Title: Spatial and temporal response of multiple trait-based indices to natural- and anthropogenic seafloor disturbance (effluents).

Authors: Pieter van der Linden[1*], Angel Borja[2], Jose German Rodríquez[2], Iñigo Muxika[2], Ibon Galparsoro[2], Joana Patrício[3], Helena Veríssimo[1], João Carlos Marques[1].

Affiliations

[1] MARE – Marine and Environmental Sciences Centre, Faculty of Sciences and Technology, University of Coimbra, 3004-517 Coimbra, Portugal

[2] AZTI – Herrera Kaia, 20110 Pasaia, Spain

[3] European Commission, Joint Research Centre, Institute for Environment and Sustainability, 21027 Ispra, Italy

* corresponding author. Tel.: +351 925092477. E-mail address: lindenvdpieter@gmail.com (P. van der Linden).

Abstract

To support ecosystem-based management and achieve the Good Environmental Status (GES) of marine waters it is important to better comprehend the relationships between biodiversity and environmental disturbance (anthropogenic and natural). Biotic indices are widely used in studies to help understanding these relationships and to assess the environmental status of waters. In recent years, trait-based indices rapidly emerged as an alternative 'functional' approach to serve this purpose. In this study, we analysed how two indices based upon the mean (community-weighted mean trait value - CWM) and the diversity of multiple traits (Rao's quadratic entropy - Rao) in a macroinvertebrate community respond to natural- and anthropogenic seafloor disturbance (effluents) and we compared their performance with the widely used AMBI and M-AMBI. Our results demonstrate that CWM and Rao were not effective in indicating anthropogenic disturbance in the Basque coast, Bay of Biscay. The main reason was probably that many traits did not have a strong link with this type of disturbance. Besides, the mechanistic links between certain traits and their response to anthropogenic seafloor disturbance in marine environments is currently not well understood. From a management perspective: the CWM does not provide a single value indicating a quality status, which makes it a difficult tool to use and interpret. This index is probably more useful for scientists who want to explore and understand different aspects of community functioning. On the other hand, Rao and other indices expressing trait diversity do provide a single value of functioning; therefore they could potentially be effectively used for management purposes. However, to improve its performance, detailed and accurate trait data is required, which is currently lacking for many marine species.

Keywords: ecosystem functioning, impact assessment, Marine Strategy Framework Directive, macroinvertebrates, biodiversity, ecological indicators

1 Introduction

Understanding how biodiversity relates to environmental disturbance has been one of the hot topics of aquatic environmental research over the past 40 years (e.g. Pearson and Rosenberg, 1978; Warwick, 1986). A better understanding of this relationship can ultimately help us to preserve and improve the quality of marine ecosystems. During this period, indices based on species traits emerged as an alternative approach to study this relationship (e.g. Bremner et al., 2006; Bremner, 2008), as opposed to the use of mostly structural approaches (e.g. taxonomic-based indices, see Borja et al., 2015). Indeed, increasing evidence suggests that a species ability to deal with environmental disturbance is at least partly driven by its traits (Pearson and Rosenberg, 1978; Bremner et al., 2003; Culhane et al., 2014). As such, trait-based indices have the potential to determine the cause of change in systems by investigating the type of traits affected (Dolédec et al., 1999).

In 2008, the European Union (EU) approved the Marine Strategy Framework Directive (MSFD: European Commission, 2008). The main goal of the MSFD is to protect efficiently the marine environment across European seas; in particular, it aims to achieve Good Environmental Status (GES) of the EU's marine waters by 2020. To assess the current environmental status, the European Commission (2010) has indicated different indicators. Among these are the indices to assess benthic community condition and functionality, in relation to seafloor integrity (see van Hoey et al., 2010; Rice et al., 2012). As the MSFD follows an ecosystem-based approach, the selected indices should be oriented not only to determine structural changes in species assemblages, but also functional (Borja et al., 2013). The inclusion of trait-based indices could help to study these functional changes and, by doing so, they potentially allow to better assess the response of species communities to disturbance (Vandewalle et al., 2010).

Nowadays, one of the most used and established disturbance indices, on benthic invertebrate communities in marine environments (Borja et al., 2015), is the AZTI's Marine Biotic Index (AMBI: Borja, 2000) and its multivariate version: M-AMBI (Muxika et al., 2007).

Since their introduction, both indices have been successfully used to indicate various types of disturbances in different environments and biogeographical regions worldwide (Borja et al., 2015), and are officially incorporated into the regulations of several European countries in the context of aquatic directives (Borja et al., 2009). AMBI is based on the sensitivity (response) of benthic invertebrate species to anthropogenic pressures, and species are allocated to five sensitivity (ecological) groups ranging from sensitive to opportunistic (Borja, 2000). M-AMBI incorporates AMBI with species richness and Shannon diversity (Muxika et al., 2007). This index is based on the observation that benthic communities respond to an improvement in environmental quality in three stages. Firstly, species abundance increases, subsequently species diversity rises, and finally the opportunistic species become dominant with the subsequent reduction in species abundance and diversity (Pearson and Rosenberg, 1978; Paganelli et al., 2011).

Both indices can essentially be classified as trait-based indices, because the AMBI ecological groups (EG's) are mostly determined by the response of multiple species traits (e.g. feeding strategy, size, life span, larval development) to anthropogenic disturbance (e.g. Marchini et al., 2008; Culhane et al., 2014). However, these traits are 'fixed' within these EG's, meaning that these indicators cannot be used to analyse each of these 'individual' traits separately. Yet, a number of studies demonstrated that analysing each of these individual traits separately, might also be useful for detecting anthropogenic disturbance (e.g. Reise, 2002; Bremner et al., 2003; Cooper et al., 2008; Paganelli et al., 2012; van der Linden et al., 2012; van Son et al., 2013; Törnroos et al., 2015; Weigel et al., 2016).

Two trait-based indices in particular have been increasingly used to assess the response of species communities to disturbance that can handle 'multiple' different types of traits (Vandewalle et al., 2010; Ricotta and Moretti, 2011). These are the 'community-weighted mean trait value' – CWM (Garnier et al., 2004) and 'Rao's quadratic entropy' – Rao (Botta-Dukát, 2005). CWM can be adequately used to analyse shifts in mean trait values within communities due to environmental selection for certain traits. While, Rao can be effectively used to analyse patterns of trait (functional) diversity, i.e. a decrease or increase in trait diversity compared to a random expectation (Vandewalle et al., 2010; Ricotta and Moretti, 2011). The employment of these indices to assess disturbance is based upon the 'habitat templet concept' of Southwood (1977), which states that the habitat provides the template upon which evolution forges species traits. When disturbance increases, only species with specific combinations of traits suitable for survival pass through the environmental filter. Ricotta and Moretti (2011) showed that these two indices may be used to describe two complementary aspects of community structure, such as the mean and the diversity of traits within a given species assemblage, and that using them simultaneously can provide an effective framework to assess the effects of environmental disturbance on species communities. Despite the potential utility of these two trait-based indices, surprisingly few studies used them simultaneously (as a framework) to assess disturbance on benthic communities in marine environments (e.g. Paganelli et al., 2012; Culhane et al., 2014; de Juan et al., 2015; Barnes and Hendy, 2015; Weigel et al., 2016).

Taking this into consideration, the main purpose of this study was to assess how the community-weighted mean trait value (CWM) and trait diversity (expressed by Rao) responded to seafloor disturbance relative to the performance of AMBI and M-AMBI. We only analysed disturbance caused by anthropogenic effluents and wave impact, although many other factors may contribute to its disturbance, namely fisheries, dredging and sediment deposit, among others. Based on the obtained results, we could give a recommendation on whether CWM and Rao might be implemented as useful seafloor disturbance indices for the MSFD.

2 Materials and Methods

2.1 Study area, anthropogenic- and natural seafloor disturbance

Environmental and benthic community data were collected annually in winter, between 1995 and 2012, from sixteen marine off-shore sampling stations along the Basque coast, in northern Spain, Bay of Biscay (Fig. 1A, B). All stations are located at sedimentary areas and situated at a depth of around 30 m, ranging from muddy to sandy. In general, there are not important sources of anthropogenic disturbance in the area. However, there is one particular station (identified as L_UR20) that is located in an area where urban and industrial wastewaters are discharged (driving to increases in organic matter content in sediment and consumption of oxygen) (Borja et al., 2009). This station is regarded as the most disturbed of the study area, especially between 1995 and 2001, when untreated wastewaters were directly discharged in the close vicinity of this station (Fig. 1C), affecting the benthic communities due to poor quality of the sediment. In 2001, a submarine outfall was constructed which, to date, transports the already biologically treated wastewater (since 2006) to a location approximately 1.2 km offshore. Since then, sediment quality steadily improved (Borja et al., 2009). Other stations that are subjected to an above average level of anthropogenic disturbance are L_N20 and L_OI20. Station L_N20 is situated close to the Nervion estuary, which was historically disturbed, but in recuperation since 1989 (Borja et al., 2006). In addition, this station is close to a historical disposal site, which can, to some extent, affect the condition of the benthic assemblages of this area (Borja et al. 2008). On the other hand, station L_OI20 is situated in the vicinity of the other disturbed estuary (Oiartzun). In addition, close to this station there are some disposal sites of dredged sediments (see Galparsoro et al., 2010). For the whole area, all stations are more or less affected by natural disturbance (e.g. wave activity that can affect the sediment dynamics - Galparsoro et al., 2013).

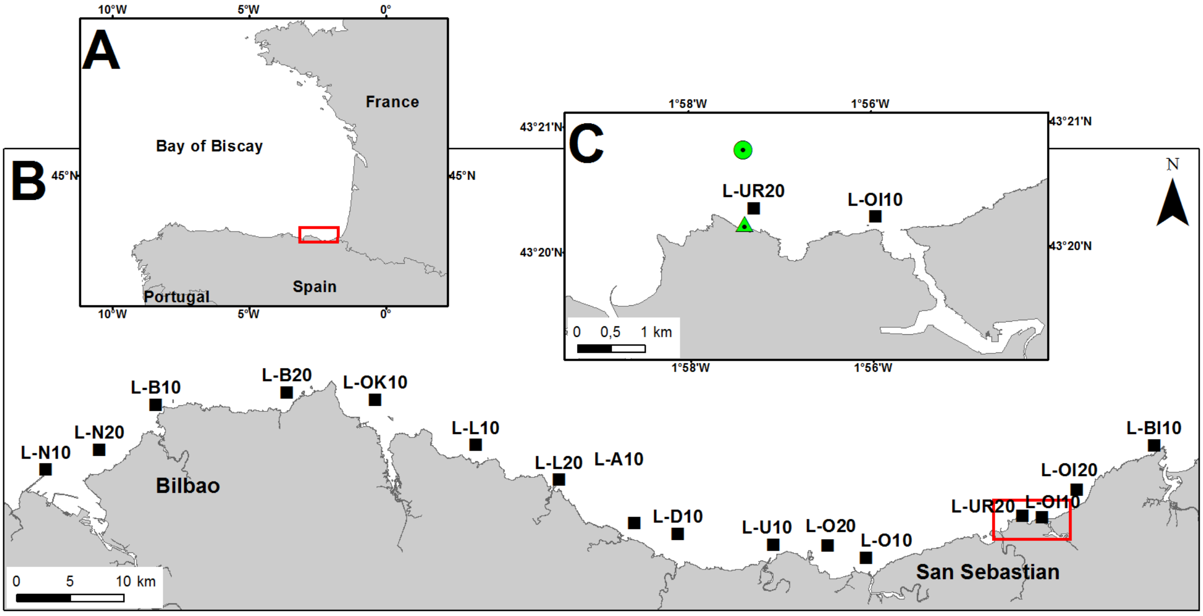

Figure 1. Study area within the Bay of Biscay (A) and the position of the 16 off-shore sampling stations along the Basque coast (Spain) (B). Diagram C shows the urban wastewater discharge locations (the green triangle points out the discharge location prior to 2001, and the green circle points out the current location, which became operational in 2001).

2.2 Data collection

At each station, three benthic samples (replicates) were taken with a van Veen grab (0.1 m^2) and sieved in situ through a 1 mm mesh. Subsequently, the benthic invertebrates were sorted and identified to the lowest possible taxonomic level. Biomass was initially estimated as dry weight (g m^{-2}), but subsequently converted to ash-free dry weight by using the conversion factors as in Ricciardi and Bourget (1998). This benthic community data was then compiled into a ‘taxa-biomass-by-sample’ matrix.

An additional sediment sample was taken at each station to analyse the variables: mud-content (%), organic-matter-content (%) and redox-potential values (mV). The correspondent limit for organic-matter-content is usually considered to be 5% (Holmer et al., 2005). Redox-potential values indicate the oxidation-reduction status of the sediments, with high values (>300) indicating aerobic sediments, and negative values indicating anaerobic sediments (Pearson and Stanley, 1979). We also measured ‘wave-flux’ as an environmental variable producing natural induced disturbance. Wave-flux (kW/m) is a measure of energy per meter of wave front (for further details, see Galparsoso et al., 2013). The above mentioned environmental variables were used to explain possible spatial and temporal variation in species assemblages. Organic-matter content and redox-potential served as a proxy to indicate anthropogenic disturbance. We considered mud-content as a proxy to indicate the potential natural characteristics of the study area, and wave-flux to indicate natural induced disturbance. These environmental variables were compiled into an 'environmental-variables-by-sample' matrix.

2.3 Species traits

Species traits were gathered from a variety of published sources (e.g. species identification guides, scientific papers and established online databases such as MarLIN (2006) and WoRMS Editorial Board (2014)). A total of six traits containing 28 trait categories were chosen for their potential ability to reflect anthropogenic- and natural induced environmental disturbance conditions (see Table 1 for details). The lack of available traits information in the literature, prevented our assignment of the trait categories for many taxa at the 'species' level. Instead, the trait categories were adjusted at the 'genus' level and data was coded using a 'fuzzy coding' approach (Chevenet et al., 1994). Records of taxa not identified to at least 'genus' level (6.9% of records) were excluded. The trait categories were given an affinity score between '0' and '3', with '0' indicating no affinity of a species to a trait category, and '3' indicating a high affinity to the trait category. The fuzzy coding procedure allows to capture variation in the affinity of a given taxa to the different categories of a given trait, thereby addressing spatial or temporal variation in the traits of a given taxa (Statzner and Bêche, 2010). These scores were then compiled into the 'taxa-by-trait' matrix (336 genus and 28 trait categories). To give the same weight to each taxa and each trait in further analysis, the scores were standardised so that their sum for a given taxa and a given trait equalled 1 (or 100%).

Table 1. Species traits (categories), labels and their *a-priori* expected response after disturbance.

Trait	Category	Labels	Expected response after disturbance
Feeding-strategy	Suspension	F_SUS	The proportion of suspension feeders in a community is expected to decrease after disturbance caused by organic pollution[2]
	Deposit	F_DEP	The proportion of deposit-feeders and grazers in a community are expected to increase after disturbance caused by organic pollution[2,4]
	Grazer	F_GRA	
	Scavenger	F_SCA	No particular response expected for scavengers and predators after disturbance
	Predator	F_PRE	
	Omnivore	F_OMN	The proportion of omnivores in a community is expected to increase after disturbance caused by organic pollution (i.e. better resilience capacity)[2]
	Parasite	F_PAR	No particular response expected after disturbance
Maximum size	Very small (< 1 cm)	S_1	The proportion of smaller sized taxa in a community is expected to increase after disturbance (i.e. better resilience capacity)[1,4]
	Small (1-3 cm)	S1_3	
	Medium (3-10 cm)	S3_10	
	Medium-Large (10-20 cm)	S10_20	No particular response expected after disturbance
	Large (> 20 cm)	S_20	The proportion or larger sized taxa in a community is expected to decrease after disturbance (e.g. fine sediment deposits)[1,4]
Life-span	Very short (< 1 year)	L_1	The proportion of short-lived taxa in a community is expected to increase after disturbance (i.e. better resilience capacity)[2,4]
	Short (1-3 years)	L1_3	
	Medium (3-10 years)	L3_10	No particular response expected after disturbance
	Long (> 10 years)	L_10	The proportion of longer-lived taxa in a community is expected to decrease after disturbance (e.g. fine sediment deposits)[2,4]
Living-position	Tube dwelling	LH_TD	The proportion of tube dwellers and burrow dwellers in a community are expected to increase after disturbance (e.g. anoxic conditions, organic pollution and fine sediment deposits), as opposed to free living species and species that are attached to the substratum, because they can hide in their fixed tubes or burrows[3,4]
	Burrow dwelling	LH_BD	
	Free living	LH_FL	
	Attached	LH_ATT	
Larval-development	Planktotrophic (feeding at least in part on materials captured from the plankton)	DT_PLAN	The proportion of taxa with a planktotrophic larval development (high dispersal potential) are expected to increase after disturbance, because the extinction risk of taxa with a lecithotrophic (medium dispersal potential) and direct larval development (no dispersal potential) is higher[5]
	Lecithotrophic (development at the expense of internal resources, i.e. yolk)	DT_LEC	
	Direct (development without larval stage)	DT_DIR	
AMBI ecological (sensitivity) groups (EG's)	(I) very sensitive species	EG_I	The proportion of taxa belonging to EG III, IV and V in a community are expected to increase after disturbance, while EG I is expected to decrease[6]
	(II) indifferent	EG_II	
	(III) tolerant	EG_III	
	(IV) 2nd order opportunists	EG_IV	
	(V) 1st order opportunists	EG_V	

[1] Townsend and Hildrew, 1994
[2] Pearson and Rosenberg, 1978
[3] Reise, 2002
[4] Statzner and Bêche, 2010
[5] McHugh and Fong, 2002
[6] Borja, 2000

2.4 Data analysis

For the data analysis and the computation of the indices, three matrices were used: 1) 'taxa-biomass-by-sample' matrix; 2) the 'environmental-variables-by-sample' matrix; and 3) the 'taxa-by-trait' matrix. Data in the 'taxa-biomass-by-station' matrix were explored by means of Correspondence Analysis (CA), after log-transforming (log 1 + x) the biomass values, using R-package 'ade4' (Chessel et al., 2004). The standard affinity scores for each taxa in the 'taxa-by-trait' matrix were multiplied by the taxa biomass in each sample (taxa-biomass-by-sample matrix), which resulted in the 'trait-by-sample' matrix.

2.5 Calculation of the indices

The main purpose of this study was to assess how CWM and Rao responded to natural- and anthropogenic seafloor disturbance relative to the response of AMBI and M-AMBI. Therefore, we assessed their response at the spatial scale (between all stations) and temporal scale (using station L_UR20 as a test case). To better interpret the response of M-AMBI, the responses of its individual components were also assessed. These are: genus richness (the standard procedure is to use species richness in the M-AMBI calculation), the Shannon index and AMBI. To better interpret the response of Rao, the Simpson index was included because Rao is a generalised form of the Simpson index (Botta-Dukát, 2005). This allowed understanding the relationship between species diversity and functional diversity (Stuart-Smith et al., 2013). Genus richness and the Shannon index (log x) were calculated using R-package 'ade4' (Chessel et al., 2004)

2.5.1 AMBI and M-AMBI calculation

Usually, AMBI and M-AMBI are calculated with species density, however, in order to make a viable comparison between all indices, AMBI and M-AMBI had to be calculated using genus biomass. Warwick et al. (2010) and Muxika et al. (2012) already tested the usefulness of AMBI using species biomass instead of species density. Moreover, two studies by Cai et al. (2014, 2015) also aimed to assess environmental disturbance by using both species density and species biomass in the calculation of AMBI and M-AMBI. These authors found a significant correlation between both methods in regards to environmental disturbance. However, we are not aware of studies that tested the correlation between M-AMBI calculated with species density and genus biomass. Therefore, we tested this correlation using an Spearman's rank correlation analysis. Moreover, we tested how both calculation methods responded to the temporal variation in disturbance conditions at station L_UR20. The non-parametric Wilcoxon signed-rank test was used for this purpose. These outcomes are excluded from the results section of this paper as it was not the main purpose of this study. Instead, they are presented as supplementary material in Fig. A.1 and Fig. A.2. These outcomes indicated a significant correlation between both calculation methods in their response to disturbance. Taking this into account, we were confident enough to use AMBI and M-AMBI, calculated with genus biomass, for the purpose of this study. These indices were calculated using AMBI 5.0 software (freely available at http://ambi.azti.es) and the November 2014 species list. Since the reference conditions for the area are based on species, the reference conditions for the M-AMBI calculation based on genus were set as following: genus richness was set as the 0.95 percentile of its maximum observed value in the dataset, the Shannon index was set at the 0.95 percentile of its maximum observed value in the dataset and AMBI was set as lowest observed value in the dataset. As for the ‘bad’ status, the reference values used were 0 for diversity and richness, and 6 for AMBI.

2.5.2 CWM and Rao calculation

The CWM was calculated for each of the 28 trait categories. The trait values were weighted by genus biomass (e.g. the biomass of filter-feeding taxa identified at genus level) (Garnier et al., 2004; Ricotta and Moretti, 2011). This index can be adequately used to summarize shifts in mean trait category values within communities due to environmental selection for certain traits (Ricotta and Moretti, 2011). As such, the calculation of this index allowed us to test how each trait category responded to the environmental variables. This index was calculated, using R-package ‘ade4’ (Chessel et al., 2004)

As mentioned before, Rao is a generalised form of the Simpson index, which measures the amount of trait diversity between two random individuals in the community (Botta-Dukát, 2005; Lepš et al., 2006). In fact, if diversity between all species pairs is maximum, then Rao is identical to the Simpson index (Botta-Dukát, 2005). The Simpson index, as a result, represents the maximum potential value Rao can reach in a given community where the species completely differ in their trait categories. This index can be effectively used to analyse patterns of trait (functional) diversity, i.e. a decrease or increase in trait diversity compared to a random expectation (Vandewalle et al., 2010; Ricotta and Moretti 2011). An Excel macro file (available from http://botanika.bf.jcu.cz/suspa/FunctDiv.php; Lepš et al., 2006) was used to calculate the Simpson and Rao index. Rao provided the mean dissimilarity values for each of the six traits (feeding-strategy, size, life-span, living-position, larval-development, and the AMBI ecological groups - EG's) for each station and subsequently a mean of the index values calculated across all these six traits.

2.6 Statistical treatment

Non-parametric Kruskal-Wallis tests were performed in order to test whether the median values for environmental variables and indices showed significant differences between the stations and between the periods 1995-2001 (non-diverted and untreated discharges) and 2002-2012 (diverted, and since 2006, treated discharges) at station L_UR20 (α: 0.05). Correlations among indices and between the indices and the environmental variables were tested with a Pearson correlation test. When testing for correlation between the indices and the environmental variables, the reported pairwise p-values (α: 0.05) were adjusted using the 'false discovery rate' (Benjamini and Hochberg, 1995).

3 Results

3.1 Environmental conditions

The sediment conditions within most stations were relatively similar, despite mud-content, organic-matter content and redox-potential displaying significant differences between stations (Kruskal-Wallis, p-value: < 0.01). Nevertheless, station L_UR20 stood out from the rest because of higher mud content and lower redox potential values (Fig. 2). Wave-flux values were also significantly different between stations (Kruskal-Wallis, p-value: < 0.01), with the highest values at stations L_N20, L_OI20, L_BI10 and the lowest values at stations L_L20, L_A10 and L_O20 (Fig. 2). Regarding the temporal variation of the sediment conditions at station L_UR20, only organic-matter content showed a significant difference (Kruskal-Wallis, p-value: 0.0005) between the two periods, with higher values in the period with the non-diverted and untreated discharges (1995-2001) (Fig. 3).

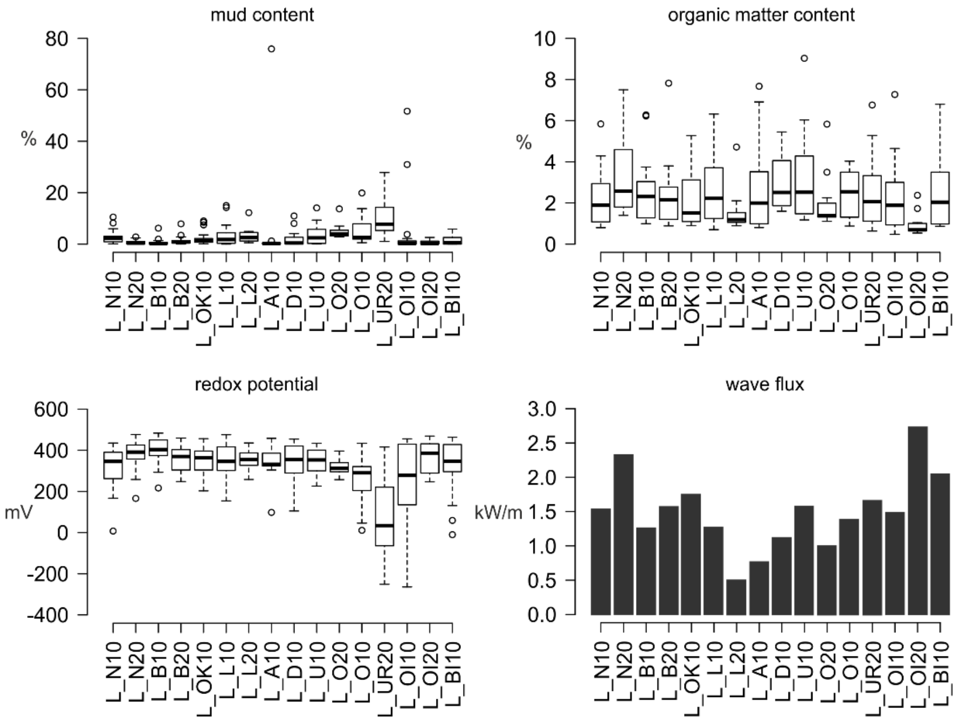

Figure 2. Spatial variation of environmental variables.

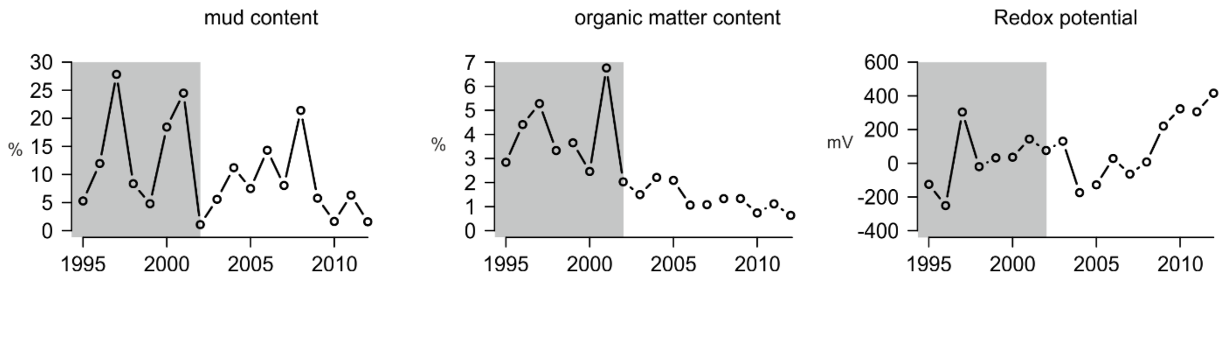

Figure 3. Temporal variation of environmental variables measured in the surficial sediment at station L_UR20. The period with the non-diverted and untreated discharges (1995-2001) is highlighted in grey.

3.2 Indices

The list of taxa (genus level) identified in this study, together with the associated traits can be consulted in Table A.1, in Supplementary Material.

3.2.1 Spatial variation

Almost all indices (except for CWM) displayed significant differences in their median values between stations (Kruskal-Walllis, p-value: < 0.01). Besides, many of these indices showed a very similar spatial variation pattern (Fig. 4). They were all significantly correlated with each other. These correlations were mostly positive, with the exception of genus richness versus AMBI, and AMBI versus M-AMBI, which were negatively correlated, since the scale of AMBI is opposite to the others (lower values indicate better status, whilst for the others this is indicated by higher values). Noticeable are the bell-shaped patterns in the spatial variation of most indices median values (except for AMBI), i.e. generally lower median values at the outer stations, and higher median values at the inner stations. This shape is especially clear for genus richness. The CWM showed considerable variation in their values for most of the trait categories (see Figure A.3, at Supplementary Material).

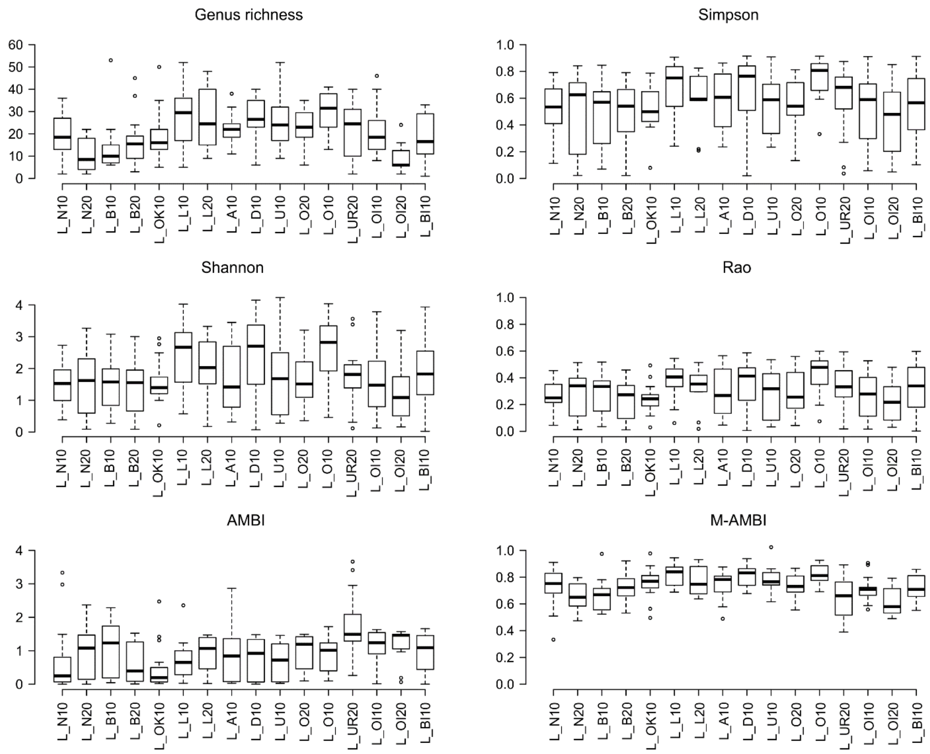

Figure 4. Spatial variation in the indicator values (for the results of the CWM index, see Figure A.3 at Supplementary Material).

3.2.2 Temporal variation

The temporal variation of the indices mean values were assessed at station L_UR20 (Fig. 5 and 6). Genus richness and M-AMBI showed a slight increase towards the latter years, while AMBI showed a general decrease. Simpson, Shannon and Rao did not show slope patterns. Genus richness and M-AMBI were positively correlated (Pearson, r: 0.87, df: 16, p-value: < 0.0001). Rao was positively correlated with Simpson (Pearson, r: 0.93, p-value: < 0.0001) and Shannon (Pearson r: 0.94, df: 16, p-value < 0.0001). AMBI and M-AMBI were negatively correlated (Pearson r: -0.84, df: 16, p-value < 0.0001) and neither of them were significantly correlated with Rao. When comparing the values between the period with the non-diverted and untreated discharges (1995-2001) and the period with the diverted, and since 2006, treated discharges (2002-2012), significant differences were found for genus richness (Kruskal-Wallis, p-value: 0.04), AMBI (Kruskal-Wallis, p-value: 0.003) and M-AMBI (Kruskal-Wallis, p-value: 0.004). All these three indices indicated higher seafloor disturbance during the period with the non-diverted and untreated discharges.

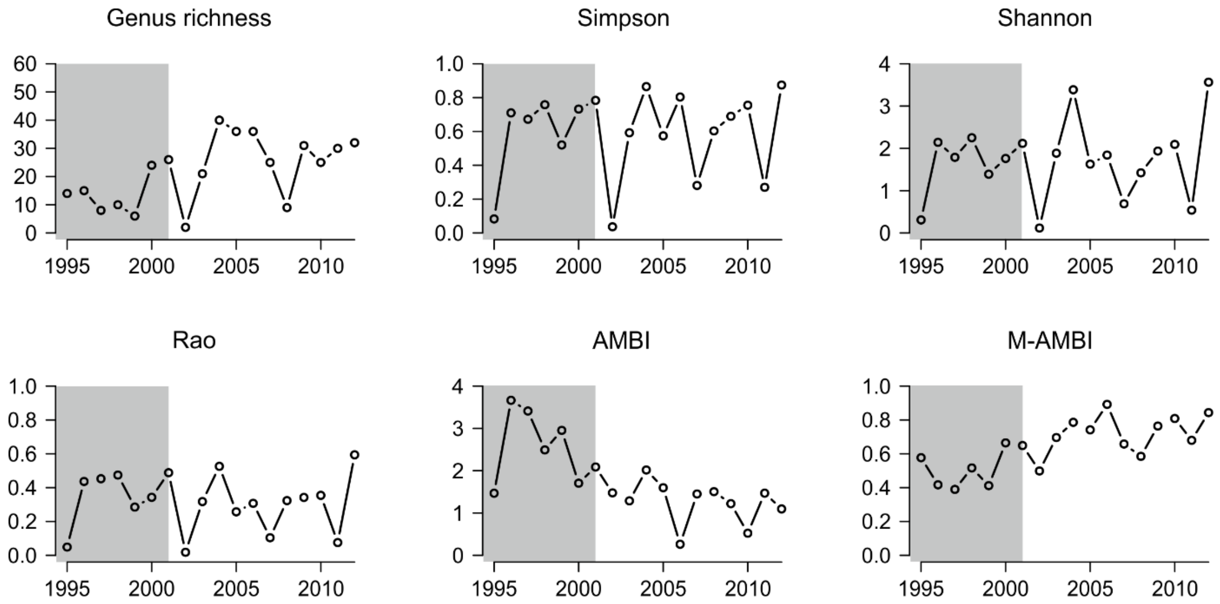

Figure 5. Temporal variation in the indicator mean values at station L_UR20 (for the results of the CWM index, see Fig.6). The period with the non-diverted and untreated discharges (1995-2001) is highlighted in grey.

The CWM index showed some subtle differences in the mean trait values between the two periods (non-diverted and untreated discharges: 1995-2001 versus diverted, and since 2006, treated discharges: 2002-2012) (Fig. 6). When comparing the values between these two periods, significant differences were found for deposit-feeders (Kruskal-Wallis, p-value: 0.05), scavengers (Kruskal-Wallis, p-value: 0.002), very small sized species (Kruskal-Wallis, p-value: 0.03), short lived species (Kruskal-Wallis, p-value: 0.04) and opportunistic species–EG V (Kruskal-Wallis, p-value: 0.002). CWM for deposit-feeders, short lived-, and opportunistic species were higher during the period with the non-diverted and untreated discharges, and the CWM for scavengers and very small sized species were higher during the period with the diverted, and since 2006, treated discharges.

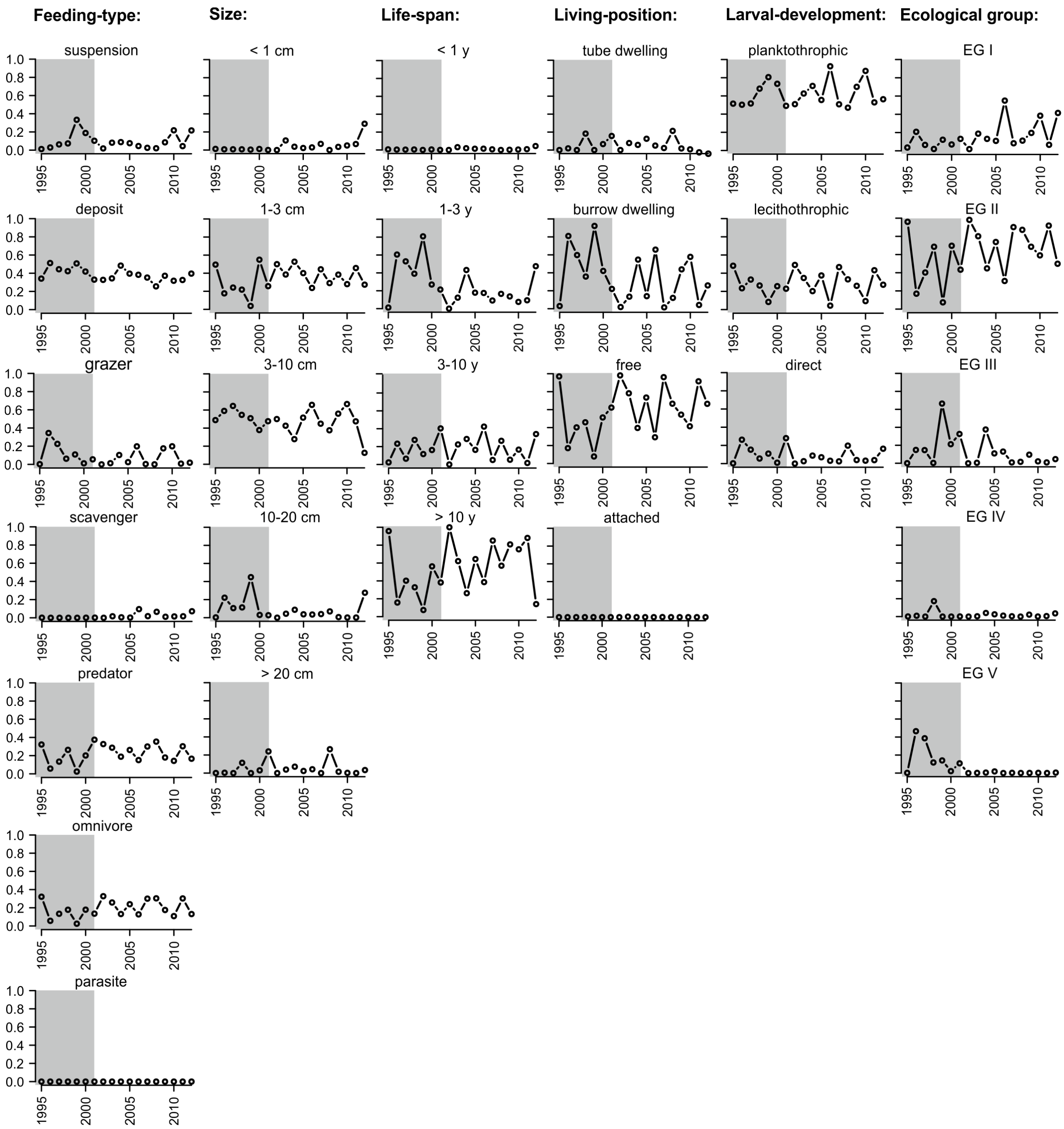

Figure 6: Temporal variation in the CWM values at station L_UR20. The period with the non-diverted and untreated discharges (1995-2001) is highlighted in grey.

3.3 Correlation between the CWM and the AMBI ecological groups (EG's)

Table 2 summarises the results of the correlation analysis between all trait categories and the EG's. For all traits, the category with the highest positive correlation is shown. Sensitive species (EG I) correlated with suspension-feeders, medium size, medium life-span, burrow-dwellers and species with a planktotrophic larval-development. Opportunistic species (EG V) correlated with species displaying a very short life-span and a direct larval-development.

Table 2. Correlations (Pearson, df: 260, pairwise p-values) between the EG's and the CWM (traits) (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Only the highest correlation for each cell is presented.

CWM (traits)	**EG I** (sensitive species)	**EG II** (indifferent species)	**EG III** (tolerant species)	**EG IV** (2nd order opportunistic species)	**EG V** (1st order opportunistic species)
Feeding	suspension (0.61***)	omnivore (0.71***)	deposit (0.42***)	suspension (0.14*)	-
Size	medium (0.33***)	very small (0.16*) large (0.16*)	very large (0.16*)	small (0.13*)	-
Life-span	medium (0.16*)	Short (0.13*)	short (0.27***)	-	very short (0.42***)
Living-position	burrow-dwelling (0.51***)	free (0.55***)	-	-	tube-dwelling (0.18**)
Larval-development	planktotrophic (0.26***)	lecithotrophic (0.34***)	direct (0.21**)	-	direct (0.19**)

3.4 Correlation between the indices and the environment

Considering the spatial variation, all indices showed significant correlations with one or more environmental variables (see Table 3 for details). The taxonomic indices (genus richness, Simpson and Shannon) were all negatively correlated with wave flux (genus richness showed the strongest correlation). Simpson, Rao and AMBI were positively correlated with mud-content (AMBI showed the strongest correlation). Only AMBI and M-AMBI were correlated with redox-potential. Regarding the CWM, most size traits were correlated to either organic-matter content, redox-potential or wave-flux, but not with mud-content. Short- and long life-span and a variety of feeding traits were mostly correlated with organic-matter content and wave-flux, while the living-habit traits (tube-dwelling and attached) and the larval-development traits (planktotrophic and lecithotrophic) correlated with organic-matter content and redox-potential. EG's I, III, IV and V were correlated with mud-content and redox potential. Considering the temporal variation at station L_UR20, AMBI, direct larval-development and EG V were positively correlated with organic-matter content, while M-AMBI was negatively correlated (see Table 4).

Table 3. Significant correlations (Pearson, df: 260, adjusted pairwise p-values) between the indices and the spatial variation of environmental variables (* p < 0.05, ** p < 0.01, *** p < 0.001).

Index	Trait (categories)	Mud-content	Organic-matter content	Redox-potential	Wave-flux
Genus richness	-				-0.33***
Simpson	-	0.17*			-0.16*
Shannon	-				-0.15*
AMBI	-	0.28***		-0.35***	
M-AMBI	-			0.19**	-0.27***
Rao	-	0.16*			
CWM	Size (very small: < 1 cm)			0.16*	0.25***
CWM	Size (small: 1-3 cm)		0.27***	-0.15*	-0.16*
CWM	Size (medium: 3-10 cm)		-0.22**		
CWM	Size (large: > 20 cm)		0.26***		
CWM	Life-span (short: 1-3 year)		0.15*		0.24***
CWM	Life-span (long: > 10 year)		-0.14*		
CWM	Feeding-strategy (suspension)				-0.16*
CWM	Feeding-strategy (deposit)		-0.14*		
CWM	Feeding-strategy (grazer)		-0.16*		
CWM	Feeding-strategy (scavenger)			0.17*	0.24***
CWM	Feeding-strategy (predator)		0.19**		0.20**
CWM	Feeding-strategy (omnivore)		0.15*		0.17*
CWM	Living-position (tube-dwelling)			-0.19**	
CWM	Living-position(attached)		0.17*		
CWM	Larval-development (planktotrophic)		-0.23***	0.15*	
CWM	Larval-development (lecithotrophic)		0.21**	-0.25***	
CWM	EG I	-0.14*		0.22***	
CWM	EG III			-0.19**	
CWM	EG IV	0.28***			
CWM	EG V	0.225***		-0.314***	

Table 4. Significant correlations (Pearson, df: 16, adjusted pairwise p-values) between the indices and the temporal variation of environmental variables measured in the surficial sediment at station L_UR20 (* p < 0.05, ** p < 0.01).

Index	Trait (categories)	Mud-content	Organic-matter content	Redox-potential
AMBI	Ecological groups		0.76**	
M-AMBI	Ecological groups		-0.63*	
CWM	Larval-development (direct)		0.61*	
CWM	EG V		0.69*	

4. Discussion

4.1 AMBI and M-AMBI

AMBI was able to indicate the effects of anthropogenic seafloor disturbance. According to this index, the seafloor was most disturbed at station L_UR20, and more than average disturbed at stations L_N20 and L_OI20 (also disturbed by anthropogenic pressures). At station L_UR20 it was also able to distinguish between the two periods with different levels of disturbance (i.e. higher disturbance during 1995-2001 and lower disturbance during 2002-2012). Station L_UR20 is regarded as the most disturbed of the dataset, especially between 1995 and 2001, when untreated urban wastewater was directly discharged in the close vicinity of this station, affecting the benthic communities due to poor sediment quality (i.e. high organic matter content and low redox potential values). In 2001, a marine outfall was constructed, which, to date, transports the biologically treated (since 2006) wastewater to a location approximately 1.2 km offshore. Since then, sediment quality steadily improved by reducing the organic matter and increasing the redox potential (Borja et al., 2009), as can be seen in Figure 3.

M-AMBI showed a slightly different response. According to this index, not station L_UR20 but stations L_N20 and L_OI20 were the most disturbed over the whole period (1995-2012). This response can be attributed to the influence of richness and diversity in its calculation. In particular, genus richness, but also the Shannon index, showed very low values at stations L_N20 and L_OI20. Also, the method used to calculate M-AMBI for this study influenced its performance. M-AMBI was calculated at genus level. Therefore, genus richness and the Shannon index were slightly different from those calculated based on species level. In fact, M-AMBI detected the worst seafloor quality at station L_UR20 when based on species level identification, after Borja et al. (2009).

To adequately compare the performance of all indices, both AMBI and M-AMBI were calculated with ‘genus biomass’ instead of ‘species density’ which is the common calculation method used in most studies (e.g. Borja et al., 2009; Paganelli et al., 2011). The results demonstrated a strong correlation between both calculation methods regarding their response to anthropogenic seafloor disturbance in this marine environment. However, some performance loss did occur due to the exclusion of certain taxa at a lower resolution (nematodes, oligochaetes, etc.) that mostly belonged to ecological group (EG) V (1^{st} order opportunists). Previous studies by Warwick et al. (2010), Muxika et al. (2012) and Cai et al., (2014) already demonstrated a strong relationship between AMBI (the two former studies) and M-AMBI calculated with 'species biomass' versus 'species density'.

In summary, both AMBI and M-AMBI were able to adequately assess the effects of anthropogenic seafloor disturbance in this coastal environment. They responded to changes in the redox-potential (spatial variation) and organic-matter content (temporal variation at station L_UR20). However, the performance of the indices was influenced by other factors. AMBI, for instance, also responded to mud-content, which can be considered a natural characteristic of the area. M-AMBI responded to wave-flux, which is a natural type of disturbance. The impact of wave-flux on the seabed was generally higher at the stations that are more exposed to the most common swell direction (coming from the north-west, e.g. L_N20 and L_OI20). These stations are situated in front of the stretch of coastline that is most perpendicular orientated towards this swell direction.

4.2 Community-weighted mean trait values (CWM)

The CWM was used to summarize shifts in the mean trait category values within communities due to environmental selection for the traits (Ricotta and Moretti, 2011). As such, we expected that all six-trait groups (28 trait categories) would be indicative of anthropogenic- and natural seafloor disturbance.

In general, the EG's were the most indicative of anthropogenic seafloor disturbance, which was obviously reflected in the performance of AMBI and, subsequently, M-AMBI. EG's I (sensitive species), III (tolerant species) and V (1st order opportunists) all responded to the spatial variation of redox-potential values, while the latter also responded to the temporal variation of organic-matter content (station L_UR20 showed a relatively high mean for EG V, especially during the period with the non-diverted and untreated discharges).

The strength of the EG's, and therefore AMBI and M-AMBI as anthropogenic disturbance indicators, is that they synthesise information regarding functioning based on multiple traits (Marchini et al., 2008). Indeed, each EG was correlated with at least two or more individual traits. For example, EG V was positively correlated with short-lived, tube-dwelling species with a direct larval-development. This wide spectrum of traits might have caused an advantage over each individual trait. Each individual trait does not always contribute with unique information on functioning (Verberk et al., 2013). In this respect, the use of a smaller number of strategies capturing the most relevant differences in trait combinations could help improve the signal-to-noise ratio, resulting in higher discriminatory power (Verberk et al., 2013).

The individual traits that seemed most indicative of anthropogenic seafloor disturbance were tube-dwelling, lecithotrophic- and direct larval-development. Tube-dwelling and lecithotrophic larval-development showed the strongest correlation with the spatial variation of redox-potential values. Direct larval-development was correlated with the temporal variation of organic-matter content at station L_UR20. Besides, these traits responded solely to anthropogenic disturbance and not to natural disturbance in the form of wave-flux.

At first glance, also the traits that correlated with the spatial variation of organic-matter content appear to be indicative of anthropogenic disturbance. However, this correlation was only observed regarding the spatial variation, which did not change much. Considering the temporal variation at station L_UR20, none of these traits responded to the considerable decrease of organic-matter content. Besides, some of these traits were also influenced by natural disturbance (small size, short life-span, predators and omnivores). This suggested that these traits were not particularly indicative of anthropogenic seafloor disturbance in this environment. However, a number of studies observed an increase of small-sized species with increasing organic-matter content (e.g. Dauer et al., 1992; Pacheco et al., 2010; van Son et al., 2013).

As mentioned before, tube-dwellers, lecithotrophic- and direct larval-development categories seemed the most indicative of anthropogenic disturbance. Indeed, for tube-dwellers this response was expected (Reise, 2002) but not for lecithotrophic and direct larval-development. Taxa with a planktotrophic larval-development was *a-priori* expected to increase in abundance with seafloor disturbance (Table 1). High larval mobility usually indicates an unstable habitat (Paganelli et al., 2012). However, Villnäs et al. (2011) and van Son et al. (2013) found that lecithotrophic larval-development characterised organic enriched environments. This study does not support their findings because it was not correlated with organic-matter content. As such, a clear mechanistic link for why lecithotrophic- and direct larval-development might be used to indicate anthropogenic seafloor disturbance is missing.

In summary, the CWM of most individual traits was not indicative of anthropogenic seafloor disturbance in this coastal ecosystem. This might have been due to different reasons: the links between the traits and the environmental variables that are associated with anthropogenic seafloor disturbance were weak; the mechanistic links between certain traits (e.g. larval-development) and their response to seafloor disturbance in marine environments is currently not well understood (Berthelsen et al., 2015). Besides, other anthropogenic pressures exist in the area, like fishing and dredging or sediments deposits, which may have contributed to mask the results obtained. Moreover, many traits were also influenced by wave-flux (natural disturbance), which made it difficult to understand whether they were influenced by anthropogenic- or natural disturbance, or by a combination of both.

4.3 Trait diversity (Rao)

We *a-priori* expected that trait diversity, which was expressed by the Rao, would be lowest at the most disturbed stations (L_N20, L_UR20 and L_OI20), especially at station L_UR20 during the period with the non-diverted and untreated discharges (1995-2001). However, this was not the case, Rao values at these stations were similar to those of most other stations, and its values during 1995-2001 were not much different from the period with the diverted, and since 2006, treated discharges (2002-2012). Based upon these results, Rao was not a useful indicator to detect anthropogenic seafloor disturbance in this particular environment. However, this outcome does not necessarily mean that Rao or any other measure for trait diversity is useless for detecting seafloor disturbance. A number of studies demonstrated a clear response of Rao to anthropogenic seafloor disturbance (e.g. Cooper et al., 2008; Paganelli et al., 2012; Wan Hussin et al., 2012). As previously mentioned when discussing the CWM results, also the performance of Rao depends on which types of traits are considered. Rao will perform better if traits have more strong and clear links with the particular type of disturbance that is being studied, and if there is none or little distortion between anthropogenic- and natural disturbance. The performance of Rao was also similar to that of genus richness and the Simpson index (strongly correlated). This reflects the relationship between species richness and trait (functional) diversity in that with the loss or addition of a species, unique traits were being lost or added to the community (Culhane et al., 2014; van der Linden et al., 2016). Most studies found a strong correlation between Rao and Simpson (e.g. Vandewalle et al., 2010; Culhane et al., 2014; van der Linden et al., 2016).

4.4 From a management perspective

AMBI and M-AMBI were able to adequately assess the effects of anthropogenic seafloor disturbance in the form of organic-matter enrichment and oxygen depletion of the surficial sediments in this marine system. Their strength lies in the ability of their ecological groups to capture a wide range of information about the response of multiple individual traits to this particular type of disturbance. The CWM of the individual traits and the diversity of these traits, as expressed by the Rao index, were not effective in indicating this disturbance. The main reason was probably that many of the individual traits did not have a very strong and clear mechanistic link with this type of disturbance. Besides, some traits also responded to natural disturbance in the form of wave-flux, which makes it difficult to unravel the effects of both types of disturbance. A clear advantage by using the CWM of the individual traits is that it gave a more detailed understanding on how the two types of disturbances (anthropogenic and natural) affected the individual traits, and thus the functioning of species communities as a whole. This knowledge might aid in the development of existing- or to be developed indices. For instance, if you know that small sized species will respond to natural disturbance in your study area, one might exclude this trait from that particular index. However, from a management perspective, which aims to simply monitor the quality and health of the site, a full understanding of a site may not necessarily be required (Culhane et al., 2014). Moreover, the CWM of multiple traits does not provide a single number that indicates a quality status, which makes it a difficult tool to use and interpret, especially for managers. It is probably more useful for scientists who really want to explore and understand different aspects of community functioning. In this aspect, AMBI and M-AMBI are easier and more straightforward to use. That is why several European Member States have used them in the first MSFD phase of GES assessment. Unlike the CWM, trait diversity (Rao in this case) provides a single value of functioning, having therefore real potential to effectively be used for management purposes. However, to improve its performance, detailed and accurate traits data are required. This is currently lacking for many marine species (Munari, 2013; Berthelsen et al., 2015). We therefore suggest that more research is needed into quantifying a larger number of traits and to understand their links with anthropogenic seafloor disturbance, before effectively utilising trait (functional) diversity for this purpose. Perhaps, when doing so, trait diversity will not be as strongly correlated to species diversity, which is now questioning the use of trait diversity as an effective tool for management purposes.

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Supplementary material

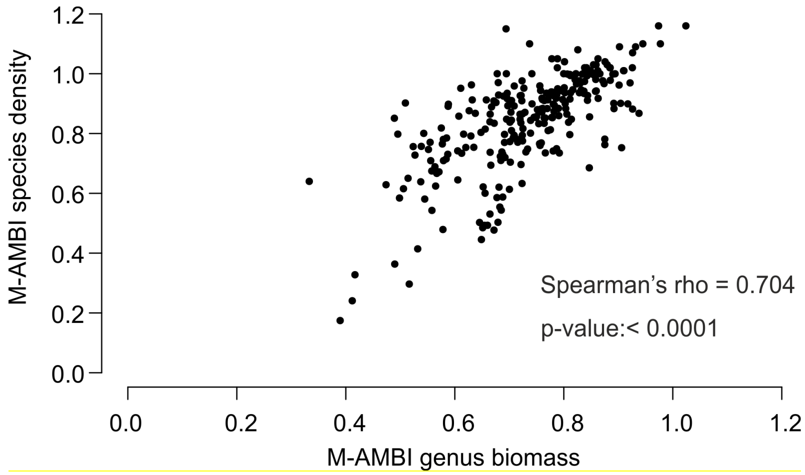


Figure A.1 Relation between M-AMBI calculated with species density and genus biomass. Results of the Spearman's rank correlation analysis are shown.

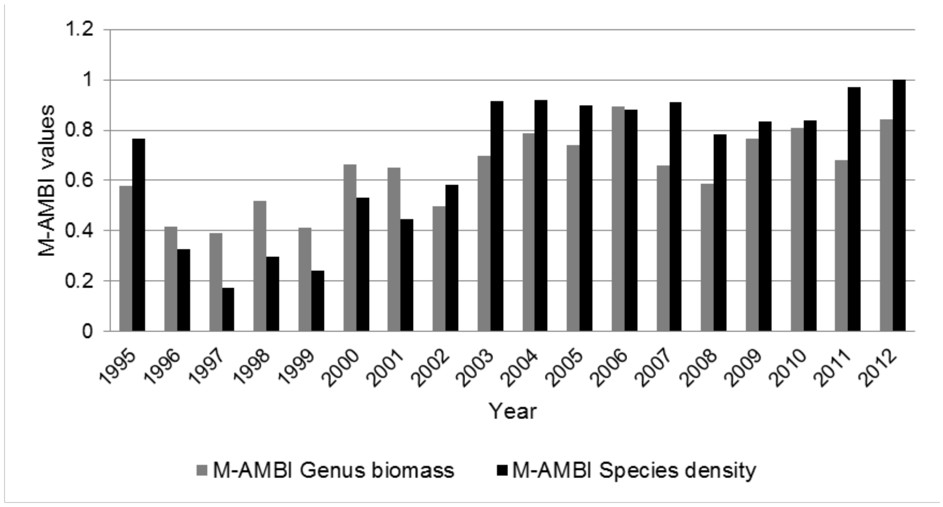
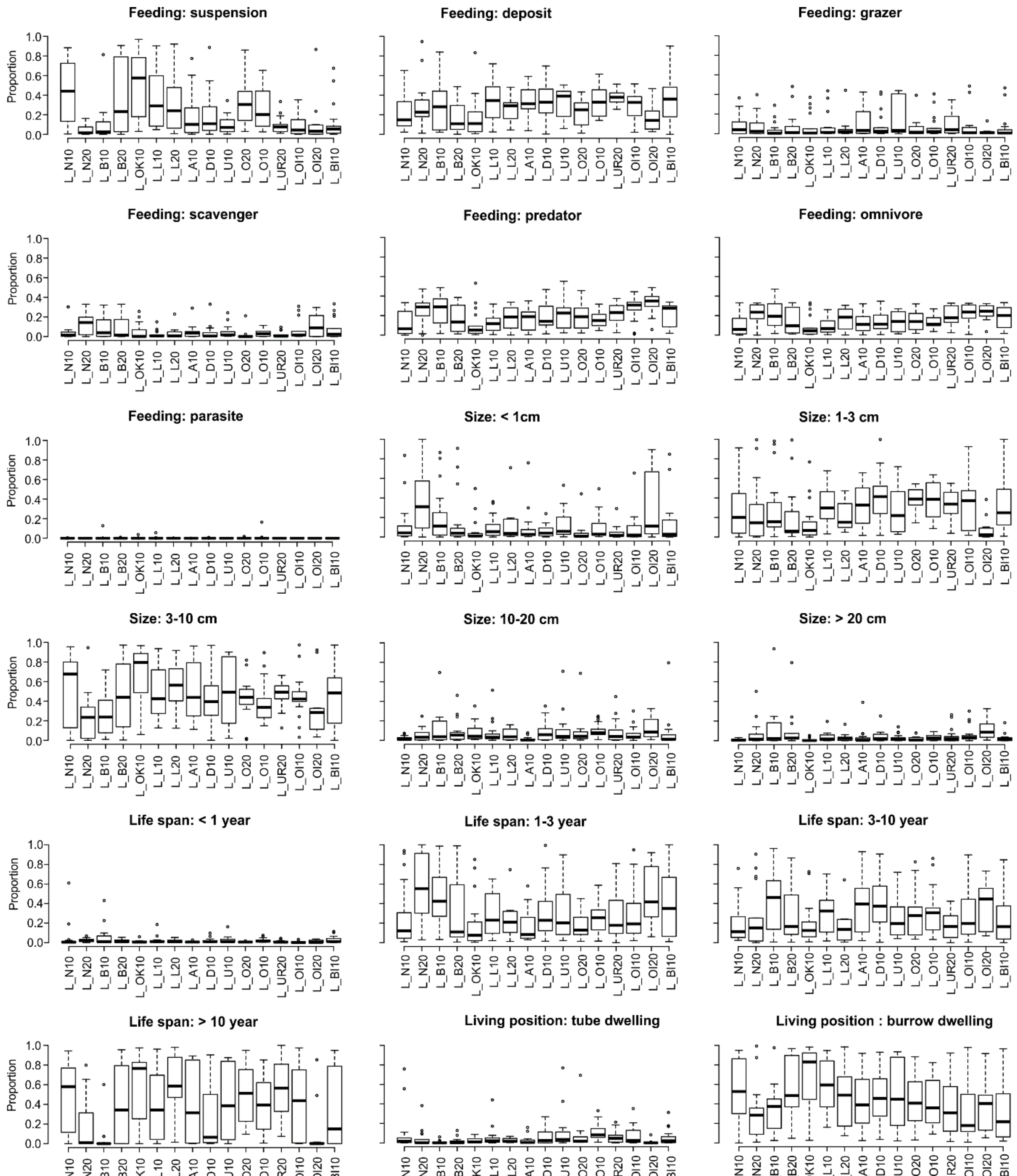


Figure A.2 M-AMBI values calculated with species density and genus biomass at station L_UR20. From 1996 to 2001 (and in 2006), M-AMBI values calculated with genus biomass exceeded the values of M-AMBI calculated with species density. The opposite can be observed for the other years. The reason for this difference is that M-AMBI calculated with species density (standard calculation of M-AMBI) included taxa at a lower resolution than genus (nematodes, oligochaetes, etc.). As most of these taxa belong to ecological groups IV and V (opportunists), M-AMBI calculated with species density responded more obviously to disturbance during the initial years, which is in accordance with the expected disturbance pattern at this station. Nevertheless, both calculation methods showed similar patterns. The Wilcoxon signed-rank test results indicated non-significant differences between the two calculation methods (p-value: 0.369).


Feeding: suspension
Feeding: deposit
Feeding: grazer
Feeding: scavenger
Feeding: predator
Feeding: omnivore
Feeding: parasite
Size: < 1cm
Size: 1-3 cm
Size: 3-10 cm
Size: 10-20 cm
Size: > 20 cm
Life span: < 1 year
Life span: 1-3 year
Life span: 3-10 year
Life span: > 10 year
Living position: tube dwelling
Living position : burrow dwelling
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
L_N10
L_N20
L_B10
L_B20
L_OK10
L_L10
L_L20
L_A10
L_D10
L_U10
L_O20
L_O10
L_UR20
L_OI10
L_OI20
L_BI10

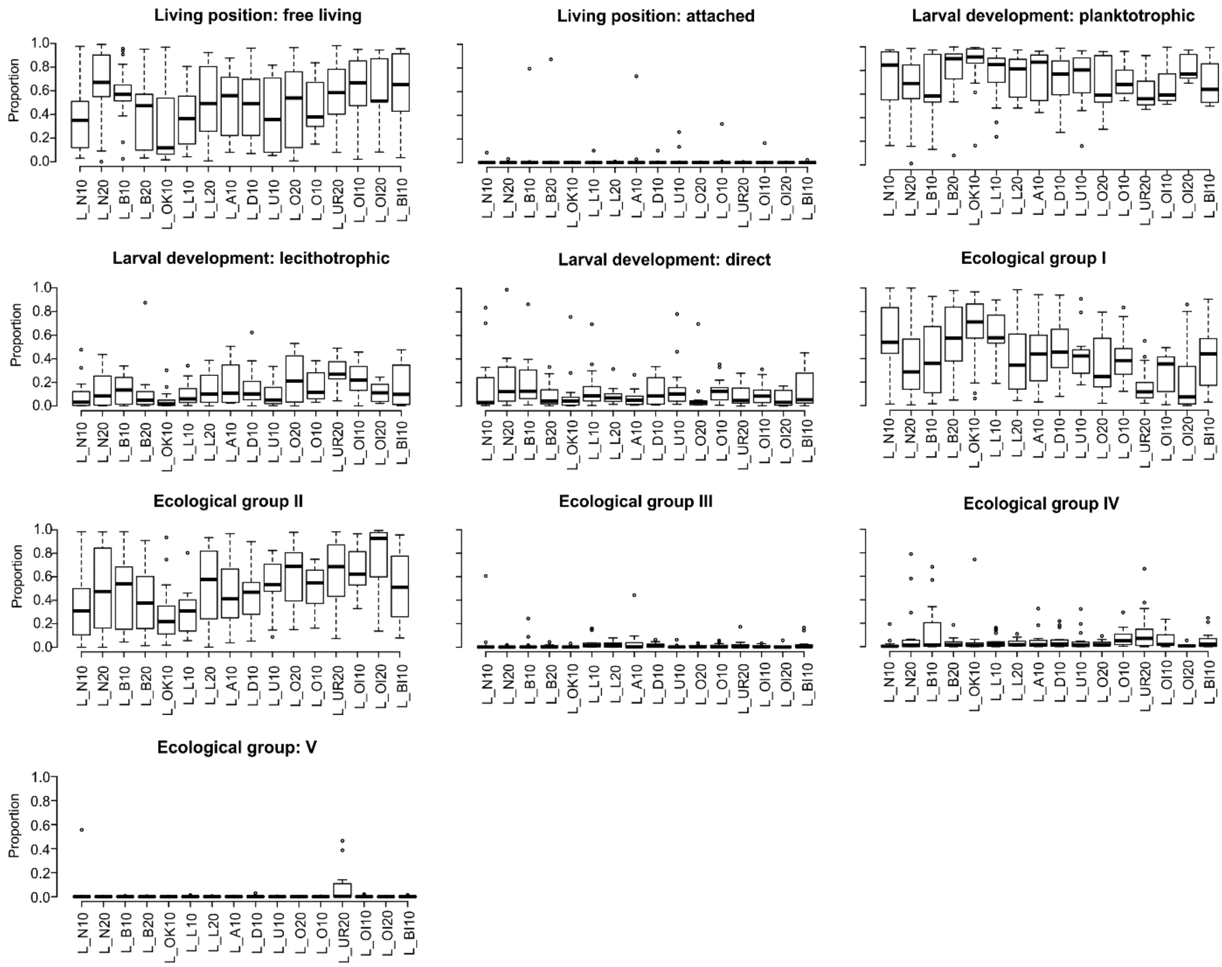


Figure A.3 The community weighted mean trait values for each of the 28 trait categories for each station.

Table A.1 The list of taxa (genus level) identified in this study, together with the associated traits (See Table 1 for the meaning of the labels).

Genus	S_1	S1_3	S3_10	S10_20	S_20	L_1	L1_3	L3_10	L_10	F_SUS	F_DEP	F_GRA	F_SCA	F_PRE	F_OMN	F_PAR	LH_TD	LH_BD	LH_FL	LH_ATT	DT_PLAN	DT_LEC	DT_DIR	EG_I	EG_II	EG_III	EG_IV	EG_V
Abarenicola	0	0	0	1	0	0	0	1	0	0	2	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0
Abludomelita	1	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0
Abra	0	1	0	0	0	0	3	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Abyssoninoe	0	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Acanthocardia	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Acrocnida	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Acteon	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0
Aglaophamus	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0
Alvania	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Amathia	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Ampelisca	1	1	1	0	0	1	3	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Ampharete	1	1	2	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0
Amphibalanus	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Amphictene	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Amphipholis	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Amphiura	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Anapagurus	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Anchialina	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
Animoceradocus	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Anoplodactylus	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Aonides	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Aora	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Aphelochaeta	0	0	1	0	0	0	2	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Apherusa	1	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Apistobranchus	2	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Apohyale	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Aponuphis	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Aporrhais	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Apseudes	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Aricidea	1	2	0	0	0	3	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0
Armandia	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Ascorhynchus	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Aspidosiphon	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Astarte	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Astropecten	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0
Atylus	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0
Autonoe	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
Barleeia	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Bathyporeia	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Bela	2	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Bittium	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Bodotria	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0
Branchiomaldane	1	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Branchiostoma	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Brania	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Caecum	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0
Callianassa	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Capitella	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
Caryophyllia	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0
Caulleriella	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0
Cellepora	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
Cerastoderma	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0
Cerebratulus	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Chaetozone	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
Chamelea	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Cheirocratus	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Chone	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0
Cirolana	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Cirrophorus	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0
Clausinella	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Cleantis	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Clytia	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Colomastix	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0
Comarmondia	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0
Corbula	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0
Coryne	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Corystes	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Cossura	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0
Cumella	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cylichna	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Cymia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cymodoce	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Dardanus	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Diastylis	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0

	Digitaria	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0
	Diogenes	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
	Diopatra	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1	0	0	0
	Dioplosyllis	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0
	Diplocirrus	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
	Dispio	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0
	Donax	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
	Dosinia	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
	Dynamene	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
	Ebalia	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
	Echinocardium	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0
	Echinocyamus	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0
	Echiurus	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0
	Edwardsia	0	1	0	0	0	0	0	1	3	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
	Embletonia	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
	Ensis	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
	Eocuma	1	0	0	0	0	2	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
	Epitonium	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
	Epizoanthus	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0
	Erinaceusyllis	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
	Euclymene	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	2	2	0	0	0	0	0
	Eulalia	0	0	1	1	0	0	1	3	0	0	0	0	1	1	1	0	0	0	1	0	3	1	0	0	1	0	0	0
	Eulimella	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0
	Eumida	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0
	Eunice	0	0	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
	Eunicella	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0
	Eupolymnia	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
	Eurydice	1	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0
	Eurysyllis	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0
	Euspira	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0
	Eusyllis	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0
	Exogone	0	1	0	0	0	3	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
	Galathea	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
	Galathowenia	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
	Gammarella	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
	Gammaropsis	1	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
	Gammarus	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0
	Gari	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0
	Gastrosaccus	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	2	0	0	0	1	0	1	0	0	0
	Glycera	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0
	Glycinde	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
	Glycymeris	0	0	1	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0
	Goniada	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
	Goniadella	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
	Goodallia	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
	Gouldia	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	Grania	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
	Gregariella	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
	Guernea	1	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
	Gyptis	1	2	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
	Haplostylus	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0
	Harmothoe	0	1	1	0	0	0	1	1	0	0	0	0	0	2	1	0	1	0	3	0	1	0	0	0	1	0	0	0
	Harpinia	1	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0	1	1	0	0	0	0
	Hediste	0	0	0	1	0	1	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0
	Hesionura	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
	Hesiospina	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
	Heterodrilus	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
	Hiatella	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
	Hippomedon	1	1	0	0	0	1	2	0	0	0	1	0	0	2	1	0	0	0	1	0	0	0	1	1	0	0	0	0
	Hyalinoecia	0	0	1	1	1	0	1	3	0	0	1	0	0	0	1	0	3	1	0	0	0	0	1	0	1	0	0	0
	Idotea	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0
	Idunella	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
	Iphinoe	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0	1	1	0	0	0	0
	Jaera	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0
	Jassa	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1
	Kefersteinia	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0
	Kurtiella	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0
	Lacydonia	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0
	Laevicardium	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	Lagis	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
	Lanassa	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	Lanice	0	0	0	1	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
	Laonice	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
	Lekanesphaera	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
757	*Lepidepecreum*	1	0	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0

Lepidonotus	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Leptochelia	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Leptoplana	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Leptosynapta	0	0	0	0	1	0	1	2	0	0	1	1	0	0	0	0	0	2	1	0	0	0	1	1	0	0	0	0
Leucothoe	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Levinsenia	0	0	1	0	0	0	1	1	0	1	2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Limaria	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Limatula	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0
Liocarcinus	0	1	1	0	0	0	0	3	0	0	0	0	0	3	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Lophogaster	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	0	0
Loripes	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Lucinella	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Lumbrinerides	0	0	1	0	0	0	1	1	0	0	1	0	0	2	1	0	0	1	3	0	0	1	1	0	1	0	0	0
Lumbrineriopsis	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0
Lumbrineris	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0
Lutraria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Lysidice	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	3	0	1	0	0	0	1	0	0	0
Lysilla	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Macrochaeta	1	0	0	0	0	0	1	1	0	1	2	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0
Mactra	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Maerella	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Magelona	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Malacoceros	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Malmgreniella	0	1	1	0	0	0	0	1	0	0	0	0	0	2	1	0	1	1	3	0	1	0	0	0	1	0	0	0
Mangelia	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Marphysa	0	0	1	2	2	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	0	0
Mediomastus	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	3	1	0	0	1	0	0	0	0	1	0	0
Megaluropus	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Megamphopus	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Melanella	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0
Melinna	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	3	0	0	0	0	1	0	0	0	1	0	0
Mesochaetopterus	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0
Mesonerilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microdeutopus	1	1	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0
Microjaera	1	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Micromaldane	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0
Microspio	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0
Modiolula	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Moerella	0	1	1	0	0	0	0	1	0	1	3	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Monoculodes	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	1	3	0	0	0	1	1	0	0	0	0
Montacuta	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	3	1	0	1	0	0	0	1	0	0	0
Monticellina	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Musculus	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0	0
Myrianida	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Myriochele	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Mysta	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	3	0	0	1	1	0	0
Mystides	1	2	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Mytilaster	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Nassarius	0	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0
Natatolana	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Nebalia	0	1	0	0	0	1	0	0	0	3	1	0	0	0	0	0	0	0	1	0	3	0	1	0	0	0	0	1
Necallianassa	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
Nephasoma	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
Nephtys	0	0	1	1	1	0	1	3	0	0	1	0	0	2	1	0	0	1	1	0	3	1	0	0	1	0	0	0
Nereimyra	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	0	1	0	0
Nereiphylla	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Nereis	0	0	1	1	0	0	0	1	0	0	1	0	0	2	1	0	0	1	0	0	0	1	2	0	0	1	0	0
Nicomache	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Nothria	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Notocirrus	0	0	0	1	1	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
Notomastus	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	2	0	0	0	1	0	0
Nucula	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	3	0	1	0	0	0	0
Odontosyllis	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Onuphis	0	0	0	1	0	0	1	1	0	0	0	0	0	2	1	0	1	0	0	0	0	0	1	0	1	0	0	0
Ophelia	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Ophiopsila	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Ophiura	0	1	1	0	0	0	0	1	0	1	1	0	0	3	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Ophryotrocha	1	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Opisthodonta	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	1	0	0
Orbinia	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Orchomene	1	0	0	0	0	1	2	0	0	0	0	0	0	2	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Owenia	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Oxydromus	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0
Pagurus	0	1	1	0	0	0	0	1	0	1	1	0	0	2	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Pandora	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0

Papillicardium	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Paradialychone	1	1	0	0	0	0	1	0	0	2	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	0
Paradoneis	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Paraehlersia	0	1	0	0	0	0	1	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	1	0	1	0	0	0
Parahaustorius	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0
Paranaitis	0	1	2	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Paraonis	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Parapionosyllis	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0
Pariambus	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Perioculodes	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	3	0	0	0	1	0	1	0	0	0
Phascolion	0	0	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Phaxas	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Pherusa	0	0	1	0	0	0	0	1	0	1	2	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0
Philine	0	1	1	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Philocheras	0	0	1	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Phoronis	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0
Phtisica	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Phyllodoce	0	0	1	1	0	0	3	1	0	0	0	0	0	1	1	0	0	1	2	0	1	1	0	0	1	0	0	0
Pinnotheres	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Pionosyllis	1	0	0	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	1	0	0	1	1	0	1	0	0	0
Pisione	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Pista	0	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0
Pistella	0	0	1	0	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Plakosyllis	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	1	0	0	0
Plumularia	0	1	1	2	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	0
Podarkeopsis	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0
Podocoryna	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Poecilochaetus	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Polybius	0	0	1	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Polycirrus	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	3	0	0	1	0	0	0	0	1	0
Polydora	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	3	1	0	0	1	0	1	0	0	0	1	0
Polygireulima	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0
Polygordius	0	0	1	0	0	1	3	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Polyophthalmus	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	3	0	0	0	1	1	1	0	0	0	0
Pontocrates	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	3	0	0	0	1	0	1	0	0	0
Portumnus	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Prionospio	0	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0
Processa	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Prosphaerosyllis	2	1	0	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0
Protodorvillea	0	1	1	0	0	0	1	0	0	0	0	0	0	2	1	0	0	0	1	0	0	0	1	1	1	0	0	0
Protodriloides	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Protodrilus	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Protomystides	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0
Psamathe	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0
Psammechinus	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0
Pseudocuma	1	0	0	0	0	1	3	0	0	1	1	0	0	0	0	0	0	1	3	0	0	0	1	0	1	0	0	0
Pseudomystides	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Pseudopolydora	1	1	1	0	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0
Pseudoprotella	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Pseudopythina	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Retusa	1	1	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	1	0	0	1	0	0	0	1	0	0	0
Rissoa	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Rocellaria	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Sabella	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Sabellaria	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Saccocirrus	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Salvatoria	1	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Sarsinebalia	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Scalibregma	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
Scaphander	0	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0
Schistomeringos	0	0	1	0	0	0	1	1	0	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0
Sclerocheilus	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Scolaricia	0	0	0	1	0	0	1	3	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Scolelepis	0	1	1	1	0	3	1	0	0	2	3	0	0	1	1	0	0	1	1	0	3	0	1	0	0	1	0	0
Scoletoma	0	0	1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	0	0
Semivermilia	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
Sertularella	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Sigalion	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Siphonoecetes	1	0	0	0	0	1	0	0	0	2	2	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Sipunculus	0	1	1	1	0	0	1	0	0	0	2	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Socarnes	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0
Spadella	1	1	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Spatangus	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Sphaerosyllis	1	0	0	0	0	0	1	0	0	0	3	0	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0
Sphenia	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0

Spio	0	1	1	0	0	1	1	0	0	1	2	0	0	0	0	0	1	0	0	0	3	0	1	0	0	1	0	0
Spiochaetopterus	0	0	1	0	0	0	0	1	0	1	2	0	0	0	0	0	3	1	0	0	1	0	0	0	0	1	0	0
Spiophanes	0	0	1	0	0	0	1	0	0	1	2	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0
Spirobranchus	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0
Spisula	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Sthenelais	0	0	1	1	0	0	0	1	0	0	0	0	0	2	1	0	0	0	1	0	1	0	0	0	1	0	0	0
Streblospio	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Streptosyllis	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Sycon	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Syllides	1	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	0
Syllis	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	3	0	1	0	0	0
Synchelidium	1	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	1	3	0	0	0	1	1	0	0	0	0
Tellimya	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	3	1	0	1	0	0	0	1	0	0	0
Tellina	1	1	0	0	0	1	1	2	0	1	2	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Tharyx	0	1	1	0	0	0	1	3	0	1	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0
Thia	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Thracia	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Thyasira	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0
Timoclea	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Tricolia	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Triphora	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0
Trypanosyllis	1	1	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0
Tryphosella	1	0	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Tryphosites	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
Tubulanus	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0
Tubularia	0	0	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0
Turbonilla	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0
Turritella	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Uca	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0
Unciola	0	1	1	0	0	1	0	0	0	1	2	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
Urothoe	1	0	0	0	0	0	1	0	0	1	2	0	0	0	0	0	0	1	3	0	0	0	1	1	0	0	0	0
Vaunthompsonia	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Venus	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Verruca	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Volvulella	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0
Websterinereis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Xenosyllis	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0