS	NS	−0.12	NS	NS	0.66 (0.62)	1.89
Partial r^2					0.66				
Surface-traces density	8.55	NS	NS	NS	−0.12	NS	NS	0.59 (0.55)	2.32
Partial r^2					0.59				
Relief-traces density	0.16	0.01	NS	NS	NS	NS	−0.13	0.44 (0.30)	0.17
Partial r^2		0.25					0.19		
Grey sed density ($\sqrt{\sqrt{}}$)	−9.95	NS	NS	NS	−0.02	13.00	−0.08	0.66 (0.51)	0.08
Partial r^2					0.19	0.34	0.13		
Total-traces diversity ($\log_{10}$)	0.40	NS	NS	NS	NS	0.84	NS	0.16 (0.07)	0.01
Partial r^2						0.16			
Surface-traces diversity	−305.79	−0.02	9.12	NS	NS	NS	NS	0.31 (0.14)	2.89
Partial r^2		0.15	0.16						
Relief-traces diversity	−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		
***J'* total-traces**	−0.21	NS	NS	NS	NS	0.12	−0.03	0.46 (0.32)	0.02
Partial r^2						0.22	0.24		
***H'* total-traces**	−0.59	NS	NS	NS	NS	0.27	−0.06	0.47 (0.34)	0.08
Partial r^2						0.24	0.23		

developed by Lévesque (2009) and Lévesque et al. (2008) suggests oxygen saturation as one of the explanatory variables influencing the biodiversity of the EGSL. Taken together, these studies suggest that the community structure of the LSLE is dominated by species tolerant to the prevailing hypoxic conditions.

The stress caused by this level of hypoxia is known to affect many taxonomic groups. Mobile vertebrate and invertebrate taxa are reported to avoid hypoxic areas while less mobile invertebrate taxa try to escape low-oxygen conditions or even die if they cannot escape (Rabalais et al., 2001; Vaquer-Sunyer and Duarte, 2008; Levin et al., 2009). We observed some individual *Ophiura* sp. raising on their arms and elevate their central disc at the hypoxic station 24 in a manner similar to that reported for other ophiuroids trying to escape low-oxygen concentrations (Baden

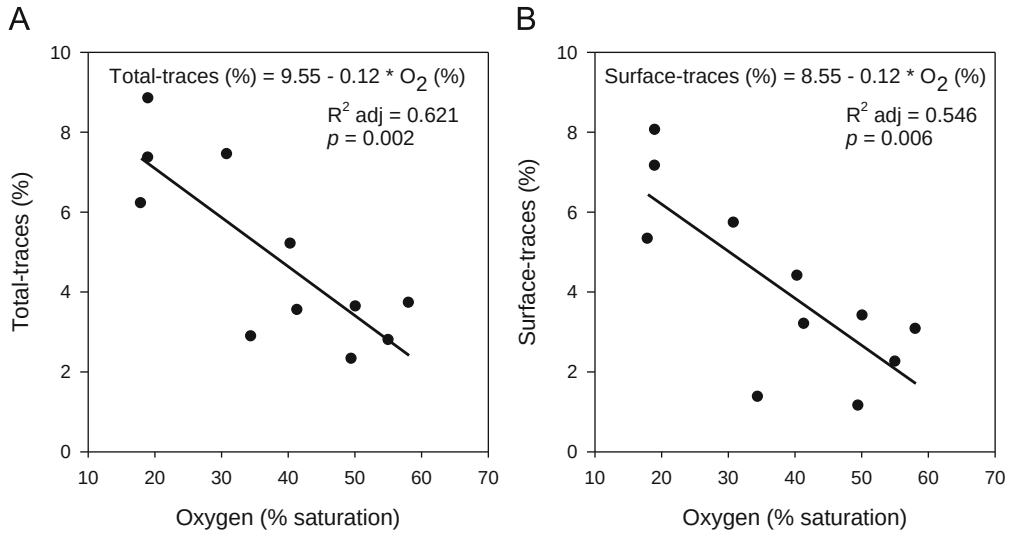

Fig. 5. Relation between oxygen saturation (%) and (A) total-traces density (%) and (B) surface-traces density (%) at the 11 stations sampled in the Estuary and Gulf of St. Lawrence in 2006 and 2007.

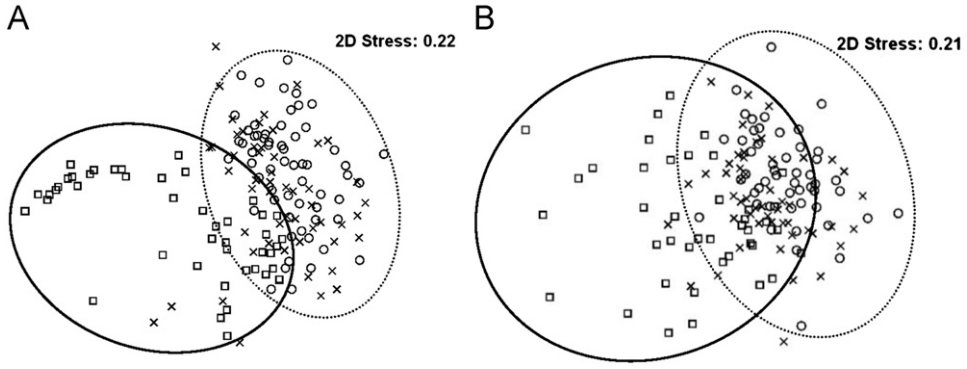

Fig. 6. Non-metric multi-dimensional scaling (nMDS) plots of total-traces density per oxygen level based on (A) untransformed data and (B) presence/absence-transformed data. Oxygen levels: hypoxic stations (□); oxy− stations (x); oxy+ stations (○). Contour lines: hypoxic station samples (-); oxy+ station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

Table 5
Permutational analysis of variance (PERMANOVA) (Anderson, 2001; McArdle and 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.

Source of variation	df	MS	Pseudo-*F*	*P* (perm)
Total-traces density				
O_2 level	2	33669.0	1.92	0.0314
Station (O_2 level)	8	17900.0	10.61	0.0002
Residuals	146	1687.7		
Total-traces density (presence/absence)				
O_2 level	2	16157.0	2.42	0.0346
Station (O_2 level)	8	6814.7	15.65	0.0002
Residuals	146	435.6		
Organism density				
O_2 level	2	57002.0	1.41	0.1644
Station (O_2 level)	8	41344.0	41.74	0.0002
Residuals	146	990.6		
Organism density (presence/absence)				
O_2 level	2	58653.0	2.08	0.0710
Station (O_2 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.

Trace	Contr. (%)	Trace	Contr. (%)
Oxy+ & Hypox (Avg. dissim. = 82.86)		**Oxy− & Hypox (Avg. dissim. = 81.77)**	
Ophiura traces (%)	33.69	*Ophiura* traces (%)	30.21
Simple ploughs (%)	19.03	Simple ploughs (%)	17.01
		Double ploughs (%)	11.56
Oxy+ & Oxy− (Avg. dissim. = 69.65)			
Simple ploughs (%)	20.42		
Shrimp trails (%)	17.86		
Imprints-depressions (%)	17.51		

et al., 1990; Rabalais et al., 2001). Crustaceans such as *Pandalus* sp. should be able to move out of hypoxic regions while less mobile crustaceans could possibly have died out at the hypoxic stations. More tolerant taxa such as cnidarians (Diaz and Rosenberg, 1995; Vaquer-Sunyer and Duarte, 2008; Levin et al., 2009) were found at the hypoxic stations (*Actinauge* sp. and *Cerianthus* sp.), and these could be less affected by the low-oxygen conditions in the LSLE. However, at slightly lower oxygen concentrations (1.5–1.0 mg L^{-1}), the large burrowing anemones *Cerianthus* sp. become severely affected by hypoxia and extend partly or completely from their tubes, lying motionless on the seafloor (Rabalais et al., 2001; Levin et al., 2009).

While this study and other recent studies conducted in the EGSL suggest that different benthic community structures in the

EGSL are due to hypoxia, differences in community structure may also be influenced by biogeographic differences. Brunel et al. (1998) divided the EGSL into 20 distinct zones based on bathymetric, biogeographic, oceanographic and physiographic criteria. Each zone would have particular species assemblages reflecting local regional characteristics. However, on the weight of the evidence presented here and elsewhere, we favour the hypothesis whereby the community structure differences mostly reflect the oxygen regime.

4.2. Bioturbation traces

In agreement with our hypothesis, the results of this study show a strong relationship between dissolved oxygen in the bottom water and the area of seafloor covered by bioturbation traces. The degree of oxygen saturation alone explains 62% and 55%, respectively, of the variability in total-traces and surface-traces. The densities of total and surface-traces is also higher in hypoxic regions than in normoxic regions, which does not agree with our hypothesis, nor with reports that bioturbation is reduced in hypoxic areas (Diaz and Rosenberg, 1995, 2008; Levin et al., 2009; Middelburg and Levin, 2009). The oxygen concentration (18% or 56.6 μmol L^{-1}) although within the range of hypoxia, is still high compared to the near-anoxia levels in studies reporting reduction of bioturbation. Thereby, the oxygen concentration may not be low enough to reduce surface manifestations of bioturbation. The SIMPER analyses indicated two types of surface-traces that explain most of the dissimilarity between the hypoxic and the oxy+ regions. These are *Ophiura* traces (only found at hypoxic stations) and simple ploughs (more abundant at hypoxic stations). This indicates that the high density of *Ophiura* sp. is responsible for the higher densities of total and surface-traces at the hypoxic stations. Since mobile surface deposit feeders such as *Ophiura* sp. move around on the seafloor to find food, they should produce higher density of traces than sedentary species. The active feeding mode and the high density of *Ophiura* sp. could be the primary explanation why we found the highest density of total and surface-traces at the hypoxic stations. An additional factor explaining the high traces density, could be behavioural, i.e. the stress imposed by low oxygen could well be affecting the activity of *Ophiura* sp., and therefore the density of traces.

Traces diversity, species richness, Pielou's evenness, and Shannon–Wiener's diversity were not significantly different for different oxygen saturation regimes. However, we did find significant differences among stations with similar levels of oxygen saturation, indicating some spatial heterogeneity in the characteristics of bioturbation traces and diversity of the benthic macrofaunal community.

The surface area analysed was similar at all station (10.07–12.63 m^2) except for station CA (4.87 m^2). However, indices used in this study did not show any distinctive discrepancy between this station and the others, so we do not expect that the difference in area of seafloor analysed affects the results of this study.

The resolution of the photographic images limits the identification of traces and organisms to features ≥ 5 mm. However, organisms and traces smaller than 5 mm, especially small burrows, were always present and sometimes in high abundance. This limitation may have affected our calculations of the density of some of the organisms and traces. Benthic studies conducted with microscale photography (Gage and Tyler, 1991) and sediment profile cameras (Rhoads, 1974; Solan et al., 2003) have shown an almost continuous disturbance of the sediment. If these techniques were to be applied in the EGSL, they would likely record much higher microrelief features of the seafloor than the ones reported here.

5. Conclusions

The negative oxygen gradient from the well-oxygenated Gulf of St. Lawrence to the hypoxic Lower St. Lawrence Estuary does not cause a significant difference in macrobenthic species richness between the hypoxic and normoxic stations. It is possible that the oxygen concentration in the Lower St. Lawrence Estuary bottom water is not low enough to cause a significant difference in macrobenthic species richness between the hypoxic stations of the Lower St. Lawrence Estuary and the normoxic stations of the Gulf of St. Lawrence.

The benthic macrofauna community structure in the hypoxic regions of the Lower St. Lawrence Estuary differs from the structure in the normoxic regions of the Gulf of St. Lawrence. In the former region, surface deposit feeders and low-oxygen tolerant species dominate over suspension feeders and low-oxygen intolerant species. The observations suggest that the community structure of the Lower St. Lawrence Estuary is dominated by species tolerant to the prevailing hypoxic conditions.

The dissolved oxygen concentration in the bottom water influences the fraction of the seafloor that is covered by bioturbation traces. The degree of oxygen saturation alone explains 62% and 55%, respectively, of the variability in total-traces and surface-traces. The high density of *Ophiura* sp. is responsible for the higher densities of total and surface-traces at the hypoxic stations. The active feeding mode and the high density of *Ophiura* sp. could be the primary reasons for the high density of total and surface-traces at the hypoxic stations.

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