

Article

Macrozoobenthic Diversity along an Oxygen Gradient in the Deep Trough of the Gulf of St. Lawrence (Canada)

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Abstract: In 2015, we studied the macrozoobenthic community composition along a dissolved oxygen gradient in the deep trough of the Gulf of St. Lawrence (Canada). We sampled the seabed at nine stations using box corers (three replicates per station), starting in the outer Gulf and ending in the Lower St. Lawrence River Estuary. We found four different communities dominated by polychaetes, crustaceans, and molluscs, with the emphasis shifting from mollusc to polychaete communities as oxygen saturation decreased. Contrary to our expectations, the stations furthest upstream in the estuary with the lowest oxygen saturation levels had the highest species diversity, and also the highest density and biomass values. Key genera of the hypoxic zone included bivalves (*Thyasira*), cumaceans (*Diastylis*), amphipods (*Harpinia*), and polychaetes such as *Ampharete*, *Ceratocephale*, *Galathowenia*, and *Trochochaeta*. We attribute this to the stability of the environmental conditions and the absence of stress, where the constant supply of oxygen, even at low concentrations, seems to be more important than the absolute oxygen concentration.

Keywords: biodiversity; hypoxia; stress; macrofauna



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1. Introduction

Climate change and its effects on the stratification of water masses make oxygen deficiency an increasing problem for benthic organisms worldwide, especially in coastal seas. This affects the estuaries of large rivers with their high nutrient loads, as well as upwelling areas on the west coasts of the continents, e.g., [1–5]. Tolerance to low oxygen is greater for smaller taxa than for larger ones, and greater for less-mobile taxa than for mobile ones. Climate change is therefore likely to lead to shifts in the relative abundance of species due to oxygen deficiency [6]. Minimum oxygen requirements for survival vary between species. The duration, periodicity, and severity of low oxygen concentrations have a significant influence on survival and activity. Apart from environmental factors, different survival strategies of organisms have developed, which have occasionally led to the evolutionary adaptation of zoobenthos in oxygen-minimum zones [7–9]. This can occur, for example, by means of symbioses or physiological mechanisms. For instance, in the Baltic Sea, a relatively young sea of 8000 years with an estuarine character, hardly any such mechanism can be observed, so that a large part of the benthic community disappears during regularly observed periods of oxygen deficiency with values below 1 mL per litre, e.g., [10]. However, in the geologically old (several million years) upwelling area off Namibia [11], it was observed that, even at the lowest oxygen concentrations of less than 0.02 mL per litre (!), diverse benthic life still prospers, e.g., [12]. Compared with a few days of anoxia in the Baltic, leading to population breakdown, such phases in the upwelling area off Namibia can last several weeks without drastic effects on macrobenthos populations. Results on structural adaptations of macrofauna communities are also reported from other upwelling areas, such as off Chile [13,14]. In order to classify the resilience of estuarine benthic populations in a system that is geologically older than the Baltic Sea, but younger than the upwelling regions on the continental west coasts, this study was carried out in the

Laurentian Trough, a 300–500 m deep submarine valley that traverses the Estuary and Gulf of St. Lawrence on the Canadian east coast, and intersects the continental shelf (Figure 1). The deep water in the trough derives from the northwestern Atlantic, and as it flows slowly inland, it loses oxygen by respiration, resulting in a negative gradient of dissolved oxygen from east to west. For decades, there has been a decreasing trend in the average oxygen supply, especially in the deeper reaches of the Lower St. Lawrence River Estuary (LSLE) and the Gulf, e.g., [15,16]. The reasons are both due to physical and biogeochemical processes, but are weighted and discussed quite differently [17,18]. The persistence of hypoxic conditions in the LSL and Gulf is due to the year-round stratification of the water column and estuarine circulation [16,19,20]. The benthos in the inner part of the estuary (LSLE) is regularly affected by hypoxia (<20% saturation), whereas, in the middle part, rather moderate oxygen values, and in the outer part, good saturation values are sustained; see [21]. As other environmental variables apart from depth and oxygen did not differ very much, this transect provided a suitable proving ground for our study.

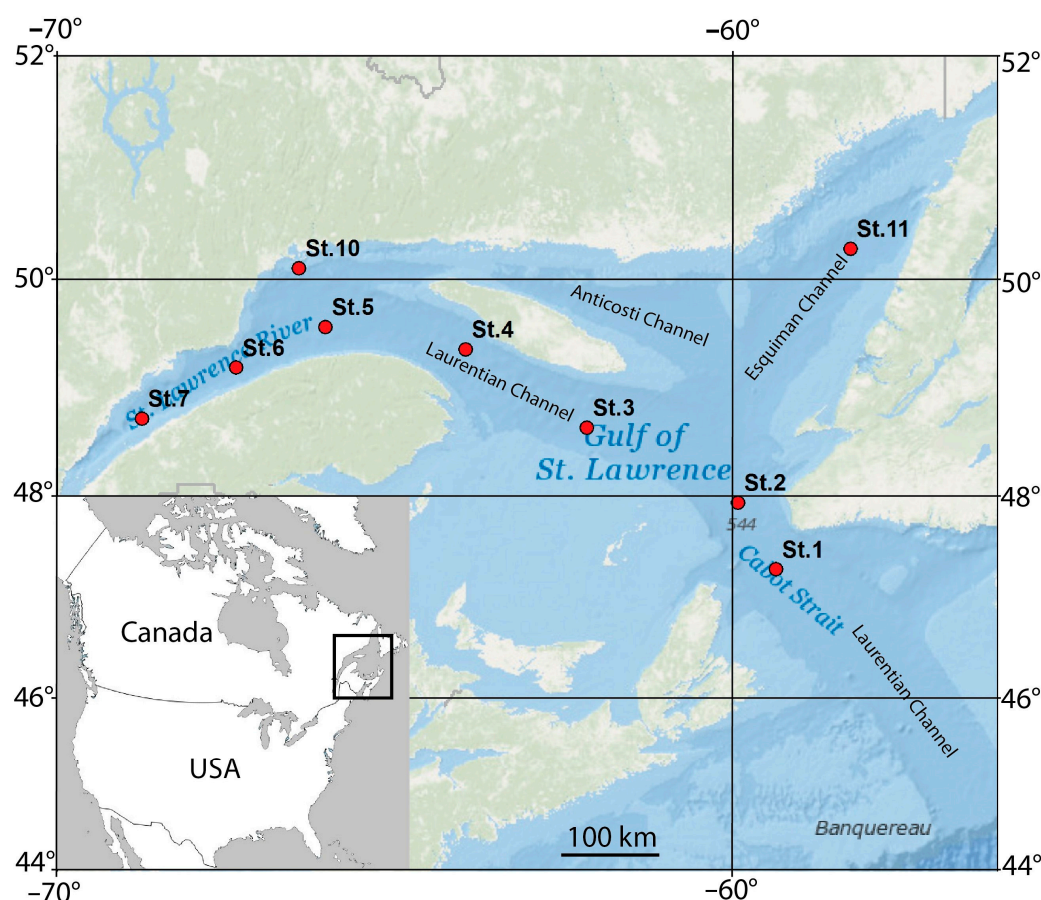


Figure 1. Estuary and Gulf of St. Lawrence, with stations 1 to 11. The black box in the overview map marks the area that has been zoomed out.

Brunel et al. [22] summarised in their catalogue the knowledge on marine invertebrates gained from more than 100 years of research in the St. Lawrence Estuary area. This inventory yielded more than 2200 species, subspecies, and varieties, a large proportion of which can be attributed to the benthic habitat. Over the last 20 years, research has focused increasingly on the changing oxygen conditions of the Estuary and Gulf and the resulting impact on marine life. In general, the effects of oxygen deficiency on the marine environment depend on the oxygen concentration and the sensitivity of the species. But, as the former comparison between different oxygen-minimum areas indicates, additional adaptational factors may impact the response as well. While the influence of the oxygen gradient in the St. Lawrence River Estuary and the Gulf of St. Lawrence on the epibenthic and

fish fauna has been relatively well studied, information on the endobenthic communities is almost lacking [21,23–29].

We therefore investigated the distribution patterns of endo- and epibenthic species in the central Laurentian Channel considering the traditional hypothesis that oxygen concentration is one of the most important environmental variables influencing the density and diversity of benthic macrofauna [5], and that, therefore, the hypoxic region of the Lower St. Lawrence Estuary (LSLE) should have lower species richness and species diversity than the normoxic regions in the Gulf of St. Lawrence (GSL).

2. Materials and Methods

2.1. Study Area

The Estuary and Gulf of St. Lawrence (EGSL) is located on the southeast coast of Canada (Province of Quebec) in the North Atlantic. The EGSL has two major connections with the Atlantic Ocean, through the Cabot and Belle-Isle straits, and receives significant freshwater inflows, mainly from the St. Lawrence River (Figure 1).

The bathymetry of the Gulf is characterised by the deep Laurentian Channel, with a maximum depth of 535 m. A cold layer (1 to 2 °C) situated between 50 and 60 m separates the warmer mixed surface (14 °C in summer) and deep (6 °C) layers (Figure 2).

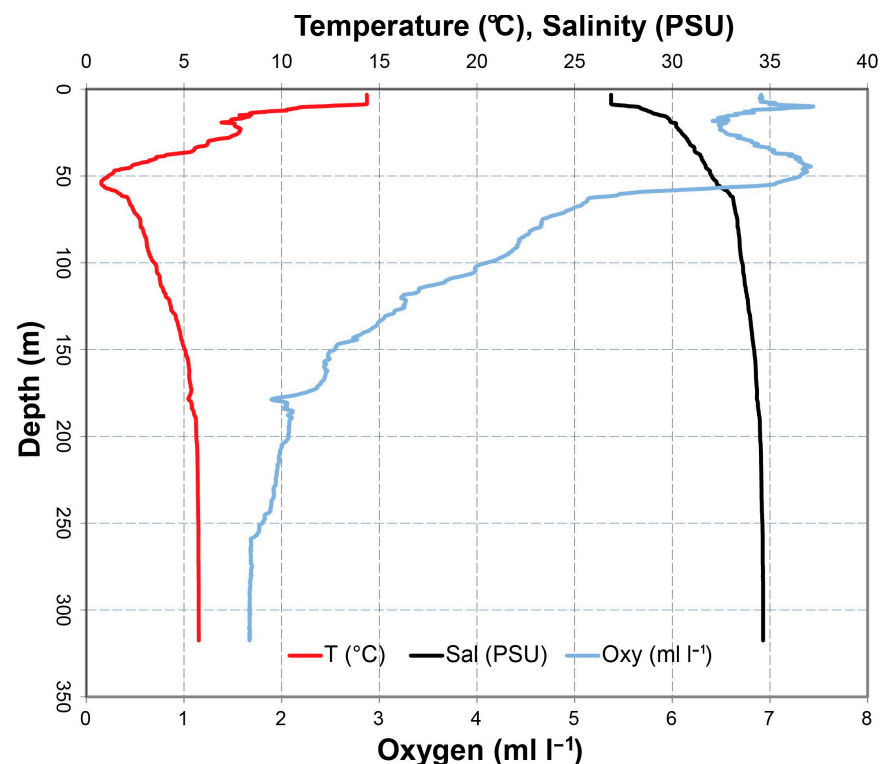


Figure 2. An example of a CTD profile (here, Stn. 6) with temperature, salinity, and oxygen.

Estuarine circulation occurs by water flowing seaward in the surface layer and landward in the deep layers [20]. The seabed of the deep Laurentian Channel is relatively homogeneous and consists of fine mud [30].

The effect of benthic respiration can be observed in the profiles of the apparent oxygen utilisation (AOU) along the stations (Figure 3). This difference between the current oxygen content and the saturation value (the oxygen content at the time of surface water mass formation) shows the oxygen decrease in the bottom water during the landward flow of the water mass from the open ocean by close to 90%.

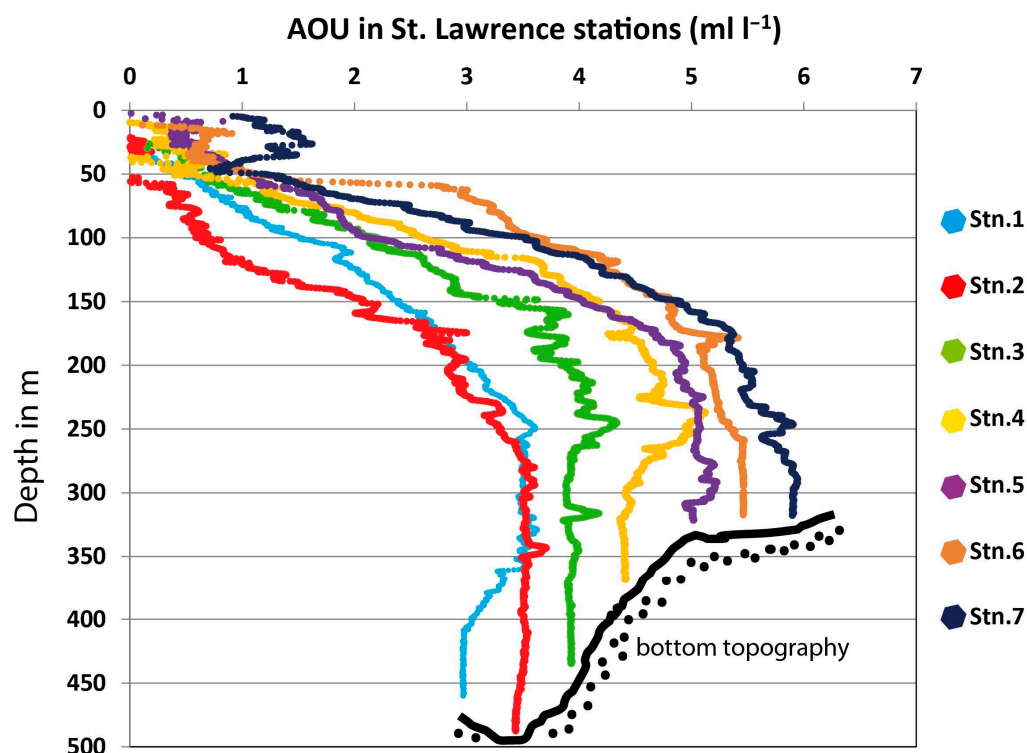


Figure 3. Apparent oxygen utilisation (AOU) along the oxygen gradient in the Gulf and Estuary of St. Lawrence. Stations 10 and 11, which are not on the transect, have been omitted.

2.2. Sampling

Macrozoobenthos samples were obtained along a transect (see Figure 1) on board of the RV Maria S. Merian during the CECAS Expedition MSM46 (25 August 2015–26 September 2015). Biological studies included benthic macrofauna along the oxygen gradients from the Gulf of St. Lawrence (GSL) to the Lower St. Lawrence Estuary (LSLE). Triplicate benthic samples were taken with a 0.1 m² box corer at each station. All samples were sieved through a 1 mm² sieve and animals were preserved on board in 4% buffered formaldehyde. Sorting procedures were conducted at the laboratory with a Zeiss stereomicroscope Discovery V8 with 10–40× magnification. All macrofauna samples were identified to the lowest taxonomic level whenever possible. The nomenclature was checked following the World Register of Marine Species (WoRMS: <http://www.marinespecies.org/index.php>, accessed on 5 January 2023). Environmental variables, such as salinity, temperature, and oxygen concentration in the water column down to the sediment boundary, were recorded by means of a profiling CTD system (SBE 911, Seabird, Bellevue, WA, USA) with an attached oxygen probe (Seabird, Bellevue, WA, USA) and a 13-bottle sampling rosette. Oxygen sensors were calibrated by an immediate potentiometric Winkler titration of three samples per water column, including the closest position to the sediment, in the ship's laboratory. An additional sediment sample was taken from the box corer to extract the upper surface sediment layer (≤ 20 mm) for analyses of the median grain size (laser particle sizer Cilas 1180L) and organic matter estimation by weight loss upon ignition (afdwt).

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2.3. Statistical Analyses

For each benthic sample, the density and biomass of the species were estimated. Following this, the replicate data were averaged to a total amount per square meter at each station (no pooling).

Multivariate analysis was conducted by complete linkage hierarchical clustering based on the Bray–Curtis similarities of the square-root-transformed density data for 9 stations. Superimposing the clustering results on nonmetric multidimensional scaling (nMDS) supported the validity of the classification of stations to 4 distinct benthic assemblages [31]. The significance of the classification results was tested with a one-way PERMANOVA based on the Bray–Curtis similarity matrix using 786 permutations. PERMANOVA is suitable for unbalanced data and heterogeneous dispersions among groups, and helps to avoid the normality assumption [32]. The species responsible for classification were determined by applying SIMPER exploratory analysis and visual re-examination of the modified data matrix, whereupon the benthic assemblages had been determined and described. The distance-based redundancy analysis (dbRDA) was performed to explore the relationship between the background oxygen concentration and other environmental variables with the ecological data from PRIMER; see [33]. We disregarded collinearity between environmental variables. It is important to note that we consider our statistical results as purely exploratory and descriptive, and acknowledge that our sampling size is too small to draw solid statistical relationships.

3. Results

The environmental conditions for macrofauna were variable within the stations over the whole grid. Table 1 and Figure 4 display the characteristic values for the bottom-water and sediment variables of the stations sampled during this study. All stations > 300 m water depth showed a very homogeneous development of sediment characteristics and salinity. Only in the case of oxygen a gradient from west to east could be observed. The oxygen bottom-water concentrations varied between 1.12 and 5.35 mL L⁻¹ over the stations. The onset of bottom-water oxygen deficiency (20 to 30% saturation) was observed only at the innermost stations of the estuary (see Figure 3). The organic content of the surface sediment varied between 1.69 and 10.5%. Except at the shallowest station, station 10 (outside the Laurentian Channel), the grain sizes were very similar, ranging from 7 to 9 µm.

Table 1. Characteristic environmental variables in bottom water and sediment in 2015. B T: bottom-water temperature; B O₂: bottom-water oxygen concentration; B O₂ Sat: bottom-water oxygen saturation; B S: bottom-water salinity; Sed Org: sediment organic content; Sed GS: sediment grain size.

Station	Latitude	Longitude	Depth (m)	B T (°C)	B O ₂ (mL/L)	B O ₂ Sat (%)	B S (PSU)	Sed Org (%)	Sed GS (µm)
Stn. 1	47.1859	−59.5380	476	5.6	4.03	82.23	34.9	9.11	9
Stn. 2	47.8333	−60.0835	500	5.6	3.55	72.57	34.9	no data	no data
Stn. 3	48.5503	−62.2495	449	5.7	3.05	62.40	34.9	10.50	8
Stn. 4	49.2903	−63.9893	382	5.9	2.54	52.19	34.8	7.86	8
Stn. 5	49.5005	−65.9982	335	5.8	1.94	39.89	34.7	10.40	7
Stn. 6	49.1196	−67.2796	326	5.8	1.52	31.03	34.6	9.30	8
Stn. 7	48.6390	−68.6319	329	5.5	1.12	22.77	34.5	5.84	8
Stn. 10	50.0441	−66.3791	202	1.6	5.35	97.53	32.9	1.69	22
Stn. 11	50.2230	−58.4656	328	6.3	2.21	45.91	34.6	9.37	8

The number of species is relatively high at most stations, ranging from 30 to 40 and with a Hurlbert index (ES50) between 15 and 20 (Figure 5A). The highest diversity was observed at station 6. Stations 5 and 11 were the least species-rich, with 18 and 21 taxa, respectively (Figure 5A). In terms of density, stations 5 and 11 were again conspicuous, with very low values (323 and 287 ind m⁻², respectively); at all other stations, more than twice the density of individuals (1000 to 1500 ind m⁻²) was recorded (Figure 5B). With over 4500 individuals per square metre, station 7 clearly stands out. In terms of biomass, the highest values per square metre were observed at stations 4–10 (Figure 5B) with 48 to 78 g. At the other stations, the biomass varied between 4 and 6 g.

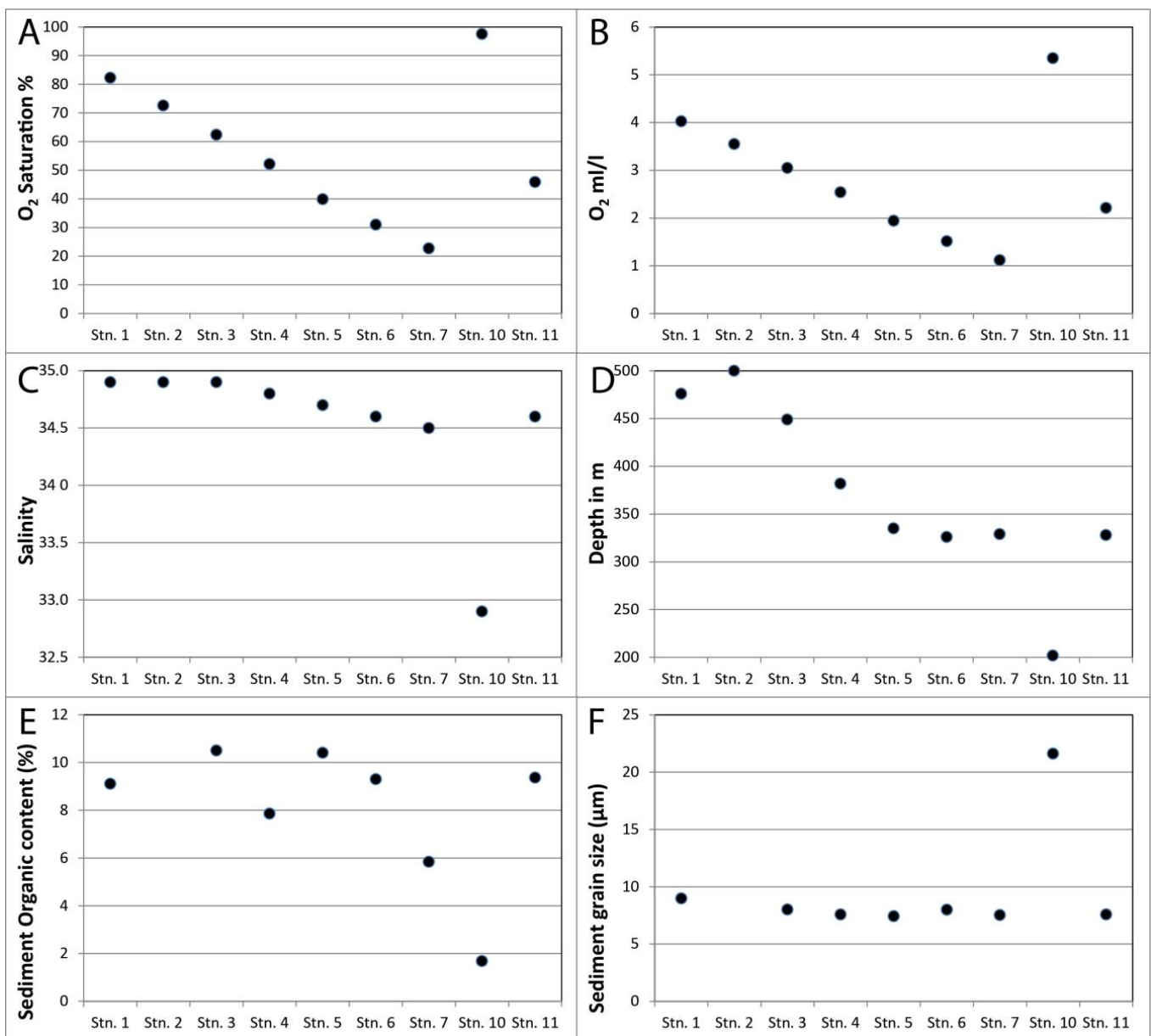


Figure 4. Oxygen saturation (A), oxygen content (B), salinity (C), depth (D), sediment organic content (E), and sediment median grain size (F) along the sampled stations 1 to 11.

Although taxonomic identification could not be completed for all groups (due to the poor condition of some calcareous materials), we were able to present an extensive list of taxa. A total of 108 taxa were identified at the 9 stations surveyed. With 40 taxa, the Polychaeta were the most diverse class, followed by the Malacostraca (33 taxa) and the Bivalvia (13 taxa) (Figure 6). Except for Gastropoda (six), Anthozoa (three), and Ophiuroidea (two), all classes occurred with only one taxon. Twenty-four of these achieved a relative density of at least 5% in at least one station and are listed in the Table 2. Some of them are shown in Figure 7. Representatives of seven classes belong to the dominant taxa. Depending on the community, different species are characteristic. We found four different communities dominated by polychaetes, crustaceans, and molluscs, with the emphasis shifting from mollusc to polychaete communities as the oxygen saturation decreased. Among the bivalves, *Mendicula ferruginosa* (Forbes, 1844) and *Thyasira* sp. are particularly noteworthy. Within the crustaceans, the cumacean *Diastylis abbreviata* G.O. Sars, 1871 and *D. goodsiri* (Bell, 1855) play a major role, as do the amphipods *Dyopetos monacanthus*

(Metzger, 1875) and *Harpinia* sp. The most comprehensive class is that of the polychaetes, from which Capitellidae, *Ceratocephale loveni* Malmgren, 1867, *Galathowenia oculata* (Zachs, 1923), and *Prionospio steenstrupi* Malmgren, 1867, among others, are to be highlighted. Finally, the epibenthic anthozoan *Pennatula aculeata* Danielssen, 1860 and the brittle star *Amphiura* sp. should be mentioned.

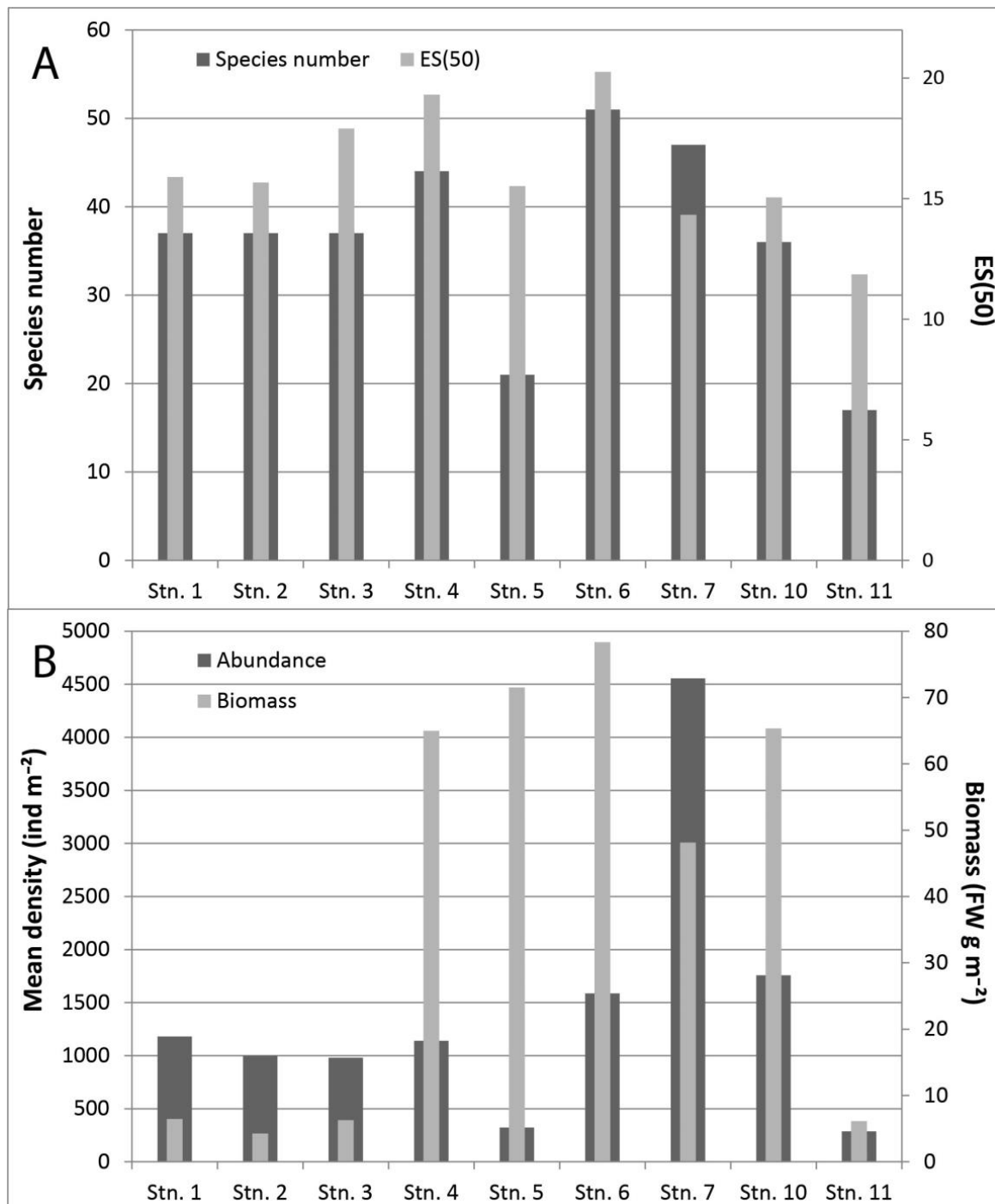


Figure 5. Species number and Hurlbert index (A), density, and biomass (B) along the sampled stations 1 to 11.

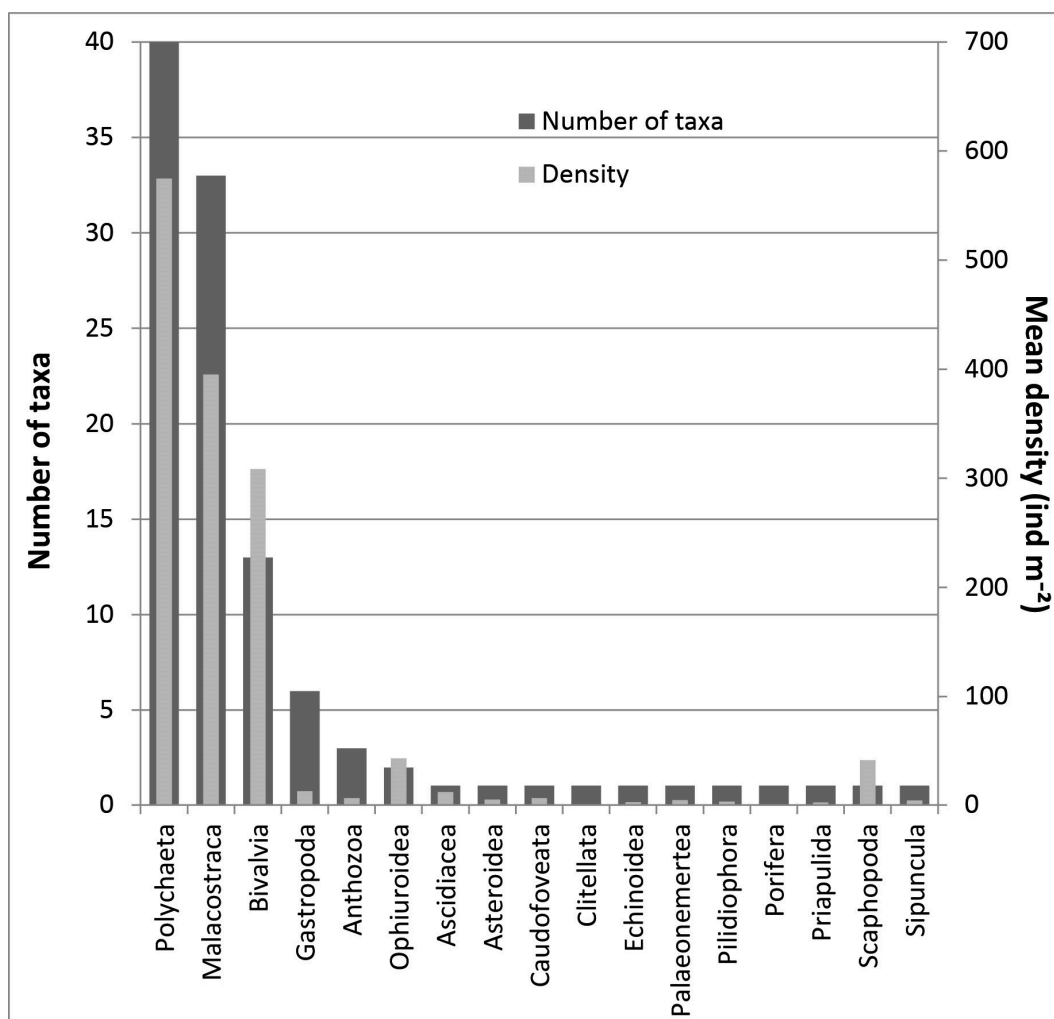


Figure 6. Number of taxa and mean density at all sampled stations together.

Four distinct communities could be distinguished during the study based on hierarchical clustering (Figure 8), nMDS (not shown here for brevity), and SIMPER results (Supplementary Data). Community structure differed significantly between the delineated communities (PERMANOVA $F_{1,8} = 4.9$, $p = 0.001$). At the entrance of the GSL (stations 1 to 4) in water depths between 382 and 500 m, and with an oxygen saturation ranging from 52 to 82%, the first community was separated by the similarity analysis (Figure 8). Diagnostic species were the amphipod *Harpinia* sp., the thyasirid bivalve *Mendicula ferruginosa*, and the scaphopod *Antalis* sp. The second cluster was situated in the innermost part of the LSLE (Stations 6 and 7) in water depths between 323 and 329 m and with an oxygen saturation ranging from 23 to 31%. The overall species diversity was highest. Characteristic taxa belonged mainly to polychaetes (*Ampharete* sp., *Ceratocephale loveni*, Cirratulidae, *Galathowenia oculata*, *Lumbrineris* sp., and *Trochochaeta multisetosa* (Örsted, 1844)) as well as the thyasirid bivalves *M. ferruginosa* and *Thyasira* sp. The third cluster consisted of only one station (stn. 10), which is outside the Laurentian Channel in more shallow waters (202 m) and with a high oxygen saturation (98%), and can be described as an outsider. Four species were characteristic of the station. Chaetopterid (cf. *Chaetopterus* sp.) and spionid (*Prionospio steenstrupi*) polychaetes reached high densities. In addition, the mussel species *Nucula* sp. and *Thyasira* sp. were prominent. The fourth cluster consisted of two stations that were far away from each other. Station 5 is located in the Laurentian Channel at the entrance to the LSLE. Station 11, on the other hand, is located in the Esquiman Channel, at the northern exit of the GSL. Both showed similar oxygen saturation values (40 vs. 46%) at similar

water depths (335 vs. 328 m). Characteristic species were the polychaetes Capitellidae, *Ceratocephale loveni* and *Lumbrineris* sp., and the thyasirid bivalve *Thyasira* sp. The very low density of individuals and the low number of species were striking at both stations (see Table 2 and Figure 5B).

The results of the dbRDA (Figure 9) show the relationship between the environmental predictors that best explain the variation in the macrofauna composition in the four sampled communities. When all stations were included in the analysis, the first two axes explained 55.8% of the total variation. The dbRDA1 was mainly driven by depth and salinity, and the dbRDA2 by sediment organic content and size. When two stations outside the main transect were removed from the species matrix, the dbRDA1 was mainly related to depth and bottom oxygen saturation. We have, however, to state again, that the present statistical results in our study should be treated as purely exploratory and descriptive, as the sampling size is too low to determine solid relationships.

Table 2. Mean macrobenthic faunal density (ind m⁻²) per taxa and per station for the nine stations sampled in the Estuary and Gulf of St. Lawrence in 2015 (n = 3). Only the 24 most common taxa (>5% dominance in at least one station) are shown (SoD = sum of density; TD = total density; TSN = total species number).

Stations	Stn. 1	Stn. 2	Stn. 3	Stn. 4	Stn. 5	Stn. 6	Stn. 7	Stn. 10	Stn. 11
Depth (m)	476 m	500 m	449 m	382 m	335 m	326 m	329 m	202 m	328 m
Oxygen Saturation (%)	82	73	62	52	40	31	23	98	46
Anthozoa									
<i>Pennatula aculeata</i>	0	0	0	10	20	3	13	0	3
Scaphopoda									
<i>Antalis</i> sp.	103	110	113	50	0	0	0	0	0
Bivalvia									
<i>Mendicula ferruginosa</i>	303	293	220	93	0	87	77	0	0
<i>Thyasira</i> sp.	70	87	43	47	27	167	700	83	20
<i>Yoldiella</i> sp.	17	30	53	7	3	7	0	0	3
Malacostraca									
<i>Diastylis abbreviata</i>	0	0	0	0	0	0	1600	0	0
<i>Diastylis goodsiri</i>	0	0	0	0	0	20	107	0	0
<i>Dyopedos monacanthus</i>	3	30	0	0	0	3	70	0	0
<i>Harpinia</i> sp.	247	160	153	200	37	103	97	0	13
<i>Ischyrocerus</i> sp.	0	0	0	0	0	33	73	0	0
<i>Leptostylis</i> sp.	0	0	0	7	0	110	0	0	0
Polychaeta									
<i>Ampharete</i> sp.	0	3	7	23	13	53	227	3	0
Capitellidae	30	23	17	60	27	120	10	23	27
<i>Ceratocephale loveni</i>	0	0	0	13	23	143	197	0	103
Chaetopteridae	7	3	0	7	0	3	0	130	3
Cirratulidae	0	3	7	70	20	67	70	17	7
<i>Diplocirrus</i> sp.	53	13	27	43	0	7	10	0	0
<i>Galathowenia oculata</i>	20	13	37	177	0	177	617	0	0
<i>Lumbrineris</i> sp.	27	10	13	73	20	87	13	33	60
<i>Prionospio steenstrupi</i>	10	23	33	10	0	3	3	890	0
<i>Trochochaeta multisetosa</i>	0	0	0	0	0	43	170	0	13
Ophiuroidea									
<i>Amphiura</i> sp.	13	30	47	33	70	70	27	0	0
<i>Ophiura</i> sp.	90	0	3	7	0	0	0	0	0
Ascidacea									
<i>Molgula</i> sp.	0	0	0	0	0	10	97	0	0
SoD (above)	993	833	773	930	260	1317	4177	1180	253
TD density (all taxa) ind m⁻²	1180	997	980	1140	323	1587	4554	1757	287
TSN (all taxa)	37	37	37	44	21	51	47	36	17

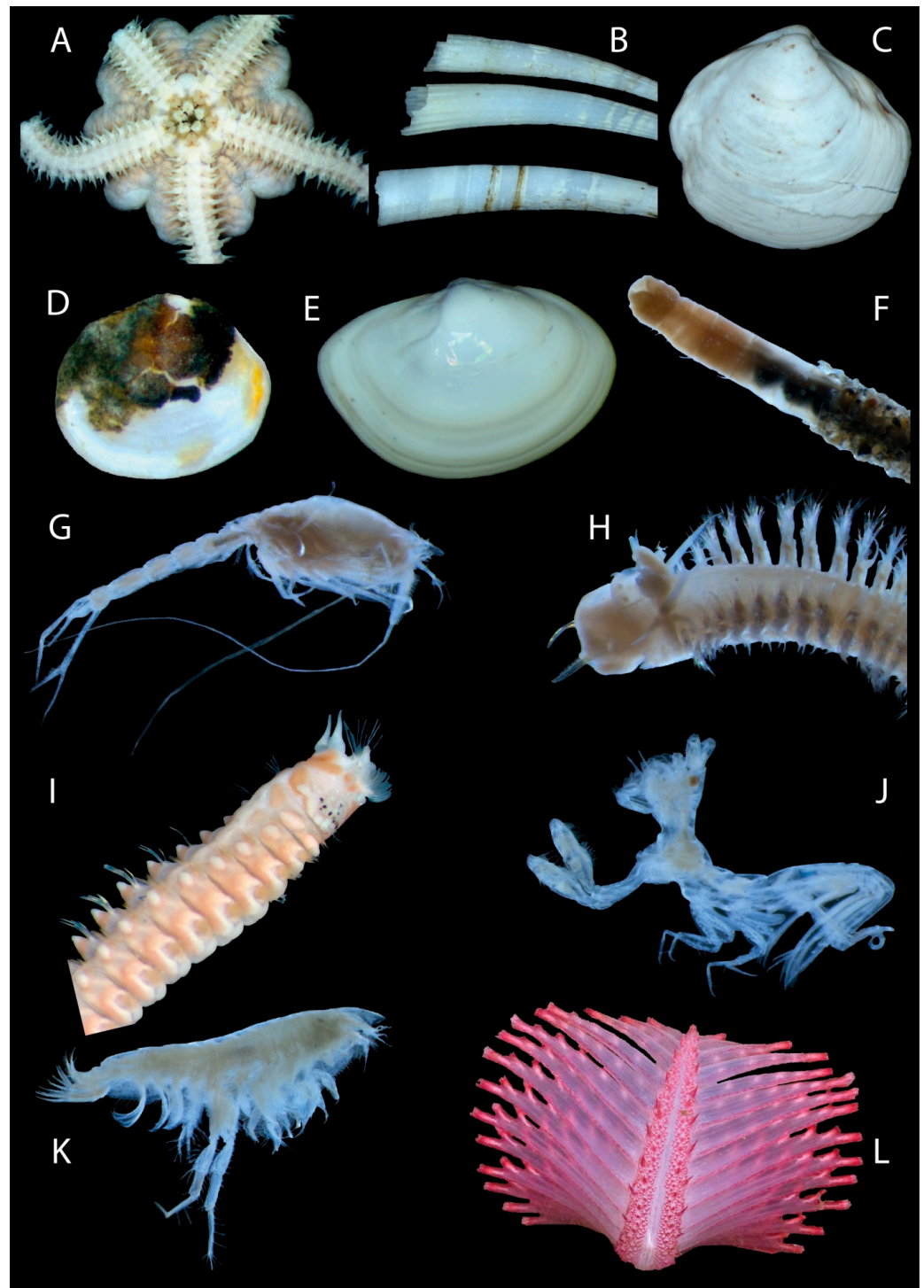


Figure 7. Key species of macrozoobenthic communities of the Estuary and Gulf of St. Lawrence. (A) *Amphiura* sp. (13 mm); (B) *Antalis* sp. (25 mm); (C) *Thyasira* sp. (5 mm); (D) *Mendicula ferruginosa* (Forbes, 1844) (1.5 mm); (E) *Yoldiella* sp. (2.6 mm); (F) *Galathowenia oculata* (Zachs, 1923) (15 mm); (G) *Diastylis abbreviata* G.O. Sars, 1871 (6 mm); (H) *Ceratocephale loveni* Malmgren, 1867 (10 mm); (I) *Trochochaeta multisetosa* (Örsted, 1844) (12 mm); (J) *Dyopodos monacanthus* (Metzger, 1875) (5 mm); (K) *Harpinia* sp. (6 mm); (L) *Pennatula aculeata* Danielssen, 1860 (150 mm).

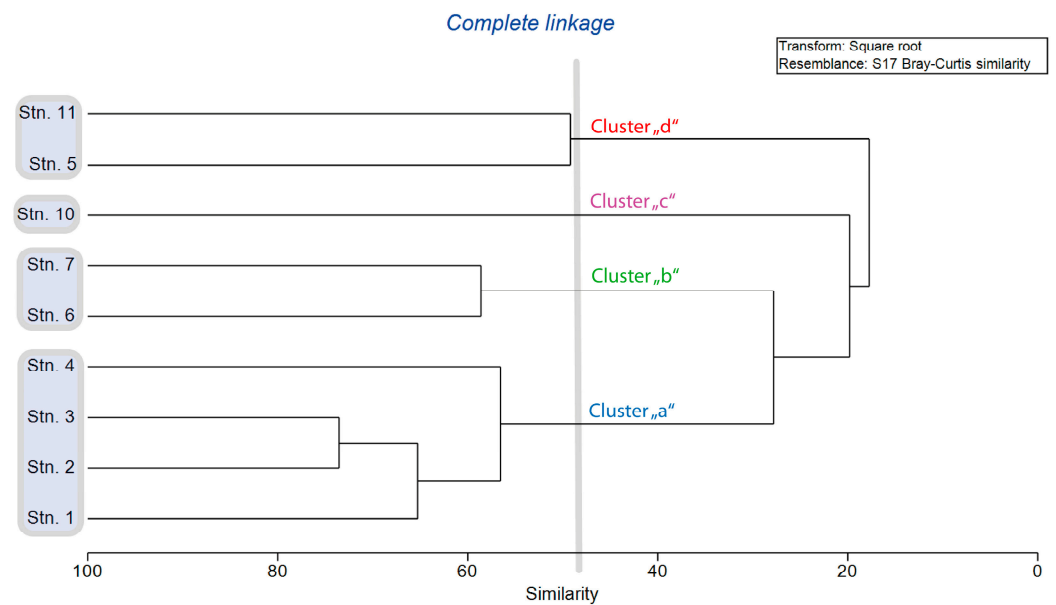


Figure 8. Dendrogram showing similarity of 9 sampled stations based on the abundance of 108 taxa recorded. The line of separation to delineate the communities is indicated.

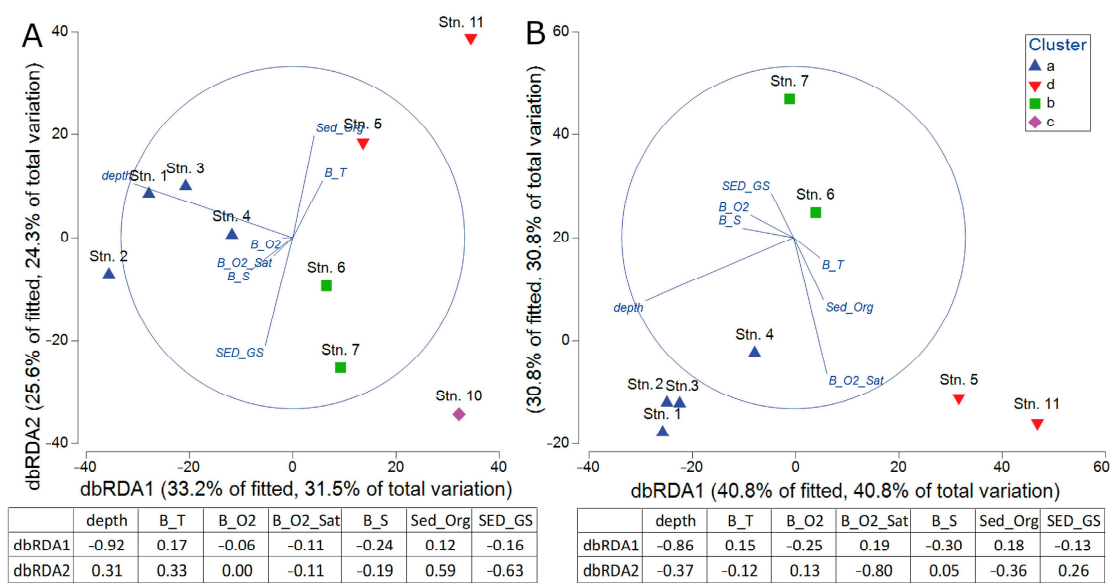


Figure 9. Distance-based redundancy analysis (dbRDA) ordination plot for the fitted macrofauna data (based on Bray–Curtis after the square-root transformation of abundances) versus environmental variables (A) for all species and stations, and (B) excluding stations 10 and 11 located outside the main transect. Environmental variables are shown by vectors abbreviated, as in Table 1, and vector length related to the effect induced by the environmental variable on species assemblages. Values in boxes below each ordination plot depict the multiple partial correlations between the dbRDA1 and dbRDA2 axes and environmental variables.

4. Discussion

It is known from the literature that oxygen values in the LSLE can be as low as $63 \mu\text{mol L}^{-1}$ ($=1.41 \text{ mL L}^{-1}$), e.g., [34]. Long-term studies also showed that, since about the mid-1980s, oxygen levels have varied between 50 and $80 \mu\text{mol L}^{-1}$, but have never reached values above $100 \mu\text{mol L}^{-1}$, as in the decades before [15,16,35]. In the present study, a bottom oxygen gradient from west (GSL) to east (LSLE) was clearly detected (Figures 3 and 4A). Similar to previous investigations, hypoxic conditions were found in

the LSLE. The two hypoxic stations showed values between 50 and 67 $\mu\text{mol L}^{-1}$ (1.12 and 1.52 mL L^{-1}) and were thus within the range of the long-term studies (see also Table 1 and Figure 4A). We can therefore assume that our 2015 survey year was not exceptional in terms of oxygen conditions.

The hypothesis that the hypoxic region of the Lower St. Lawrence Estuary (LSLE) has a lower benthic diversity than the normoxic region of the Gulf of St. Lawrence (GSL) could not be confirmed in this study. On the contrary, the stations furthest upstream in the estuary with the lowest oxygen saturation levels showed the highest species diversity and also the highest density and biomass values. These results are contrary to our expectations, so it is possible that the oxygen values of 1.12 and 1.52 mL L^{-1} are not yet sufficient to reach the physiological threshold values of most organisms present.

Species-specific studies showed that hypoxia thresholds vary greatly across marine benthic organisms (several hundred tested) and that the conventional definition of 2 $\text{mg O}_2 \text{ L}^{-1}$ (1.4 mL L^{-1}) to designate waters as hypoxic is probably too high for more than half of the tested organisms [36]. As a rough estimate, the mean threshold value of the sublethal O_2 concentration (2.24 $\text{mg L}^{-1} = 1.6 \text{ mL L}^{-1}$) determined by the authors for all organism groups is widely adopted. However, the sensitivity of the organisms is definitely very different, and therefore the wide species-specific range of thresholds for oxygen deficiency in benthic marine organisms cannot be adequately described by a single, universal value. The decapod crustacean *Calocaris macandreae* Bell, 1846, for example, occurring also in the GSL, which switches from an aerobic to anaerobic metabolism below its threshold (0.085 $\text{mg L}^{-1} = 0.1 \text{ mL L}^{-1}$), is one of the most tolerant species worldwide [37]. In general, still the most sensitive organism groups are crustaceans, whereas molluscs and cnidarians with highest resilience against low oxygen concentrations are the groups most tolerant to hypoxia [36]. These include, for example, thyasirid bivalves, as recorded in the oxygen-minimum zones and methane springs around the world [38–41], and our own results from Namibia. Two representatives of this family were also found in high abundance in the present study.

The formation of clusters, especially of the two hypoxic stations 6 and 7, indicates that the community is different from the normoxic ones (with only 30% similarity). Only present at the hypoxic stations, and therefore very characteristic, are the amphipods *Cheirocratus* sp. and *Ischyrocerus* sp., the cumacean *Diastylis goodsiri*, the spionid *Spiophanes kroyeri* Grube, 1860, as well as the ascidian *Molgula* sp. They are all not very typical of oxygen-minimum zones. However, we observed that species (or at least the genus) known to be tolerant of low oxygen, such as *Thyasira* sp., *Ampharete* sp., *Ceratocephale loveni*, *Galathowenia oculata*, and *Trochochaeta multisetosa*, were very abundant (Table 2).

A very similar observation was made by Belley et al. [21], who investigated the hypoxic effects on bioturbation activities. They found that 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. They therefore suspect 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 along the oxygen gradient. However, they observed that there are major differences in the feeding mode and low-oxygen tolerance between the hypoxic and normoxic communities. Interestingly, they found by image analysis an increased bioturbation (traces on the sediment surface) in the hypoxic region. They explained this by the high densities of the brittle star *Ophiura* sp. and its active feeding mode. In our study, however, *Ophiura* was only found at the normoxic stations, but the related species *Amphiura* sp. reached high densities in the LSLE. Both genera are known for their pronounced low-oxygen tolerance [42].

An explanation for the counterintuitive fact of a more diverse benthic community with a higher biomass at threshold oxygen values could be based on the stability of the environmental conditions. Whereas in other coastal areas or enclosed brackish seas, episodic events in both bottom water renewal and nutrient supply lead to large fluctuations

in population dynamics with alternating collapse and rebuilding of benthic populations, e.g., [43], the LSLE benthos simply lacks this stress. A constant lateral supply of oxygen allows species to extend their population growth right towards the border of their specific oxygen-minimum level and allows communities to adapt by gradual changes in their species inventory. Thus, the constant supply of oxygen, even at low concentrations, seems to be more important than the absolute oxygen concentration. Nutrient input from the surface layer is likely dampened by the fact that even our shallowest station is already 350 m deep and has already been preceded by a major processing of organic material from the surface. But sedimented organic particles originating from rivers can also be introduced by the lateral, near-bottom, seaward flow, thereby achieving a similar uniform nutrient supply mode as the provision with oxygen in the reverse direction. Although the supply of food was not measured in our sampling scheme, it could very well be superimposed on the impact of oxygen in the regulation of diversity and biomass in the gradient between the river mouth and open ocean in the LSLE. The fact that the innermost station of the deep-water transect (stn. 7) showed the lowest amount of accumulated carbon in the sediment at the highest macrofauna diversity and biomass values, but the lowest oxygen concentrations, indicates a still very effective turnover of food, and thereby a well-functioning benthic system. In our opinion, the general lack of stress in the benthos of the LSLE promotes diversity and biomass in suboxic stations, which also appears to be an important regulator of population dynamics in other systems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15070854/s1>, The online version contains supplementary material with all abundance data and SIMPER statistics.

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