



Main Ecological Features of Benthic Macrofauna in Mediterranean and Atlantic Intertidal Eelgrass Beds: A Comparative Study

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Abstract

The present study compares the intertidal eelgrass macrofauna in two geographically and ecologically disparate localities (central Mediterranean and eastern Atlantic). Both coastal ecosystems are developed on extensive large mudflats with eelgrass beds, hosting a great diversity of water birds and providing important socio-economic assets. These two distinct and distant geographical ecosystems are affected by numerous anthropogenic pressures. By reflecting the response of the structure and functioning of benthic communities to climate change, the two eelgrass ecosystems provide a natural laboratory to investigate global warming. The macrobenthic fauna community of *Zostera (Zosterella) noltei* eelgrass beds was studied by sampling 34 stations in the Kneiss Islands and 48 stations in Arcachon Bay. A total of 148 species are identified in the Kneiss islands and 117 species in Arcachon Bay, but only 23 species are common to both ecosystems. Diversity, abundance and community structure are significantly different between the two study areas, which could be explained by differences between Mediterranean and Atlantic climatic conditions and by anthropic factors (e.g. fishing pressure, pollution, nutrient inputs) affecting each ecosystem. Multidimensional scaling (n-MDS) analysis identifies two distinct geographical station groups on the basis of species and family-level abundance. On the contrary, three assemblages are identified on the basis of trophic groups distributed between the separate ecosystems. In terms of ecological quality status, the Kneiss site appears to have a good ecological condition and hosts a variety of sensitive species. On the other hand, biotic indices indicate that the Arcachon site is moderately perturbed and that the benthic communities are unbalanced. It is expected that the present-day functioning of the Kneiss Islands ecosystem will become typical of the situation in Arcachon Bay in several decades time, with the development of warmer and drier conditions.

Keywords

Zostera noltei meadows; Benthic communities; Anthropogenic pressures; Climate warming; Kneiss Islands; Arcachon Bay

Introduction

Sheltered and semi-sheltered coastal ecosystems rank among the most productive and important aquatic ecosystems on Earth [1,2]. These complex environments fulfil several vital functions which play a key role in controlling biodiversity, such as nursery and feeding areas for fish and birds [3,4]. Coastal ecosystems are often formed by a mosaic of interlinked habitats that should not be considered in isolation. However, each habitat has its own characteristics and hosts particular benthic assemblages [5-7].

Eelgrass meadows are distributed in intertidal and subtidal areas from tropical to temperate zones [8-10], representing important ecological and economic components of coastal zones worldwide [11,12]. Eelgrass meadows provide high-value ecosystem services with among the highest levels of primary production for submerged aquatic communities [13]. As engineer species, they attract and support rich faunistic assemblages [14,15] providing food and refuge for many commercial species and enhancing nutrient cycling, water quality and sediment stabilization [16-18].

The Kneiss Islands (Central Mediterranean) and Arcachon Bay (North-Eastern Atlantic) are two coastal ecosystems sharing many similar features (Table 1). They both comprise extensive mudflats covered with *Zostera noltei* meadows, alternating with a network of shallow tidal channels [6,19,20]. They host a great diversity of water birds species with different ecological requirements, and have consequently been recognized as Important Bird Areas [21]. Indeed, more than 45,000 water birds belonging to 50 species have been counted yearly on the wetlands of the Kneiss Islands [22] and more than 115,000 individuals belonging to 66 species in Arcachon Bay [23].

Likewise, the intertidal areas are of both ecological and socio-economic interest, especially for traditional activities such as crustacean fishing, bait digging and clam harvesting [24] (Table 1). The latter activity is mainly artisanal in Tunisia and both artisanal and professional in France, plays an important economic role in both countries. For example, clam harvesting provides up to 45% of the total production in Tunisia [25], while ca. 40% of the aquaculture production of the Manila (Asari) clam *Ruditapes philippinarum* in France comes from Arcachon Bay [26].

Arcachon Bay has also developed intense activities involving oyster culture and tourism (including power boating), while the Kneiss Islands is subject to stronger influence from industrial fishing as well as artisanal bottom trawling which is banned in Arcachon Bay.

However, we consider that climate is the most significant factor which could impact the functioning of communities in these two broadly similar seagrass ecosystems, with the Kneiss Islands on average undergoing drier and warmer conditions than Arcachon Bay (Table 1). According to climate change predictions [27], warmer and drier conditions could prevail in Arcachon Bay in the future, leading to a situation comparable to the present-day Kneiss Islands. It is well accepted that climatic variation along latitudinal gradients provides an excellent natural laboratory to investigate the role of temperature and the potential impacts of climate warming at different sites [28-30]. Moreover, the climatic gradient is expected to have an even greater impact in intertidal/shallow systems than in deeper subtidal systems [31-33].

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The main aims of this study are: 1) to compare the structural assemblages and diversity of the benthic macrofauna community associated with *Zostera noltei* intertidal eelgrass beds in the Kneiss Islands and Arcachon Bay ecosystems based on taxonomic and ecological approaches as well as the study of trophic groups. While taxonomic differences are expected between contrasted biogeographic areas, this study focuses on similarities and proposes some possible

explanations (exotic species present in one area or in both, species with particularly extensive range worldwide, eventually related to efficient larval dispersal); 2) to provide a reliable assessment of the general ecological status in each ecosystem, testing different benthic indicators of ecological quality. The expected discrepancies between index values (between ecosystems but also within ecosystems) can help reveal the strengths and weaknesses of these indices in these

Table 1: General characteristics of Kneiss Islands, and Arcachon Bay.

	Parameters/ Ecosystem	Kneiss Islands, Tunisia	Arcachon Bay, France
Geomorphology	Latitude-Longitude	34°20'N,10°9'E	44°40'N,1°10'W
	Surface (km ²)	220	180
	Freshwater input (m ³ yr ⁻¹)	Low	1.25×10 ⁹
	Sea communication	Mediterranean Sea	Atlantic ocean
	Presence of islands	Four	One
	Intertidal flats (km ²)	147	117
	Tidal channels (km ²)	73	63
	Mean and maximal depth (m)	6 and 10	8 and 15
Climate Water body	Annual rain flow (mm)	180-200	800-900
	Tidal range (m)	0.3-2.3	0.9-4.9
	Temperature: mean (range) (°C)	22 (11-32)	15 (5-25)
	Salinity	37-41	25-35
	pH	7.80-8.15	8.2
	Dissolved oxygen (mg.L ⁻¹)	7-8	6-10
	Transparency: mean (range) (FNU)	3 (2-8)	2 (1-6)
Sediment	Organic matter (%)	3-7	0-10
	Sediment type	Mud & muddy sand	Sand & mud
	Schorre (km ²)	6	8
	Intertidal <i>Zostera noltei</i> (km ²)	68	70
	Subtidal angiosperms (km ²)	5	3
Status, vertebrate occurrence	National importance	Nature reserve	Marine National Park
	International importance	SPAMI, IBA, RAMSAR	IBA, Site Natura 2000
	Mammal and turtles	Dolphin, turtle	Seal
	Water birds (number of species)	50	66
Anthropic factors	Alien species (number)	139	50
	Shellfishing	Clam, razor clam, mussels, crustaceans	Clam, cockle, mussel, shrimp
	Finfishing	Present	Present
	Cephalopod fishing	Cuttle fish, octopus	Cuttle fish
	Bait digging	Present	Present
	Aquaculture	Fish	Oyster
	Bottom trawling	Present	Absent
	Oil pollution	Not significant	Not significant
	Nutrients input	Absent	Present
	Macroalgae blooms	Not significant	Locally, occasionally
	Phytoplankton blooms	Present	Present
	Toxic blooms	Present	Present
	Dredging & sediment deposition	Absent	Present
	Phosphate industry	Present	Absent
	Coastal urbanisation	Not significant	Significant
	Coastal tourism	Absent	Significant
	Large coastal towns	Absent	Significant
Agricultural activities	Not significant	Significant	
Tourism activities	Absent	Significant	
	Marinas	Absent	Present
	Commercial port	Skhira (hydrocarbons and phosphates)	Absent
	Fish port	One	One (small)

particular habitats (seagrasses); 3) to identify the role of the main environmental factors that determine the structure and functioning of the benthic community, using the latitudinal gradient to predict the response of benthic communities in these geographically distinct ecosystems; and 4) to compare one aspect of functional trait diversity (i.e. trophic diversity) in seagrass habitats of the Kneiss Islands and Arcachon Bay. This comparison aims to hierarchize the factors structuring benthic communities in seagrass environments, leading us to consider two main alternative hypotheses: either **i)** both areas display a similar trophic diversity, and we can assume that *Zostera noltei* is a highly effective engineer species structuring benthic functional diversity (in this case trophic functioning), independently of other factors (climate, anthropic activity, sediment grain-size, etc.); or **ii)** trophic guilds are contrasted between the two studied areas, suggesting that the presence of seagrass does not on its own ensure the stability of functioning of this habitat and that functioning of the benthic communities can be modified by global change independently of the physical presence of eelgrasses.

Materials and Methods

Study area

Kneiss islands: The Kneiss Islands are located in the Gulf of Gabès (South Eastern Tunisia), characterized by an extensive continental shelf (34°10'-34°30' N and 10-10°30'E) (Figure 1 and Table 1). Shoals of shallower depth are developed around four islets. The total surface-area of the studied area (220 km²) can be divided into two main sectors: the subtidal channels (maximum depth of 10 m) and the intertidal zone [20,34]. The tide is semi-diurnal, with amplitude varying from 0.3 to 2.3 m [35]. The seawater temperatures vary seasonally between 11.3°C to 32.0°C. The salinity ranges between 37 and 41 ppt, according to annual precipitation, which does not

exceed 200 mm, as well as inputs of freshwater from Ouadrane wadi during flood periods. At low tide, the Kneiss Islands are surrounded by vast mud and sand flats [36], with an abundant and diversified benthic macrofauna [20], making this site the most important area for wintering of migratory waders in the Mediterranean region [37]. The intertidal mudflats of the Kneiss Islands are colonized by *Zostera noltei* eelgrass beds (68 km²). Due to their marine biodiversity, the Kneiss Islands were established as a "Specially Protected Area of Mediterranean Importance" (SPAMI) in 2001, an "Important Bird Area" (IBA) in 2003 and designated as a "RAMSAR site" since 2007.

Arcachon Bay

Arcachon Bay is a triangular-shaped macro-tidal area situated on the South Western coast of France (44°40' N, 1°10' W) (Figure 1 and Table 1). It communicates with the Atlantic Ocean through a 2km wide channel. The tide is semi-diurnal, with amplitude varying from 0.8 to 4.6 m. The average sea water temperatures vary seasonally between 6°C and 22.5°C, and fluctuations in freshwater inputs from rivers and rainwater influence the water salinity, which ranges between 22 and 35. The total surface-area of the bay (180 km²) can be divided into two domains: the subtidal channels (63 km²), and the intertidal zone (117 km²). The main channels have a maximum depth of 25 m and are fed by a secondary network of shallower channels. The intertidal zone comprises sandy to sandy-mud flats, with most of their area (60%, i.e. 70 km²) being covered by *Zostera noltei* eelgrass beds (70 km²) [6,38]. The lagoon receives freshwater inputs mostly from the Leyre River, situated in the South-Eastern part of the Bay, which contributes 73% of the total annual freshwater inflow (813 million m³y⁻¹). Arcachon Bay represents a site of international interest in terms of ornithological diversity (Important Bird Area) [23] and Natura 2000 site.

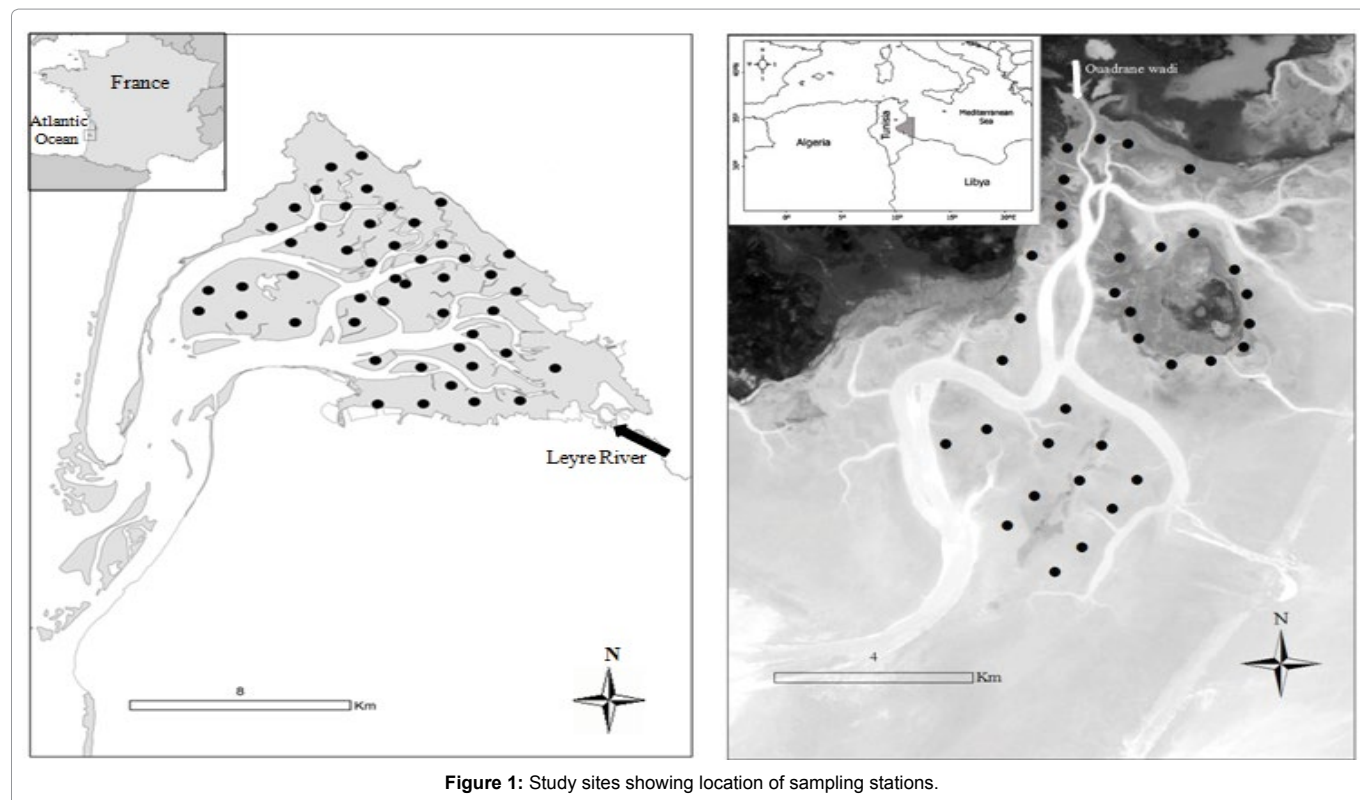


Figure 1: Study sites showing location of sampling stations.

Sampling procedure

The sampling method was similar for the two study areas. At low tide, the top 20-30 cm of the sediment was collected with a 0.0225 m² corer, covering a total sampling area of 0.09 m² (i.e. four replicates per station). Using an unbalanced design, a total of 34 and 48 stations were sampled during the spring campaigns of 2013 and 2014 (Figure 1) in the Kneiss Islands (Figure 1) and 2002 in Arcachon Bay, respectively, when the eelgrass beds fully extended over the tidal flats. Sediment was sieved through a 1-mm mesh; the retained fraction was fixed in 4% buffered formalin and stained with Rose Bengal. In the laboratory, the macrofauna was sorted, identified to the lowest possible taxonomic level (usually species level) and counted.

Sediment analysis and organic matter

The topmost 3 cm sediment layer was also sampled for grain-size analysis. Sediment from each sample was homogenized and wet-sieved through a 63 µm mesh to separate mud (including silt and clay) and sandy fractions (retained in the sieve). After being oven dried to constant weight at 60°C, sandy fractions were separated using a mechanical shaker (column of six sieves of mesh sizes 2000, 1000, 500, 250, 125 and 63 µm) during 10 min. All fractions (including <63 µm) were then weighed and their percentages determined. For the organic matter content analyses, sediment samples were dried at 60°C to constant weight and ground to a fine powder. Organic matter content was determined on the powder samples by 'loss on ignition' at 450°C for 4 h.

Data analysis

Univariate analysis: Faunal parameters were calculated at each station to compare the macrozoobenthic biodiversity and ecological status of the studied areas: abundance A (number of individuals per m²), species number S (number of species per 0.09 m²), Shannon-Wiener index H' [39] and evenness J' [40]. The abundance of trophic groups was compared to highlight differences in the functioning of the benthic food web among both eelgrass systems. Species were classified into six trophic groups: non-selective deposit feeders (NSDF; burrowers which ingest the sediment from which they take their food), selective deposit feeders (SDF; taxa feeding on organic particles on the sediment surface), suspension feeders (SF; taxa feeding on suspended food in the water column), carnivores (C; predatory animals), herbivores (H; species mainly feeding from macrophytes, and micro-grazers (µG; feeding on benthic microalgae, bacteria and detritus). Identified species were classified into trophic groups according to Fauchald and Jumars [41] and notably modified by Grall and Glémarec [42], Hily and Bouteille [43], Afli and Glémarec [44], Pranovi et al. [45], Afli et al. [46] and Jumars et al. [47].

One-factor ANOVAs (Analyses of Variance) were carried out to test the differences in the values of abundance (total abundance), species richness, diversity index and evenness between the samples from Kneiss Islands and Arcachon Bay (Table 2). A *post hoc* Tukey test ($p < 0.05$) was used for *a posteriori* multiple comparisons. Analyses to test the normality (Kolmogorov-Smirnov) and verify the homogeneity of variances (Barlett) were carried out prior to each ANOVA. A chi-square test was used to determine the significance of differences in phylum and the trophic-group abundance between the ecosystems. These statistical procedures were performed using the software SYSTAT 20 (SPSS).

Ecological indicators: Four currently available Benthic Indicators (BIs) were used, namely AMBI (AZTI Marine Biotic Index) [48], M-AMBI [49], BO2A (Benthic Opportunistic Annelids Amphipods Ratio) [50,51] and d-MISS (Macrobenthic Index in Sheltered Systems) [19,52]. The first three biotic indices (BIs) are based on a classification of species into ecological groups according to their level of sensitivity/tolerance to stress. AMBI (AZTI Marine Biotic Index) is based on previous studies by Grall and Glémarec [42]. It considers five ecological groups [53] ranging from sensitive species (EGI) to first-order opportunistic species (EGV) [48]. M-AMBI (Multivariate AMBI) combines AMBI with the Shannon diversity and species richness, which are very strongly dependent on habitat type and many other factors. The application of M-AMBI requires the definition of reference conditions related to the typology under study [49]. The BO2A (Benthic Opportunistic Annelids Amphipods index) is based on the ratio of opportunistic polychaetes (i.e. polychaetes of ecological groups IV and V of the AMBI) and amphipods (except for the genus *Jassa*). The d-MISS (Macrobenthic Index in Sheltered Systems) index is a multimetric approach using 14 metrics describing the biological integrity of the macrobenthic fauna [19,54].

Multivariate analysis: Multivariate analysis was performed to compare the macrozoobenthic community structure of the two areas. Abundances were square-root transformed to minimize the influence of the most dominant taxa (for species and families). A non-metric multidimensional scaling method (n-MDS) based on the Bray-Curtis similarity allowed us to visually assess differences in macrofaunal assemblages among stations of the studied areas. SIMPER tests were used to determine which species contribute to within-group similarity. These analyses were performed using PRIMER^{v6} [55].

A similarity matrix was constructed from the fourth-root transformed abundance data using the Bray-Curtis similarity measure; non-metric multidimensional scaling (n-MDS) ordination was then applied to assess the differences in trophic groups between the two ecosystems.

Table 2: Main characteristics of structural indices used to qualify the ecological status (EcoQ) of the benthic macrofauna in both ecosystems: ns, not significant; (*), significant. EcoQ scores are given here for different biotic indices (AMBI, M-AMBI, BO2A, d-MISS).

	Kneiss Islands	Arcachon Bay	ANOVA test	
			F	p
Total number of species / site	148	117		
Mean S (per 0.09 m ²)	39	27	24.85	p<0.01*
Mean A (ind/m ²)	14,709	20,553	3.39	p>0.05 ns
Mean H'	4.4	2.2	149.71	p<0.01*
Mean J'	0.85 Good	0.45 Moderate	125.7	p<0.01*
Mean AMBI	0.74 Good	0.43 Moderate	200	p<0.01*
Mean M-AMBI	0.029 High	0.113 Good	213.71	p<0.01*
Mean BO2A	0.8 Good	0.7 Good	39.02	p<0.01*
Mean d-MISS	1.6 Good	3.5 Moderate	112.18	p>0.05 ns

Results

Sediment characteristics

Sediment grain-size analysis shows that sediments in the Kneiss Islands consist of muddy to muddy sands depending on the station, with median grain-size varying from 120 to 380 μm . In Arcachon Bay, sediments are mainly mud (mean grain-size=33-59 μm) with high silt and clay content (mean=57-75%). Organic matter content ranges from 3 to 7% in the Kneiss Islands and from 3 to 10% in Arcachon Bay. A comparison of sediment grain-size and organic matter contents between the two ecosystems reveals no significant difference ($p>0.05$).

Macrofaunal characteristics

In the Kneiss Islands, a total of 148 species are identified from 34 stations, with an unequal distribution among sampling stations. The number of species in a sample (S) varies between 22 and 64 species per 0.09 m^2 , with a mean of 39. Abundance (A) varies from 9,200 to 36,800 ind. m^{-2} (with a mean abundance of $14,709 \pm \text{SD}=900 \text{ ind. m}^{-2}$), evenness (J') from 0.79 to 0.92 (mean= 0.85) and Shannon index (H') from 3.5 to 5.2, with a mean of 4.4 bits ind^{-1} (Figure 2 and Table 2). In Arcachon Bay, 117 species are identified from 48 stations. The mean number of species observed in a sample (S) is 27.5, ranging from 8 to 49 species per 0.09 m^2 . Abundance (A) ranges between 1,700 and 64,000 ind. m^{-2} , with a mean abundance of $20,553 \pm 2,100 \text{ ind. m}^{-2}$. Finally, evenness (J') varies from 0.19 to 0.87 (mean= 0.45) and Shannon index (H') from 1.2 to 4.1, with a mean of 2.2 bits ind^{-1} . The average values of S, J' and H' are higher in the Kneiss Islands than in Arcachon Bay (one-

factor ANOVA; S: $F=24.85$; $p<0.01$; J': $F=125.7$; $p<0.01$; H': $F=149.7$; $p<0.01$). Abundance is similar in the Kneiss Islands and Arcachon Bay (ANOVA; $F=3.39$; $p>0.05$) (Figure 2A and Table 2). A total of 23 species are common to both ecosystems (Table 3), while 125 species are restricted to the Kneiss Islands, and 94 species to Arcachon Bay. The Kneiss Islands are characterized by a higher proportion of mollusc species ($X^2=5.388$; $p<0.05$), while the proportions of arthropod and annelid species are similar in both systems (with $X^2=1.49$; $p>0.05$ for arthropods and $X^2=0.66$; $p>0.05$ for annelids) (Figure 2B).

For both ecosystems, annelids and molluscs are the dominant groups in terms of abundance, followed by arthropods (Table 4). In the Kneiss Islands, *Scrobicularia plana*, *Cerithium scabridum* and *Pirenella conica* are the three most abundant mollusc species (18% of total abundance), whereas *Peringia ulvae*, *Abra segmentum* and *Bittium reticulatum* are dominant in Arcachon Bay (47% of total abundance). In the Kneiss Islands, *Cirratulus cirratus*, *Perinereis cultrifera* and *Euclymene lumbricoides* are the most abundant annelid species. In Arcachon Bay, oligochaetes represent 33% of the total abundance.

Based on the analytical model of Ugland et al. [56], the number of species recorded in the Kneiss Islands is approaching an asymptote, while the number of species continues to rise with sampling effort in the case of Arcachon Bay. This suggests that, in the case of Arcachon Bay, the sampling effort has probably been insufficient to record all the species present in this habitat (Figure 3). For a similar effort (34 stations), the expected number of species is 148 in the Kneiss Islands, as against 117 for Arcachon Bay (Figure 3).

The trophic structure analysis shows that, in the Kneiss Islands, carnivores (40%) and NSDF (18%) are the dominant trophic groups

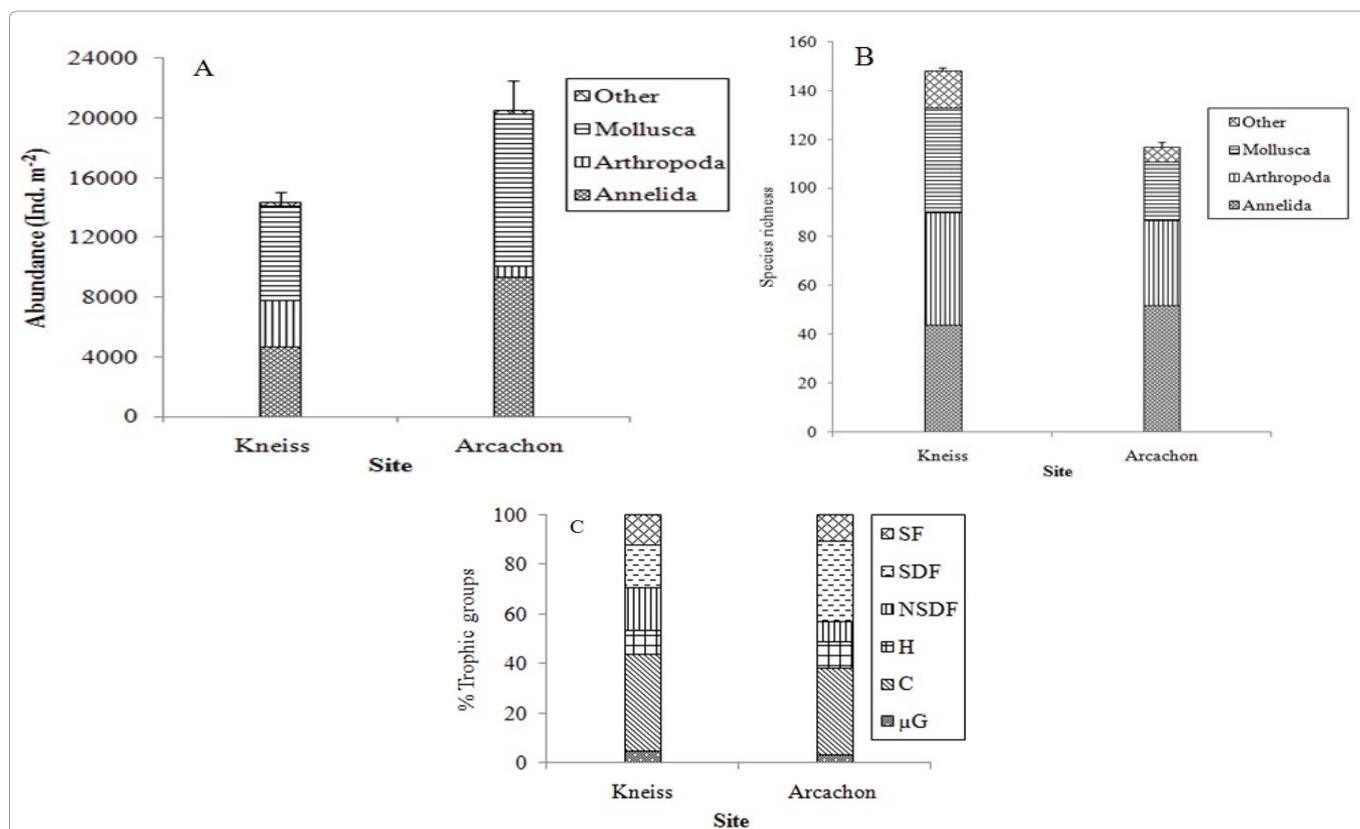


Figure 2: Comparison of the main benthic macrofauna parameters: mean abundance (\pm SD), specific richness (S) and Trophic groups in two study areas (C: carnivores; SDF: selective deposit feeders; NSDF: non-selective deposit feeders; SF: suspension feeders; H: herbivores; μG : micrograzers).

in terms of abundance. In Arcachon Bay, carnivores (36%), and SDF (33%) are the two most abundant trophic groups. However, SDF is the only trophic group displaying a different proportion (higher in Arcachon Bay) (micrograzers: $X^2=0.02$; $p>0.05$; carnivores: $X^2=0.22$; $p>0.05$; NSDF: $X^2=2.79$; $p>0.05$; suspension feeders: $X^2=0.48$; $p>0.05$; SDF: $X^2=4.90$; $p<0.05$) (Figure 2C).

Ecological status

Out of the four biotic indices compared between the two studied areas, three of them provide different results in terms of ecological quality status. AMBI and M-AMBI indicate that the Kneiss Islands have a good ecological status compared to Arcachon Bay, which shows a moderate status. BO2A yields a high status for the Kneiss Islands and a good status for Arcachon Bay ($p<0.01$). The values of d-MISS are similar in both ecosystems, and correspond to good ecological status (ANOVA, $F=112.18$; $p>0.05$) (Table 2).

Identification of macrofaunal assemblages

Using the MDS ordination plot based on species, we can discriminate two different groups, one corresponding to the Kneiss Islands and the other to Arcachon Bay (Figure 4A). Both ecosystems are also clearly separated on the basis of clades (i.e. molluscs, arthropods, annelids, etc.) (Figure 4B). Conversely, we find certain trends of similarity on the basis of trophic groups (Figure 4C). Three groups of stations are distinguished. Based on trophic groups (Figure 4C), the largest group (A) includes all the stations in the Kneiss Islands and the most of the stations in Arcachon Bay (67%). The two other groups (B and C) are restricted to stations in Arcachon Bay, located in a more exposed oceanic position: the station group B (12 stations) is dominated by NSDF, and is mostly represented by *Heteromastus filiformis* and oligochaetes. The station group C (4 stations) mainly includes SDF and carnivore species, such as *Melinna palmata*, *Hexaplex trunculus* and Anthozoa.

According to SIMPER analysis, Arcachon Bay is mainly characterized by the mud snail *Peringia ulvae*, as well as Oligochaetes, *Heteromastus filiformis*, *Abra segmentum*, *Idotea chelipes*, Nemertina,

Ruditapes philippinarum and *Bittium reticulatum*. The macrofaunal community in the Kneiss Islands is represented by *Cerithium scabridum*, *Cirratulus cirratus*, *Scrobicularia plana*, *Pirenella conica*, *Loripes orbiculatus*, *Ruditapes decussatus*, *Cerastoderma glaucum*, *Euclymene lombricoides* and *Cerithium vulgatum*.

Discussion

Many studies on macrobenthic eelgrass bed communities have compared parameters such as abundance, biomass or species

Table 3: List of species, occurring both in the Kneiss Islands and Arcachon Bay.

Phylum	Species
Annelida	<i>Arenicola marina</i>
	<i>Cirriiformia tentaculata</i>
	<i>Euclymene oerstedii</i>
	<i>Eunice vittata</i>
	<i>Leiochone clypeata</i>
	<i>Marphysa sanguinea</i>
	<i>Melinna palmata</i>
	<i>Lysidice unicornis</i>
	<i>Nephtys hombergii</i>
	<i>Hediste diversicolor</i>
<i>Platynereis dumerilii</i>	
Crustacea	<i>Ampelisca brevicornis</i>
	<i>Melita palmata</i>
	<i>Microdeutopus gryllotalpa</i>
	<i>Corophium insidiosum</i>
Mollusca	<i>Cyathura carinata</i>
	<i>Polittapes aureus</i>
	<i>Ruditapes philippinarum</i>
	<i>Scrobicularia plana</i>
	<i>Bittium reticulatum</i>
Echinodermata	<i>Cyclope neritea</i>
	<i>Loripes orbiculatus</i>
	<i>Amphipholis squamata</i>

Table 4: Top dominant taxa in the Kneiss Islands and Arcachon Bay.

Site	Species	Phylum	Mean density per m ²	% of presence
Kneiss Islands	<i>Scrobicularia plana</i>	Mollusca	1010	71
	<i>Cerithium scabridum</i>	Mollusca	866	91
	<i>Pirenella conica</i>	Mollusca	812	73
	<i>Cirratulus cirratus</i>	Annelida	780	79
	<i>Loripes orbiculatus</i>	Mollusca	529	85
	<i>Perinereis cultifera</i>	Annelida	528	38
	<i>Euclymene lombricoides</i>	Annelida	430	73
	<i>Gammarus insensibilis</i>	Crustacea	414	62
	<i>Bittium reticulatum</i>	Mollusca	392	50
	<i>Euclymene oerstedii</i>	Annelida	335	53
Arcachon Bay	<i>Peringia ulvae</i>	Mollusca	9002	96
	Oligochaeta	Annelida	6795	40
	<i>Heteromastus filiformis</i>	Annelida	967	94
	<i>Abra segmentum</i>	Mollusca	592	94
	<i>Melinna palmata</i>	Annelida	332	37
	<i>Pygospio elegans</i>	Annelida	274	48
	<i>Idotea chelipes</i>	Crustacea	189	90
	<i>Bittium reticulatum</i>	Mollusca	149	69
	Chironomidae	Crustacea	144	52
	Nemertina	Nemertina	137	92

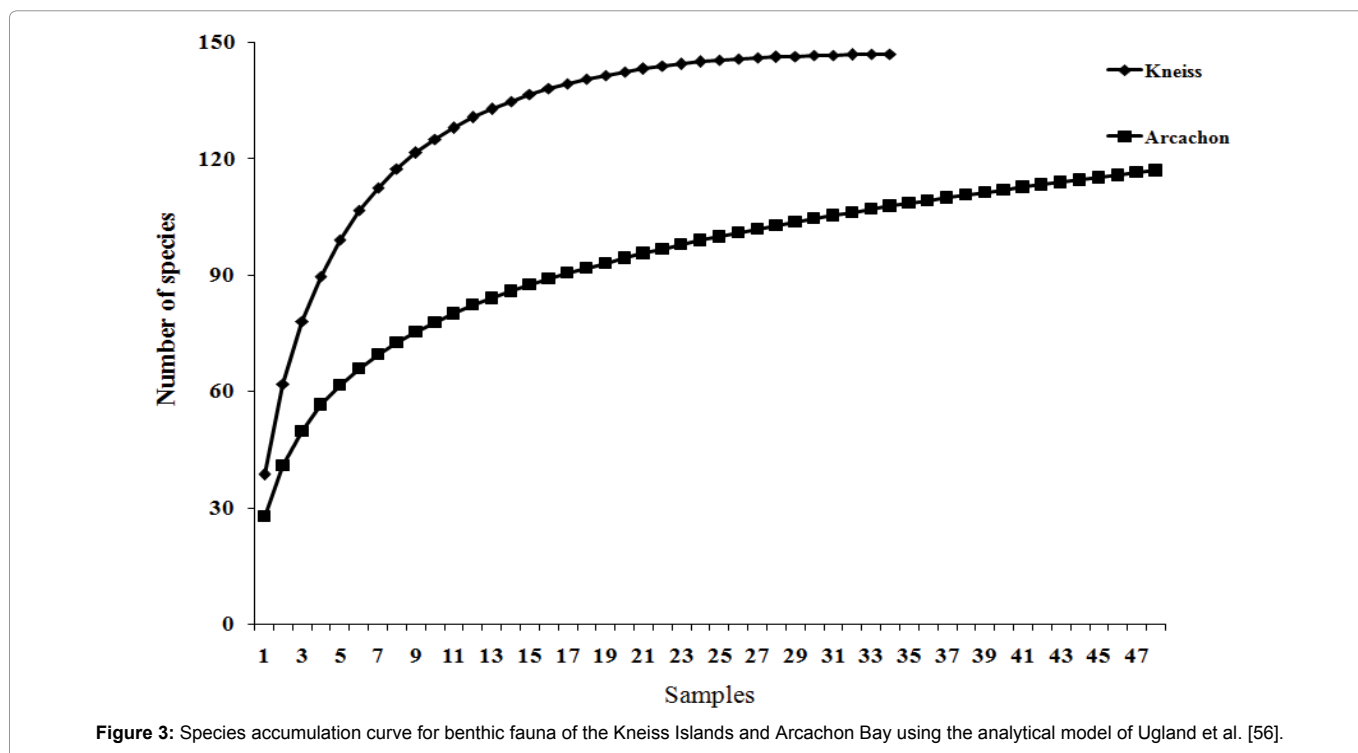


Figure 3: Species accumulation curve for benthic fauna of the Kneiss Islands and Arcachon Bay using the analytical model of Ugland et al. [56].

richness between adjacent sediments with or without vegetation [57,58], or between areas with different kind of vegetation [59,60]. On the other hand, there are few studies comparing macrobenthic communities in eelgrass beds at different spatial scales [61]. The originality of the present study is to compare the structure of benthic communities associated with intertidal *Zostera noltei* beds in two geographically distinct ecological communities, i.e. a Mediterranean ecosystem (Kneiss Islands) and a French Atlantic coastal ecosystem (Arcachon Bay). The aim of this approach is to identify differences and similarities between two similar habitats in terms of spatial heterogeneity (i.e. eelgrass physical presence) and to understand the response of benthic communities to other environmental variables, particularly climate, independently of the biogeographic area. In other words, we investigate whether the structure and functioning of macrofaunal communities in *Z. noltei* meadows can be compared at a large scale

A total of 232 taxa are recorded, associated with eelgrass beds, unequally distributed among the sampling stations. Annelids and molluscs are the dominant groups at both sites. High species diversity and abundance are frequently reported for macrofauna from seagrass habitats [61-66] compared with unvegetated sediments. Eelgrass meadows increase habitat complexity and provide living space and shelter for a diverse animal community [67,68]. These differences are related to the above-ground component of eelgrass, favouring the successful recruitment and colonization of animals, and the belowground structural complexity of the interlacing rhizome layer and roots increasing sediment stability [69-71].

A total of 148 species are identified in the Kneiss Islands and 117 species in Arcachon Bay, these values describing the γ -diversity of each site. The total number of species in the Kneiss Islands is higher on average than in Arcachon Bay, even when taking into account the difference in sampling effort. The species-accumulation curve for the

Kneiss Islands stabilizes around an asymptotic value suggesting a correct assessment of γ -diversity. However, the lack of an asymptotic value for Arcachon Bay implies that the sampling effort is insufficient to provide an exhaustive assessment of diversity. This curve also indicates that diversity is not homogeneously distributed within Arcachon Bay, where an increased number of stations would have yielded 'more species'. This may be related to a greater diversity of habitats within the eelgrass beds in Arcachon Bay compared to the Kneiss Islands, i.e. a higher β -diversity [72].

A comparison of faunal composition between *Z. noltei* meadows at the two sites shows the existence of 23 'shared' species (i.e. common to both sites). *Loripes orbiculatus* Poli, 1791 (lucinid bivalve) is the most common bivalve species. This species has also been observed in other climatic zones and is present in 97% of tropical eelgrass sites, 90% of subtropical meadows, and 56% of temperate eelgrass beds. The presence of *L. orbiculatus* in eelgrass is also related to the special adaptation of lucinid bivalves to sulphide-rich sediments, due to symbiosis with gill bacteria [73]. Thus, seagrass meadows may offer an optimal habitat for these bivalves and their symbionts by indirectly stimulating sulphide production through high organic matter input, while also providing oxygen through radial oxygen release from the roots. In turn, lucinids remove sulphide from the sediment, which could relieve stress on eelgrass growth caused by sulphide accumulation due to the degradation of organic matter [73-75].

The abundance of macrobenthic fauna communities in both ecosystems is similar, but with different patterns. The Kneiss Islands represent a balanced species abundance pattern, as shown by high values of H' and J' . By contrast, the macrobenthic community associated with *Z. noltei* beds in Arcachon Bay is dominated by small grazing molluscs such as *Peringia ulvae* (Pennant, 1777) (44% of total abundance), and oligochaete deposit-feeders (33% of total abundance). The abundance of these dominant taxa is similar to that

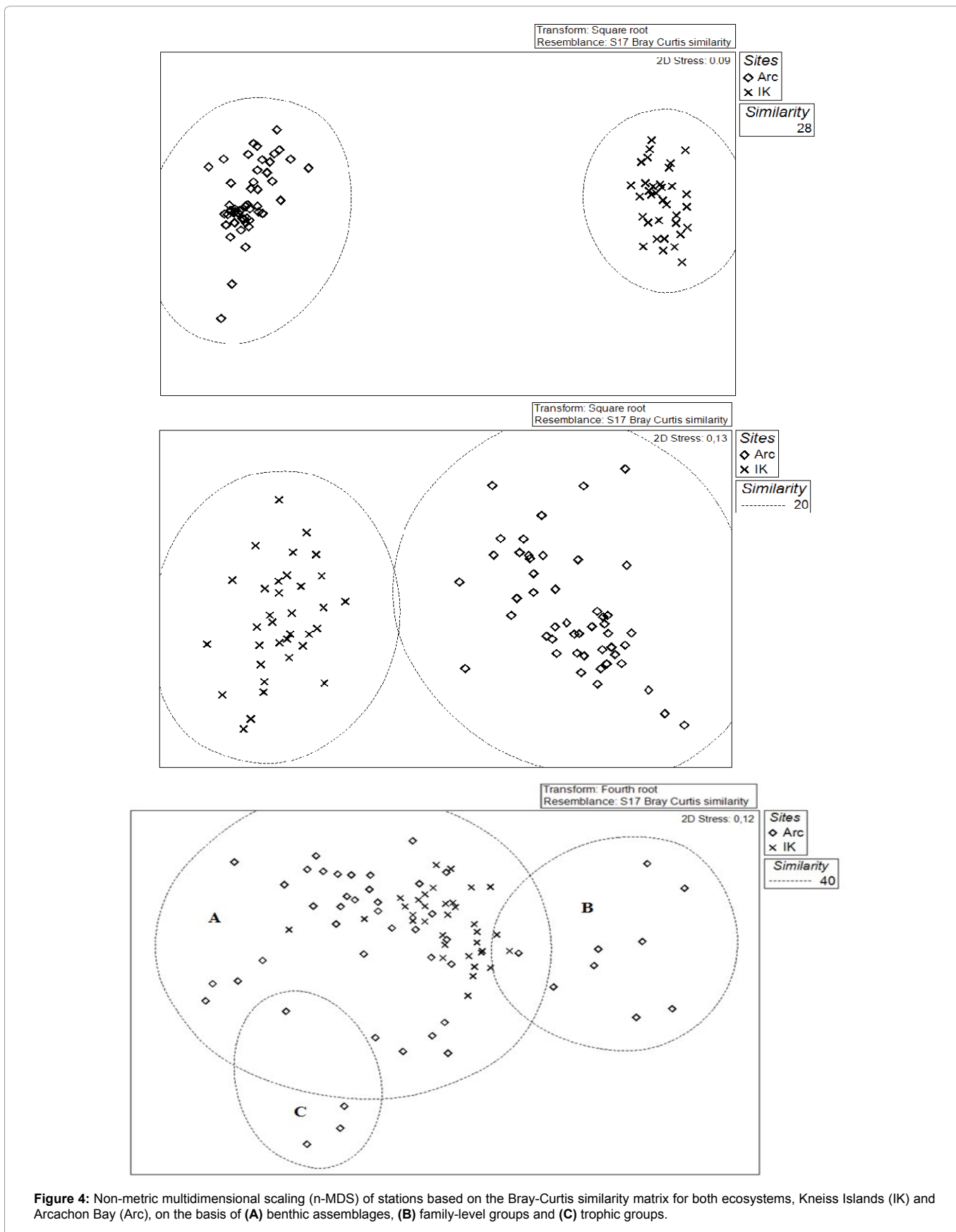


Figure 4: Non-metric multidimensional scaling (n-MDS) of stations based on the Bray-Curtis similarity matrix for both ecosystems, Kneiss Islands (IK) and Arcachon Bay (Arc), on the basis of (A) benthic assemblages, (B) family-level groups and (C) trophic groups.

observed in other Atlantic *Z. noltei* beds, including brackish habitats in the North Sea and Atlantic areas [69,76-78].

The differences in diversity between Arcachon Bay and the Kneiss Islands is probably a response to human activities (e.g. fishing pressure, port and aquaculture activities, as well as nutrient inputs), environmental factors (sediments characteristics, salinity) and different climatic conditions. In fact, the Gulf of Gabès is a semi-arid Mediterranean coastal zone [79], characterized by an arid climate (average annual precipitation: ≤ 200 mm year⁻¹) with higher temperature and salinity. The invertebrate macrofauna in this inshore region is directly under the influence of salty and warm Mediterranean waters well known for their high intrinsic diversity [80,81]. General oceanographic conditions in the Mediterranean basin have been described in detail elsewhere [82-84]. Areas bordering the Mediterranean Sea have a dry-summer subtropical type climate. The summer is hot and dry, and the winter is cool and rainy. These general features, along with some other regional characteristics such as fluctuations in fluvial inputs, temperature and salinity, give rise to the particularities of Mediterranean communities [85,86]. Afi et al. [46,87] proposed that environmental conditions, particularly temperature and salinity, play a major role in the structuring of communities and the exclusion of certain species or groups of species in Mediterranean ecosystems. This explains why the Kneiss Islands have a larger number of species not common to both sites and why a taxonomy-based MDS allows a clear discrimination between the sea grass habitats (Kneiss Islands and Arcachon Bay).

In both studied areas, the abundance of species within trophic groups appears similar. This suggests the consistency of a similar functioning of the benthic food web in these two geographically distant *Zostera noltei* habitats. In both ecosystems, the trophic structure is dominated by carnivores. Normally, the presence of carnivores in a balanced ecosystem should not exceed a certain proportion. Their role is to control the community and prevent the monopolization of resources (food and space) as well as competition from prey populations [44,88]. The results of the MDS analysis clearly show that three functional trophic groups can be identified in both eelgrass ecosystems: the major group is represented by all the stations of the Kneiss Islands and the majority of Arcachon stations, strongly dominated by carnivores, NSDF and SDF. The two other groups are restricted to the Arcachon Bay stations, mainly dominated by NSDF such as oligochaetes, and SDF such as *Melinna palmata* and *Cirratulus cirratus*. The similarity in trophic functioning detected between the two different eelgrass beds shows that, in response to the climate difference between the Mediterranean and the Atlantic Ocean, many species in the Kneiss Islands play the same ecological role in Arcachon Bay.

Beyond comparing the specific and trophic functioning of the Kneiss Islands and Arcachon Bay, we also analyse the biotic indices (BIs) (*sensu* Water Framework Directive). Most of these BIs are based on sensitivity to environmental stress. Therefore, independently of species composition, BIs represent a relevant way to compare the seagrass communities in terms of fitness, or at least the distribution of associated species according to their resistance to stress (mainly related to organic matter in the sediment). The overall pattern of ecological quality status is different according to the selected BI. All BIs, except d-MISS, reveal a difference between the ecosystems ($p < 0.01$). AMBI, M-AMBI and BO2A all classify the Kneiss Islands seagrass as having good or high ecological status (unpolluted status), highly dominated by sensitive species (GI). The fact that the

Shannon index tends to increase slightly in finer sediments is due to the important influence of species richness and abundance and the lack of ecological terms in the formulae. However, these three BIs classify Arcachon Bay as having a poor to moderate ecological status. These lower values are more closely related to the sediment type than pollution conditions and physical disturbances [89]. Indeed, eelgrass in Arcachon Bay is associated with fine sediments and high organic matter content. Consequently, since the proportion of opportunistic species is high, this also influences the BIs [89]. Generally, most of these BIs (e.g., AMBI and BO2A) yield poor scores for semi-enclosed ecosystems where the natural benthic habitat consists of muddy, organic matter enriched sediments [52,89]. As a result, biotic indices based on these functional groups (e.g., BENTIX and AMBI) are not well adapted to study different types of pollution, such as physical pollution or metal contamination [46,87,90]. d-MISS is based on 14 metrics describing the ecological community, trophic composition and pollution indicator species, and is considered to be more efficient than other BIs in detecting perturbations in this kind of ecosystem [19,52]. Unlike the other calculated indices, the d-MISS index places both the Kneiss Islands and Arcachon Bay ecosystems in the good ES category.

Climatic conditions in Arcachon Bay will change over the next decades [27]. Indeed, the temperature is expected to increase by 10°C up to 2100, and may induce lower fluvial input (-5% to -35%) around the years 2046-2065. These conditions will be similar to those occurring currently in the Gulf of Gabès. Change in climatic conditions in the eastern Atlantic means that western stenothermal cold water species would be negatively affected by any future warming, ultimately leading to an increase of species diversity and a reduction in the abundance, biomass and benthic primary production of invertebrates resulting in modifications of the structure and functioning of the ecosystem [31,91]. Kröncke et al. [33] showed that most shifts in the community structure are directly or indirectly correlated with the variability of the North Atlantic Oscillation Index (NAOI) in winter, especially the increase in NAOI since the late 1980s. This has resulted in the increase in warm-temperate species, a decrease in cold-temperate species and/or the invasion of non-indigenous species (NIS).

In conclusion, this study shows that biogeography (and the associated climate conditions) is of prime importance in structuring benthic communities at the scale of the planet. Indeed, two comparable seagrass ecosystems under different climatic conditions host different species. Conversely, the habitat itself shapes the functioning of an ecosystem: seagrass habitats in the Kneiss Islands (arid climate) and Arcachon Bay (temperate oceanic climate) display similarities in terms of distribution of trophic guilds and overall characteristics (d-MISS). Besides, we also propose an interesting way to predict the response of benthic communities to climate warming by comparing two contrasted ecosystems in coastal areas of the Mediterranean Sea and Atlantic Ocean. The direct effects of climate change impact the performance of individuals at various stages in their life history cycle through changes in physiology, morphology and behaviour. Climate also has an impact at the population level via changes in transport processes that influence dispersal and recruitment [92,93]. Community-level effects are mediated by interacting species (e.g. predators, competitors, etc.), and include climate-driven changes in both the abundance and per capita interaction capability of these species. The combination of these proximal impacts leads to emergent ecological responses, which involve modifications in species distributions, biodiversity, productivity and micro-evolutionary processes. Crucially, the long-term research programme over the

coming decade should provide much of the additional information that is required to assess and mitigate the potential impacts of climate change in the seagrass ecosystems of the Kneiss Islands and Arcachon Bay.

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