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Effects of a salmon fish farm on benthic habitats in a high-energy hydrodynamic system: the case of the Rade de Cherbourg (English Channel)

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ABSTRACT

The Rade de Cherbourg (RdC), in the North Cotentin (Normandy, English Channel) is the only French coastal zone where an offshore salmon farm has been in operation over the past three decades. Our study leads to the identification of the Ecological Quality status of benthic habitats based on a one-year survey (2013-2014) underneath and near the cages as well as in non-impacted areas lying outside the influence of salmon farming. The semi-diurnal high tide regime of the Rade de Cherbourg (5 to 8 m tidal range from neap to spring tide) should prevent any significant accumulation of Organic Matter (OM) under the cages. Nevertheless, higher Total Organic Carbon (TOC) and the presence of opportunistic species at sampling stations under and near the cages indicate an impact of salmon farming on the benthic habitats. Three benthic assemblages are identified, corresponding to three sediment types with different levels of OM enrichment. The presence of several indicator species, such as the polychaete worm *Capitella minima* belonging to the Capitellidae, reflects the local impact of fish farming without long-term accumulation of OM in the shallow waters of the RdC.

Moreover, one of the main characteristics of the macrofauna of the RdC and neighbouring zones is the current very high abundance and dominance of the tanaid *Apseudopsis latreillii* in diverse sediment types. Benthic indices (AMBI, M-AMBI, and BO2A) were also able to distinguish three main zones in relation to the distance to salmon cages.

Keywords: Macrobenthic communities; Sediment characteristics; Salmon fish farm; Benthic indices; TOC enrichment

1. Introduction

The impact of aquaculture on benthic habitats had been highlighted since the end of the 1980s (Brown et al., 1987). More recently, Yokoyoma (2002), Buschmann et al. (2006, 2009); Burridge et al. (2010), Wilding et al. (2012) and Lu et al. (2017) have described the impact of aquaculture on sediment characteristics and macrofauna. The main impact leads to the enrichment of Organic Matter (OM) in sediments that are initially oxygenated and the accumulation of toxic compounds derived from aquaculture waste products (mainly H_2S and NH_3). Under salmon cages sediment contains generally high levels of organic matter due to waste products (feces, uneaten food, etc.), the driving force for most primary diagenetic redox reactions (Kasten and Jørgensen, 2000). The high organic matter flux creates anoxic conditions (oxygen consumption by aerobic respiration). The sulphate reduction process becomes predominant because of the availability of high concentrations of sulphate in seawater, which leads to the production of sulphides in sediment (Jørgensen, 1977; Bo Barker, 1977). This phenomenon may induce changes in the benthic communities: i.e. an increase in the abundance and biomass of species on a seabed enriched in OM (Brown et al., 1987; Carroll et al., 2003; Hyland et al., 2005; Kalantzi and Karakassis, 2006).

Pearson and Black (2001) produced a review of the environmental impacts of marine fish cage culture showing the effects of fish farming on coastal ecosystems, concerning the influence of increased organic matter inputs on benthic habitats. Most of these previous studies indicated that the impact of fish farming is local and depends greatly on factors such as fish density, start date of activities, water depth, initial sea bottom site characteristics and hydrodynamic regime (Frid and Mercer, 1989; Morrisey et al., 2000; Merceron et al., 2002; Yokoyama, 2002; Tomassetti and Porrello, 2005; Kalantzi and Karakassis, 2006; Kuty et al., 2007; Borja et al., 2009; Giles et al., 2009; Chang and Page, 2011; Wang et al., 2017).

Most of these studies reveal a change in sediment biogeochemistry and benthic ecology around the cages extending to some metres distance away, in accord with the model of Pearson and Rosenberg (1978) which describes the response of macrofauna to OM enrichment in the sediment. The extreme accumulation of OM tends to create an anoxic/azoic zone where both the oxygen demand and depletion are maximal (Brooks and Mahnken, 2003; Brooks et al., 2004; Hargrave, 2010; Chang et al., 2013; Backman et al., 2009; Bannister et al., 2014; Brooks et al., 2003; Wilding et al., 2012). Moreover, Fernandez-Gonzalez et al. (2016) has highlighted the role of biofouling in fish farms appears to be an important vector for colonization of the surrounding soft-bottom communities impacted by aquaculture.

The Rade de Cherbourg (RdC) is a protected semi-open area situated on the north coast of the Cotentin Peninsula (central part of the English Channel), under a semi-diurnal high tide regime (5 m to 8 m tidal range from neap to spring tide). It is sheltered from the swell by breakwaters that enclose the outer harbour. In spite of 3.7 km of breakwaters interrupted by two mains channels in the north of the RdC and a smaller channel in the east tidal currents (up to 1 m/s) allow the mixing of water bodies and a significant concentration of suspended particulate matter in the seawater (Merceron and Gaffet, 1994; Poizot et al., 2016). Due to these conditions, the RdC has been recognized as a suitable place for the development of aquaculture due to both the presence of highly mixed waters and presence of breakwaters suppress swell impacts. Consequently, a trout farm has been established in the RdC since the beginning of the 1990s, becoming a salmon farm (*Salmo trutta fario* then *Salmo salar*) during the early years 2000. Today, this site hosts the only marine salmon farm in France, covering an area of ~17 ha currently producing ~600 tons of salmon per year (data available in 1993, 1995, 2001, 2002, 2006, 2011, 2013, 2016 and 2017, with respective production volumes of 144, 290, 400, 800, 2300, 1200, 350, 250, 600 t) (Saumon de France, 2015).

The first study on the quality of the water column, sediments and benthic macrofauna around the fish farm was carried in the early 1990s (Merceron and Gaffet, 1994; Bentley et al., 1997; Kempf et al., 2002; Merceron et al., 2002). Nevertheless, in these studies, the surveyed area was limited to the immediate vicinity of the aquaculture cages, and only the dominant species of the macrobenthic fauna were identified.

The development of aquaculture in a high-energy hydrodynamic regime over the past 30 years has offered the opportunity to study the impact of human pressures on the benthic habitats of the RdC. Moreover, Baux et al. (2017) have highlighted the great diversity of benthic communities and habitats in the RdC and have identified three habitat types corresponding to EUNIS codes giving in the classification of European benthic habitats

(EUNIS, 2012) as well as two types so far not attributed to any known benthic habitat, in addition to one habitat characterized by the presence of *Zostera marina* beds. In this context of rich diversity, it is also interesting to study in more detail the benthic communities as well as the impact of the salmon farm.

The objective of this study is to assess the ecological quality status of benthic habitats and to determine the impact of salmon farm on these benthic habitats, by considering the sediment characteristics and macrofauna patterns in relation to distance from the salmon cages. To study the impact of salmon farming on benthic communities, univariate, multivariate analyses and benthic indices are used to assess the quality of benthic habitats.

2. Materials and methods

2.1. Study site

The RdC which construction ends in 1895 is the Europe's largest, extending over a total area ~1,500 ha (Baux et al., 2017). The 'Grande Rade' (1,300 ha) is isolated from the open sea by three breakwaters, with three channels allowing exchanges with open sea water (West Channel, East Channel and Collignon Channel; Fig. 1). The oscillating water volume is about 80,000 m^3 at spring tide, with a tidal range of 5.3 m (Merceron et al., 2002). Several small rivers and urbanized outfalls can give to minor fresh water inputs, into the RdC. The maximum depth is ~20 m with a mean depth ~13 m (Gregoire et al., 2019). The mean winter water temperature is 8-9 °C and reaches 17-18 °C at the end of the summer. The predominant current is easterly during the flood tide and westerly during the ebb. The flood stream enters by the 'West Channel' and flows out mainly by the 'East Channel' and to a lesser extent by the 'Collignon Channel'. This is opposite to the situation at ebb tide. During flood and ebb tide, depending on the interactions between bathymetry, coastline morphology and tidal currents, gyres may form locally with a counterclockwise rotation (Merceron and Gaffet, 1994; Poizot et al., 2016).

The RdC sea bed is covered by four main sedimentary facies (Baux et al., 2017). The western sector is generally made up of organic-rich mud with decaying marine algae and coarse sand. The centre of the RdC consists of silty mud, while the east is covered by fine sand. Gravel and coarse sand are found in the channels which connect the RdC with the open sea.

The salmon farm consists of cylindrical and cubic nets aligned along an East-West axis, the concession area being located only 50 m south of the main breakwater, extending over a distance of 1.5 km with a width of 100 m at a depth of ~12 m (Saumon de France, 2015) (Fig. 1). The average height of the nets ranges from 7 to 8 m below the sea surface, and the distance above the seabed is ~ 3 to 7 m due to deformation of the fishnet cage under the influence of the variable tidal currents and range. Inside the RdC, tidal currents are mainly oriented East-West and reversely during the tide with current velocities up to 1 m/s. At the fish farm site, a gyre (Merceron and Gaffet, 1994) is responsible of an asymmetric regime of the currents velocities from flood to ebb. At neap tide, the flood currents are oriented west-east 30% of the time and ebb currents are oriented east-west 70% of the time. During spring tide, this asymmetric is reduced to respectively 40% (flood currents) and 60% (ebb currents). This asymmetry is related to the establishment of a gyre within the concession area (Merceron and Gaffet, 1994).

2.2. Sampling and laboratory treatment

Following an East-West axis parallel to the main breakwater where the cages are located and according to the main tidal currents in this area in the RdC, six benthic stations (~ 10-11 m depth) were sampled during five campaigns over an annual cycle in 2013-2014 (C1: 31 October 2013, C2: 19 February 2014, C3: 8 April 2014, C4: 13 June 2014 and C5: 18 September 2014) to identify the impact of this salmon farm. One station (CC8) was located under a cage, two stations (OR and ER) outside the fish farm (> 600 m from the central cages), and three others (OC8, EC8 and EC16) near the central cages (OC8: 50 m to the west; EC8: 50 m to the east; EC16: 500 m to the east; Fig. 1). During the five sampling campaigns, five replicates were collected using a 0.1 m^2 Van Veen grab covering a total sampling surface area of 0.5 m^2 at each station for the macrofauna analysis plus one supplementary sample for grain-size analysis. At station CC8, the Van Veen grab was manipulated by hand from the cage structure between the salmon nets. The sampled faunal material was sieved onboard on a 1-mm circular mesh. Fauna was preserved in 10% buffered formaldehyde prior to sorting, identified to species as far as possible. Some species are grouped to the higher classification rank when the morphological determination is doubtfully.

The taxonomic richness (TR) and abundance (A) are expressed in number of taxa and number of individuals per 0.5 m^2, respectively. Species (or taxa) names were checked against the World Register of Marine Species (http://www.marinespecies.org) on 1 September 2018.

The fine fraction (<50 µm) was measured by wet sieving and rinsed with fresh water to remove the salt. Other sediment fractions were dried and sieved on a sieve shaker. Eight-sieve column was used (8, 4, 2, 1, 0.5, 0.250, 0.125 and 0.050 mm). The sediment was classified according to Wentworth's grain-size scale (Wentworth, 1922): <50 µm: silt clay; 50–125 µm: very fine sand; 125–250 µm: fine sand; 250–500 µm: medium sand; 500–1000 µm: coarse sand; 1000–2000 µm: very coarse sand; 2000–4000 µm: gravel; and >8000 µm: pebbles). The results are expressed in percentage relative to the total dry weight of the sample. Finally, we consider four grain-size classes for the definition of sediment types: fine fraction (< 50 µm, denoted FF), fine sand (50-250 µm), medium and coarse sand (500–2000 µm) and gravels (> 2000 µm).

Sediments for Total Organic Carbon (TOC) analysis were freeze-dried and homogenized. The coarse fraction was removed with a 2-mm sieve to keep only the fine fraction. The weight of the sample was reduced to obtain 50 mg aliquots using a manual quartering method (random separation of sample aliquots). Sediment samples were acidified by H3PO4 (1 M), to remove carbonates, dried on a hot plate at 40° C and measured for TOC content by combustion in a LECO CS 744 Carbon Sulfur analyzer. Two or three replicates were analyzed per sample. The results of organic carbon measurements are expressed in percent of dry sediment. The precision determined from replicate subsampling was ± 0.05% organic carbon.

2.3 Current measurements

Two Acoustic Doppler Current Profilers (ADCPs: Teledyne RDI Sentinel S50 and V50) were installed at a distance of 20 m (East) and 50 m (West) from the eastern cage (Fig. 1). Measurements were conducted between 6 and 24 October 2016, allowing the acquisition of current velocity data during a tidal cycle (spring/neap tides). The two ADCPs measured currents at the same height in the water column, running the same firmware, and were configured for the same depth-cell size. Both ADCP's use 22 cells, with a depth-cell size of 0.5 m. Even if dates of velocities and directions measurements took place at a different moment than the bottom sampling, they were considered as characteristics of flow conditions at the studied site. The fish farm structures and shapes did not change between the two sampling surveys.

2.3. Data analysis

2.3.1. Univariate analyses

Data were used to calculate the abundance A (0.5 ind.m^{-2}) and the most commonly used biodiversity indices for each station, *i.e.* Taxonomic Richness (TR), Shannon-Weaver diversity index (H') in log$_2$ (Shannon and Weaver, 1963) and Pielou's evenness (J) (Pielou, 1966) for the six stations and five sampling dates. Data analysis was performed using the PRIMER® version 6 software package (Plymouth Routines in Multivariate Ecological Research) (Clarke & Gorley, 2006).

The Ecological Status indicating the quality of the station was estimated from H' values according to the thresholds defined previously by Vincent et al. (2002) i.e.: bad 0-1; poor 1-2; moderate 2-3: good 3-4 and high > 4. Dauvin et al. (2017) proposed thresholds for the taxonomic richness and J', respectively i.e: bad <10, <0.20; poor 10-20, 0.20-0.40: moderate 20-30, 0.40-0.60; good 30-40, 0.60-0.80 and high >40, > 0.80.

The biotic indices AMBI, M-AMBI and BO2A were also calculated to assess the ecological status of the macrofauna (Borja et al., 2000; Dauvin et al., 2012, 2016). The five ecological statuses of the European Water Framework Directive were used to assess the benthic macrofauna according to the thresholds between these statuses proposed by Borja et al., (2000) and Dauvin et al. (2012, 2016).

AMBI (AZTI Marine Biotic index) (Borja et al., 2000) is based on an *a priori* classification of macrofauna species in five ecological groups (EG) according to their sensitivity to OM. EG-I corresponds to taxa very sensitive to organic enrichment and disturbance which are usually only present under unpolluted conditions, EG-II to taxa indifferent to enrichment or disturbance, EG-III to taxa tolerant of excess OM enrichment, which may occur under normal conditions, but which are stimulated by organic enrichment, EG-IV, to second-order opportunistic species and EG-V, to first-order opportunistic species, able to resist strong disturbance. The relative abundances of each EG serve to calculate benthic indices following the formula given in Borja et al. (2000).

$$AMBI = 0\ EG_{I} + 1.5\ EG_{II} + 3\ EG_{III} + 4.5\ EG_{IV} + 6\ EG_{V}$$

The index is computed using the AZTI program (version 5.0) freely available online at http://www.aziti.es. AMBI values lying between 0 and 6 can be converted into EcoQ using the fixed scale provided by Borja et al. (2000).

M-AMBI is a multimetric index for assessing the ecological quality status of marine and transitional waters (Bald et al., 2005; Muxika et al., 2007). It is based on benthic macro-invertebrates and combines AMBI, which is a biotic index based on species sensitivity/tolerance, with diversity and taxonomic richness. The M-AMBI algorithm incorporates different metrics by means of factor analysis (FA). Reference values are considered to represent an unperturbed environment, in which the Taxonomic Richness (TR) and H' values are highest for the same type of benthic communities (respectively 50 for TR and 3.5 for H'). We also assume that, in an unperturbed environment, first-order opportunistic species (EG V of the AZTI list) would be absent or poorly represented with a AMBI value of 2.5.

The BO2A (Benthic Opportunistic Annelids Amphipods Ratio) (Dauvin and Ruellet, 2009; Dauvin, 2018) is calculated following the formula:

$$BO2A= \log_{10} [f_{oa}/(f_{sa} +1) +1]$$

where f_{oa} is the frequency of opportunistic annelids (Clitellata and Polychaeta) (i.e., number of opportunistic polychaetes corresponding to Ecological Groups IV and V of Grall and Glémarec (1997) and used for calculating AMBI (Borja et al., 2000), plus the Oligochaeta and Hirudinea, divided by the total number of individuals in a sample), and f_{sa} is the sensitive amphipod frequency (i.e., number of amphipods, excluding the opportunistic *Jassa* amphipods, divided by the total number of individuals in a sample), and $f_{oa} + f_{sa} \leq 1$.

A two-way ANOVA is used to test spatio-temporal changes (stations and campaigns factors) for TS, A, H', J, AMBI, M-AMBI and BO2A. A Shapiro-Wilk normality test and a Bartlett test for homogeneity of variances are performed prior to each ANOVA. The Tukey Honestly Significant Difference test is applied when ANOVA shows significant differences.

2.3.2. Multivariate analysis

The spatial structure of the sediment characteristics and the benthic community are analysed using a multivariate analysis following Clarke and Gorley (2006) with the PRIMER software package (Plymouth Routines In Multivariate Ecological Research). Data analysis is performed using non-metric multidimensional scaling ordination (MDS), and a Hierarchical Ascendant Classification (HAC) is created by group average linking using the Bray-Curtis similarity measure (Beals, 1984). In comparison with other similarity measures, the Bray-

Curtis is known to be one of the more efficient indexes to highlight the similarity between samples (Bloom, 1981).

Sorensen's coefficient for Presence/Absence of taxa, and Log_{10}+1-transformed abundances (0.5 ind.m²) are used to down-weight the effect of very abundant species**.** To identify the species within different groups which principally account for the observed assemblage differences, SIMPER (SIMilarity PERcentage) routines are performed using a decomposition of Bray-Curtis similarity on log-transformed abundance data (Clarke and Warwick, 1994).

3. Results

3.1. Hydrological conditions

Table 1 summarizes the main characteristics of the water column during the year 2013-2014. While the temperatures show considerable seasonal variations, with a maximum at the end of summer in September-October (17.9 °C) and a minimum in winter in February (8.2 °C), the salinity remains stable throughout the year with values included between 34.4 and 34.7. The diurnal oxygen saturation reaches a maximum in September 2014 (123%), probably in relation with a high primary production at that time; the turbidity is low, with very low values (1.2 NTU) at both of the early sampling dates and low values during the rest of the year (< 14 NTU).

3.2. Currents near the cages

Ebb currents flow westward at almost 270°, while flood currents flow eastward at almost 90°. Ebb currents start to flow a few hours before high tide, and flood currents start after low tide during spring tides and before low tide during neap tides. During neap tides, the ebb current runs for 60% of the time, and the flood current for 40% (Table 2). During spring tides, flood currents run for 30% of the time, and ebb currents make up the remaining 70%. At West ADCP location, mean velocities and directions highlight a more erratic behaviour during ebb currents (270°) than at East ADCP location. This is the reverse for flow currents (90°) in a lesser extent. At both ADCPs, the maximum velocity increases twofold between neap tide and spring tide. The maximum velocity is three times higher during spring tide compared with neap tide.

3.3. Sediment characteristics

Using HAC and MDS to analyse the grain-size characteristics of the sediments from the five stations at the five sampling dates, we can distinguish three main groups (Fig. 2).

The first group is made up of five observations, four from CC8 and one from OC8. For this group, the mean percentage of Fine fraction (FF)= 11.4, fine sand= 51.3, coarse sand and gravel= 37.3. The sediment type corresponds to sand and gravel with a low percentage of FF, mainly restricted to station CC8 located under the cage.

The second group comprises 10 observations, 4 from EC8, 4 from EC16 and those from OR in October 2013 and OC8 in June 2014. For this group, the mean % FF= 16.2, fine sand= 76.2, coarse sand and gravel= 7.6, corresponding to fine sand sediment mainly represented at EC8 and EC16 (two stations in the eastern part of the salmon cages).

The third group comprises 14 observations, including the five sampling dates at ER, four at OR (except at OR in October), the observation from EC16 in June 2014, three observations from OC8 (February, April and September 2014), one from CC8 in September, and one from EC8 in June 2014. For this group, the mean % FF= 14.9, fine sand= 60.1, coarse sand and gravel= 25.0, corresponding to heterogeneous muddy sediment, according to the Wentworth classification (Wentworth, 1922). This group comprises both reference stations OR and ER plus station OC8 in the western sector of the salmon cages.

The TOC levels remain relatively stable throughout the year (Table 3) with a global mean of 0.55 +/- 0.04%. While seasonal changes are very slight, there are nevertheless some differences in TOC between the stations, with a minimum at station EC8 in the eastern part of the salmon cages (0.35+/-0.06%) ranging up to a maximum at station CC8 under the cages (0.82 +/- 0.05%).

Figure 3 shows the mean annual values of TOC for the five stations as a function of FP (fine particles < 50 µm). The mean values of TOC at four stations (OR, EC8, EC16 and ER) follow a linear trend from 0.3% TOC and 5% FP to 0.6% TOC and 16% FP. The reference stations OR and ER also yield the highest TOC, with the latter being the richest in FP content. The stations (EC8 and EC16) located in the eastern sector of the salmon cages are characterized by lower fine fraction percentage (6-8%) and TOC (0.3-0.4%). For these four stations, there is no organic matter enrichment. Station CC8 under the cages and OC8 in the western sector of the cages show different patterns, with a low percentage of FP and, on the contrary, relative high percentages of TOC (>0.6%) in comparison with other stations.

The similarity between the stations is high (80 %), but three groups can be identified with granulometric data combined with those of FP and TOC (Figs. 2 and 3; Table 3). Firstly, stations CC8 and OC8 under and near the western sector of the cages are characterized by mixed sediment with high TOC%. Secondly, stations EC8 and EC16 in the eastern sector of the cages are located on fine sand with low TOC%. Lastly, the reference stations OR and ER are distant from the cages, showing high percentages of fine particles correlated with high percentages of TOC on heterogeneous mixed sediment.

3.4. General characteristics of the fauna

A total of 182 taxa are identified during the study, the polychaetes dominate in terms of diversity with 71 taxa representing 38% of the TR (Taxonomic Richness), the molluscs with 36 taxa (20% of TR) and the amphipods with 32 taxa (17% of TR). These three dominant zoological groups comprise a total of 139 taxa (75% of the fauna recorded). A total of 119,296 individuals are sampled, with 98 taxa being represented only by a few number of individuals (<10), making up only 0.27% of the collected fauna. The tanaids account for 61% of the recorded individuals, followed by the polychaetes (25%), amphipods (6%) and molluscs (1.5%). The TR varies from 22 to 78 and the abundances from 455 to 11,355 individuals. 0.5m^{-2} without any clear seasonal pattern or differences between the six stations (Table 3).

Moreover, the ten most abundant species account for 106,921 individuals making up 89.6% of the macrofauna. The tanaid *Apseudopsis latreillii* represents 60.3% of the total number of collected individuals, then the polychaetes *Notomastus latericeus* (9.4%) and *Dipolydora giardi* (9.0%), the Maldanidae, mainly represented by *Euclymene oerstedii* (4.3%), the amphipod *Ampelisca tenuicornis* 1.7%, the polychaetes *Phyllodoce mucosa* (1.3%) and *Capitella minima* (1.3%), the amphipod *Phtisica marina* (1%), the polychaete *Chaetozone gibber* (0.7%) and the bivalve *Thyasira flexuosa* (0.7%).

To summarize, although the fauna is diversified, it is dominated numerically by a small number of species, especially by the tanaid *Apseudopsis latreillii* (species identified in December 2017 by specialist P. Pesquete, Aveiro University, personal communication).

3.4. Spatio-temporal patterns of the macrofauna

Using the abundance data and applying a Bray-Curtis similarity level of 50%, the HAC and MDS analyses allow us to identify three groups (Fig. 4). Group 1 includes the 10 observations from stations OC8 and CC8. Group 2 corresponds to the observations from reference sites OR and ER, plus two sampling dates for EC16 (June and September) and June for EC8. Group 3 includes seven observations from EC8 (four dates) and EC16 (three dates). Table 4 show significant differences in abundances, H' and J' between stations, while only differences of TR are observed between ER and EC8.

Finally, analyses of sediment characteristics and macrofauna abundance lead to the identification of a spatial pattern with three groups of stations: two stations (CC8 and OC8) located under the cages and in the western sector of the cages, two stations (EC8 and EC16) in the eastern sector of the cages, and, finally, the reference stations OR and ER. A weak pattern is observed at the scale of the observations during the 2013-2014 sampling year (Tables 3 and 4). Table 4 shows significant differences of Taxonomic Richness between C1 and C5, while significant differences in abundances are observed between C4 and C5, and for both diversity indices H' and J' between C2 and C4.

The tanaid *Apseudopsis latreillii* dominates the macrofauna in the three groups of stations, with an abundance $\geq$ 2,000 ind.0.5m²; similarly, the polychaete *Notomastus latericeus* shows noteworthy abundance in all three groups, but decreases in abundance from stations under and in the western sector of the cages towards the reference stations (Table 5). Opportunistic species (GIV and GV) are only abundant in the first group of stations (CC8 and OC8); conversely, sensitive species are present and abundant at both references stations (OR and ER) (Table 5).

3.5. Ecological quality status

The values of the three benthic indices (AMBI, M-AMBI and BO2A) and their corresponding Ecological Quality Status (EcoQS) allow us to identify three groups of stations without seasonal changes: references stations ER and OR plus EC16 and OC8 show a good to high EcoQS, station EC8 shows moderate to high EcoQS depending on the sampling campaign or the biotic index, and station CC8 shows a moderate EcoQS. The diagnosis based on H' and J' yields a poor to moderate EcoQS, but both of these indices are clearly influenced by high *Apseudopsis latreillii* abundances which lower their values.

4. Discussion

The Rade de Cherbourg has hosted a salmon farm since the beginning of the 1990s (Kempf et al., 2002; Merceron et al., 2002). Our recent study (2013-2014) offered the opportunity to assess the ecological quality status of benthic habitats in the RdC three decades after the initial establishment of aquaculture in this zone (firstly a trout farm and then a salmon farm). Bachelet (2014) highlighted the effects of anaerobic degradation due to sulphate-reducing processes at the water-sediment interface in areas east of the salmon cages, as well as high ammonium concentrations resulting from faeces and non-consumption of feed for farmed fishes at the station located under the cages (Bachelet, 2014). Both the high-energy hydrodynamic regime in the RdC and the acceleration of currents under the cages (Poizot et al., 2016), has led to the dispersal of excess organic waste. The increase of current velocity under the fishnets is also responsible of erosion, which has resulted in modifications of the bottom morphology. As measured during this study, the maximum current velocity reaches 0.7 $m.s^{-1}$, which is two times higher during Spring tide compared with Neap tide. Nevertheless, this maximum velocity is very slow in comparison with values recorded off the North Cotentin coast especially in the Raz Blanchard, a zone where the maximum velocity can reach 5.0 $m.s^{-1}$ during Spring tide (Salomon and Breton, 1991, 1993). Velocity measurements near the cages show that the fish farm is always under the influence of tidal currents, including during neap tides. The water within the farm is regularly replenished and homogenized (Poizot et al., 2016). The strong asymmetry of the tidal currents (as regards both duration and intensity of flow) leads us to consider that ebb current is dominant on the farm (Poizot et al., 2016). These conditions correspond to the coastal farming classification of Holmer (2010), preventing the accumulation of OM under the cages due to dispersal of the residual organic matter derived from the waste-feed and faeces, in contrast to enclosed salmon farms such as in Norwegian fjords (Kutti et al., 2007; Holmer, 2010). Moreover, the moderate fish production over the past 25 years (mean ~ 700 tonnes of salmon per year) has caused a negligible supplementary input of organic matter in the RdC (Murat et al., 2012).

The six stations chosen in this study are located in two main EUNIS benthic habitats (Baux et al., 2017): A5.334 *Melinna palmata* in mixed muddy fine sand (OC8, CC8, and EC8) and a new habitat with *Spio decorata* and *Apseudopsis latreilli* in very fine sand and fine sand (OR, ER and EC16). Analyses of the six stations sampled during the five campaigns show that the macrofauna can be separated at a similarity of 50 % in three benthic assemblages (Fig. 4; Table 5).

The first group corresponds to reference stations OR and ER at some distance from the cages, with high percentages of fine particles (≅ 14%) higher than at other studied stations (≅ 7%) and relatively high mean TOC (≅ 0.56%) on heterogeneous mixed sediment. The relationship between TOC and fine particles suggests that both stations are in dynamic equilibrium outside the influence of the cages (Fig. 3).

The second group of stations EC8 and EC16 is located in the eastern sector of the cages on fine sand (≅ 7.2% of FP) with low TOC content (0.37%). These lower values (FP and TOC) are consistent with higher energy hydrodynamic conditions (stronger currents and enhanced turbulence) linked to an acceleration of currents under the cages (Poizot et al., 2016). These hydrodynamic conditions result in a winnowing of fine particles and organic matter.

The third group corresponds to stations CC8 and OC8 (under and near the cages in their western sector), which are characterized by mixed sediment with the highest TOC% (≅ 0.73%) and the lowest FP% (≅ 6.5%). Low FP percentage of the sediment is linked to the impact of cages on water flow (higher turbulence and current intensity) (Poizot et al., 2016). In contrast to the stations in the second group, stations CC8 and OC8 do not appear to have a faunal community consistent with fish farm (high OM content) due to the presence of faeces and feed-waste. Despite the high-energy hydrodynamic conditions, the input of organic matter is sufficient to enrich the underlying sediment.

During the present study, very high densities of the tanaid *Apseudopsis latreillii* are observed under salmon cages, as well as in other muddy sand habitats of the RdC. This species is known to have an affinity with clean fine sands (Bakalem et al., 2009). The three benthic assemblages for each of the three communities identified are dominated by *A. latreillii* with very high abundances both in terms of time (year scale) and space. High abundances of this species are observed in most of the benthic habitats of the RdC except the mud habitat (Baux et al., 2017). This species is widely distributed all along the North Cotentin coastline, and a very high abundance is found outside the fish farm and the RdC in its eastern part (Martinez, 2017) as well as in some sand and gravel habitats in the western sector of the RdC (personal observations). Such high abundances have been observed in other marine areas (Table 6), but the present study represents the first report of such high abundances of this species associated with a fish farm. The abundances observed in the RdC and in its eastern part (20,000-23,000 ind.m^{-2}) are among the highest recorded values. Only the abundance observed in the Persian Gulf (Dubai creek) reaches higher values, with 43,000 ind.m^{-2}, but this site is subject to the impact of organic pollution (Saunders et al., 2007). The relationship between fish farm and its increasing of Organic Matter and abundance of *A. latreillii* need to be clarified in the future.

Except for the Aber Wrach in the western part of the English Channel along the Brittany coast where the abundance exceeds 3,000 ind.m^{-2} (Dauvin and Gentil, 1990; Hily and Bouteille, 1999), *A. latreillii* is a rare species in the benthic communities of the English Channel. It is mostly associated with the *Melinna palmata* muddy sand community as in the Rivière de Morlaix station in the Bay of Morlaix, in an area naturally enriched in OM (Dauvin, 2000), and is very rarely recorded in the eastern part of the English Channel. Moreover, *A. latreillii* never occurs as dense populations or as a dominant species such as observed in the North Cotentin. Abundant populations occur elsewhere principally on fine sand and muddy fine, in *Zostera marina* meadows (Hily and Bouteille, 1999; Esquete et al., 2011; Gamito et al., 2011), and rarely on coarse sand (Lourido et al., 2008).

The response of *A. latreillii* to pollution continues to be debated, and the sensitivity of this species to pollution is unclear since it is reported as being both tolerant and sensitive (de-la-Ossa-Carretero et al., 2010). It is classified in the list of tolerant species (GIII in AMBI, Borja et al., 2000; Table 5). Along the Castellon coast (W. Mediterranean) de-la-Ossa-Carretero et al. (2010) has shown that the species responds negatively to sewage pollution, displaying reduced abundances near outfalls with a higher input of suspended solids, nutrients and a possible trend to hypoxia at stations near the discharge channels. As *A. latreillii* is a GIII species largely dominant in the three benthic assemblages recorded under and near the cages, the AMBI and M-AMBI benthic indices lead mainly to the attribution of a good EcoQS at the stations except for station CC8 under the cages where a moderate EcoQS is obtained (Table 3). The use of BO2A yields the same EcoQS for the six stations (Table 3). Nevertheless, both diversity indices (H' and J; Table 3) assign degraded poor and moderate EcoQS for these stations in relation to high abundances of the dominant species *A. latreillii* and the poorly structured distribution of abundances between species.

Apart from the top dominant species, the other dominant taxa show different patterns of abundances in the three assemblages (Table 5). Opportunistic species such as the polychaetes *Dipolydora giardi*, *Capitella minima*, *Chaetozone gibber*, *Caulleriella alata* and *Cirriformia tentaculata* and the amphipod *Jassa herdmani* (EG IV and V) are abundant at stations under and near the cages (OC8 and CC8) or in the eastern sector of the cages, and rare at the reference stations. EG III species such as the polychaetes *Phyllodoce mucosa* and *Neanthes acuminata,* the amphipod *Gammarella fucicola* and the tanaid *Zeuxo holdichi* show similar patterns with decreasing abundance from the stations under the cages to the reference stations. Conversely, the polychaetes Maldanidae (mainly *Euclymene oerstedii*), *Melinna palmata*, *Hilbigneris gracilis* and *Acromegalomma vesiculosum*, the bivalve *Thyasira flexuosa* and the tanaid *Apseudes talpa* are abundant only at the reference stations (Table 5). The amphipods sensitive to organic pollution (*Ampelisca tenuicornis* and *Phtisica marina*) and the polychaete *Lanice conchilega* show similar abundances at both eastern stations and at the reference stations (Table 5).

In summary, these is a decrease in abundance of opportunistic species away from stations OC8 and CC8 near the cages and, conversely, an increase in abundance of sensitive species from stations under and near the cages towards the reference stations (OR and OR). The abundances of both opportunistic and sensitive species show intermediate abundances at stations in the influence zone (EC16 and EC8).

All the results (sediment type, fine particles, TOC percentages, macrofauna abundances and biotic indices), show that the fish farm impact remained relatively low in this tidal regime: but three benthic habitats can be distinguished:

i) an impacted zone (under the cages and in the western sector of the cages; stations CC8 and OC8), exhibits moderate accumulation of OM and an enhanced hydrodynamic regime;

ii) an influenced zone (stations EC8 and EC16 in the eastern sector of the cages) with a single impact (enhanced hydrodynamics);

iii) A non-impacted zone corresponding to both reference stations (ER and OR) (Tables 3, 5 and Figs. 2, 4).

Our results highlight a local impact of the salmon fish farm, with a relative lower number of species under cages and the reduction in the rate of degradation of benthic OM inputs since the establishment of fish farming in the 1990s. In addition, these observations appear to support the Intermediate Disturbance Hypothesis, which proposes that the diversity and abundance of organisms increases when the disturbance is intermediate in frequency and intensity (Huston, 1979; Wilson, 1994; Dial and Roughgarden, 1998; De Backer et al., 2014; Pezy et al., 2018).

Although tidal currents prevent the accumulation of OM in the RdC, Bachelet (2014) observed the presence of local anaerobic degradation by sulphate-reducing processes at the water-sediment interface to the east of the salmon cages, as well as high ammonium flux under the cages, resulting from faeces and waste-feed derived from the salmon farm at the station under the cages. Again, the impact in the RdC appears very limited.

Moreover, many studies have shown that certain parameters play a major role in determining the impact of farms, such as high fish density, age of the concession, water depth, previous sediment types located at the site and hydrodynamic regime (Frid and Mercer, 1989; Morrisey et al., 2000; Merceron et al., 2002; Borja et al., 2009; Giles et al., 2009; Chang and Page, 2011). The current velocity appears to be one of the most important parameters because it favours the dispersal of waste and ensures the absence of anoxic conditions under the fish cages (Black et al., 1996; Keeley et al., 2013). Facing with the large increase of OM in sediments under the cages and in surrounding habitats in coastal ecosystem with weak currents, fish farmers have chosen to develop aquaculture in deeper waters, mainly in Norwegian fjords and in higher energy hydrodynamic regimes (Holmer, 2010; Falconer et al., 2013; Bannister et al., 2014).

In the case of the RdC, the abundances of opportunistic and sensitive species are clearly linked to the impact of salmon cages; opportunistic species are more abundant in the assemblages impacted by the farm and, in the contrary, sensitive species are more abundant in the reference non-impacted assemblages (Table 5). Moreover, in this particular megatidal environment, the benthic habitats are impacted by two main factors: the input of OM in relation to the fish farm and the increase in currents near and under the fish cages. The RdC is particularly suitable for aquaculture, with an increase of current velocities under the cages in shallow waters due to the reduction of the open water column under the cages. This phenomenon prevents a large accumulation of OM under the cages and favours the dispersal of OM outside the fish farm, which is reinforced by tidal currents.

In their prospect, the ‘GMG Saumon de France’ company envisaged the transfer of cages to the neighbouring eastern part of the RdC, which exhibits a higher energy hydrodynamic regime than in the RdC. Our results do not justify this repositioning of the fish farm outside the RdC, the existing salmon cages showing a relative low and local impact. Some studies had shown that after the cessation of fish production or after fallowing (i.e. period during which there is a pause in production), the opportunistic taxa undergo a decline in only two months (Zhulay et al., 2015), or six months (Brooks et al., 2013a), whereas the impact could have a duration of several years (Brooks et al., 2004; Pereira et al., 2004; Keeley et al., 2012a,b, 2015). In the case of the cessation of activity in the RdC salmon farm, it will be interesting to survey the resilience of benthic habitats in this area.

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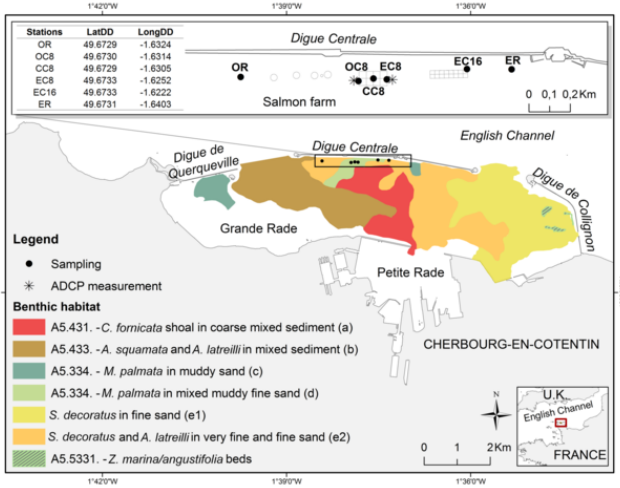
Figure 1. Location of the six sampling stations near the salmon farm in the Rade de Cherbourg and benthic habitats identified by Baux et al. (2017). * Location of the two sites used for ADCP current measurements.

Fig. 2. HAC and MDS analyses of sediment characteristics for the five stations at the five sampling dates. A. Dendrogram using group average linking of Bray-Curtis similarities on square root transformed sediment data. B. MDS ordination based on standardized and square root sediment data and Bray-Curtis similarities (see Fig. 1 for location of stations; oct13: October 2013; feb: February 2014; apr14: April 2014; jun14: June 2014; sept14: September 2014).

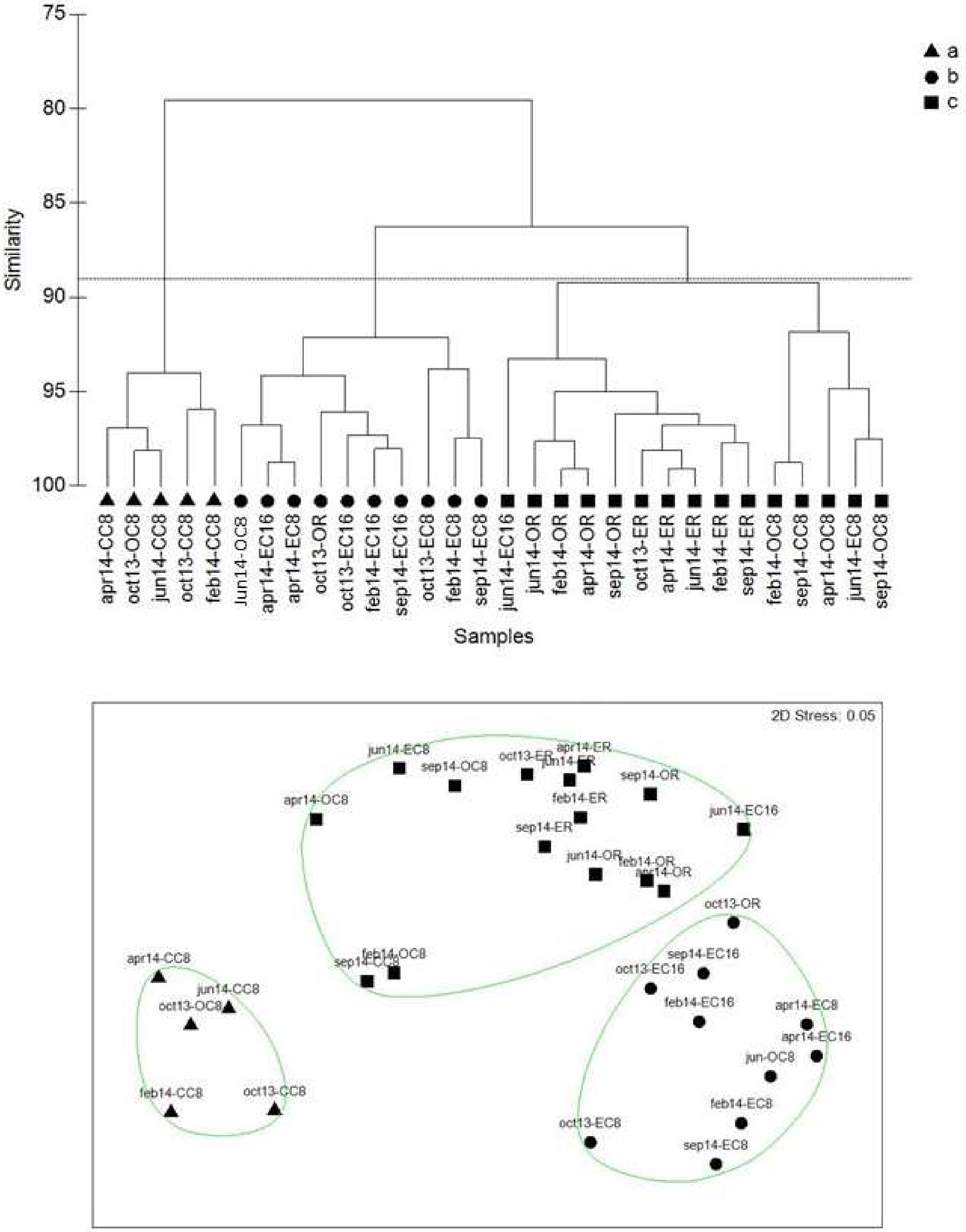
Fig. 3. Relationship between percentage of TOC and fine particles (< 50 µm), showing evidence of the enrichment of TOC at stations CC8 and OC8 (see Fig. 1 for location of stations).

Fig. 4. **A**: Dendrogram showing hierarchical clustering of data from 30 sites in the Rade de Cherbourg, using group average linking of Bray-Curtis similarities on Log(x+1) abundance of the taxa. The three groups of samples are separated at 50% similarity. **B**: MDS ordination of the 30 sites sampled in the Rade de Cherbourg, based on standardized and Log (x+1) transformation of abundances and Bray-Curtis similarities. (see Fig. 1 for location of the stations; oct13: October 2013; feb: February 2014; apr14: April 2014; jun14: June 2014; sept14: September 2014).



Stations	LatDD	LongDD
OR	49.6729	-1.6324
OC8	49.6730	-1.6314
CC8	49.6729	-1.6305
EC8	49.6733	-1.6252
EC16	49.6733	-1.6222
ER	49.6731	-1.6403

Figure 2


75
80
85
90
95
100
Similarity
Samples
▲ a
● b
■ c
apr14-CC8
oct13-OC8
jun14-CC8
oct13-CC8
feb14-CC8
Jun14-OC8
apr14-EC16
apr14-EC8
oct13-OR
oct13-EC16
feb14-EC16
sep14-EC16
oct13-EC8
feb14-EC8
sep14-EC8
jun14-EC16
jun14-OR
feb14-OR
apr14-OR
sep14-OR
oct13-ER
apr14-ER
jun14-ER
feb14-ER
sep14-ER
feb14-OC8
sep14-CC8
apr14-OC8
jun14-EC8
sep14-OC8
2D Stress: 0.05
jun14-EC8
sep14-OC8
oct13-ER
apr14-ER
jun14-ER
sep14-OR
apr14-OC8
feb14-ER
jun14-EC16
sep14-ER
jun14-OR
feb14-OR
apr14-OR
oct13-OR
sep14-EC16
oct13-EC16
feb14-EC16
apr14-EC8
apr14-EC16
jun-OC8
feb14-EC8
oct13-EC8
sep14-EC8
sep14-CC8
feb14-OC8
apr14-CC8
jun14-CC8
oct13-OC8
feb14-CC8
oct13-CC8

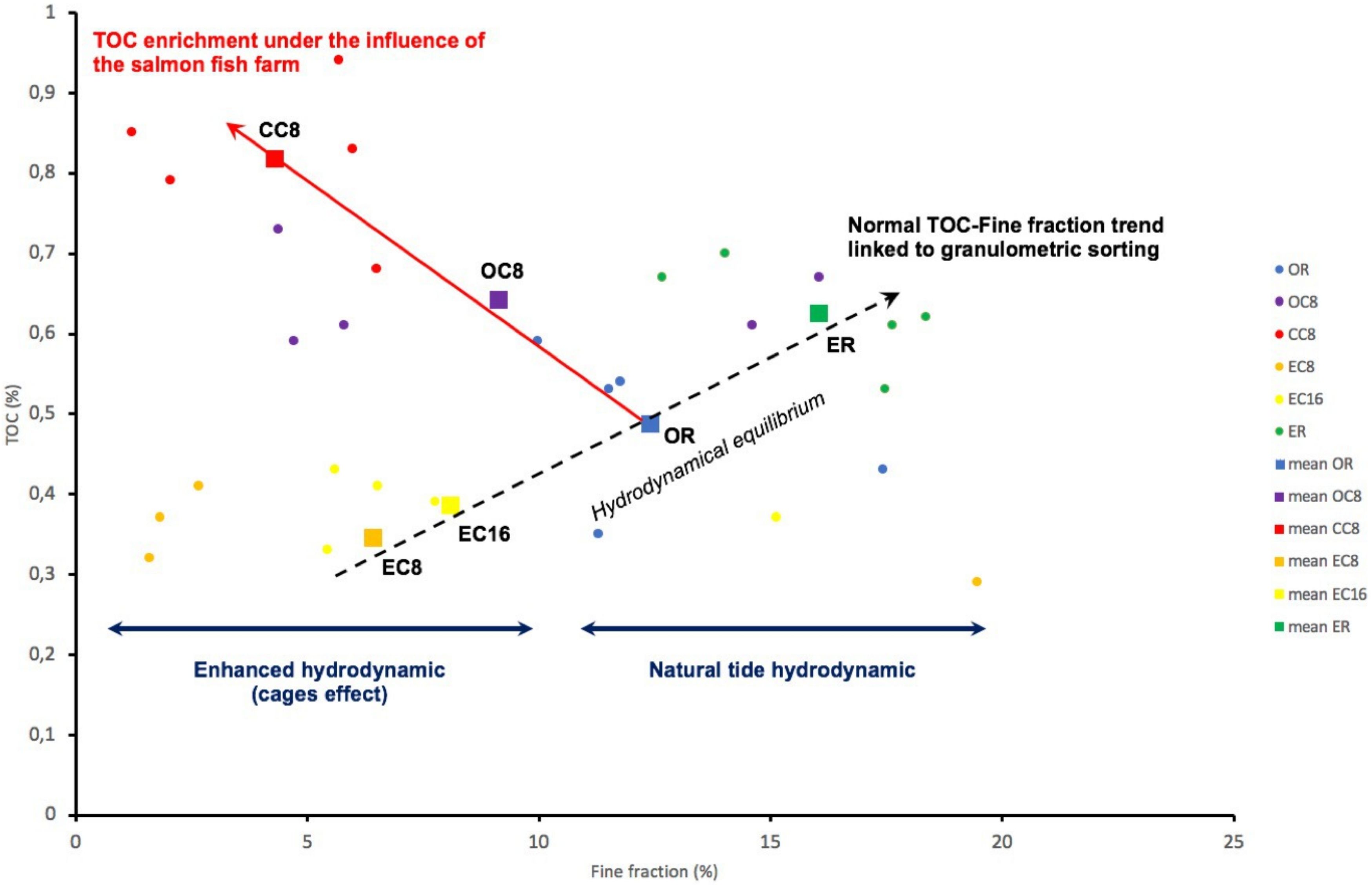

TOC enrichment under the influence of the salmon fish farm
CC8
OC8
OR
ER
EC16
EC8
Normal TOC-Fine fraction trend linked to granulometric sorting
Hydrodynamical equilibrium
Enhanced hydrodynamic (cages effect)
Natural tide hydrodynamic
TOC (%)
Fine fraction (%)
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
5
10
15
20
25
OR
OC8
CC8
EC8
EC16
ER
mean OR
mean OC8
mean CC8
mean EC8
mean EC16
mean ER

Figure 4

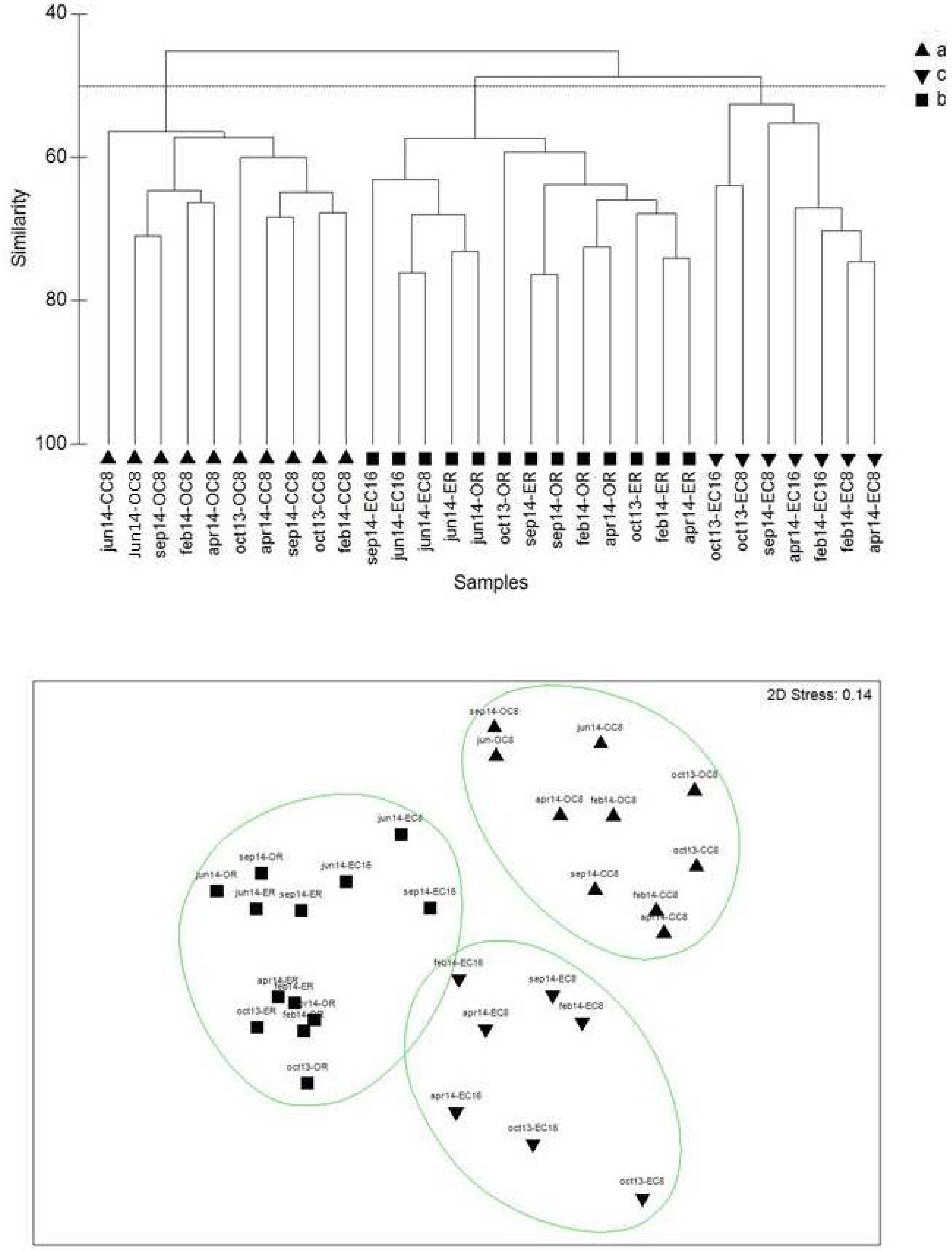

40
60
80
100
Similarity
▲ a
▼ c
■ b
jun14-CC8
Jun14-OC8
sep14-OC8
feb14-OC8
apr14-OC8
oct13-OC8
apr14-CC8
sep14-CC8
oct13-CC8
feb14-CC8
sep14-EC16
jun14-EC16
jun14-EC8
jun14-ER
jun14-OR
oct13-OR
sep14-ER
sep14-OR
feb14-OR
apr14-OR
oct13-ER
feb14-ER
apr14-ER
oct13-EC16
oct13-EC8
sep14-EC8
apr14-EC16
feb14-EC16
feb14-EC8
apr14-EC8
Samples
2D Stress: 0.14
sep14-OC8
jun-OC8
jun14-OC8
oct13-OC8
apr14-OC8
feb14-OC8
oct13-CC8
sep14-CC8
feb14-CC8
apr14-CC8
jun14-EC8
sep14-OR
jun14-EC16
jun14-OR
jun14-ER
sep14-ER
sep14-EC16
apr14-ER
feb14-ER
apr14-OR
oct13-ER
feb14-OR
oct13-OR
feb14-EC16
sep14-EC8
feb14-EC8
apr14-EC8
apr14-EC16
oct13-EC16
oct13-EC8

Table 1. Mean seawater characteristics during the five sampling campaigns. C1: 31 October 2013, C2: 19 February 2014, C3: 8 April 2014, C4: 13 June 2014 and C5: 18 September 2014.

	C1	**C2**	**C3**	**C4**	**C5**
Salinity (psu)	34.5	34.4	34.6	34.7	34.6
Temperature (°C)	17.7	8.2	11.1	14.7	17.9
Oxygen saturation (%)	102	101	103	107	123
Turbidity (NTU)	1.2	2.1	14.0	11.0	8.0

Table 2. Main characteristics of tidal currents measured by the eastern ADCP.

Main characteristics	**Neap tide**	**Spring tide**
Tidal range (m)	2.0	6.5
Maximum flood current velocity ($m.s^{-1}$)	0.10	0.20
Maximum ebb current velocity ($m.s^{-1}$)	0.30	0.70
Flood current (% of time)	40%	33%
Ebb current (% of time)	60%	66%

Table 3. Characteristics of sediments and macrofauna collected from sampling stations. TOC (%): Total Organic Carbon; FP (%): Fine Particles < 50 µm in dry sediment. TR: Total taxonomic richness per 0.5 m^2; A: Total abundance (ind.0.5m^2); H': Shannon-Weaver diversity index in $\log_2$; J': Pielou's evenness index. Mean values of the Benthic Indices (AMBI, M-AMBI, and BO2A) calculated with the five replicates for each station. C1: 31 October 2013, C2: 19 February 2014, C3: 8 April 2014, C4: 13 June 2014 and C5: 18 September 2014. Ecological Quality Status (EcoQS), red: bad; poor: orange; moderate: yellow; good: green; high: blue.

Stations/campaigns		**TOC (%)**	**% FF**	**TR**	**A**	**H'**	**J'**	**AMBI**	**M-AMBI**	**BO2A**
OR	**C1**	0.59	10.0	55	3,920	1.53	0.26	2.72	0.69	0.002
	C2	0.53	11.5	59	3,381	1.70	0.29	2.64	0.73	0.005
	C3	0.35	11.3	51	3,340	1.64	0.29	2.63	0.69	0.005
	C4	0.54	11.8	44	2,935	2.30	0.42	2.32	0.76	0.008
	C5	0.43	17.4	78	7,022	211	0.34	2.37	0.88	0.005
ER	**C1**	0.53	17.5	70	3,250	3.14	0.51	2.42	0.95	0.024
	C2	0.70	14.0	58	3,089	2.63	0.45	2.28	0.86	0.012
	C3	0.62	18.4	55	3,190	2.51	0.43	2.27	0.83	0.010
	C4	0.61	17.6	45	3,065	2.56	0.47	2.51	0.77	0.031
	C5	0.67	12.7	57	7,792	2.21	0.38	2.39	0.80	0.010
EC16	**C1**	0.41	6.5	38	1,248	1.74	0.33	3.03	0.61	0.046
	C2	0.43	5.6	49	3,007	2.59	0.46	3.01	0.75	0.072
	C3	0.33	5.5	33	2,164	2.08	0.41	2.21	0.70	0.008
	C4	0.37	15.1	47	8,451	2.06	0.37	2.71	0.71	0.024
	C5	0.39	7.8	53	3,889	2.28	0.40	3.02	0.73	0.065
EC8	**C1**	0.32	1.6	22	445	2.65	0.59	3.13	0.63	0.123
	C2	0.41	2.7	32	1,973	2.91	0.58	3.66	0.65	0.142
	C3	0.34	6.5	34	3,119	1.97	0.39	2.81	0.64	0.024
	C4	0.29	19.5	39	7,324	1.70	0.32	3.21	0.60	0.077
	C5	0.37	1.8	45	2,054	2.23	0.41	3.50	0.65	0.147
OC8	**C1**	0.59	4.7	37	1,502	2.17	0.42	2.75	0.68	0.022
	C2	0.61	5.8	57	3,648	2.36	0.40	3.04	0.76	0.052
	C3	0.61	14.6	55	6,913	1.78	0.31	2.99	0.69	0.015
	C4	0.73	4.4	59	11,355	1.76	0.30	3.19	0.69	0.039
	C5	0.67	16.1	65	7,964	2.36	0.39	3.25	0.77	0.082
CC8	**C1**	0.79	2.1	48	3,177	3.07	0.55	3.79	0.72	0.162
	C2	0.85	1.2	35	2,113	2.80	0.55	3.88	0.63	0.157
	C3	0.68	6.5	43	1,693	2.34	0.43	2.97	0.70	0.031
	C4	0.94	5.7	34	3,284	2.04	0.40	3.52	0.58	0.065
	C5	0.83	6.0	48	2,989	2.35	0.42	3.60	0.66	0.164

Table 4. Results of two-way ANOVA statistical tests. C1: 31 October 2013, C2: 19 February 2014, C3: 8 April 2014, C4: 13 June 2014 and C5: 18 September 2014.

			F	p-value	Tukey test
Taxonomic richness	Dates	4	2.82	<0.05	C1≠C5
	Stations	6	2.31	<0.05	ER≠EC8
Abundance	Dates	4	14.43	<0.001	C2≠C4, C5 C1≠ C4, C5 C3≠ C4, C5
	Stations	6	6.57	<0.001	OC8≠EC16, CC8, EC8, ER, OR
H’	Dates	4	3.87	<0.01	C2≠C3, C4
	Stations	6	4.41	<0.001	OR≠ER, CC8 OC8≠ER, CC8 CC8≠EC16
J’	Dates	4	4.42	<0.01	C4≠C1, C2
	Stations	6	11.67	<0.001	OR≠EC16, ER, EC8, CC8 CC8≠EC16 OC8≠ER, EC8, CC8
AMBI	Dates	4	2.45	<0.05	C5≠C3
	Stations	6	24.75	<0.001	ER≠EC16, OC8, EC8, CC8 OR≠OC8, EC8, CC8 EC16≠OC8, CC8 CC8≠OC8
M-AMBI	Dates	4	1.14	0.34	-
	Stations	6	4.73	<0.001	ER≠EC16, EC8, OC8, CC8
BO2A	Dates	4	6.37	<0.001	C3≠C1, C2, C5 C5≠C2
	Stations	6	23.3	<0.001	OR≠OC8, CC8, EC8 ER≠EC8, CC8 EC16≠EC8, CC8 OC8≠EC8, CC8 CC8≠EC16
∑		143			

Table 5. Mean abundances per 0.5 m² for dominant taxa in the three zones identified around the salmon cages in the Rade de Cherbourg. EG: Ecological Group from AZTI consulted on 15th February 2018 (see Fig. 1 for location of the six stations).

Taxa	**EG**	**CC8/OC8**	**EC16/EC8**	**OR/ER**
Apseudopsis latreillii	III	2538.9	1980.8	2669.5
Notomastus latericeus	III	574.3	375.0	169.4
Dipolydora giardi	IV	554.9	452.1	68.0
Capitella minima	V	115.2	34.0	1.8
Phyllodoce mucosa	III	66.3	70.7	15.5
Gammarella fucicola	III	65.9	-	1.1
Chaetozone gibber	IV	60.8	12.7	11.8
Jassa herdmani	V	60.2	0.3	0.2
Caulleriella alata	IV	50.0	10.3	7.6
Cirriformia tentaculata	IV	44.6	16.7	2.6
Cheirocratus intermedius	I	41.8	3.9	8.2
Zeuxo holdichi	III	39.1	6.5	5.5
Abludomelita obtusata	II	38.5	1.4	9.7
Steromphala umbilicalis	I	19.6	-	0.5
Neanthes acuminata	III	15.8	7.7	0.1
Ampelisca tenuicornis	I	4.0	99.9	99.5
Phtisica marina	I	0.3	60.0	62.0
Maldanidae	I	1.1	59.4	450.1
Lanice conchilega	II	1.1	34.7	31.9
Tritia reticulata	II	15.1	12.7	9.0
Hilbigneris gracilis	III	5.0	9.3	34.6
Melinna palmata	III	-	0.9	80.7
Thyasira flexuosa	III	0.1	6.4	77.6
Acromegalomma vesiculosum	I	2.9	1.0	38.7
Apseudes talpa	II	-	0.1	25.8
Abra alba	III	3.9	7.4	12.0

Table 6. Sites and habitats showing high abundance (mean abundance and maximum abundance ind.m²) of the tanaid *Apseudopsis latreilli* in the World Ocean. OM: % Organic Matter in dry sediment.

Sites		**Benthic habitat**	**Abundance**		**OM (%)**	**Reference**
			mean	**max**		
English Channel	Rade de Cherbourg, Normandy, France	Mixed, coarse sand and gravel	5,078	20,700	3.5	This study
		Muddy fine sand	4,339	10,320	3.0	This study
		Fine sand	3,962	14,640	2.5	This study
		A. squamata and *A. latreilli* mixed sediment	3,151	4,777	3.7	Baux, 2015
		M. palmata muddy sand	2	3	6.5	Baux, 2015
		M. palmata mixed muddy fine sand	2,690	4,720	3.2	Baux, 2015
		S. decorata fine sand	453	2,130	1.2	Baux, 2015
		A. latreilli and *S. decorata* in very fine sand	2,250	6,280	3.5	Baux, 2015
	Baie du Becquet, Normandy, France	*A. squamata* and *A. latreilli* mixed sediment	8,900	22,787	1.6	Martinez, 2017
		C. coarse mixed sediment	2,563	5,150	2.0	Martinez, 2017
		Amphipods and polychaetes in muddy sand	6,822	13,770	1.7	Martinez, 2017
	Aber Wrach, Brittany, France	Intertidal *S. decorata* fine sand	740	-	-	Hily and Bouteille, 1999
		Intertidal *Z. marina* meadows	3,086	-	-	Hily and Bouteille, 1999
		Fine sand *A.alba-H. bilineata* community	2,535	3,608	-	Dauvin and Gentil, 1990
Atlantic	Galicia, Ria de Grove, Spain	Subtidal *Z. marina* meadows	5,940	9,640	-	Esquete et al., 2011
		Fine sand community	398	2,161	1.8	Lourido et al., 2008
		Coarse sand community	348	2,289	1.5	Lourido et al., 2008
		Muddy fine sand community	1,778	5,321	3.1	Lourido et al., 2008
	Ria de Formosa, Portugal	Subtidal *Z. marina* meadows	1,528	-	2.8	Gamito et al., 2012
Mediterranean Sea	South-eastern Spain	Sandy soft-bottom in Portman Bay	1,432	-	-	Marin-Guirao et al., 2005
		Marine caves of Granada's coast	2,106	-	-	Navarro-Barranco et al., 2013
	Castellon coast Spain	Well-sorted fine sand community	-	1,033	-	De-la-Ossa-Carretero et al., 2010
	western Italian coast	Well-sorted fine sand community, Pisa	4,335	-	-	Tataranni and Lardicci, 2010
Marmara Sea, Turkey		Well-sorted fine sand community	80	166	2.85	Ates et al., 2014
Persian Gulf, Dubai creek		Muddy sediment under organic pollution	17,650	43,000		Sauders et al., 2007