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To cite this version:

Elisa Baldrighi, Jacques Grall, Nolwenn Quillien, Rita Carriço, Valentin Verdon, et al.. Meiofauna communities' response to an anthropogenic pressure: The case study of green macroalgal bloom on sandy beach in Brittany. Estuarine, Coastal and Shelf Science, 2019, 227, pp.1-14. 10.1016/j.ecss.2019.106326 . hal-02622934

HAL Id: hal-02622934
https://hal.inrae.fr/hal-02622934v1

Submitted on 20 Jul 2022

Meiofauna communities' response to an anthropogenic pressure: the case study of green macroalgal bloom on sandy beach in Brittany

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Abstract: Open sandy beaches support key ecological functions and a distinctive biodiversity, but are threatened by an increasing anthropogenic pressure. Among these threats is the occurrence of green tides of *Ulva* spp., expression of the eutrophication phenomenon. Our study aimed at determining the impact of green macroalgal accumulations on benthic meiofauna inhabiting two macrotidal sandy beaches of Brittany: Saint Nic (impacted) and Anse de Dinan (unimpacted). The presence of *Ulva* enhanced total meiofaunal abundance and nematode functional diversity when compared to a state free from macroalgal mats. The stranded *Ulva* supported high values of meiofaunal β-diversity as well. This unexpected response was likely due to the highly dynamic nature of open sandy beaches that prevents O_2 depletion within sediments. Natural seasonal changes in meiofaunal biomass and composition were also evident at both beaches and changes in environmental features, apart from eutrophication alone, do drive the variability in meiofaunal biomass and nematodes diversity.

Keywords: Meiofauna, macroalgal bloom, sandy beach, nematodes, Brittany, anthropogenic impact, *Ulva* spp.

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Declaration of interest: none

1. Introduction

There is growing scientific evidence that our coastlines are suffering from catastrophic ecological damage as a result of anthropogenic activities (Cloern et al., 2016). Eutrophication is a process of natural or man-made enrichment with inorganic nutrient elements (e.g. nitrogen and phosphorus) beyond the maximum critical level of the self-regulatory capacity of a given system for a balanced flow and cycling of nutrients (Fletcher, 1996). It is a direct consequence of increasing population densities along coastal areas and the use of fertilizers for agriculture (Grall and Chauvaud, 2002). Increased nutrient loading leads to stimulated primary production and, in particular conditions, such as shallow and enclosed areas with low water turnover, eutrophication may induce opportunistic green or brown macroalgal blooms (Liu et al., 2009). The term ‘‘Green Tides’’ (here after GT) or macroalgal blooms covers a heterogeneous set of events that share two characteristics: they are caused predominantly by green macroalgae, and have negative impacts on the environment (Garcia and Johnstone, 2006; Ye et al., 2011). Thus, although macroalgal blooms can be in some cases a natural phenomenon, the global problem of green tides has increased both in extent and in its public perception over the last three decades. GT occur mainly in the North Temperate Zone, with America, Europe and the Asia-Pacific being the most seriously affected (Morand and Merceron, 2004). In Brittany (Western France), the first green algal bloom was recorded on the southwestern channel bays in the early 70’s. Nowadays, many coastal areas and beaches around Brittany are affected by green tides. In 2012, green macroalgal blooms were reported from 51 beaches and 33 estuaries for a total volume of 40,000 m^3 of fresh algae (CGDD 2014). From 1997 to 2015 the number of sites affected by green tides increased from 34 to 63, while the number of Brittany coastal cities affected by GT increased from 60 to 138 (http://www.ceva.fr/fre/MAREES-VERTES). In 1986, 25,000 m^3 of *Ulva* spp. accumulated in Lannion Bay in a single season (Charlier et al., 2006).

Sandy beaches are the most extensive intertidal system worldwide (Wright and Short, 1983) and dominate a majority of temperate and tropical coastlines where they represent both important recreational assets and functions as well as buffer zones against the sea (Sun et al., 2014). Sandy beaches are known to be among the most dynamic soft bottom habitat, with abundant biological resources (McLachlan and Brown, 2010) and act as nurseries and feeding areas for commercially important fishes and bivalves (surf clams) (Schlacher et al., 2008). Sandy beach ecosystems are populated by many organisms that are specialized and adapted to life in mobile substrate and their peculiar harsh environment. These species all play important roles in the ecological functioning of the beach system, e.g. as primary producers (diatoms and algae), decomposers (bacteria), consumers (heterotrophic bacteria, meiobenthos and macrobenthos). From regional to global scales, sandy beaches also highly contribute to β-diversity (Schlacher et al., 2008). As a transition zone between land and sea, sandy beach ecosystems suffer from various anthropogenic disturbances such as coastal development and pollution (Schlacher et al., 2007; Defeo et al., 2009); as well as from green macroalgal blooms mainly caused by nutrient enrichment of coastal waters by human activities (Quillien et al., 2015a, 2016). These macroalgae can form stranded mats along beaches, such as the documented large *Ulva* spp. mats along Brittany beaches (CGDD 2014). The presence of such free-living macroalgal mats affects exchange between sediments and water and modifies local hydrodynamics (Hull, 1987) and primary production (Liu et al., 2009) and affects benthic macro- and meiofauna fauna (e.g. Dolbeth et al., 2007; Carriço et al., 2013; Quillien et al., 2015a, 2015b; Sun et al., 2014) and fish populations (Le Luherne et al., 2016).

The majority of the studies and monitoring programs dedicated to the evaluation of anthropogenic impacts (e.g. eutrophication, algal blooms) in the marine environment focus on benthic macrofauna, as well as microbial and epiphyte communities; only few included hitherto meiofauna especially in the case of macroalgal bloom impacts (Villano et al., 1995; Neira et al., 1996; Garcia and Jonhstone, 2006; Carriço et al., 2013). Nevertheless, meiofauna has recently started to be recognized as useful biological indicators, since the community may contain information that macrofauna cannot provide (Zeppilli et al., 2015; Bianchelli et al., 2016; Schratzberger and Ingels, 2017). Relative to macrofauna, meiofauna exhibits a shorter response time and many perturbations are detectable due to their asynchronous reproduction, rapid turnover rate, and lack of larval dispersal. As a result, the abundance of meiofauna is more sensitive to environmental fluctuations and is therefore useful as indicator of disturbances (Schratzberger et al., 2000; Austen and Widdicombe, 2006). Free-living nematodes, usually the dominant meiobenthic taxon, have been pointed out as potential indicators for the effects of anthropogenic disturbance on biodiversity in aquatic ecosystems (Moreno et al., 2008; Vanaverbeke and Vincx, 2008; Semprucci et al., 2015, 2016; Zeppilli et al., 2015). Moreover, nematodes direct development coupled to the one to three months long life-cycle, permit observing changes in the community structure readily observable in short term benthic studies (Moens et al., 2014a).

The aim of the present study was to assess the impact of eutrophication by green macroalgae (i.e. *Ulva* spp.) on benthic meiofauna, and particularly nematodes, inhabiting macrotidal sandy beaches of Brittany. To reach this objective, the meiofaunal communities inhabiting two beaches in the bay of Douarnenez (south of Finistère, France) with different impact of GT were investigated. The beach of Saint Nic, is impacted seasonally by GT while the beach of Anse de Dinan was considered as unimpacted since it has never harboured GT. The meiobenthic communities were sampled at different seasons, since meiofauna can show natural seasonal variations in relation to changes in environmental conditions (Liu et al., 2008). Hence, the following hypotheses were studied: (1) meiofaunal and nematode abundance, biomass, structural and functional diversity are affected by the presence of *Ulva* spp.; (2) natural seasonal environmental changes differently affect the meiofauna populations inhabiting impacted and unimpacted sandy beaches. Because an integrated approach considering different benthic components appears to be the most suitable when assessing environmental impacts and ecological status of coastal zones (Patrìcio et al., 2012), our main results will be discussed in perspective with the macrofaunal results previously published for the same ecosystem (Quillien et al., 2015a, 2015b).

2. Material and Methods

2.1 Study area and sampling strategy

The study was performed in two sandy beaches located in the bay of Douarnenez (Brittany, France): Anse de Dinan and Saint Nic (Fig. 1). The two sandy beaches consist of large areas (up to 500 m from shore during spring tides) that are uncovered at low tide (mean tidal regime = 6.5 ± 0.5 m) and have lengths ranging from 2.1 to 3.0 km (see more detailed description in Quillien et al., 2015a). The unimpacted beach of Anse de Dinan (AD, 48°14.109'N, 4°32.545'W) never harbored green tides and the anthropogenic impact is negligible (a wetland area located just behind the beach filters terrestrial water inputs and has limited urbanization); conversely the impacted beach of Saint Nic (SN, 48° 10.132'N, 4° 17.465'W) is characterized by the presence of spatially heterogeneous GT blooms, mainly *Ulva* sp., since the early 80's (Charlier et al., 2007). In order to characterize the meiofaunal communities, sediment sampling was conducted manually in the intertidal zone during three months - May, July and December 2012 - using Plexiglas corers ($10cm^2$). At each site two separated sediment replicates of 15 cm depth were collected and stored frozen (-20°C) until the laboratory analyses. At both sites a single sediment core (inner diameter: 11.3cm; depth: 15cm; surface: $100cm^2$) was collected from which grain size and organic matter content characteristics were determined. Seawater temperature, salinity, and dissolved oxygen content were measured at each sampling occasion using an YSI-OMS v2 multi-parameter probe.

2.2 Samples processing

Meiofauna and nematode analyses. For meiofaunal extraction, sediment samples (0-15 cm) were sieved through a 1000 µm mesh. The fraction remaining on a 40 µm mesh was centrifuged three times with Ludox HS40 (diluted with water to a final density of 1.18 g cm^{-3}) and stained with Rose Bengal (0.5 g l^{-1}) (Heip et al., 1985). Meiofauna was counted and classified to higher taxonomic level under a stereomicroscope after which the density (n. of individuals/10 cm^{-2}) and taxon richness of the communities were estimated.

The determination of meiofaunal biomass was performed using the volumetric method that consists of indirect estimates of biomass extrapolating organism weight from a volume (Danovaro, 2010). From each sample, 100 randomly collected nematodes were mounted on slides after a formalin–ethanol–glycerol treatment to prevent dehydratation (Danovaro, 2010) and then identified to the genus level according to Platt and Warwick (1983, 1988), Warwick et al. (1998), and the NeMys database (http://nemys.ugent.be). The different nematode morphotypes were reported under the name of the genus and then as putative species sp1, sp2 and so on. The nematode biomass was calculated from the biovolume, which was estimated from all specimens per replicate using the Andrassy formula ($V=L \times W^2 \times 0.063\times10^{-5}$, with body length, L, and width, W, expressed in μm; Andrassy, 1956). The carbon contents was considered as 40 % of the dry weight (Feller and Warwick, 1988).

Species richness (SR) was calculated as the total number of species collected at each site. Nematode species diversity (H, using log base e) was measured using the Shannon–Weaver diversity index (Shannon and Weaver, 1949), with the evenness as the Pielou index (J; Pielou, 1975). In order to facilitate comparison among samples, the expected number of nematode species for a theoretical random sample of 51 individuals, $ES_{(51)}$, was calculated. All indices were calculated using PRIMER v6.0+ (Plymouth Marine Laboratory, UK; Clarke and Gorley, 2006).

The trophic diversity of the nematodes was determined by analyzing trophic groups, as reported by Wieser (1953). The nematodes were divided into four groups, as follows: no buccal cavity or a fine tubular one, as selective (bacterial) feeders (1A); large, but unarmed, buccal cavity, as non-selective deposit feeders (1B); buccal cavity with scraping tooth or teeth epistrate or epigrowth feeders (2A); and buccal cavity with large jaws, as predators/omnivores (2B). The index of trophic diversity (ITD) was calculated as Θ, where $\Theta=g_1^2+g_2^2+g_3^2\ldots+g_n^2$, and g is the relative contribution (in terms of number of specimens) of each trophic group to the total number of individuals, and n is the number of trophic groups (Heip et al., 1985). For n=4, Θ ranges from 0.25 (highest trophic diversity; i.e. each of the four trophic groups accounts for 25 % of the nematode abundance) to 1.0 (lowest diversity; i.e., when one trophic group accounts for 100 % of the nematode abundance). Nematode trophic structure was calculated based on the nematode biomass matrix. The maturity index (MI) of nematode populations was calculated from life strategies (r - K) of the nematodes for which these strategies are known (Bongers, 1990; Bongers et al., 1995). In order to identify colonization strategies, nematodes are divided into “colonizers” (comparable to r-strategists, characterized by a short life cycle, high colonization ability, and tolerance to disturbance, e.g., eutrophication) and “persisters” (K-strategists with a low reproduction rate, long life cycle, and low colonization ability and tolerance to disturbance; the list of species with different life strategies is reported by Bongers et al., 1991). The MI was calculated according to the weighted mean of the individual genus scores: MI=Σ v (i) X f (i), where v is the c–p value (colonisers–persisters; ranging from 1, i.e. only opportunistic colonizers, to 5, i.e. only persisters) of the genus i (Bongers et al., 1991) and f (i) is the frequency of that genus.

Environmental variable analyses. Grain size was measured by dry-sieving the sediment, using a series of 16 sieves from 63 to 10,000 µm. The sorting index (SI) was calculated based on the first and third quartile ratio (√Q25/Q75, where Q25 and Q75 denote the first and the third quartiles of the sediment grain size, respectively), and the median (Q50) was equal to the second quartile of the sediment grain size value (hereafter referred to as ‘median’; Quillien et al., 2015a). Organic matter content was measured by weight loss after combustion at 450°C for 5h. *Ulva* biomass was estimated by CEVA (www.ceva.fr/fre) through monthly aerial surveys (for estimation of surface area covered by mats) and field sampling (for conversion into biomass). Monthly mean values for wave height were taken from the publicly available database PREVIMER. PREVIMER estimates the wave height using the model WW3 (grid = 200 m).

2.3 Data analyses

Principal component analysis (PCA) with Euclidean distance was carried out on environmental data, previously normalized, in order to visualize the comparison of the two sandy beaches based on the main abiotic variables.

Uni- and multivariate analyses were carried out in order to assess temporal and spatial differences in meiofauna and nematode assemblage composition. The sampling design included two fixed and orthogonal factors: beach (2 levels: Saint Nic and Anse de Dinan) and month (3 levels: May, July and December). Pair wise tests were carried out to verify the significance of the differences among beaches at different months. The distance-based permutation analysis of variance (PERMANOVA; Anderson, 2001) in either univariate (separately for each meiofauna and nematode diversity index) or multivariate data (for both meiofaunal assemblages and nematode communities) was used for testing for differences in community structure between beaches and seasons. Faunal data (square-root transformed) were analyzed using tests based on Bray-Curtis similarity matrices and on Euclidean-distance similarity matrices for univariate data. PCA analysis was performed to visualize the spatial (i.e. beaches) and temporal (i.e. seasons) patterns in the meiofaunal assemblages and to identify the meiofaunal taxa mainly responsible for the spatio-temporal variability.

Afterwards, the relative contribution of each nematode species to the average dissimilarities between beaches and periods (i.e. months) was calculated using SIMPER test (using 90% as cutoff). The ß diversity provides indications of any change in community composition and can be expressed as percentages of dissimilarity (e.g. based on a Bray–Curtis similarity matrix; Gray, 2000). The SIMPER analysis was used to determine the contributions of each species to the average Bray–Curtis dissimilarity (Clarke and Warwick, 2001). This analysis of dissimilarities was based on a square-root transformation matrix. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis similarity matrix was used to visualize spatio-temporal patterns on nematode assemblages at the two sandy beaches.

Multivariate multiple regression analyses (DistLM forward, Anderson et al., 2008) were performed to test the influence of abiotic variables (wave hight, seawater temperature (SWT), salinity, oxygen concentration (O_2), *Ulva* biomass, median grain size (MGS) and organic matter (OM) into the sediment) on meiofaunal standing stock and community composition, nematode species composition, trophic diversity and nematode life strategy. The DistLM forward was carried out using the routine included in the PRIMER v6.0 + software (Clarke and Gorley, 2006). This analysis was based on Bray-Curtis dissimilarities with 4999 permutations of residuals. PERMANOVA, pair wise tests, PCA, SIMPER and nMDS were carried out by means of the software PRIMER v6.0 + (Clarke and Gorley, 2006).

3. Results

3.1 Environmental characterization

Environmental characteristics of the Anse de Dinan (AD, unimpacted) and Saint Nic (SN, impacted) beaches are reported in Table 1. Seawater temperature, salinity, and dissolved oxygen did not show significant differences (see also Quillien et al., 2015a) between the two beaches, but lower seawater temperatures were reported during winter time. The two environments were well oxygenized during all sampling periods. Organic matter content (from 3.19% to 4.90% at SN in December and AD in May, respectively) were comparable between the two sampling sites but a decreasing trend was observed from May to December (Table 1). Higher values of sorting index and median grain size were found at AD compared to SN, particularly in May (Table 1). However, both sampling sites characteristics were part of dissipative sandy beaches definition (Carriço et al. 2013). Actually, the presence (SN, until 1445.8 10^3 kg in July; Table 1) or absence of *Ulva* (AD) was the most important environmental variable that made the difference between the two beaches.

The PCA visualized data trends of the multivariate characteristics of the two sandy beaches over different sampling periods (Fig. 2). The two axes, PC1 and PC2, explained 82% of the differences between Saint Nic and Anse de Dinan (Supplementary Material 1). In particular, PC1 axis accounted for 50.3% of differences between beaches and they were separated into two groups according to the season (December and May-July) related to differences in organic matter (OM), oxygen (O_2 %), wave height (WH), salinity (Sal) and seawater temperature (SWT) (Fig. 2). Along the PC2 axis, beaches were ordinated according to the presence/absence of *Ulva* and to the grain size (MGS, SI) and clearly separated impacted (SN) and unimpacted (AD) beaches (Fig.2).

3.2 Spatial and temporal variations in meiofaunal standing stock and composition

Meiofauna standing stock. Total mean meiofaunal abundance varied from 221.8 ind.10 cm^{-2} (AD in July) to 933.9 ind.10 cm^{-2} (SN in July; Fig. 3a, Table 2). PERMANOVA tests based on meiofaunal abundance data highlighted significant spatial variation (i.e. significant differences between beaches; Table 3), with higher meiofaunal abundance at SN beach compared to AD beach. Total meiofaunal biomass ranged from 13.8 µg C/10 cm^2 (AD in December) to 91 µg C/10 cm^2 (SN in July; Fig. 3b, Table 2).

PERMANOVA tests demonstrated significant temporal variation in the meiofaunal biomass (Table 3). More specifically, the pairwise tests revealed higher meiofaunal biomass in the "warmer" months May and July compared to the "colder" December month ($P< 0.05$).

Meiofauna community composition. A total of 14 *taxa* were identified: Amphipoda, Bivalvia Cladocera, Copepoda with their *nauplii*, Cumacea, Gastrotricha, Halacaridae, Isopoda, Nematoda, Oligochaeta, Ostracoda, Platyhelminthes, Polychaeta and Tardigrada. Eight was the highest mean number of taxa, at SN beach during December, while two was the lowest mean number of taxa, at AD in December (Table 2). The results of the PERMANOVA tests reported a major significant effect of the interaction between Beach x Month on the number of meiofaunal higher taxa (Table 3). Overall**,** a higher mean number of meiofaunal taxa characterized the impacted beach (SN), with the only exception for May during which the number of taxa was comparable between the two beaches (Table 2).

Nematoda phylum was always the most represented group, accounting for 91-99% of meiofauna (Fig. 4a; Supplementary Material 2). The second most represented group was Crustacea (i.e. Amphipoda, Copepoda, Cumacea, Isopoda and Ostracoda) in both beaches (accounting for 73-82% of the group of 'others'), with the only exception for AD in December where Platyhelminthes was more dominant (Fig. 4b). At Saint Nic, Copepoda with their *nauplii* constituted the majority of the crustaceans followed by Ostracoda. Differently, at Anse de Dinan, Copepoda (with their *nauplii*) and Cumacea were the most abundant groups followed by Amphipoda. Other taxa were reported just in one of the two beaches and not at all sampling periods. For instance, a high contribution of Platyhelminthes found at both beaches during winter period; a unique presence of Gastrotricha and Isopoda in May at AD and Bivalvia found only at SN especially during the warmer sampling months. Taxa such as Cumacea, Amphipoda, Isopoda, Polychaeta and Tardigrada were more abundant during warmer seasons; whereas Platyhelminthes (at SN and AD) and Ostracoda (at SN) coped were more abundant during colder month. Three taxa never appeared in SN - Gastrotricha, Tardigrada and Isopoda; four taxa were never detected at AD - Bivalvia, Halacaridae, Oligochaeta and Cladocera (Fig. 4b; Supplementary Material 2). PERMANOVA tests revealed a significant spatial (Beach) and temporal (Month) effect on meiofaunal community structure (Table 3). In particular, the pairwise test demonstrated a significant difference on the meiobenthic community composition between July vs December at AD beach ($P< 0.05$) (Fig. 4b).

The PCA visualized the contribution of taxa to the spatial and temporal variability in the meiofauna community structure (Fig. 5). PC axis 1, which explained 33% of the variability, grouped samples related to the beach (AD on right side and SN on the left side of the graph) and was driven by the taxa: Cumacea, Amphipoda, Polychaeta, Copepoda + *nauplii*, Nematoda, Ostracoda and Bivalvia (Fig. 5; Supplementary Material 2). PC axis 2 explained 27% of the variability and samples were grouped according to season ('colder' samples on the upper part and 'warmer' samples on the lower part of the graph). Platyhelminthes, Copepoda, Cumacea and Nematoda contributed the most to the separation of these samples (Fig. 5; Supplementary Material 3).

3.3 Nematode structural and functional diversity.

Nematode diversity. A total of 76 putative species, 59 genera and 21 families of nematodes were identified (Supplementary Material 4). Xyalidae was the most diversified family with 10 genera, followed by Desmodoridae (seven genera), Axonolaimidae, Chromadoridae and Thoracostomopsidae (all four genera). Selachinematidae was the most abundant family representing 28% of the total nematode fauna (characterized the AD site), followed by Xyalidae (21%), Desmodoridae (12%) and Thoracostomopsidae (11%) characterizing both AD and SN sediments. The diversity indices (SR, H and $ES_{(51)}$) did not show any significant differences between impacted (SN) and unimpacted (AD) beaches and over different sampling periods (Table 2). PERMANOVA tests only revealed significant effects of factor Beach on the equitability values (J; Table 3) with lower mean values in the equitability index at AD (0.7 ± 0.1) compared to SN (0.8 ± 0.0).

PERMANOVA results based on nematode species composition revealed spatial and temporal significant differences (Table 3). Saint Nic and Anse de Dinan beaches were characterized by a specific nematode community inhabiting impacted and unimpacted beaches which changed also between wormer and colder months. More specifically, the pairwise tests reported significant differences in nematode species composition between May vs. December ($p<0.01$) at both beaches and July vs. December ($p<0.01$) only at AD beach.

The results of SIMPER analyses (Table 4) showed a 64.5% of dissimilarity in nematode species composition between the impacted and unimpacted beaches. The dissimilarity between the two beaches was mainly due to the dominance of *Richtersia* spp. at Anse de Dinan and the higher abundance of *Promonhystera* sp1, *Microlaimus* sp1, *Viscosia* sp1 and *Marylynnia* sp1 at Saint Nic. The highest dissimilarity percentage (75.4%) was reported among sampling periods: May vs December and July vs December (Table 4). Differences among sampling periods were due to the presence of some 'warmer' species, such as *Omicronema* sp1; *Daptonema* sp1, *Promonhystera* sp1 and *Trileptium* sp2 vs 'colder' species such as *Molgolaimus* spp. and *Endeolophos* sp1. Overall, a total of 24 exclusive species were encountered at Anse de Dinan, whereas 21 exclusive species characterized Saint Nic (Supplementary Material 4). Spatio-temporal dissimilarities in nematode species composition were clearly shown by the nMDS graph (Fig. 6). Along the horizontal axis stations followed a seasonal gradient and they were distributed in the space from 'warmer' to 'colder' seasons, whereas along the vertical axis stations were grouped according to the beach from unimpacted to impacted one.

Nematode trophic diversity and life strategy. The results of PERMANOVA highlighted a significant 'beach' effect on the trophic structure of nematodes (Table 3). Predators (2B) and non-selective deposit feeders (1B) were the most represented trophic groups at SN beach (45.2% and 26.6%, respectively), where the contribution of epistrate feeders (2A, 21.3%) and selective deposit feeders/bacterivores (1A, 6.8%) should not be neglected (Fig. 7). Differently, at AD beach the 1B (82.8%) group dominated over all the other feeding groups. The contribution of the other groups varied between 1% (1A) and 9 % (2B) (Fig. 7). No seasonal variation in the nematode trophic structure was observed for the beaches of Saint Nic and Anse de Dinan (Fig. 7). The mean ITD value of 0.31 at SN indicated almost equal distribution of nematodes in each trophic group whereas at AD dominance of a single group (i.e. 1B = non-selective deposit feeders) was indicated with a mean ITD value of 0.56.

Mean values of nematode maturity index (MI) were very similar between the two beaches (2.06±0.81 and 1.97±0.64 at AD and SN, respectively) and indicated "r-strategy" communities of nematodes. PERMANOVA tests revealed a significant 'month' effect on the MI (Table 3), with lower MI values in the winter (Table 2). Indeed, pairwise tests reported significant differences in the nematode maturity index between May-July and December ($P < 0.01$) at both beaches.

The results of PERMANOVA tests demonstrated a significant effect on the interaction between Beach x Month on contribution of males, females and juveniles (Table 3). The contribution of males remained quite constant during all the sampling periods in both beaches, while the percentage of females (gravid and non-gravid) was higher during the warmer periods. Instead, the percentage of juveniles increased during winter particularly at AD beach (Table 2).

3.4 Meiobenthic community and nematode composition related to environmental features

The results of DistLM forward analyses revealed that total meiofaunal abundance was significantly and highly explained by *Ulva* biomass (65%), while total meiofaunal biomass was significantly explained by seawater temperature (SWT) and salinity (73%; Table 5).
Salinity and SWT significantly explained the meiofaunal diversity (n° taxa; 52%); while the variability in meiofaunal community structure was mostly explained by *Ulva* biomass and SWT (61%; Table 5). Nematode trophic structure is explained by median grain size (MGS), salinity and SWT, whereas MI is explained by O_2, salinity and SWT (Table 5). Nematode assemblages composition were significantly explained by O_2, salinity, *Ulva* biomass, organic matter (OM) and SWT, cumulatively explaining 82% of the observed variance (Table 5; Fig. 8). The dbRDA graph (Fig. 8) clearly showed a separation of samples according to season (along axis 1; 47% explained) and according to impacted and unimpacted beach (along axis 2; 30 explained). None of the environmental variables considered could explained nematode diversity (SR, H and $ES_{(51)}$).

4. Discussion

Eutrophication in estuaries and coastal waters in the form of green macroalgal blooms occurs all over the world (Liu et al., 2009; Ye et al., 2011). Increasing degradable organic matter may strongly affect biogeochemical cycling and nutrient processes, leading to oxygen depletion and the accumulation of toxic sulphide (Diaz and Rosenberg, 1995). High organic loads usually has negative effects on the abundance and diversity of zoobenthic communities and causes massive benthic fauna mortality and/or disappearance of sensitive taxa (e.g. McLachlan, 1978; Villano and Warwick, 1995; Garcìa and Johnstone, 2006; Sun et al., 2014).

Most of the studies concerning the effects of eutrophication on meiobenthic communities have been conducted on sheltered coastal systems (McLachlan, 1978; Villano and Warwick, 1995; Garcìa and Johnstone, 2006), or by *in situ* (Neira and Rackemann, 1996; Gambi et al., 2009; Bohórquez et al., 2013) or laboratory experiments (Wang et al., 2011). Reduced sediment layers, due to a dramatic fall in oxygen levels following algal blooms, frequently occur in sheltered beaches whereas open sandy beaches generally remain well oxygenated (McLachlan, 1978, 1985). In these cases, the effect of eutrophication on the macrobenthic communities may be subtle although objective (Quillien et al., 2015a, 2015b) while they can cause significant increase in meiofaunal abundance and diversity (Koop and Griffiths, 1982; Giere, 2009).

4.1 Effect of Ulva bloom on meiobenthic communities inhabiting open sandy beaches.

In the present study, the impacted beach of Saint Nic demonstrated overall higher values in meiofaunal standing stock (i.e. abundance and biomass) and diversity (i.e. number of major taxa). Total meiofaunal abundance appeared to be positively affected by the presence of *Ulva*, while the total biomass was subjected to the natural seasonality of meiofauna communities with lower values during winter (e.g. Alongi, 1990; Guidi-Guilvard and Buscail, 1995), independently of the presence/absence of *Ulva* mats. A variety of factors are considered to control seasonal oscillations in benthic standing stock and feeding mode such as temperature fluctuation, and food availability (Ólafsson and Elmegren, 1997; Garcìa and Johnstone, 2006; Liu et al., 2008). Seasonal fluctuation in algal abundances, for instance, can imply a shift in meiofaunal diets and ingestion of other food sources, such as bacteria (Pascal et al., 2009).

Meiofaunal abundance values reported from the Bay of Douarnenez (i.e. SN and AD beaches) were in the range of values documented for other pristine sandy beaches and sandy littoral sites from northern Europe and elsewhere (Gheskiere et al., 2002, 2004a; Kotwicki et al., 2005 and literature therein). Abundance values found in this study were higher when compared to those from sheltered impacted sandy beaches (e.g. Garcìa and Johnstone, 2006) by macroalgal blooms. The depletion of oxygen in Moreton Bay (Garcìa and Jonhnstone, 2006), not reported in our case of study could explain the lower values in the meiofaunal abundance when compared to SN and AD.

The presence of *Ulva* mats could only partially explained the variability in meiofaunal community structure, which also highlighted a certain seasonality. The significant interaction of the two factors ‘beach’ and ‘month’ explaining the variation of meiofaunal community composition suggests that the effects of the presence of GT (factor sites) depends on the month (factor time). The dominance of nematodes, as the most ubiquitous and tolerant taxon, followed by copepods has been described as a classic feature for meiofauna inhabiting many marine habitats (Gheskiere et al., 2004a, 2004b; Giere, 2009). All the remaining taxa, even if scarcely represented (1-9%), were usually found characterizing sandy beach systems (Gheskiere et al., 2002, 2004a; Kotwicki et al., 2005; Albuquerque et al., 2007) e.g. the high relative abundance of Platyhelminthes particularly during winter time (McLachlan, 1978; Rzeznik-Orignac et al., 2003). Gastrotricha and Tardigrada, the most sensitive taxa which are generally strongly affected by a stressed environment (Zeppilli et al., 2015) never appeared at the impacted beach of SN. Nevertheless, other taxa such as Bivalvia, Halacaridae, Ostracoda, Cumacea and Amphipoda, usually found characterizing not impacted systems (e.g. Kotwicki et al., 2005; Gambi et al., 2009; Wang et al., 2011), were reported from the impacted beach of SN.

No clear negative effect of *Ulva* mats on meiobenthic community structure was demonstrated. Meiofaunal diversity (i.e. number of major taxa) was highest at SN during December, when *Ulva* biomass showed minimum biomass value. While at AD meiofaunal diversity decreased from warmer to colder months. Carriço et al. (2013) reported a negative effect of stranded *Ulva* on meiofauna composition, with number of higher taxa depressed at the impacted beach of Saint Nic (i.e. only three taxa identified), but authors did not consider the seasonal variability. When considering a longer time scale (present study), such a negative effect was far from evident. As already reported from the macrofaunal community studies (Quillien et al., 2015a), our findings indicated that meiofauna community structure and diversity were dependent both on time of the year and on the beach system considered. Results on meiofaunal standing stock, community composition and diversity supported the hypothesis of an *Ulva* effect on meiobenthic populations. This effect, somehow subtle, may not be regarded as negative, especially from sheltered sandy beach systems (e.g. McLachlan, 1978; Evans, 1993; Villano and Warwick, 1995).

Our second hypothesis, regarding the different effect of seasonality on meiobenthic communities at impacted and unimpacted beaches, is also only partially verified. Indeed, the total meiofaunal biomass changed seasonally at both beaches and showed lower values during winter time. For other meiofaunal descriptors, such as meiofaunal community structure and diversity, the seasonality was less evident and the effects of the presence of GT (factor sites) are not the same depending on the month (factor time). A similar subtle response was reported by Quillien et al. (2015a) for macrobenthic communities inhabiting open sandy beaches. They sustained the theory of intermediate disturbance (Connell, 1978), in which benthic communities have a positive response to a moderate disturbance by an increase in abundance and diversity (see for example Pearson and

Rosenberg, 1978). It appears that open sandy beach systems would be able to support high stranded biomass of algae while avoiding reduced conditions in the sediments and thus a direct, strong disturbance effect on meiobenthic communities.

4.2 Nematode structural and functional response to green macroalgal bloom

Nematodes, the dominant meiofaunal taxon (from 50 to over 90% of the total meiofauna abundance; Merckx et al., 2009), have been largely utilized as indicators of high organic loads especially when investigating the response of systems subjected to eutrophication phenomena (e.g. Gambi et al., 2009; Moreno et al., 2011; Wang et al., 2011; Sun et al., 2014; Bianchelli et al., 2018). Strong changes in nematode structural and functional diversity, assemblage composition and trophic structure occur under various scenarios of organic enrichment (Mirto et al., 2002; Moreno et al., 2008; Semprucci et al., 2015; Franzo et al., 2018). In some studies (e.g. Villano and Warwick, 1995; Gambi et al., 2009), nematode species richness was not affected during algal bloom and under hypoxic-anoxic conditions deriving from high organic loads, while beta-diversity and functional diversity changed drastically. Nematode genera such as *Rhabditis*, *Diplolaimella* and *Diplolaimelloides* were reported in extreme high abundances associated with decaying algae/plant material (Villano and Warwick, 1995; Franzo et al., 2018; Bertocci et al., 2019). Some studies reported an increase in nematode abundances under high-organic enrichment (Wang et al., 2011; Bohórquez et al., 2013), whereas other studies reported a decline in nematode and/or meiofaunal abundance values under such conditions (Neira and Rackemann, 1996; Garcìa and Johnstone, 2006). Usually, the decline in meiofauna abundance coincided with an oxygen depletion going deeper into the sediments or with formation of black spots indicating reduced oxygen concentration in surface sediments.

Nematode structural diversity (i.e. SR, H, $ES_{(51)}$) was not affected by *Ulva* mats and nematode species richness was comparable between the impacted (SN) and unimpacted (AD) sites, as reported by Carriço et al. (2013). Nematode diversity indices were in range with values from pristine sandy beach systems (e.g. Rzeznik-Orignac et al., 2003; Liu et al., 2008) and appear to be higher than values reported from highly organic enriched systems (e.g. Villano and Warwick, 1995; Jouili et al., 2017; Bianchelli et al., 2018). The high values in the nematode species evenness (J), especially at the impacted beach of SN, underlined the lack of strongly dominating species, such as tolerant nematode species, as may be expected for stressed environments (Steyaert et al., 2007). All these findings suggest that changes induced by the presence of *Ulva* mats have a minor impact in terms of structural diversity (α-diversity).

Seasonal changes were evident in nematofauna composition at both beaches, suggesting that these changes were not exclusively linked to *Ulva* cycles as may have been reported in previous studies (Villano and Warwick, 1995). In fact, not only *Ulva* biomass, but most of the environmental variables considered could help to explain the seasonal variability in nematode community composition. The variation of environmental factors such as sediment type, organic matter content, salinity and seawater temperature are fundamental factors that govern species composition inhabiting sandy beaches (Schratzberger and Warwick, 1998, 1999).

Stranded *Ulva* alone had significant effects on nematode community composition, mainly in promoting a high turnover diversity. Indeed, the presence of a high number of unique species at both sandy beaches (24 at AD and 21 at SN) indicated a high β-diversity in nematode composition, even though α-diversity was comparable between sites (Carriço et al., 2013). The presence vs. absence of *Ulva* mats may generate the spatial heterogeneity between the two sandy beaches necessary to support the high β-diversity in nematode composition. This would not be detected when merely considering the α-diversity, as the α-diversity usually does not reflect the β-diversity (Gambi et al., 2014).

Richtersia spp., abundant at the unimpacted beach of Anse de Dinan generally inhabits un-impacted systems and is a proxy for good environmental status (Moreno et al., 2011). At the impacted beach, the most represented genera *Microlaimus*, *Viscosia* and *Marylynnia* were reported as less sensitive genera, tolerant to high organic loads and proxy of a moderate quality status of the system (Jouili et al., 2017; Franzo et al., 2018; Bianchelli et al., 2018). Nevertheless, other opportunist and more tolerant genera known to be proxy of a poor environmental quality status were found at both beaches, e.g. *Daptonema*, *Parodontophora* and genera belonging to the family Chromadoridae, Desmodoridae and Xyalidae (Gambi et al., 2009; Moreno et al., 2011; Jouili et al., 2017). Many other genera reported from unimpacted sandy beach systems in the northern Europe (Gheskiere et al., 2000, 2002) characterized Anse de Dinan and/or Saint Nic beaches: *Andoncholaimus, Axonolaimus, Chromadorita, Comesoma, Daptonema, Leptolaimus, Metadesmolaimus, Oncholaimellus, Theristus* and *Trichotheristus.*

The presence of stranded *Ulva* sustained higher functional diversity at Saint Nic where all feeding types were represented equally. The presence of all feeding types indicates the input of a broad spectrum of potential food sources, e.g., microbes (involved in decomposition processes; Wang et al., 2011), detritus, freshly stranded *Ulva*, available for nematodes and all other meiofauna taxa

(McGwynne and McLachlan, 1988). Nematofauna can use, both directly and indirectly through one or more trophic intermediates, a wide range of food sources in vegetated sediments e.g., microphytobenthos, seagrass detritus, benthic bacteria and sediment particulate organic matter (Vafeiadou et al., 2014; Moens et al., 2014b; van der Heijden et al., 2019). Riera and Hubas (2003) highlighted that stranded macroalgae is another potential primary food source for meiobenthic populations inhabiting sandy beaches, thereby demonstrating that *Ulva* could directly or indirectly, through microbial loop, fuels the benthic food web. The higher relative abundance of predators at SN could be explained by a higher presence of their potential preys (other meiofauna and small macrofauna) which themselves rely on the organic enrichment associated with stranded *Ulva* (according to Jensen, 1987). Moens et al. (2014b) stated that the guts of predators can sometimes be filled with diatoms from direct grazing or from the gut contents of the nematode's prey. The high amounts of organic material derived from stranded *Ulva* enriched the growth of diatoms and ciliates which in turn contributed significantly as a food source to epistrate feeders (Pascal et al., 2009; Lebreton et al., 2011), a well represented group at SN. At the beach of Anse de Dinan the non-selective deposit feeders dominated and they were mainly represented by *Richtersia* spp; the dominance of deposit feeders is common in open sandy beaches (Gheskiere et al., 2004b) that consist of sediments rich in organic detritus (Jouili et al., 2017 and literature therein). In particular, this feeding behavior coupled with the prompt reaction of *Richtersia* to a pulsed food supply (Vanaverbeke et al., 2004), contribute to the success of the genus (Peters and Wassenberg, 1983; Moens and Vincx, 1997).

No seasonal changes were observed for the trophic structure, despite the seasonal turnover in nematode species composition. The presence vs. absence of *Ulva* mats, coupled with seasonal changes in environmental features, affected the nematode structural (species composition) diversity over time but not their functional diversity. Differently from previous studies (Semprucci et al., 2010, 2018), nematode functional diversity did not mirror their taxonomical diversity and thus these parameters provided different information on nematode communities inhabiting sandy beaches.

Open macrotidal sandy beaches are highly dynamic systems, physically stressed by waves, tidal currents and mobile sediments (McLachlan and Brown, 2006). Accordingly with Bongers's model, the r–strategists were more abundant when the hydrodynamic stress was strong. At both impacted and un-impacted beaches, c-p values between 2 and 3 were reported indicating 'r-strategy' nematode communities with relatively short life-cycles and high colonization abilities. Such life strategies were in line with the equal repartition of nematodes into juveniles and adults (male and female), suggesting a reproductive-active population of nematodes (Giere, 2009).

The Pearson-Rosenberg model (Pearson & Rosenberg, 1978) describes three successive steps of the effects of organic enrichment on qualitative characteristics of benthic communities. This depends on the organic input: 1) if organic loading increases only slightly, species abundances and biomass values increase; 2) further increase of organic input favors opportunistic organisms; 3) even more organic loading leads to disappearance of zoobenthic organisms and appearance of 'azoic' sediments. The impacted beach of Saint-Nic could be placed between step 1 and 2 of the Pearson-Rosenberg model, with an overall increas in the meiofauna standing stock, turnover diversity and promoting colonizers (i.e. opportunistic nematofauna communities). McGwynne et al. (1988) reported a similar observation describing the response of meiofaunal community inhabiting Australian exposed sandy beaches impacted by stranded macroalgae. Therefore, the beach of Saint-Nic can be seen as a system in which a balance between food and oxygen availability is reached approaching the ‘optimum point’ (McGwynne et al., 1988): abundance of food coincides with well oxygenated environment and other favorable features (e.g. grain size). In this case, *Ulva* mats does not disturb meiobenthic populations but rather stimulate species that are able to thrive on these new carbon sources.

4.3 Ulva bloom effect on meio- and macrofauna communities: a comparison

Quillien et al. (2015a) investigated the spatio-temporal variation in the distribution of macrofauna standing stock and diversity from open sandy beaches impacted and un-impacted by *Ulva* bloom, where two of those beaches corresponded to the beaches of Saint-Nic and Anse de Dinan. Conditions affecting the meiofauna are somewhat different from those affecting the macrofauna (Wang et al., 2011). Therefore, the response of meio- and macrofauna communities inhabiting open sandy beaches impacted by stranded macroalgae has been reported as different (e.g. McLachlan, 1985), or comparable (e.g. Koop and Griffiths, 1982).

The spatio-temporal changes detected for both meio- and macrofauna community composition inhabiting the investigated sandy beaches indicated that the community structure of both benthic components was dependent on beach and time (i.e. seasonal variability).

For both benthic components the response to dense *Ulva* mats was subtle and not as obvious as it may have been expected, with drastic decrease in diversity or mortality in zoobenthic communities (Neira and Rackemann, 1986; Bolam et al., 2000; Gambi et al., 2009). As reported above, an explanation could be that the highly dynamic nature of open sandy beaches, that somehow prevents the hypoxic-anoxic sediment conditions.

Quillien et al. (2015a) invoked the Pearson-Rosenberg model (Pearson & Rosenberg, 1978) to explain the observed macrofauna patterns and the concept of the intermediate disturbance (Connell, 1978), which agreed with the meiofauna and nematofauna standing stock and diversity patterns. Shifts in macrobenthic community composition and functional diversity (trophic groups; Quillien et al., 2016) between the impacted and unimpacted sandy beaches were also observed for the meiobenthos, in particular the nematofauna. For the meiofauna we did not detect the decrease in β-diversity in the presence of homogenous coverage of *Ulva*, conversely to macrofaunal community composition. This may be related to the fact that we did not consider a gradient of increasing coverage of stranded *Ulva* in our investigation, as in Quillien et al. (2015a), but a 'simple' comparison between a state with and without *Ulva*. Moreover, an heterogeneous coverage of *Ulva* in SN, instead of homogeneous *Ulva* mats, probably promoted the spatial heterogeneity and sustained the nematode diversity. The faster turnover rate of the meiobenthic population compared to the macrofauna (Balsamo et al., 2012; Semprucci et al., 2015), coupled with the ability of nematodes to adjust to all kind of environments (Tahseen, 2012), could have enhanced the high spatio- (impacted vs. un-impacted beach) and temporal turnover diversity in nematode communities.

5. Conclusions

- The response of meiobethic community to macroalgal bloom is strictly linked to the system considered. When eutrophic conditions are not associated with long-lasting O_2 depletion/limitation, meiofaunal abundance and diversity may eventually increase. As for macrofaunal communities, a minor response of meiofauna and nematofauna to *Ulva* accumulation is observed and the impact is not evident as previously reported for sheltered systems.
- As for the macrofauna (Quillien et al., 2015a), the Pearson-Rosenberg model (Pearson & Rosenberg, 1978) and the concept of the intermediate disturbance (Connell, 1978) can be used to explain the meiofauna response to *Ulva* mats affecting open sandy beaches.
- Overall, the presence of *Ulva* positively affects meiofaunal abundance, structural and functional diversity and supports the high values of β-diversity.
- Natural seasonal changes in meiofaunal biomass and composition are evident at both beaches. Changes in environmental features partially explain the variability in meiofauna and nematodes structural and functional diversity at the beaches of Saint-Nic and Anse de Dinan.

Acknowledgments

This study was supported by the national interdisciplinary Ecosphère Continentale et Côtière EC2CO-INSU MAVERIQ, the Région Bretagne and the Université de Bretagne Occidentale.
The authors thank Vincent Le Garrec, Marion Maguer, Gauthier Schaal, Sylvie Castay and Sandrine Laurand who helped in sampling and in the laboratory work.

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Tables

Table 1 Environmental characteristics of the two beaches (Anse de Dinan and Saint Nic) sampled during three different periods: May, July and December 2012 (Quillien et al., 2015a). Abbreviations: SWT= seawater temperature; O_2= dissolved oxygen; WH= wave height; MGS= median grain size; OM= organic matter; SI= sorting index.

Beach	Month	SWT (°C)	Salinity	O_2 (%)	*Ulva* biomass (10^3kg)	WH (m)	MGS (µm)	OM (%)	SI
Anse de Dinan	May	14.08	35.39	106.55	0.00	0.70	240	4.90	1.31
Anse de Dinan	July	18.92	35.04	105.25	0.00	1.37	195	4.39	1.41
Anse de Dinan	December	8.70	33.93	102.63	0.00	1.61	180	4.01	1.36
Saint Nic	May	13.30	35.56	106.66	1352.31	0.70	170	4.80	1.11
Saint Nic	July	21.43	34.69	108.07	1445.76	1.65	150	4.45	1.07
Saint Nic	December	8.17	34.60	100.06	100.00	1.91	150	3.19	1.18

Table 2 Meiofaunal abundance, biomass, diversity (as number of higher taxa), nematode maturity index (MI) and sex percentage contribution values at impacted (Saint Nic) and un-impacted (Anse de Dinan) beaches. Abbreviations: SR = species richness , H = Shannon index of diversity , ES = expected species number, J = equitability index, M = male, F = female, GF = gravid female , Ju. = juvenile.

Year	Month	Beach	Replicate	Abundance (ind. 10cm^{-2})	Biomass (µgC/10cm^{2})	n° taxa	SR	H (log$_e$)	ES$_{(51)}$	J	MI	M %	F %	GF %	J %
2012	May	AD	1	372.7	53.2	7	18	2.1	14.0	0.7	2.67	23	37	8	32
	May	AD	2	394.8	52.1	5	22	2.3	16.2	0.8	2.49	23	37	8	32
	July	AD	1	196.4	32.0	5	15	2.2	13.2	0.8	2.62	22	48	9	21
	July	AD	2	247.3	40.5	4	18	2.3	14.0	0.8	2.51	22	48	9	21
	December	AD	1	365.0	15.0	2	19	2.0	12.2	0.7	0.89	23	10	1	65
	December	AD	2	284.7	12.5	4	26	2.4	15.6	0.7	1.16	28	20	2	51
2012	May	SN	1	646.9	75.3	4	18	2.5	15.0	0.9	2.20	22	50	5	23
	May	SN	2	633.8	53.9	4	24	2.9	19.5	0.9	2.55	22	50	5	23
	July	SN	1	796.4	62.5	5	16	2.4	13.4	0.8	2.39	27	34	10	29
	July	SN	2	1071.3	119.6	5	18	2.4	14.1	0.8	2.36	27	34	10	29
	December	SN	1	209.8	10.4	9	16	2.2	12.6	0.8	1.01	34	31	4	30
	December	SN	2	627.6	24.9	6	19	2.3	13.5	0.8	1.33	38	30	5	27

Table 3 Results of PERMANOVA testing variations (A) meiofaunal standing stock (i.e. abundance and biomass), community structure and diversity (i.e. n° taxa) and (B) nematode diversity indices and species composition. dF = degree of freedom; MS = mean square; F = F statistic; ** = P < 0.01; * = P < 0.05; ns = not significant. Abbreviations: Be = beach, Mo = month, MI = maturity index, J = equitability index, ES = expected species number , H = Shannon index of diversity, SR = species richness.

A)	Source	df	MS	F	P	% explained variance	**B)**	Source	df	MS	F	P	% explained variance
Meiofauna abundance	Beach	1	5.2	5.2	**	46.6	ES$_{(51)}$, H, SR	Beach	1	0.0	0.0	ns	-14.3
	Month	2	1.2	0.6	ns	4.5		Month	2	39.1	19.5	ns	20.6
	Be x Mo	2	2.8	1.4	ns	31.9		Be x Mo	2	21.1	10.6	ns	2.5
	Residual	6	1.8	0.3		17.1		Residual	7	69.9	10.0		91.3
Meiofauna biomass	Beach	1	1.7	1.7	ns	16.1	J	Beach	1	20.0	20.0	*	50.8
	Month	2	5.7	2.9	*	44.5		Month	2	6.7	3.4	ns	3.6
	Be x Mo	2	1.5	0.8	ns	15.1		Be x Mo	2	4.8	2.4	ns	-1.3
	Residual	6	2.1	0.3		24.3		Residual	7	17.7	2.5		46.9
Meiofauna community structure	Beach	1	1654.4	1654.4	**	27.2	MI	Beach	1	0.0	0.0	ns	-0.6
	Month	2	2721.7	1360.9	**	32.6		Month	2	0.7	0.4	**	95.1
	Be x Mo	2	1067.9	533.9	*	19.2		Be x Mo	2	0.0	0.0	ns	0.6
	Residual	6	1133.5	188.9		21.0		Residual	6	0.0	0.0		4.9
n° Taxa	Beach	1	203.3	203.3	*	25.5	ITD	Beach	1	0.1	0.1	**	94.5
	Month	2	10.7	5.3	ns	-2.9		Month	2	0.0	0.0	ns	2.1
	Be x Mo	2	332.8	166.4	*	61.3		Be x Mo	2	0.0	0.0	ns	-2.9
	Residual	6	116.1	19.3		16.1		Residual	6	0.0	0.0		6.3
							Sex % contribution	Beach	1	3.3	3.3	**	9.1
								Month	2	19.1	9.5	**	41.5
								Be x Mo	2	10.6	5.3	**	44.8
								Residual	6	1.6	0.3		4.6
							Species	Beach	1	7033.3	7033.3	**	27.5

composition	Month	2	12814.0	6407.1	**	37.0
	Be x Mo	2	3792.6	1896.3	**	15.2
	Residual	7	5137.9	734.0		20.3

Table 4 Results of SIMPER tests assessing the dissimilarity levels in the nematode species composition among beaches (Anse de Dinan and Saint Nic) and sampling times. The first ten species that contributed mostly to the dissimilarity are reported.

Contrast	Dissimilarity %	Responsable species
AD vs SN	64.5	*Richtersia sp1, Richtersia sp2, Richtersia sp3 Promonhystera sp1, Microlaimus sp1, Viscosia sp1 Marylynnia sp1, Onyx sp1, Xyala sp1 Parodontophora sp1*
May vs July	44.9	*Richtersia sp3, Neochromadora sp1, Viscosia sp2 Thalassinorus sp1, Chromadorita sp1, Trichotheristus sp2 Daptonema sp1, Microlaimus sp2, Paracomesoma sp1 Richtersia sp1*
May vs December	75.4	*Omicronema sp1, Daptonema sp1, Trileptium sp2, Metadesmolaimus sp1, Microlaimus sp3, Molgolaimus sp2, Endeolophos sp1, Molgolaimus sp1, Diodontolaimus sp1, Viscosia sp2*
July vs December	75.4	*Omicronema sp1, Molgolaimus sp1, Promonhystera sp1 Trileptium sp2, Metadesmolaimus sp1, Molgolaimus sp2 Endeolophos sp1, Microlaimus sp3, Diodontolaimus sp1 Odontophora sp1*

Table 5 Results of DistLM forward to assess the role of environmental variables on meiofauna standing stock, diversity (n° taxa), community structure, nematode species composition, trophic structure, maturity index (MI) and diversity ($ES_{(51)}$, H, SR). SS = mean square; F = F statistic; ** = $P < 0.01$; * = $P < 0.05$; ns = not significant. Abbreviations: SWT = seawater temperature; OM = organic matter; MGS = median grain size, $ES_{(51)}$ = expected species number, H = Shannon diversity index, SR = species richness.

	Variable	SS	F	P	Prop %	Cum. Prop %
Abundance	*Ulva*	1276.60	18.33	**	64.7	64.7
	SWT	29.03	0.39	ns	1.5	66.2
	O_2	29.02	0.36	ns	1.5	67.6
	OM	203.15	3.27	ns	10.3	77.9
	Salinity	13.70	0.20	ns	0.7	78.6
Biomass	SWT	1900.60	11.41	**	53.3	53.3
	Salinity	695.28	6.45	*	19.5	72.8
	O_2	307.77	3.72	ns	8.6	81.4
	Ulva	156.25	2.16	ns	4.4	85.8
	MGS	84.54	1.20	ns	2.4	88.2
	OM	0.00	0.00	ns	0.0	88.2
n° taxa	Salinity	245.93	6.52	*	37.1	37.1
	SWT	100.44	5.19	*	15.2	52.3
	O_2	81.99	2.55	ns	12.4	64.6
	OM	77.24	1.32	ns	11.7	76.3
	MGS	41.07	1.33	ns	6.2	82.5
Meiofauna community structure	*Ulva*	1803.90	6.44	**	39.2	39.2
	SWT	993.43	4.95	**	21.6	60.8
	O_2	366.24	2.03	ns	8.0	68.7
	OM	378.97	2.50	ns	8.2	77.0
	Salinity	299.45	2.36	ns	6.5	83.5
Nematode species	O_2	10567.00	5.53	**	33.5	33.5
	Ulva	6858.40	4.84	**	21.7	55.2

composition	Salinity	3788.80	3.29	**	12.0	67.2
	OM	2852.80	3.04	**	9.0	76.2
	SWT	1932.80	2.42	**	6.1	82.3
	MGS	0.00	0.00	ns	0.0	82.3
Nematode trophic structure	MGS	2312.10	10.46	**	51.1	51.1
	Salinity	546.94	2.96	*	12.1	63.2
	SWT	609.36	4.62	*	13.5	76.7
	OM	268.24	2.39	ns	5.9	82.6
	O_2	215.50	2.27	ns	4.8	87.4
MI	O_2	827.27	24.63	**	71.1	71.1
	Salinity	179.25	10.30	*	15.4	86.5
	SWT	83.63	9.16	*	7.2	93.7
	Ulva	18.52	2.38	ns	1.6	95.3
	OM	0.16	0.02	ns	0.0	95.3
$ES_{(51)}$, H, SR	OM	24.61	2.63	ns	19.3	19.3
	SWT	21.89	2.70	ns	17.2	36.4
	MGS	10.01	1.27	ns	7.8	44.3
	O_2	0.95	0.11	ns	0.7	45.0
	Ulva	0.26	0.03	ns	0.2	45.2
	Salinity	0.00	0.00	ns	0.0	45.2

Figure Captions

Fig. 1. Location (Brittany, France) of the two sampled sandy beaches: the un-impacted Anse de Dinan beach (control) and the impacted Saint Nic beach.

Fig. 2. Principal Component Analysis output based on environmental variables characterizing the two beaches, Anse de Dinan (AD) and Saint Nic (SN), over three sampling periods (May, July and December 2012). Abbreviations: WH = wave height; SI = sorting index; MGS = mean grain size; OM = organic matter; Sal = salinity; O_2 = percentage of oxygen; SWT = sea water temperature. Ordination of sampling stations using the first and second Principal Component.

Fig. 3. Total meiofaunal abundance (ind.10 cm^{-2}) (a) and biomass (µg C/10 cm^2) (b) at the beaches of Anse de Dinan (AD, light orange bars) and Saint Nic (SN, green bars) at different sampling periods (May, July and December).

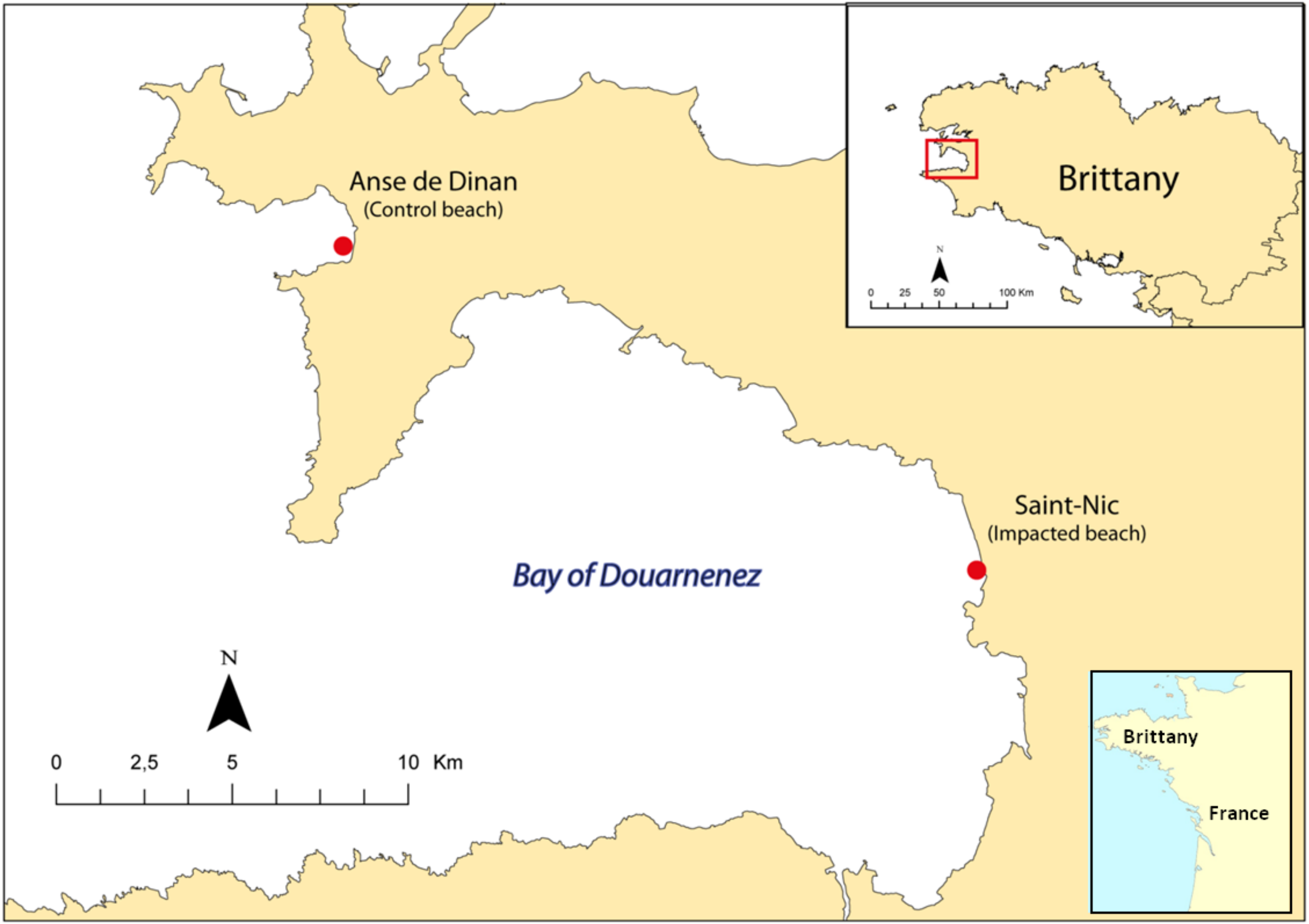
Fig. 4. Meiofaunal community structure characterizing Anse de Dinan (AD) and Saint Nic (SN) beaches over the three sampling periods. Contribution of each taxon (expressed as %) to the community composition with a focus on the contribution of the most abundant taxon of Nematoda (a) and with a focus on the contribution of taxa belonging to the group 'others' (b).

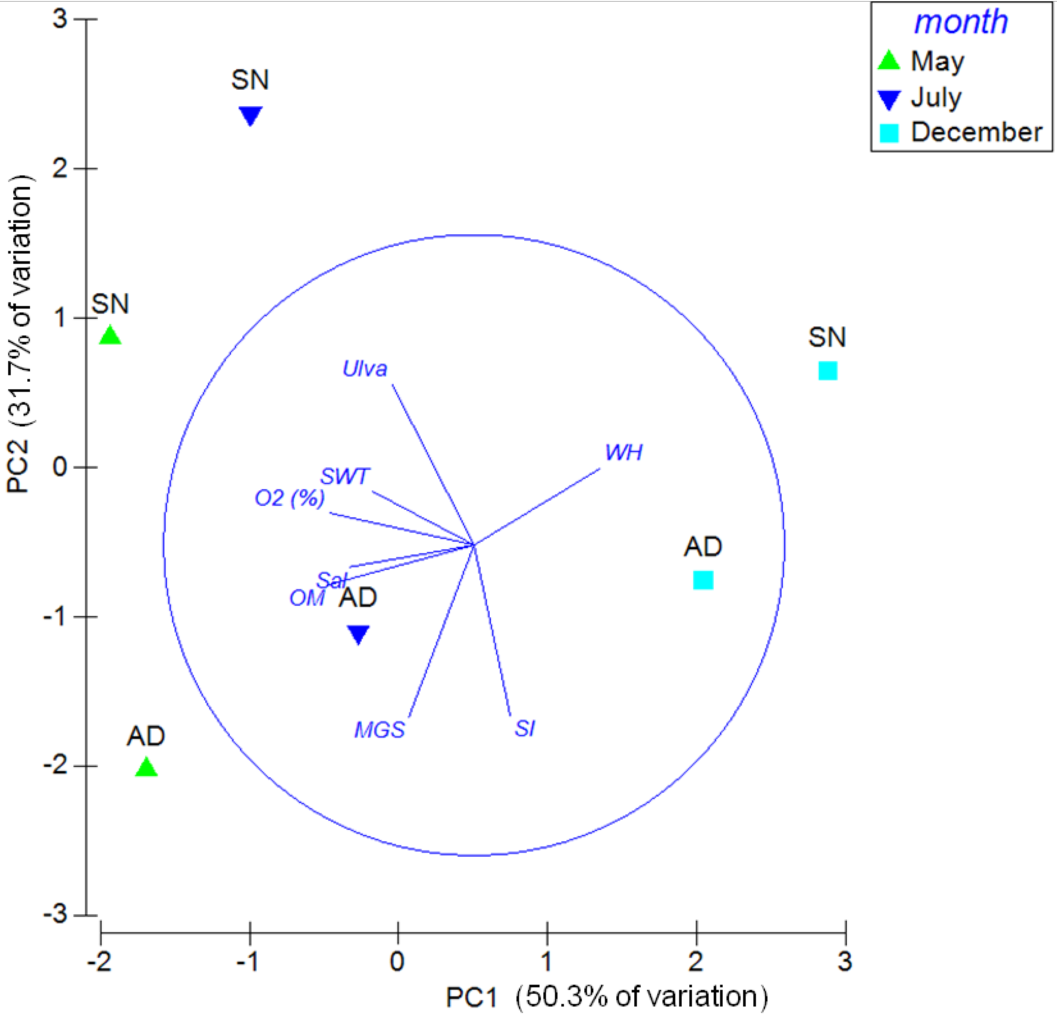
Fig. 5. Principal Component Analysis output based on meiofauna community structure at Saint Nic (SN) and Anse de Dinan (AD) beaches over three sampling periods (May, July and December). Ordination of sampling stations using the first and second Principal Component (PC).

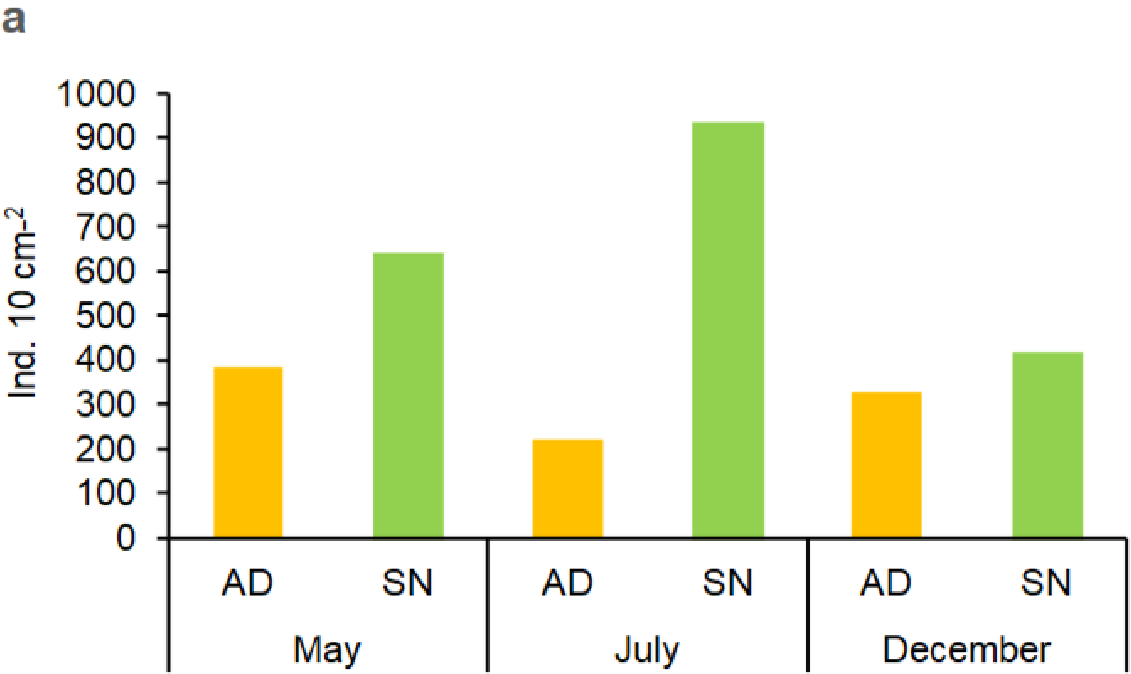
Fig. 6. nMDS of nematode assemblages characterizing Saint Nic (SN; impacted) and Anse de Dinan (AD; unimpacted) beaches over different sampling periods. All replicates are displayed.

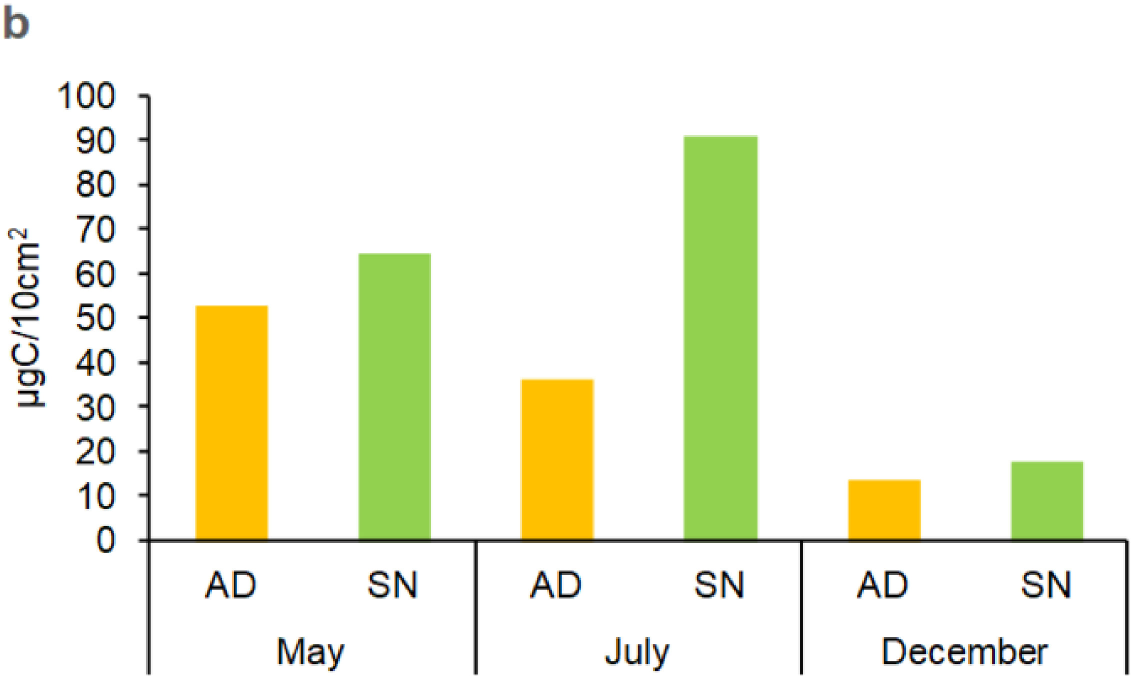
Fig. 7. Nematode trophic structure at Saint Nic (SN) and Anse de Dinan (AD) beaches over different sampling periods. The ITD (index of trophic diversity) values are reported at the top of the histogram bars. The contribution of each trophic group is expressed as % and based on nematode biomass. Abbreviations: 1A = selective deposit feeders; 1B = non-selective deposit feeders; 2A = epistrate feeders; 2B = predators/omnivores.

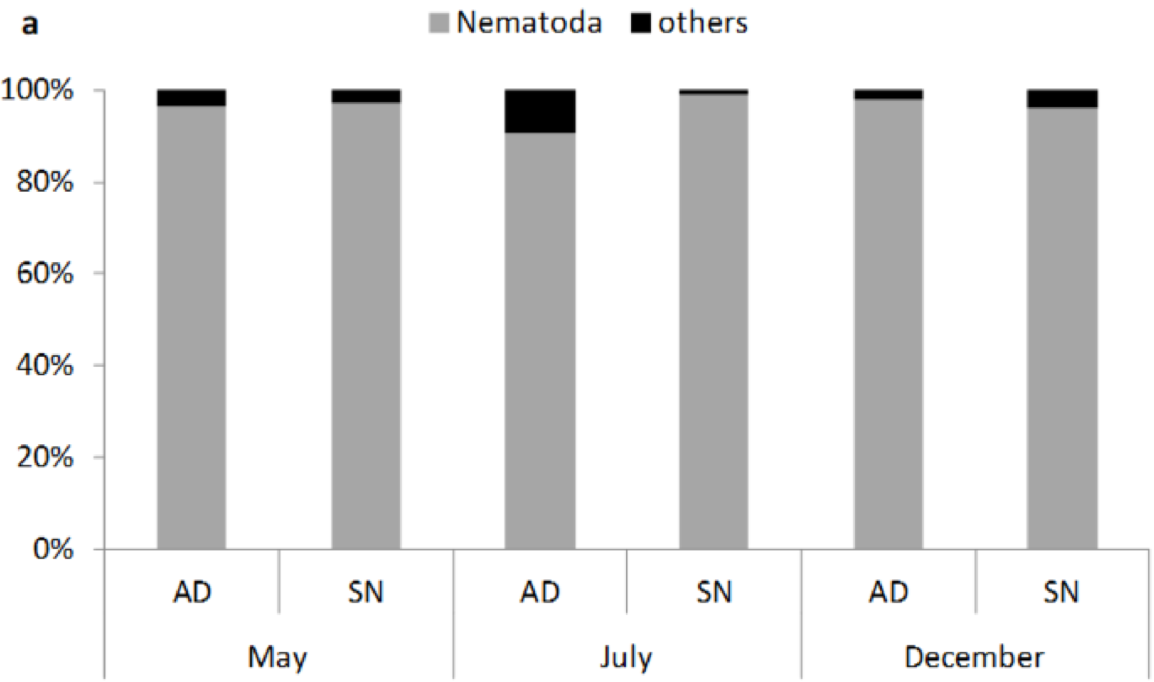
Fig. 8. DistLM (distance-based linear model) and dbRDA showing the effect of environmental variables on meiofaunal community structure. Abbreviations: AD = Anse de Dinan; SN = Saint Nic; dec = December. All replicates are shown.

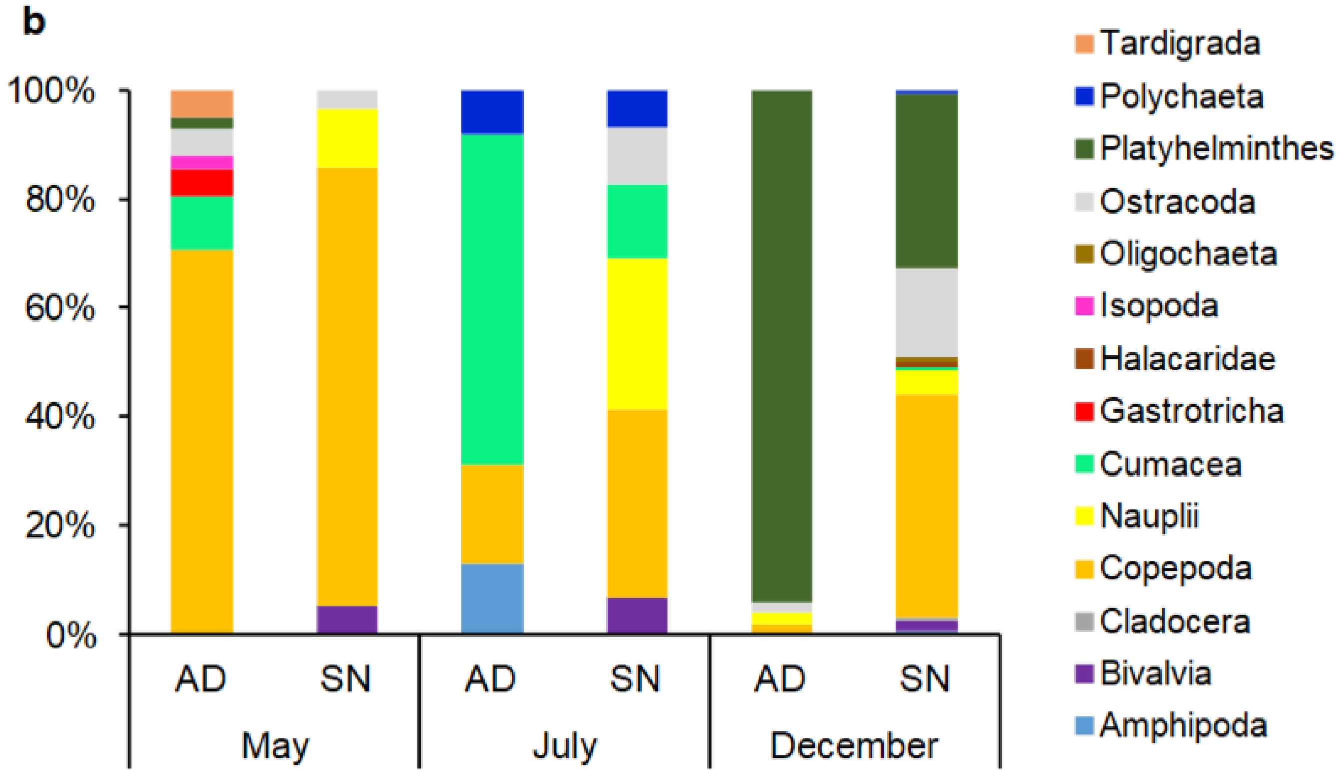

Anse de Dinan
(Control beach)
Saint-Nic
(Impacted beach)
Bay of Douarnenez
N
0
2,5
5
10
Km
Brittany
N
0
25
50
100 Km
Brittany
France

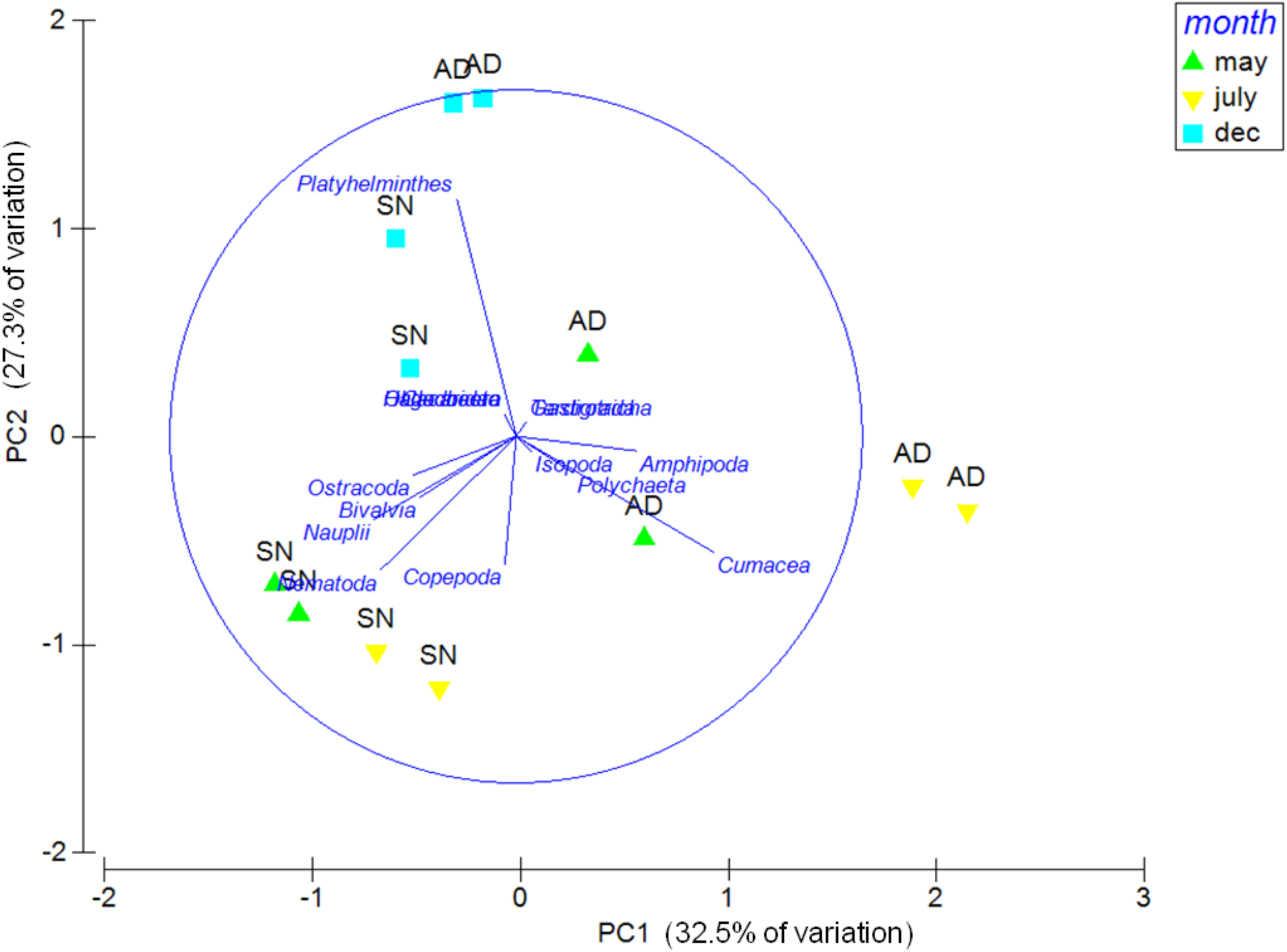

month
May
July
December
SN
SN
SN
AD
AD
AD
Ulva
WH
SWT
O2 (%)
Sal
OM
MGS
SI
PC2 (31.7% of variation)
PC1 (50.3% of variation)
3
2
1
0
-1
-2
-3
-2
-1
0
1
2
3

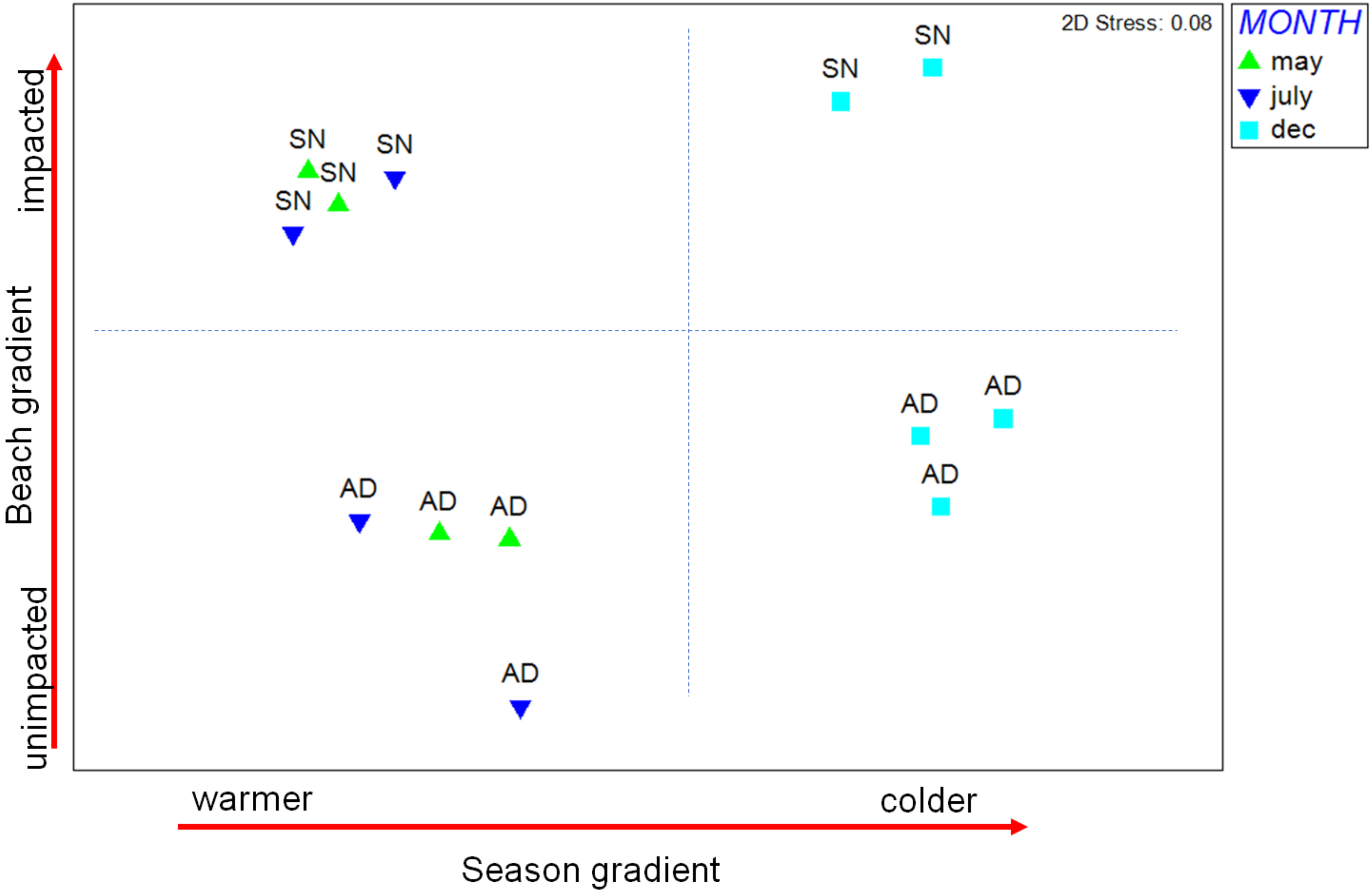

a
1000
900
800
700
600
500
400
300
200
100
0
Ind. 10 cm^{-2}
AD
SN
AD
SN
AD
SN
May
July
December

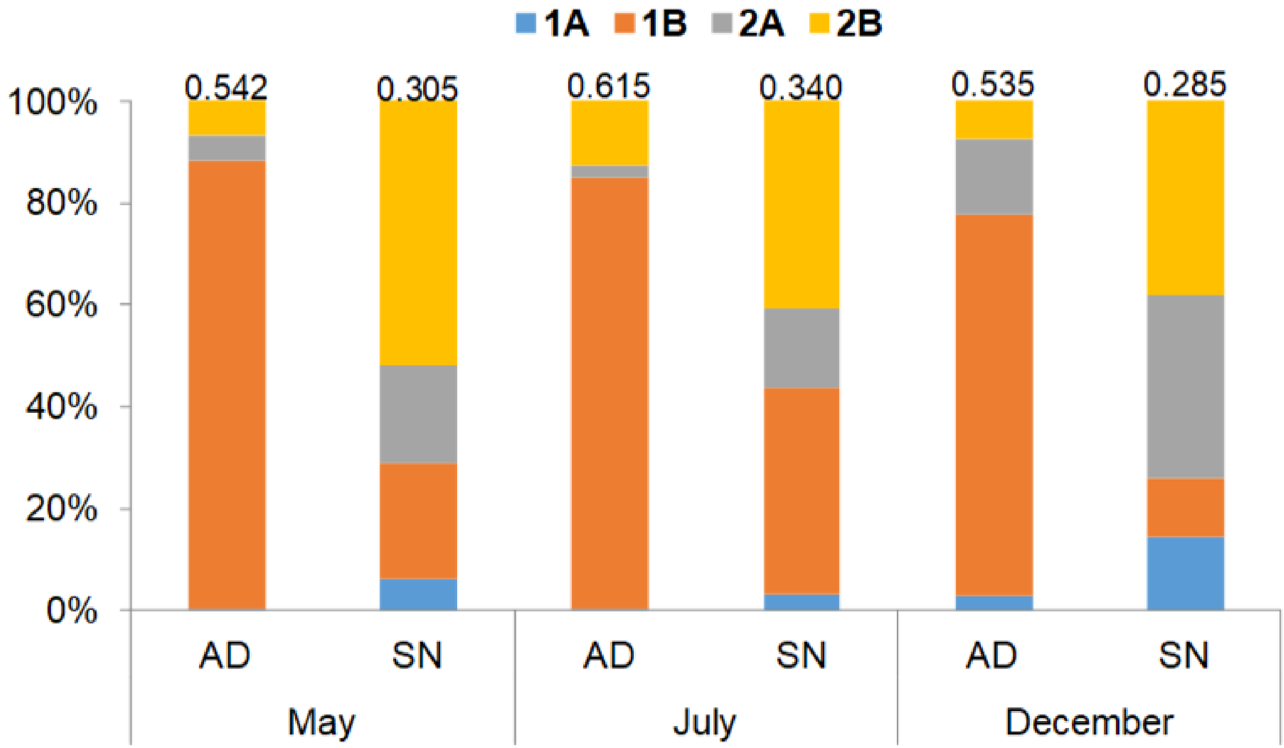

b
μgC/10cm²
100
90
80
70
60
50
40
30
20
10
0
AD
SN
AD
SN
AD
SN
May
July
December

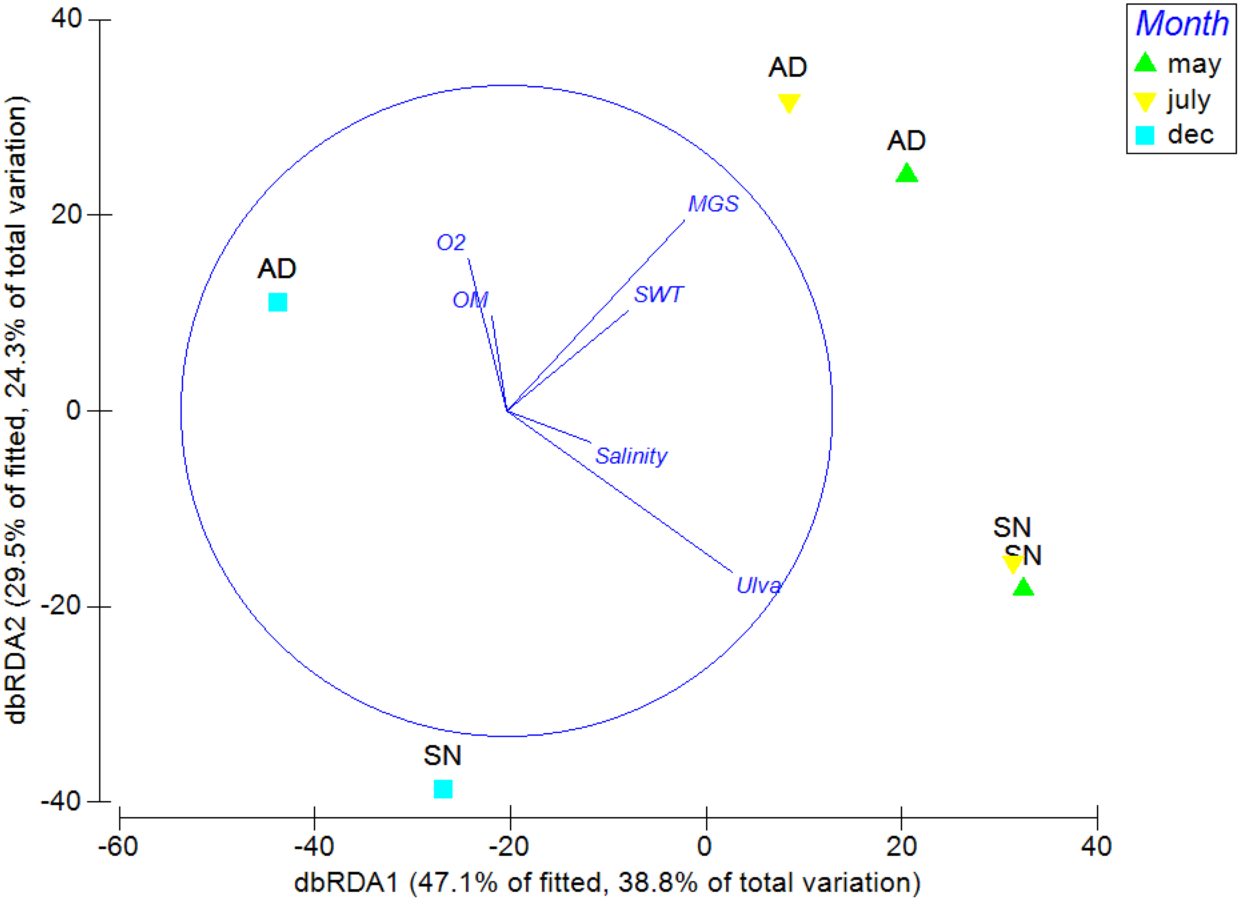

a
Nematoda
others
100%
80%
60%
40%
20%
0%
AD
SN
AD
SN
AD
SN
May
July
December


b
100%
80%
60%
40%
20%
0%
AD
SN
AD
SN
AD
SN
May
July
December
Tardigrada
Polychaeta
Platyhelminthes
Ostracoda
Oligochaeta
Isopoda
Halacaridae
Gastrotricha
Cumacea
Nauplii
Copepoda
Cladocera
Bivalvia
Amphipoda


month
may
july
dec
2
1
0
-1
-2
PC2 (27.3% of variation)
-2
-1
0
1
2
3
PC1 (32.5% of variation)
AD
AD
Platyhelminthes
SN
SN
AD
Isopoda
Amphipoda
Polychaeta
AD
Ostracoda
Bivalvia
Nauplii
SN
SN
Nematoda
Copepoda
Cumacea
SN
SN
AD
AD


2D Stress: 0.08
MONTH
▲ may
▼ july
■ dec
SN
SN
SN
SN
SN
SN
AD
AD
AD
AD
AD
AD
AD
impacted
Beach gradient
unimpacted
warmer
colder
Season gradient


1A
1B
2A
2B
0.542
0.305
0.615
0.340
0.535
0.285
100%
80%
60%
40%
20%
0%
AD
SN
AD
SN
AD
SN
May
July
December


Month
may
july
dec
AD
AD
AD
SN
SN
SN
MGS
O2
OM
SWT
Salinity
Ulva
40
20
0
-20
-40
-60
-40
-20
0
20
40
dbRDA1 (47.1% of fitted, 38.8% of total variation)
dbRDA2 (29.5% of fitted, 24.3% of total variation)