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Title: A process-driven sedimentary habitat modelling approach, providing insights into seafloor integrity and biodiversity assessment within the European Marine Strategy Framework Directive

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Abstract

The Marine Strategy Framework Directive (MSFD) seeks to achieve good environmental status, by 2020, for European seas. The applicability of a process-driven benthic sedimentary habitat model, to be used in the implementation of the MSFD in relation to biodiversity and seafloor integrity descriptors for sedimentary habitats, has been analysed. The approach is used to project, onto a map, the major environmental factors influencing soft-bottom macrobenthic community structure and the life-history traits of species. Among the 16 environmental variables considered in this investigation, a combination of water depth, mean grain size, a wave-induced sediment resuspension index and annual bottom maximum temperature, are found to be the most significant factors explaining the variability in the structure of benthic communities in the study area. The aforementioned variables are classified into those representing the \`Disturbance´ and \`Scope for Growth´ components of the environment. It was observed that the habitat classes defined in the process-driven model reflected different structural and functional characteristics of the benthos. Moreover, benthic community structure anomalies due to human pressures could be detected also, within the model produced. Thus, the final process-driven habitat map can be considered as being highly useful for seafloor integrity and biodiversity assessment, within the European MSFD. Likewise, for conservation, environmental status assessment and managing human activities, especially within the marine spatial planning process.

Keywords: sedimentary habitat modelling, benthic processes, life-history traits, marine ecosystem, Marine Strategy Framework Directive

1. Introduction

Increasing pressure induced by human activities in the marine environment has triggered the necessity for new management requirements. Amongst others, new initiatives towards marine management, *e.g.* Marine Spatial Planning (MSP) (Douvere & Ehler, 2009; European Commission, 2010b) and Ecosystem-Based Management (EBM) (or the Ecosystem-based MSP (Foley *et al.*, 2010; Katsanevakis *et al.*, 2011)), have highlighted the need for the best available scientific knowledge on the marine environment, as well as ecosystem functioning. For example, benthic habitat maps have been identified as being the basic knowledge to permit scientists and managers to understand the distribution of living and non-living resources on the seafloor (Shumchenia & King, 2010) together with their characteristics (vulnerability, sensitivity, etc.). Such information needs to be taken into account in managing human activities to optimize the exploitation of marine goods and services, at the same time, minimizing the environmental impact of the related uses and activities. Unfortunately, scientific knowledge on the extent, geographical range and ecological functioning of benthic habitats is still poorly established. Consequently, it is difficult to manage resources effectively, protect ecologically important areas and establish legislation to safeguard the oceans.

In order to address this management requirement, there is an urgent need to develop robust methods for mapping marine ecosystems, to establish their geographical location, extent, and condition (Brown *et al.*, 2011). Specifically, in the European Marine Strategy Framework Directive (MSFD, (Council Directive 2008/56/EC, 2008), two important descriptors used in assessing environmental status of marine waters are seafloor integrity and biodiversity. “Sea Floor” is interpreted as including both the physical parameters of the seabed - bathymetry, roughness (rugosity), substrate type, etc.; and biotic composition of the benthic community. “Integrity” is interpreted as both covering spatial connectivity, such that the habitats are not fragmented unnaturally, whilst having the natural ecosystem such processes functioning in characteristic ways. “Biodiversity” includes, together with species, population and ecosystem structure, other indicators related to habitat distribution, extent and condition (European Commission, 2010a). Areas of high habitat integrity on both of these standards are resilient to perturbations. As such, human activities can cause some degree of perturbation without serious and lasting harm to the ecosystems (Borja *et al.*, 2011; Rice *et al.*, 2010; Rice *et al.*, 2012; Van Hoey *et al.*, 2010).

The environmental variables that describe a species' fundamental niche can be grouped broadly into: resource gradients, *e.g.* chemicals or energy consumed by a species; direct gradients of variables, with a physiological influence on a species but not consumed by it, *e.g.* sediment grain size or temperature; and indirect gradients of variables, correlated with direct and resource gradients but with no physiological connection to the species, *e.g.* depth and latitude (Meynard & Quinn, 2007). Considering the aforementioned assumptions, habitat modelling methods have been used to link statistically field observations of biological data to a set of environmental variables or spatial predictors, reflecting some key characteristics of the niche (Guisan & Zimmermann, 2000; Hirzel & Guisan, 2002; Hirzel & Le Lay, 2008). Physical disturbance and available food supply are known to be important in structuring benthic communities (Kube *et al.*, 1996). Thus a benthic habitat model should take these into account, together with, other information on physical processes occurring on the seafloor and oceanographic information pertaining to the near-bottom water column (Gogina *et al.*, 2010b). Consequently, the process-driven habitat template (Kostylev & Hannah, 2007), takes into consideration the aforementioned assumptions, when formulating the habitat model. The process-driven habitat template is a conceptual model, used to relate species life-history traits to the properties of the environment, transforming maps of the physical environment into a map of benthic habitat types. Such an approach has been applied to benthic marine habitat in Atlantic Canada (Kostylev *et al.*, 2005); it was applied also elsewhere in assessing how the resulting classification corresponded to distributions of a number of species, including corals, sponges, and commercially important bottom fish (Gregr, 2008). More recently, the capacity of this model to explain the spatial distribution of fish species diversity has been demonstrated (Fisher *et al.*, 2011).

Within this context, the main objective of the present study was to test the applicability of a process-driven benthic sedimentary habitat model, in the implementation of the European MSFD, in relation to the biodiversity and seafloor integrity descriptors for sedimentary habitats (Borja *et al.*, 2011; Rice *et al.*, 2010; Van Hoey *et al.*, 2010) and the MSP approach. A case study, the Basque continental shelf (Bay of Biscay) has been adopted. To accomplish this objective, the following sequential approach was applied: (i) near-bottom oceanographic and sedimentological parameters that determine species assemblages were identified; (ii) the most important environmental parameters were selected and fitted within the process-driven habitat model template; (iii) a process-driven habitat model map was produced; (iv) the structural parameters and life-history traits of species were analysed within the process-driven habitat model template; and, finally, (iv) benthic habitats were characterised in terms of species' assemblages and environmental characteristics.

2. Material and methods

The study area is located on the continental shelf of the Basque Country, in the southeastern part of the Bay of Biscay, northern Spain (Figure 1).

2.1. The process-driven habitat model template

The process-driven marine benthic habitat mapping approach, as proposed by Kostylev and Hannah (2007), is based upon ecological theory that relates species life-history traits to the properties of the environment (Huston, 1994; Margalef *et al.*, 1979; Reynolds, 1999; Southwood, 1977), transforming maps of the physical environment into those of benthic habitat types. This approach is based upon the aggregation of sets of environmental selective factors, on two axes. The 'Disturbance' axis, reflects the intensity of habitat alteration or destruction, or the durational stability of habitats, including only natural seabed processes responsible for the selection of species' life history traits, on the evolutionary time-scale. The 'Scope for Growth' (SfG) axis, which describes the amount of energy available for growth and reproduction after adjusting the available food supply by environmental stressors that pose a cost for the physiological functioning of organisms. This latter factor could be related also to the metabolic theory of ecology (Brown *et al.*, 2004). Thus, the habitat model constructed according to aforementioned assumptions should reflect the main ecological characteristics of the habitats.

2.2. Environmental data

For this investigation, soft-bottom macrobentos data and a set of 16 environmental variables were considered, which could be grouped into: (i) seafloor morphology (depth and distance to rock); (ii) sediment characteristics (mean grain size, sorting, gravel content, sand content, fine content, organic matter content, redox potential) and sediment resuspension index; and (iiii) oceanographical conditions near the seafloor (average annual chlorophyll content, average spring chlorophyll content, annual mean temperature, annual temperature range and minimum annual temperature). The characteristics of each of the datasets are described bellow.

- Seafloor morphology

High-resolution multibeam echosounder (MBES), at 1 m horizontal resolution Digital Elevation Model (DEM) and bathymetric LiDAR, at 2 m horizontal resolution grid, were available up to 100 m depth (Chust *et al.*, 2008; Galparsoro *et al.*, 2010). The information on seafloor type distribution and sediment characteristics were derived from Galparsoro *et al*. (2010). The seabed surface corresponding to sedimentary deposits is 406 km^2, representing 37% of the surface of the study area. The distance to rock map was calculated using Euclidean distance algorithm (ArcGIS) from the morpho-sedimentary map of the same study (Galparsoro *et al.*, 2010). Such a layer represents the minimum distance of each pixel to the nearest rock substratum. Each aforementioned information layer was resampled at 5 m horizontal resolution grid, to homogenise and operate between the different information layers in the GIS.

- Sediment characteristics and sediment resuspension index calculation

Sediment variables and grain size distribution maps were extracted from Galparsoro *et al*. (2010) (Figure 2). To calculate the sediment resuspension index, storm wave characteristics were propagated across the study area. The significant wave height, exceeding 12 hours per year (Hs12), and period (Tp) were derived from the oceanographic buoy *Bilbao-Vizcaya* record (period 1996-2006) (Puertos del Estado, 2007). Numerical modelling (González *et al.*, 2007; SMC, 2002) was used, with the MBES-derived DEM as an input. The spatial resolution of the resulting grid was 20 m. Wave-induced near-bottom maximum orbital velocities were derived using linear wave theory and Hs, period (Tp) and mean water depth, for each point of the computational grids. The critical current for sediment resuspension was calculated following an empirical relationship between grain size and critical current speed (Hjulström, 1935). Finally, the resuspension index was calculated by dividing the Orbital Velocity by the Critical Current, then multiplied by 100. Thus, values higher than 1 indicate areas of sediment resuspension; lower values indicate that sediment is not remobilised by wave-induced currents.

- Oceanographic data

CTD profiles from 21 monitoring stations, measured in spring, autumn, summer and winter, since 1998, were collated (Borja *et al.*, 2009) (see Figure 1, for sample locations). Oceanographic data corresponding to the same period as the benthic data (*i.e.* 2003-2010) were obtained, whilst near-bed oceanographic parameters were retained for further analysis. Subsequently, the mean value and standard deviation of each selected parameter (i.e. mean, maximum and minimum annual water temperature; annual mean and mean spring chlorophyll concentration (for measures obtained between April and May)) was derived. In order to obtain a continuous layer, each parameter was interpolated using ordinary kriging, with spherical-fitted models of semivariograms, into a grid of 5 m resolution (Surfer 8, from Golden Software).

- Biological data

Benthic biological data were collected using a Van Veen sediment grab (sampling area 0.1 m^2). The data corresponding to infauna and epifauna were extracted for the time period 2003-2010 (see Figure 1, for benthic sample locations). This selection resulted in 404 grab samples, with benthos identified at species level whenever possible (a total of 1,202 species). For each sample species richness (number of *taxa*) and Margalef index were determined. Subsequently, samples collected in areas with known human impacts, such as those located near sewage outfalls, dredging and sediment disposal sites, were identified (166 out of 404); this was in order to analyse the influence of such data on the final results of the analysis. As such, two datasets were generated; (i) containing all the available samples (404); and (ii) only with samples collected from "natural habitats" (i.e. 238).

The ecological significance of the generated process-driven habitat model, together with the resulting habitat classes, were analysed. The species lists for each habitat class, defined in the habitat template, were compared with the species life-history traits extracted from the Life Information Network (MarLIN, 2006). Eight biological traits were selected for the analysis: lifespan; maturity; generation time; size; living habit; sociability; fragility; and flexibility. Continuous values were binned into classes: (i.e. Lifespan (<2 years; 2-5 years; 5-10 years; >10 years); Maturity (<1 year, 1 year, 1-2 years, 2-3 years, 3-5 years); Generation Time (<1 year, 1 year, 1-2 years, 3-5 years); Size (Very small (<1 cm), Small (1-2 cm), Small-medium (3-10 cm), Medium (11-20 cm), Medium-large (21-50 cm), Large (>50 cm)); and Flexibility (High (>45 degrees), Low (10-45 degrees), None (< 10 degrees)). For the remaining, qualitative descriptors were retained: Living habit (Attached, Burrow dwelling, Erect, Free living, Tubiculous); Sociability (Colonial, Gregarious, Solitary); and Fragility (Fragile, Intermediate, Robust). When no information on a particular trait was available for a taxon, zero values were entered for each trait category. Then, for each habitat class, the percentage of species showing each studied trait was calculated.

- Data integration and analysis

For each benthic grab sample location, the values of environmental variables were extracted and the straight line distance to all possible pairs was calculated. Subsequently, multivariate analysis was undertaken using the PRIMER (Plymouth Routines In Multivariate Ecological Research (version 6) software package (Clarke, 1993; Clarke & Gorley, 2006). Fourth-root transformation was applied to species abundance, to reduce the influence of highly abundant species. The Bray Curtis similarity matrix (Bray & Curtis, 1957) was calculated, with a dummy variable added (value: 1).

The RELATE routine, with the Spearman rank correlation method, was used to analyse the correlation between: species composition and the spatial location of the samples; environmental variables and spatial location of samples; and *taxon* composition and environmental conditions. The BEST routine was used to investigate the significance of any relationship between *taxon* composition and environmental conditions; likewise to identify the environmental variables that best matched the distribution of *taxa* (Bremner *et al.*, 2006a; Clarke & Ainsworth, 1993; Louzao *et al.*, 2010; McArthur *et al.*, 2010; Shumchenia & King, 2010; Todd & Kostylev, 2011). BEST analysis was run with Spearman rank correlation method and Euclidean distance resemblance measure.

Finally, statistically most significant environmental variables layers were transformed, by linear scaling from 0 to 1; this was based upon the minima and maxima of each environmental variable layer, then transformed into SfG and Disturbance axis using equal weights in an additive model (Kostylev & Hannah, 2007). In order to display simultaneously two template axes in geographical space, a red-green colour map was used on the basis of a band composition algorithm. This approach created a single raster dataset, through the combination of Disturbance (red band of the image) and Scope for Growth (green band of the image) rasters.

SfG and Disturbance values for each sample location were extracted in GIS and plotted within the process-driven habitat template; this was divided then into 16 classes (4x4 squares). Subsequently, each sample was classified according to these classes. Finally, an analysis of similarity (ANOSIM) was carried out. Species richness and diversity (Shannon) of the samples were interpolated in the process-driven habitat template to analyse the ecological significance of the template. Once classes were identified, the average similarity and the representative species for each assemblage, based upon the similarity percentages method (SIMPER), were estimated. Finally, the traits of the species of each of the defined habitat classes were analysed.

3. Results

In terms of the derived environmental variables, the wave-induced near-bottom maximum orbital velocity is shown in Figure 2a. This information, together with the grain size distribution (Figure 2b), was used to calculate the sediment resuspension index (Figure 2c). Values lying close to 0 on the map indicate that sediments are not resuspended by wave action; high values indicate a higher probability of sediment remobilisation. The near-bed oceanographical, obtained from CTD data records, are shown in Figure 3.

In terms of the statistical analysis results, a significant correlation was found between *taxonomic* composition and environmental conditions, when all samples (404) were considered (RELATE; ρ = 0.35, p<0.1%). The correlation between the environmental variables and the geographical location was also significant (RELATE; ρ = 0.33, p<0.1%), as well as the correlation between the species composition and sample location (RELATE; ρ = 0.14, p<0.1%).

In contrast, when only samples from natural habitats (238) were considered (i.e. after removing stations from human-modified areas), a higher correlation was found between *taxonomic* composition and environmental conditions at the stations studied (RELATE; ρ = 0.40, p<0.1%). A significant, but lower, correlation, between the environmental variables and the spatial location of the samples, was found (RELATE; ρ = 0.13, p<0.1%). Correlation between species composition and spatial location of the samples was found also to be significant, but lower than when considering all of the samples (RELATE; ρ = 0.08, p<0.1%).

Oxygen values were found to be always near to saturation, or saturated. As the concentration was not reaching a level that could affect the organisms, O_2 values were not considered as being discriminative in terms of biological response; as such, they were not used in any further analysis. On the other hand, salinity did not show significant variations in the near-bottom (Table 1), so it was not kept for further analysis.

From the aforementioned 16 environmental parameters considered in this investigation, the best correlation between environment and *taxa* was provided by a combination of 4 environmental parameters (BEST; ρ = 0.46): mean grain size; water depth; sediment resuspension index; and maximum temperature. The associations between environmental conditions and *taxon* composition were weaker when environmental variables were considered individually. The order of importance of each of the variables resulted in: water depth (ρ = 0.42); the resuspension index (ρ = 0.34); the average annual maximum temperature (ρ = 0.33); and mean grain size (ρ = 0.33) (in all cases, with a significance level of 0.1%). Water depth could be related to all the environmental components of the investigation; meanwhile, mean grain size was used to calculate the resuspension index. Hence, the main variables driving Disturbance and SfG, within the study area, were the resuspension index and the annual maximum temperature, respectively. Both variables were transformed then into the SfG and Disturbance axes using linear scaling. The plot of the benthic samples distribution in the process-driven habitat template is shown in Figure 4a.

The analysis of similarity between habitat classes extracted from the process-driven habitat template, together with benthic community structure, showed a statistically significant correlation (ANOSIM; ρ = 0.31, $p<0.1\%$) (Figure 4b). Subsequently, for each habitat class, environmental data (Table 2) and the average similarity and the representative species for each assemblage, based upon the similarity percentages method (SIMPER) and macrobenthos species lists, were extracted (Tables 1 to 8 in Supplementary Material).

The response of the benthic structural parameters - species richness and Margalef index - to the resuspension index has indicated that species richness decreases rapidly as the resuspension index increases, up to approximately 1.5; this lies near to the threshold of sediment resuspension (Figure 5a). The Margalef index showed almost the same response, with an almost proportional decrease in comparison to an increase in the resuspension index (Figure 5b).

Within the process-driven habitat template, the Margalef index values showed an increase as the Disturbance reduced, showing a maximum for a medium range of SfG (Figure 6a). A similar pattern was observed for species richness (Figure 6b); the highest was located in a narrower range of disturbance values, but across a wide range of SfG values. When all of the benthos sample data were considered, the results showed the same general pattern, but with some differences: (i) lower Margalef values than expected (rectangle "A" in Figure 6c); and (ii) higher Margalef values than expected (rectangle "B" in Figure 6c). In the same way, species richness resulted also in the same pattern as for natural samples, with some outliers (rectangles “A”, “B”, "C" and "D" in Figure 6d).

Life-history traits information was found to be available only for 45% of the total number of species identified. The percentage of presence of species showing each trait, calculated for each habitat class defined in the process-driven template, is shown in Table 3. Here, some general patterns can be observed: species with shorter lifespan (<2 years), shorter maturity span (<1 year) and lower generation time, were present at higher percentages in areas characterized by higher SfG and low to medium Disturbance (mainly in Classes 1, 2, 3, 6, 7). In contrast, higher lifespan and maturity span species proportion decreased, as Disturbance and SfG increased. Conversely, burrow dwelling species increased as Disturbance increased, whilst free living and tubiculous proportion species decreased. The proportion of gregarious and smaller size species increased, as Disturbance and SfG increased. In contrast, the proportion of solitary and larger species decreased. In terms of fragility, flexibility and generation time, the results were unclear.

Finally, a predicted Disturbance map was produced, by linearization of the resuspension index. The derived values of Disturbance range between 0 and 1. A zero value represents zones of lower disturbance; value close to unit, representing higher disturbance. The spatial distribution is shown in Figure 7a. For comparison, the SfG map was produced by linearization of the average annual maximum temperature (Figure 7b). Values lying close to 1 occurred in shallow water areas, with a gradient to lower values towards deeper water areas. The final process-driven sedimentary habitat map is presented in Figure 7c. In general terms, highest Disturbance and SfG habitats are located within nearshore areas; this is because they are influenced by sediment dynamic processes and because of their proximity to estuaries. In contrast, the Nervion estuary shows low Disturbance and high SfG habitats; here the estuary mouth is protected from waves, by a dyke. Elsewhere, the map reveals nearshore areas with high Disturbance and low SfG, these are within very shallow waters and away from the influence of estuaries. Finally, the habitats with lower Disturbance and SfG are located in the deeper water areas of the study area, which are supposed to be associated with more stable oceanographical parameters. Such results demonstrate that the values of Disturbance and SfG are not always associated linearly, e.g. there are areas with high Disturbance, for which the SfG ranges from moderate to high (and *vice-versa*).

4. Discussion

During the preliminary steps of the analysis, it was noted that the correlation between taxonomic composition and environmental conditions was higher for samples collected in areas classified as having a low influence of human activities ("natural" habitats), than for samples collected in areas with known human pressures (i.e. with wastewater discharges and dredged sediment disposal). Such a result could be explained in terms of the environmental impact producing anomalies in species composition, due to changes in the prevailing physical and chemical conditions (sediment grain size, organic matter content, etc.), generated by human activities (Birchenough & Frid, 2009; Borja *et al.*, 2000; Boyd *et al.*, 2005).

The correlation established between macrobenthic species composition and environmental parameters was weak, but statistically significant. Nonetheless, the correlation obtained was comparable to that obtained in other habitat modelling studies, where similar algorithms have been used to relate biotic structure to environmental characteristics (Ellingsen, 2002; Gogina *et al.*, 2010a; Louzao *et al.*, 2010; Lu, 2005; Shumchenia & King, 2010). On this basis, it is considered that the improvement on the availability of environmental data (an increase in the spatial density of the oceanographic data), would derive into a higher correlation between environmental data and biological composition. Thus, these assumptions have to be taken into account, for a proper interpretation of the subsequent results.

In terms of the environmental variables identified as explaining species composition, some authors have reported differences in the order of importance of individual environmental factors. For example, Todd and Kostylev (2011) found that summer oxygen saturation was the single variable which best explained the distribution of bottom fauna on the Scotian Shelf (Canada). Further, seawater in the study area showed oxygen saturation percentages which lay always over 80% and close to 100% (Borja *et al.*, 2011). Other authors investigation the Baltic sea (Gogina & Zettler, 2010) state that changes in salinity had also a noticeable effect in the determination of suitable habitats for certain species of benthic macrofauna. Once again, in the study area, salinity within the bottom layers showed low variability (a measured range of between 35.1 and 35.5). Hence, the environmental factors with considerable ranges of variability could be those limiting, or influencing, the species assemblages. In fact, the Bay of Biscay is located in a temperate zone with no extreme oceanographic changes throughout the year

(Valencia *et al.*, 2004). As the hydrographical parameters are relatively stable, the wave energy and sediment dynamics could be identified as being the most important factors influencing benthic assemblages, in relation to the shallow water depth (Dolbeth *et al.*, 2007). Moreover, habitats characterized by relatively high disturbance and low SfG may provide areas in which to detect the strongest direct linkages, between environmental characteristics and life-history traits of species (Fisher *et al.*, 2011). In other studies, water depth may appear to be the most significant variable influencing species assemblages, being identified as the driving gradient influencing other environmental characteristics and species diversity (McArthur *et al.*, 2010). This association denotes that the environmental parameters contributing to the Disturbance and SfG components of the model depend upon the background characteristics of the location where it is due to be applied. In relation to this observation, additional studies could be carried out to investigate if the response of structural parameters and traits, to Disturbance and SfG components, are comparable across regional seas.

The model established here showed an increase of species richness and Margalef index, as the Disturbance and the SfG decrease (Figure 6a and 6c). This interpretation fits well with the initial hypothesis of the process-driven habitat template (Kostylev & Hannah, 2007) and the ecological theories on which is based (Huston, 1994; Margalef *et al.*, 1979; Reynolds, 1999; Southwood, 1977, 1988). The model obtained here is in agreement with the general assumption that shallow, eutrophic systems near coastal margins tend to have high biomass and low species richness; this is due to high productivity and extreme environmental conditions (Edgar, 2001). Such systems give way to moderate biomass and species richness on most coastal shelves (Snelgrove, 2001); this is followed by an increase in richness and decrease in biomass and abundance, in the deep sea (Levin *et al.*, 2001). According to this characteristic, in terms of the ecological implications of the process-driven habitat template, zones with low Disturbance and SfG classes were associated with deeper water areas not affected by waves; thus, the diversity of such zones, would be higher (see for example, the continental shelf area in front of Lekeitio and Higer Cape, in Figure 7c. Meanwhile, the opposite situation could be found in areas with high SfG and Disturbance; these are located in shallow water depth, adjacent to estuaries, e.g. the coastal area in front of the Nervión estuary (Figure 7c).

Samples of benthos were represented only in 8 out of the 16 theoretical classes in the process-driven habitat template, when it was divided into a 4x4 squares grid. This result is because the template is constructed for the combination of all possible environmental conditions, represented as continuous layers, together with the lack from samples for certain areas. Within this context, there was an absence of samples for the habitat types with extreme Disturbance values (i.e. samples in areas with a very low or very high disturbance values) and areas with very low SfG. The lack of samples in very low Disturbance areas is related to the absence of samples from deepest water areas of the study area were absent. Meanwhile the lack of samples from very high disturbance areas, is related to the absence of samples from extremely shallow (<7) waters. Nevertheless, it should be noted that the area corresponding to Disturbance values higher that 0.65 accounted for only 2% of the total study area surface. Moreover, there are some combinations of Disturbance and SfG that are difficult to occur naturally, such as areas with a combination of low productivity (i.e. low SfG) and high disturbance. As such, no samples are located within these classes.

The interpretation of the biological traits results suggests some ecological differences in the habitat classes, defined using the process-driven template. In general, for those habitat classes with lower SfG and Disturbance, the proportion of species with higher lifespan, maturation time, generation time and size appears to be higher (the opposite in areas with higher SfG and Disturbance), as anticipated initially. Differences in characteristics of lifespan, maturity time and sociability are particularly well reflected in the process-driven template. Such results indicate that the process-driven template reflects some of the environmental characteristics linked to metabolic theory (Brown *et al.*, 2004), combined with the ecological functioning of marine benthic assemblages and BTA (Bremner *et al.*, 2006b). Nevertheless, the results should be utilised with care, due to the absence of biological trait information for 55% of the listed species. The benthic invertebrate assemblages are incorporated into the maintenance of ecological processes and the biological traits, which can provide information about some aspects of ecosystem functioning (Bremner *et al.*, 2006a). Thus, further investigations into the characterisation of species traits is considered very valuable, for habitat modelling approaches dedicated to conservation and management purposes (Bremner, 2008). As stated by Roff *et al.* (2003), the ecosystem-based approach, which defines representative habitat types, is a fundamental prerequisite for management. In this sense, the process-driven habitat template approach fits well within this concept, of producing ecologically meaningful habitat maps derived from environmental parameters.

Understanding community-level feedbacks, such as those involving both diversity and species richness, together with disturbance, has implications for understanding the response of ecological systems to physical habitat alteration, or destruction, and human perturbation (Randall Hughes *et al.*, 2007). Given that certain human activities can increase the disturbance (*i.e.* dredged material disposal sites, dredging, trawling, sewage sludge), the result could be an acceleration of species loss beyond the expectations of direct human modification of habitats (related to biodiversity and the seafloor integrity ecosystem indicators in the MSFD (Borja *et al.*, 2011; Van Hoey *et al.*, 2010). This assumption could be observed when Margalef index and species richness for a "natural" subset and for all of the data (including human-disturbed habitats) were plotted in the process-driven habitat template. In some cases, it was noted that the species richness was lower than expected for natural habitats (rectangles "A" and "D", within Figure 6d). These corresponded to samples collected in areas of dredged material disposal, a regasification plant water disposal, and a sewage sludge area. In other cases (rectangle "B" in Figure 6c) a higher Margalef index than expected was found; this corresponded to samples collected in an area influenced by an organically-enriched sewage sludge. On the other hand, the response of the species richness and Margalef index, to the resuspension index, indicates a decrease in species richness and Margalef index for a small increase of disturbance, in environments with low natural disturbance (Figure 5). According to the results obtained, the model produced for "natural" habitats could be used to infer: (i) the expected values for structural parameters of the benthic biological communities and life-history trait, for a certain combination of values of SfG and Disturbance; and (ii) as a proxy, indicating the risk of habitat damage, or sensitivity of habitats, derived from human activities producing habitat disturbance, or seafloor physical alteration, in those areas where the natural disturbance is low, such bottom trawling disturbance (Queiros *et al.*, 2006), dredging or dredged sediment disposal (Wilber *et al.*, 2008) as processes determining the opportunistic response (Norkko *et al.*, 2006) and the recovery of sediment communities and habitats, following physical disturbance (Dernie *et al.*, 2003). Theoretically, the habitat model could be also used as a proxy of risk of overfishing taking into account the SfG of the habitats (Fisher *et al.*, 2011).

In the present investigation, the process-driven template has been tested for sedimentary habitats (which represent 37% of the case study area); nevertheless, it could be considered as being applicable to other sedimentary environments elsewhere. In addition, the same approach could be developed for hard-bottom substrata. For the latter case, some of the environmental parameters used here would be useful, e.g. wave energy in the near-bottom; temperature, etc., but new ones should be incorporated into the model, e.g. light penetration.

The use of ecosystem characteristics makes the process-driven habitat modelling approach to be considered as being useful for the implementation of management measures, *i.e.* the Habitats Directive (92/43/EEC) and MSFD, but also as a basis for MSP of human activities (Douvere & Ehler, 2009; European Commission, 2010b). The increase in availability of data, *i.e.* the spatial density of samples and information on life-history traits of species, would probably improve the statistical results and the robustness of the resulting model. It should be noted, even if habitat models are important tools for understanding the ecological niche of a particular species or communities and their ecological functioning, they must be considered carefully in relation to the representation of reality.

The rise in importance of mapping benthic marine environments, for management purposes, has resulted in a general shift from predominantly species-based management strategies to the ecosystem-based approach (Heap & Harris, 2011). For the present investigation, the process-driven habitat mapping approach (Kostylev & Hannah, 2007) was selected as an insight into biodiversity and seafloor integrity assessment, within the MSFD. In this way, the European Commission (2010a) identified 6 indicators as being suitable for seafloor integrity assessment, From the 6, 3 can be related to the approach presented here: (i) the extent of the seabed affected significantly by human activities (identified using this approach); (ii) the presence of particularly sensitive and/or tolerant species (related to some of the functional traits); and (iii) indices assessing benthic community condition and functionality. Hence, the process-driven approach is related to species composition, structure and function (biodiversity and life-history traits of species) and the main characteristics of the environment (natural and anthropogenic) influencing seafloor integrity; these could serve for the environmental assessment, as a complement to other tools proposed or used by van Hoey et al. (2010), Borja et al. (2011) and Rice et al. (2012).

For the MSFD, when assessing the environmental status, the authors are aware of the possible shortcomings of the method presented; however, it could be considered as a good approach utilising the available information, which is the criterion required by the MSFD.

Acknowledgments

This project was supported by the Basque Water Agency (URA), the Department of Environment, Land Use, Agriculture and Fisheries, of the Basque Government, the MeshAtlantic project (Atlantic Area Transnational Cooperation Programme 2007-2013 of the European Regional Development Fund) (www.meshatlantic.eu) and the project DEVOTES (DEVelopment Of innovative Tools for understanding marine biodiversity and assessing good Environmental Status) funded by the European Union under the 7th Framework Programme, 'The Ocean for Tomorrow' Theme (grant agreement no. 308392), www.devotes-project.eu". We wish to thank: Professor Michael Collins (School of Ocean and Earth Science, University of Southampton (UK) and AZTI-Tecnalia (Spain)), for kindly advising us on some details of the manuscript. Marta Pascual was funded by the Fundación Centros Tecnológicos, with a Training, Specialization and Technological Development grant. We wish to thank: Professor Michael Collins (School of Ocean and Earth Science, University of Southampton (UK) and AZTI-Tecnalia (Spain)) for kindly advising on some details of the manuscript; This paper is contribution number XXX from AZTI-Tecnalia (Marine Research Division).

References cited

Birchenough, S. N. R., C. L. J. Frid, 2009. Macrobenthic succession following the cessation of sewage sludge disposal. *Journal of Sea Research*, **62**: 258-267.

Borja, Á., J. Bald, J. Franco, J. Larreta, I. Muxika, M. Revilla, J. G. Rodríguez, O. Solaun, A. Uriarte, V. Valencia, 2009. Using multiple ecosystem components, in assessing ecological status in Spanish (Basque Country) Atlantic marine waters. *Marine Pollution Bulletin*, **59**: 54-64.

Borja, Á., J. Franco, V. Pérez, 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*, **40**: 1100-1114.

Borja, Á., I. Galparsoro, X. Irigoien, A. Iriondo, I. Menchaca, I. Muxika, M. Pascual, I. Quincoces, M. Revilla, J. Germán Rodríguez, M. Santurtún, O. Solaun, A. Uriarte, V. Valencia, I. Zorita, 2011. Implementation of the European Marine Strategy Framework Directive: A methodological approach for the assessment of environmental status, from the Basque Country (Bay of Biscay). *Marine Pollution Bulletin*, **62**: 889-904.

Boyd, S. E., D. S. Limpenny, H. L. Rees, K. M. Cooper, 2005. The effects of marine sand and gravel extraction on the macrobenthos at a commercial dredging site (results 6 years post-dredging). *ICES Journal of Marine Science*, **62**: 145-162.

Bray, J. R., J. T. Curtis, 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs*, **27**: 326-349.

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, **366**: 37-47.

Bremner, J., S. I. Rogers, C. L. J. Frid, 2006a. Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems*, **60**: 302-316.

Bremner, J., S. I. Rogers, C. L. J. Frid, 2006b. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators,* **6**: 609-622.

Brown, C. J., S. J. Smith, P. Lawton, J. T. Anderson, 2011. Benthic habitat mapping: A review of progress towards improved understanding of the spatial ecology of the seafloor using acoustic techniques. *Estuarine, Coastal and Shelf Science,* **92**: 502-520.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, G. B. West, 2004. Toward a metabolic theory of ecology. *Ecology,* **85**: 1771-1789.

Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology,* **18**: 117-143.

Clarke, K. R., M. Ainsworth, 1993. A Method of Linking Multivariate Community Structure to Environmental Variables. *MArine Ecology-Progress Series,* **92**: 205-219.

Clarke, K. R., R. N. Gorley, 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Council Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008, establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union, L164: 19-40. 22 pp.

Chust, G., I. Galparsoro, Á. Borja, J. Franco, A. Uriarte, 2008. Coastal and estuarine habitat mapping, using LIDAR height and intensity and multi-spectral imagery. *Estuarine, Coastal and Shelf Science,* **78**: 633-643.

Dernie, K. M., M. J. Kaiser, E. A. Richardson, R. M. Warwick, 2003. Recovery of soft sediment communities and habitats following physical disturbance. *Journal of Experimental Marine Biology and Ecology,* **285-286**: 415-434.

Dolbeth, M., Ó. Ferreira, H. Teixeira, J. C. Marques, J. A. Dias, M. A. Pardal, 2007. Beach morphodynamic impact on a macrobenthic community along a subtidal depth gradient. *Marine Ecology Progress Series,* **352**: 113-124.

Douvere, F., C. N. Ehler, 2009. New perspectives on sea use management: Initial findings from European experience with marine spatial planning. *Journal of Environmental Management,* **90**: 77-88.

Edgar, G. J., 2001. Australian Marine Habitats. New Holland Publishers. ISBN: 1876334533. 224 pp.

Ellingsen, K. E., 2002. Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series*, **232**: 15-27.

European Commission, 2010a. Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters (notified under document C(2010) 5956)(2010/477/EU). Official Journal of the European Union, L232: 14-24.

European Commission, 2010b. Maritime Spatial Planning in the EU - Achievements and Future Development. Communication from the Commission to the European Parlament, the Counci, the European Economic and Social Committee and the Committee of the Regions. Brussels, 17 December 2010. COM(2010) 771. 11 pp.

Fisher, J. A. D., K. T. Frank, V. E. Kostylev, N. L. Shackell, T. Horsman, C. G. Hannah, 2011. Evaluating a habitat template model's predictions of marine fish diversity on the Scotian Shelf and Bay of Fundy, Northwest Atlantic. *ICES Journal of Marine Science,* **68**: 2096-2105.

Foley, M. M., B. S. Halpern, F. Micheli, M. H. Armsby, M. R. Caldwell, C. M. Crain, E. Prahler, N. Rohr, D. Sivas, M. W. Beck, M. H. Carr, L. B. Crowder, J. Emmett Duffy, S. D. Hacker, K. L. McLeod, S. R. Palumbi, C. H. Peterson, H. M. Regan, M. H. Ruckelshaus, P. A. Sandifer, R. S. Steneck, 2010. Guiding ecological principles for marine spatial planning. *Marine Policy,* **34**: 955-966.

Galparsoro, I., Á. Borja, I. Legorburu, C. Hernández, G. Chust, P. Liria, A. Uriarte, 2010. Morphological characteristics of the Basque continental shelf (Bay of Biscay, northern Spain); their implications for Integrated Coastal Zone Management. *Geomorphology,* **118**: 314-329.

Gogina, M., M. Glockzin, M. L. Zettler, 2010a. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 1. Causal analysis. *Journal of Marine Systems*, **79**: 112-123.

Gogina, M., M. Glockzin, M. L. Zettler, 2010b. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 2. Modelling and prediction. *Journal of Marine Systems,* **80**: 57-70.

Gogina, M., M. L. Zettler, 2010. Diversity and distribution of benthic macrofauna in the Baltic Sea. *Journal of Sea Research,* **64**: 313-321.

González, M., R. Medina, J. González-Ondina, A. Osorio, F. J. Mendez, E. Garcia, 2007. An integrated coastal modelling system for analyzing beach processes and beach restoration projects, SMC. *Computers & Geosciences,* **33**: 916-931.

Gregr, E. J., 2008. An ecological classification of benthic habitat in Pacific Canadian shelf waters. Sitka, Alaska, USA. pp. *in* GEOHAB; Marine Geological and Biological Habitat Mapping. Series Ed.: Publisher: ISSN: http://www.geohab.org/agenda2008.html

Guisan, A., N. E. Zimmermann, 2000. Predictive habitat distribution models in ecology. *Ecological Modelling,* **135**: 147-186.

Heap, A. D., P. T. Harris, 2011. Geological and biological mapping and characterisation of benthic marine environments—Introduction to the special issue. *Continental Shelf Research,* **31**: S1-S3.

Hirzel, A., A. Guisan, 2002. Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling,* **157**: 331-341.

Hirzel, A. H., G. Le Lay, 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology,* **45**: 1372-1381.

Hjulström, F., 1935. Studies of the morphological activity of rivers as illustrated by the river Fyris. *Bulletin of the Geological Institute of the University of Upsala,* **25**: 221-527.

Huston, M. A., 1994. Biological Diversity: The Coexistence of Species on Changing Landscape: Cambridge University Press, Cambridge. ISBN: 0521360935. 708 pp.

Katsanevakis, S., V. Stelzenmüller, A. South, T. K. Sørensen, P. J. S. Jones, S. Kerr, F. Badalamenti, C. Anagnostou, P. Breen, G. Chust, G. D'Anna, M. Duijn, T. Filatova, F. Fiorentino, H. Hulsman, K. Johnson, A. P. Karageorgis, I. Kröncke, S. Mirto, C. Pipitone, S. Portelli, W. Qiu, H. Reiss, D. Sakellariou, M. Salomidi, L. van Hoof, V. Vassilopoulou, T. Vega Fernández, S. Vöge, A. Weber, A. Zenetos, R. t. Hofstede, 2011. Ecosystem-based marine spatial management: Review of concepts, policies, tools, and critical issues. *Ocean & Coastal Management,* **54**: 807-820.

Kostylev, V. E., C. G. Hannah, 2007. Process-Driven Characterization and Mapping of Seabed Habitats. *in Todd, B.J., and Greene, H.G., eds., Mapping the Seafloor for Habitat Characterization: Geological Association of Canada, Special Paper,* **47**: 171-184.

Kostylev, V. E., B. J. Todd, O. Longva, P. C. Valentine, 2005. Characterization of benthic habitat on Northeastern Georges Bank, Canada. *American Fisheries Society Symposium,* **41**: 141–152.

Kube, J., M. Powilleit, J. Warzocha, 1996. The importance of hydrodynamic processes and food availability for the structure of macrofauna assemblages in the Pomeranian Bay (Southern Baltic Sea). *Archiv Fur Hydrobiologie,* **138**: 213-228.

Levin, L. A., R. J. Etter, M. A. Rex, A. J. Gooday, C. R. Smith, J. Pineda, C. T. Stuart, R. R. Hessler, D. Pawson, 2001. Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics,* **32**: 51-93.

Louzao, M., N. Anadón, J. Arrontes, C. Álvarez-Claudio, D. M. Fuente, F. Ocharan, A. Anadón, J. L. Acuña, 2010. Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: Baseline biodiversity information for a marine protected area. *Journal of Marine Systems,* **80**: 47-56.

Lu, L., 2005. The relationship between soft-bottom macrobenthic communities and environmental variables in Singaporean waters. *Marine Pollution Bulletin,* **51**: 1034-1040.

Margalef, R., M. Estrada, D. Blasco, 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence, in Taylor, D.L., and Seliger, H.H., eds., Toxic Dinoflagellate Blooms: Elsevier, Amsterdam. 89-94.

MarLIN, 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. Available from <www.marlin.ac.uk/biotic>

McArthur, M. A., B. P. Brooke, R. Przeslawski, D. A. Ryan, V. L. Lucieer, S. Nichol, A. W. McCallum, C. Mellin, I. D. Cresswell, L. C. Radke, 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuarine, Coastal and Shelf Science,* **88**: 21-32.

Meynard, C. N., J. F. Quinn, 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography,* **34**: 1455-1469.

Norkko, A., R. Rosenberg, S. F. Thrush, R. B. Whitlatch, 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. *Journal of Experimental Marine Biology and Ecology,* **330**: 195-207.

Puertos del Estado, 2007. Clima medio de oleaje. Boya de Vizcaya. Banco de datos oceanográficos de Puertos del Estado (http://calipso.puertos.es/BD/informes/MED_BO_2136.pdf). 34 pp.

Queiros, A. M., J. G. Hiddink, M. J. Kaiser, H. Hinz, 2006. Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. *Journal of Experimental Marine Biology and Ecology,* **335**: 91-103.

Randall Hughes, A., J. E. Byrnes, D. L. Kimbro, J. J. Stachowicz, 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters,* **10**: 849-864.

Reynolds, C. S., 1999. Metabolic sensitivities of lacustrine environment to anthropogenic forcing. *Aquatic Sciences,* **61**: 183-205.

Rice, J., C. Arvanitidis, A. Borja, C. Frid, J. Hiddink, J. Krause, P. Lorance, S. A. Ragnarsson, M. Skold, B. Trabucco, 2010. Marine Strategy Framework Directive – Task Group 6 Report Seafloor integrity. *EUR 24334 EN – Joint Research Centre, Luxembourg: Office for Official Publications of the European Communities*: 73 pp.

Rice, J., C. Arvanitidis, A. Borja, C. Frid, J. G. Hiddink, J. Krause, P. Lorance, S. Á. Ragnarsson, M. Sköld, B. Trabucco, L. Enserink, A. Norkko, 2012. Indicators for Sea-floor Integrity under the European Marine Strategy Framework Directive. *Ecological Indicators,* **12**: 174-184.

Roff, J. C., M. E. Taylor, J. Laughren, 2003. Geophysical approaches to the classification, delineation and monitoring of marine habitats and their communities. *Aquatic Conservation-Marine and Freshwater Ecosystems,* **13**: 77-90.

Shumchenia, E. J., J. W. King, 2010. Comparison of methods for integrating biological and physical data for marine habitat mapping and classification. *Continental Shelf Research,* **30**: 1717-1729.

SMC, 2002. Coastal Modelling Aid System (SMC) developed by the Ocean and Coastal Research Group from the University of Cantabria with the support of the Directorate General to the Coast in the Environmental Ministry of Spain.

Snelgrove, P. V. R., 2001. Diversity of Marine Species. Encyclopedia of Ocean Sciences. Academic Press, Oxford. 748-757.

Southwood, T. R. E., 1977. Habitat, Templet for Ecological Strategies - Presidential-Address to British-Ecological-Society, 5 January 1977. *Journal of Animal Ecology,* **46**: 337-365.

Southwood, T. R. E., 1988. Tactics, Strategies and Templets. *Oikos,* **52**: 3-18.

Todd, B. J., V. E. Kostylev, 2011. Surficial geology and benthic habitat of the German Bank seabed, Scotian Shelf, Canada. *Continental Shelf Research,* **31**: S54-S68.

Valencia, V., J. Franco, A. Borja, A. Fontán, 2004. Hydrography of the southeastern Bay of Biscay. *Borja, A. and Collins, M. (Eds.) Oceanography and Marine Environment of the Basque Country, Elsevier Oceanography Series,* **70**: 159-194.

Van Hoey, G., A. Borja, S. Birchenough, L. Buhl-Mortensen, S. Degraer, D. Fleischer, F. Kerckhof, P. Magni, I. Muxika, H. Reiss, A. Schröder, M. L. Zettler, 2010. The use of benthic indicators in Europe: From the Water Framework Directive to the Marine Strategy Framework Directive. *Marine Pollution Bulletin,* **60**: 2187-2196.

Wilber, D. H., G. L. Ray, D. G. Clarke, R. J. Diaz, 2008. Responses of Benthic Infauna to Large-Scale Sediment Disturbance in Corpus Christi Bay, Texas. *Journal of Experimental Marine Biology and Ecology*, **365**: 13-22.

Table1
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Table 1. Mean, maximum (max.) and minimum (min.) values for each of the environmental variables analysed within the study area, in the near-bottom layer of the water column. S.D: Standard Deviation. PSU: Practical Salinity Units

Variable	**Mean ± S.D.**	**Max.**	**Min.**
Annual mean temperature (ºC)	14.2±0.6	15.6	12.5
Annual maximum temperature (ºC)	19.4±1.1	20.9	14.8
Annual minimum temperature (ºC)	11.9±0.3	12.5	11.6
Annual temperature range (ºC)	6.4±1.0	7.7	2.7
Annual mean chlorophyll concentration ($\mu g \cdot l^{-1}$)	0.69±0.19	0.96	0.14
Spring chlorophyll concentration ($\mu g \cdot l^{-1}$)	1.03±0.5	1.9	0.08
Mean grain size (Phi)	2.17±1.22	7.38	-1.69
Sorting	1.41±0.44	3.52	0.15
Gravel content (%)	3.9±11.4	93	0
Sand content (%)	69.9±32.9	100	0.06
Fine content (%)	26.3±33	99.7	0
Organic Matter content (%)	3.1±2.8	26.5	0.5
Redox potential (mV)	182.1±231.9	499	-336
Depth (m)	-41.8±23	-114	-6.7
Resuspension index	1.5±0.77	4.81	0.17
Distance to rock (m)	215.7±249.5	997.1	0
Salinity (PSU)	35.4±0.1	35.5	35.1
Oxygen saturation (%)	97.8±7.0	106.3	85.3

Table2

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Table 2. Main characteristics of each habitat class defined in the process-driven habitat template (see Figure 4a, for habitat class distribution in the process-driven habitat template). Key: NS- number of samples; GS- grain size; SORT- Sorting; OM- organic matter; RI- Resuspension index; AC- annual chlorophyll; SC- spring chlorophyll; and T- temperature.

Habitat class	NS	GS (Phi)	SORT	Gravel (%)	Sand (%)	Mud (%)	OM (%)	Depth (m)	RI	AC ($\mu g \cdot l^{-1}$)	SC ($\mu g \cdot l^{-1}$)	Mean T (ºC)	T Range (ºC)	Min T (ºC)	Max T (ºC)	Species richness (nº)	Margalef	Diversity (Shannon) (bits ind^{-1})
1	15	1.71	1.25	5.0	86.6	8.4	2.1	-46.5	1.12	0.67	0.94	14.4	7.3	11.7	19.8	23.3	3.71	2.64
2	116	1.69	1.50	2.0	91.3	6.7	2.4	-33.7	1.86	0.76	1.00	14.6	6.7	12.1	20.0	16.8	3.02	2.24
3	7	2.02	1.25	0.2	95.2	4.6	2.9	-12.9	3.04	0.65	0.83	15.3	7.1	12.4	19.6	16.0	2.27	1.77
5	35	1.82	1.18	5.3	76.6	18.1	2.4	-72.1	0.95	0.57	0.68	13.9	5.7	11.9	18.4	41.1	5.82	2.96
6	25	1.69	1.48	2.0	91.5	6.6	2.4	-46.6	1.64	0.59	0.62	14.5	6.0	12.1	18.8	25.8	4.34	2.52
7	3	1.69	1.40	0.2	96.8	3.0	2.8	-17.8	2.75	0.58	0.64	15.5	7.3	12.5	19.2	6.9	1.04	1.61
9	27	2.71	1.34	4.9	51.0	44.2	3.2	-94.3	0.71	0.32	0.28	13.1	4.2	11.8	16.8	51.9	6.81	3.28
13	10	2.87	1.26	0.9	57.8	41.3	2.5	-102.2	0.72	0.24	0.17	12.7	3.5	11.7	15.6	39.2	5.80	3.20

Table3
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Table 3. Percentage of presence of different life-history traits divided into classes, for each class defined in the process-driven habitat template (defined in Figure 4b); together with the mean percentage of presence of the life-history traits divided according to the increasing Disturbance and Scope for Growth (SfG) classes: A (habitat classes 1, 5, 9, 13); B (habitat classes 2, 6); C (habitat classes 3, 7); D (habitat classes 13); E (habitat classes 9); F (habitat classes 5, 6, 7); G (habitat classes 1, 2, 3). See Figure 4b for each habitat defined in the process-driven habitat template.

Life-history traits	**Process-driven habitat class**								**Disturbance**			**SfG**			
Lifespan	**1**	**2**	**3**	**5**	**6**	**7**	**9**	**13**	**A**	**B**	**C**	**D**	**E**	**F**	**G**
<2 years	53	52	58	44	51	60	41	37	43.8	51.5	59	37	41	51.7	54.3
2-5 years	32	33	26	40	34	40	39	47	39.5	33.5	33	47	39	38	30.3
5-10 years	9	11	0	11	11	0	15	16	12.8	11	0	16	15	7.3	6.7
>10 years	6	4	16	5	4	0	5	0	4	4	8	0	5	3	8.7
Living habit															
Attached	0	1	0	0	2	0	1	0	0.3	1.5	0	0	1	0.7	0.3
Burrow dwelling	27	35	29	32	28	50	32	35	31.5	31.5	39.5	35	32	36.7	30.3
Erect	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Free living	46	36	49	44	46	29	40	36	41.5	41	39	36	40	39.7	43.7
Tubiculous	27	28	22	24	24	21	27	29	26.8	26	21.5	29	27	23	25.7
Maturity															
<1 year	57	50	63	40	53	67	38	37	43	51.5	65	37	38	53.3	56.7
1 year	7	7	9	14	11	0	14	16	12.8	9	4.5	16	14	8.3	7.7
1-2 years	30	38	20	39	29	33	37	36	35.5	33.5	26.5	36	37	33.7	29.3
2-3 years	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3-5 years	6	5	9	6	6	0	12	12	9	5.5	4.5	12	12	4	6.7
Generation Time															
<1 year	49	36	58	26	44	0	18	20	28.3	40	29	20	18	23.3	47.7
1 year	0	1	0	0	1	0	0	0	0	1	0	0	0	0.3	0.3
1-2 years	51	63	42	74	56	100	74	73	68	59.5	71	73	74	76.7	52
3-5 years	0	0	0	0	0	0	9	7	4	0	0	7	9	0	0
Sociability															
Colonial	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gregarious	16	14	28	9	15	20	10	6	10.3	14.5	24	6	10	14.7	19.3
Solitary	84	86	72	91	84	80	90	94	89.8	85	76	94	90	85	80.7
Size															
Very small (<1 cm)	16	16	15	9	14	25	7	6	9.5	15	20	6	7	16	15.7
Small (1-2 cm)	30	28	25	33	31	25	26	24	28.3	29.5	25	24	26	29.7	27.7
Small-medium (3-10 cm)	45	42	52	44	42	38	49	51	47.3	42	45	51	49	41.3	46.3
Medium (11-20 cm)	6	10	7	8	6	13	10	11	8.8	8	10	11	10	9	7.7
Medium-large (21-50 cm)	3	3	2	4	5	0	7	5	4.8	4	1	5	7	3	2.7
Large (>50 cm)	1	1	0	1	2	0	1	2	1.3	1.5	0	2	1	1	0.7
Fragility															
Fragile	41	40	44	45	41	50	46	45	44.3	40.5	47	45	46	45.3	41.7
Intermediate	58	59	56	54	59	50	52	54	54.5	59	53	54	52	54.3	57.7
Robust	1	1	0	1	0	0	2	1	1.3	0.5	0	1	2	0.3	0.7
Flexibility															
High (>45 degrees)	70	68	76	68	60	67	74	79	72.8	64	71.5	79	74	65	71.3
Low (10-45 degrees)	12	15	13	14	21	33	9	6	10.3	18	23	6	9	22.7	13.3
None (< 10 degrees)	18	17	11	19	19	0	17	16	17.5	18	5.5	16	17	12.7	15.3

Figure1 Colour

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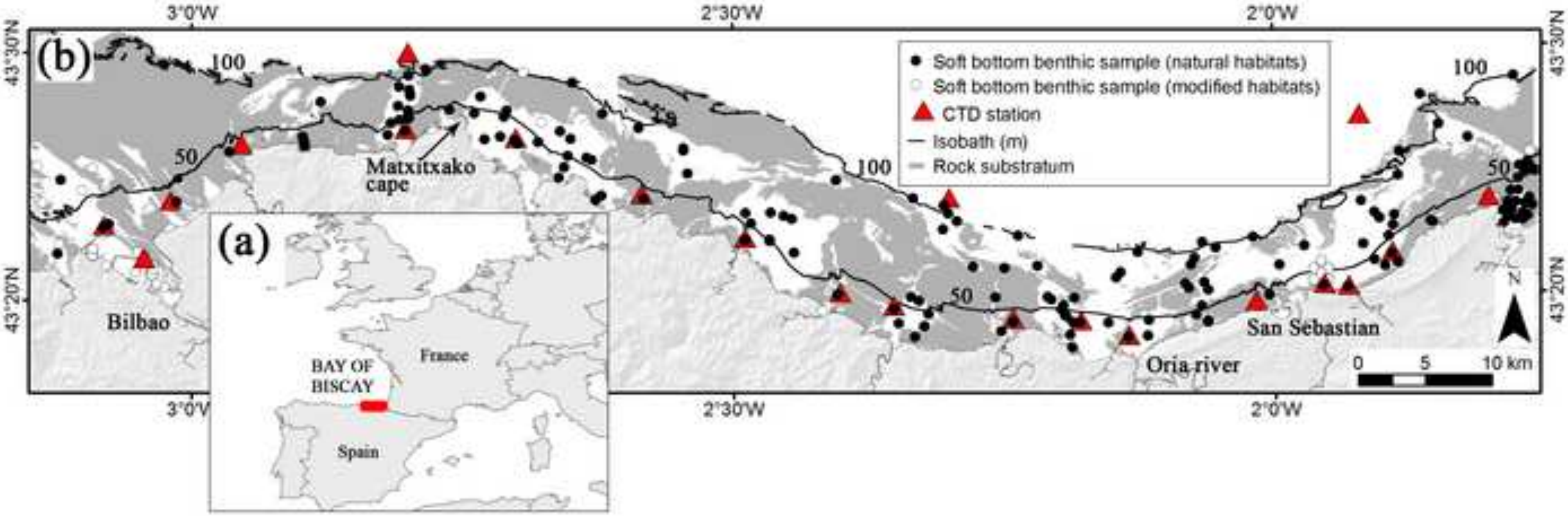

Figure2 Colour

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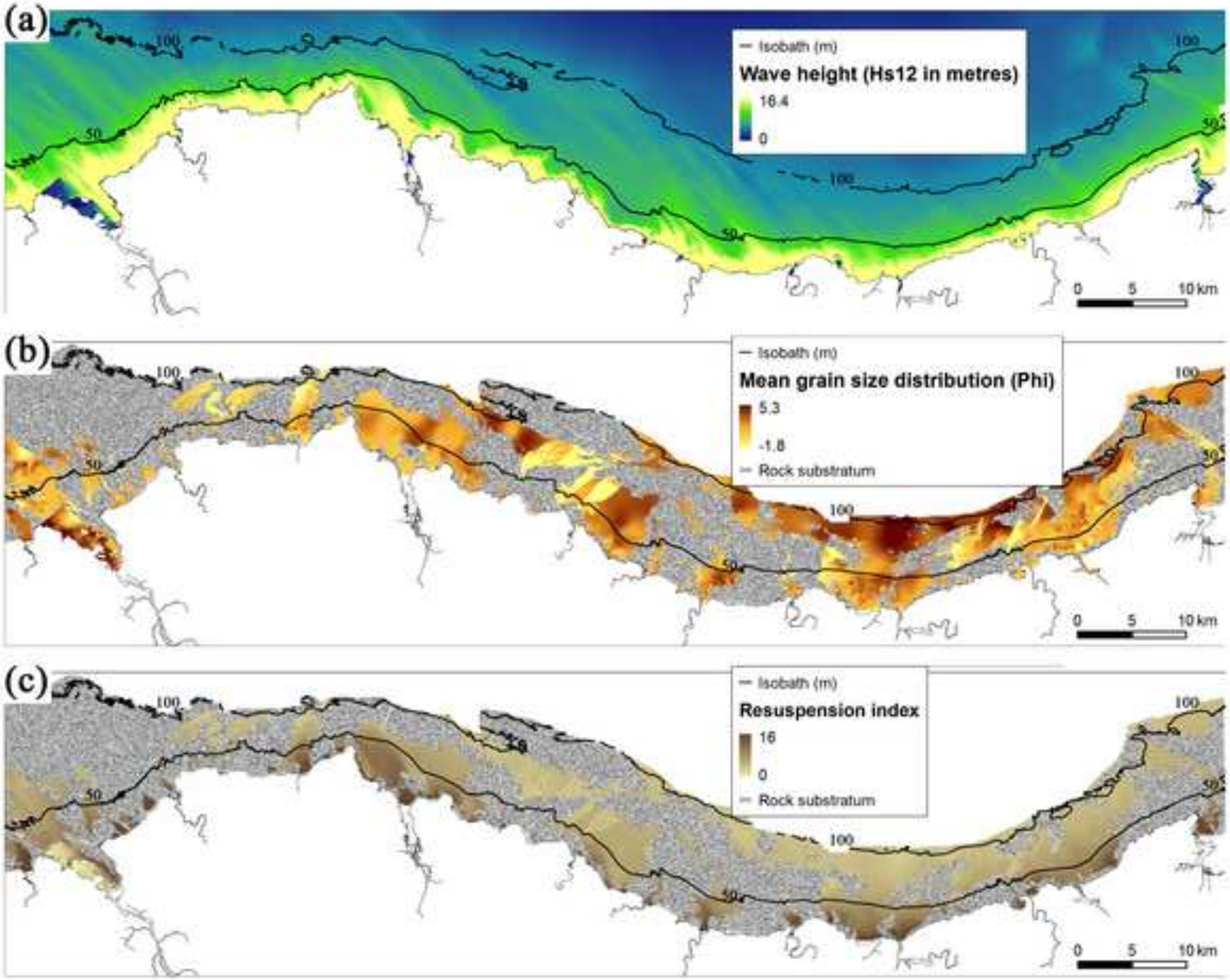

Figure3 Colour
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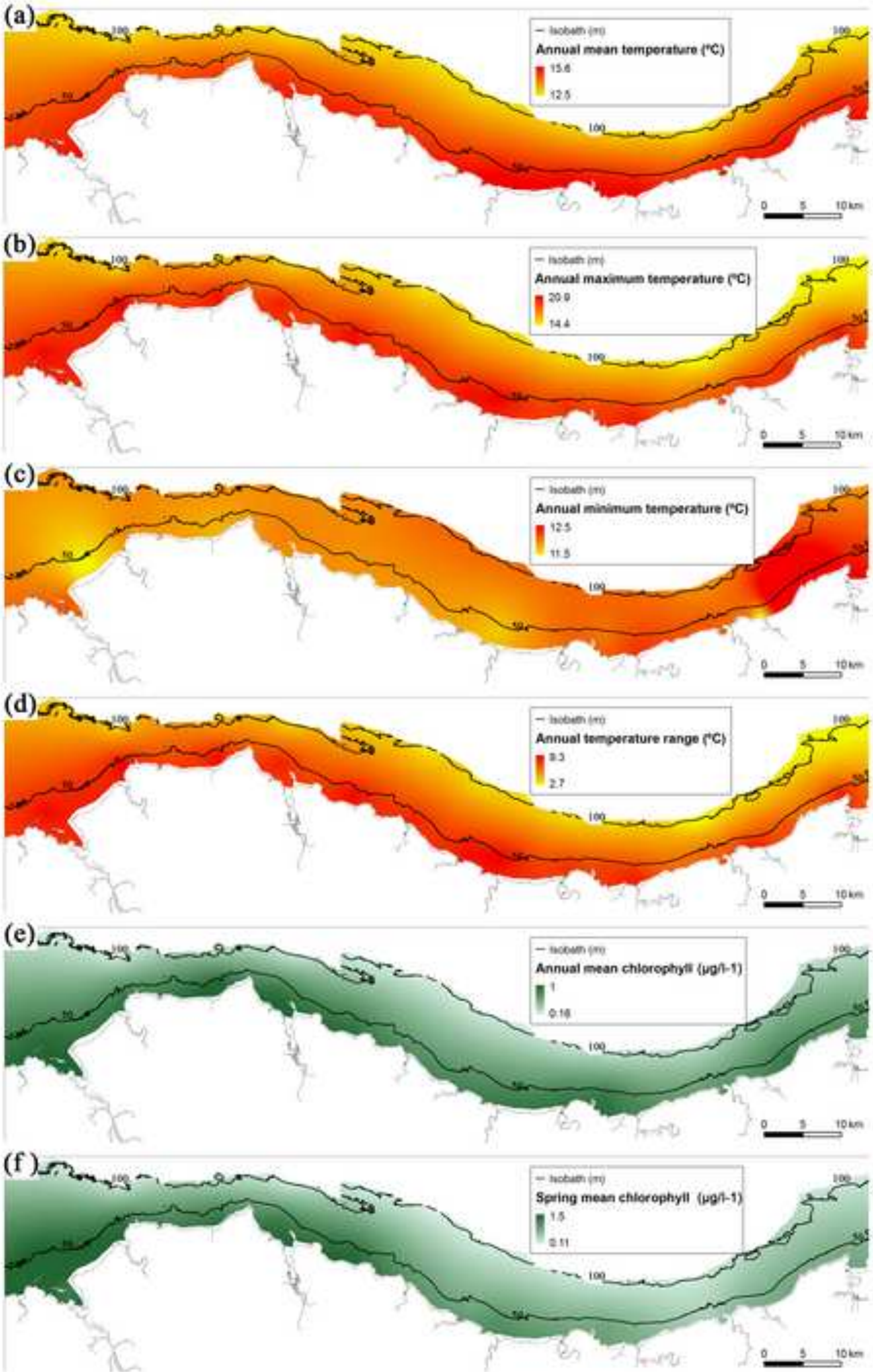

Figure4 Colour
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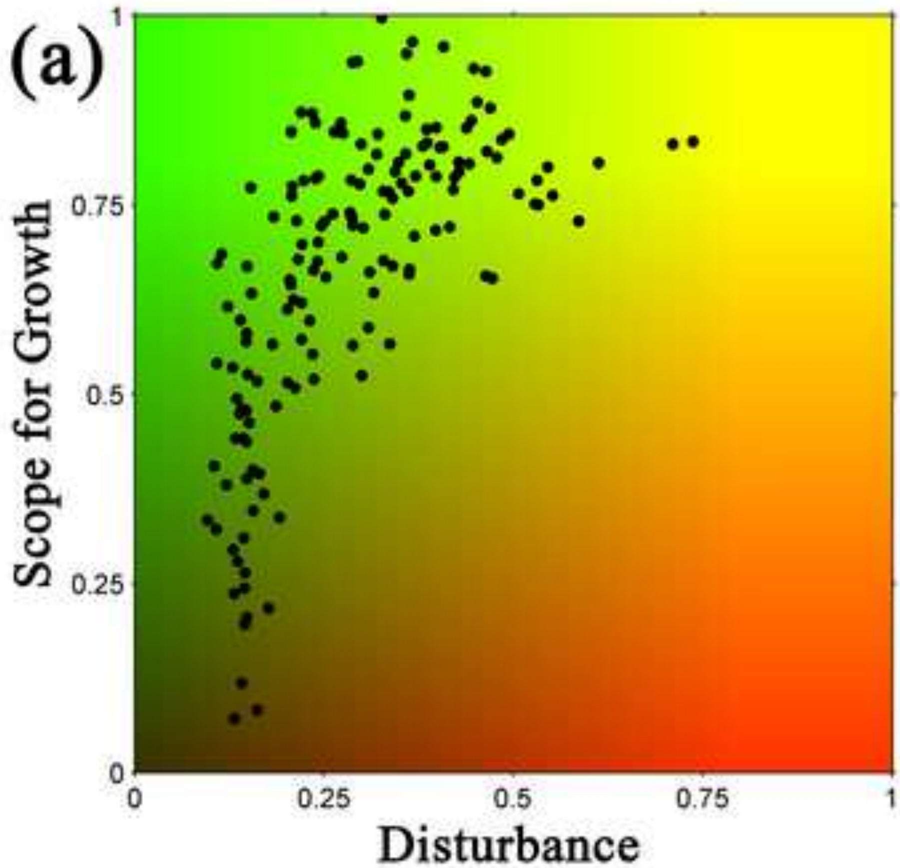

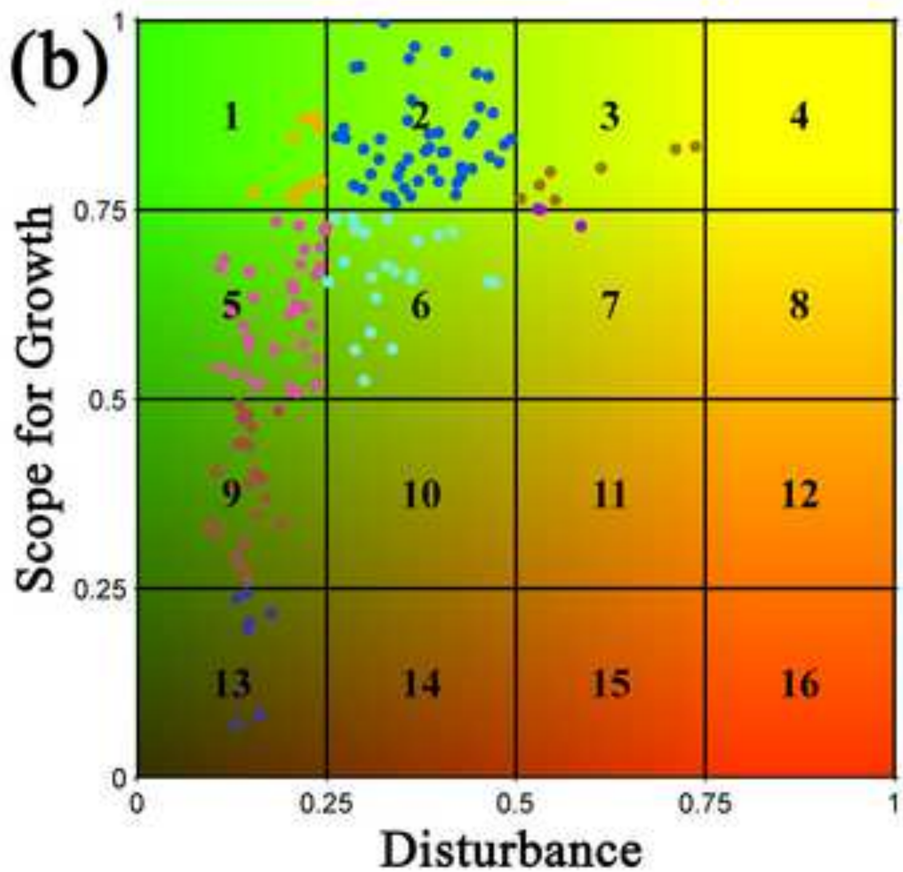

Figure5
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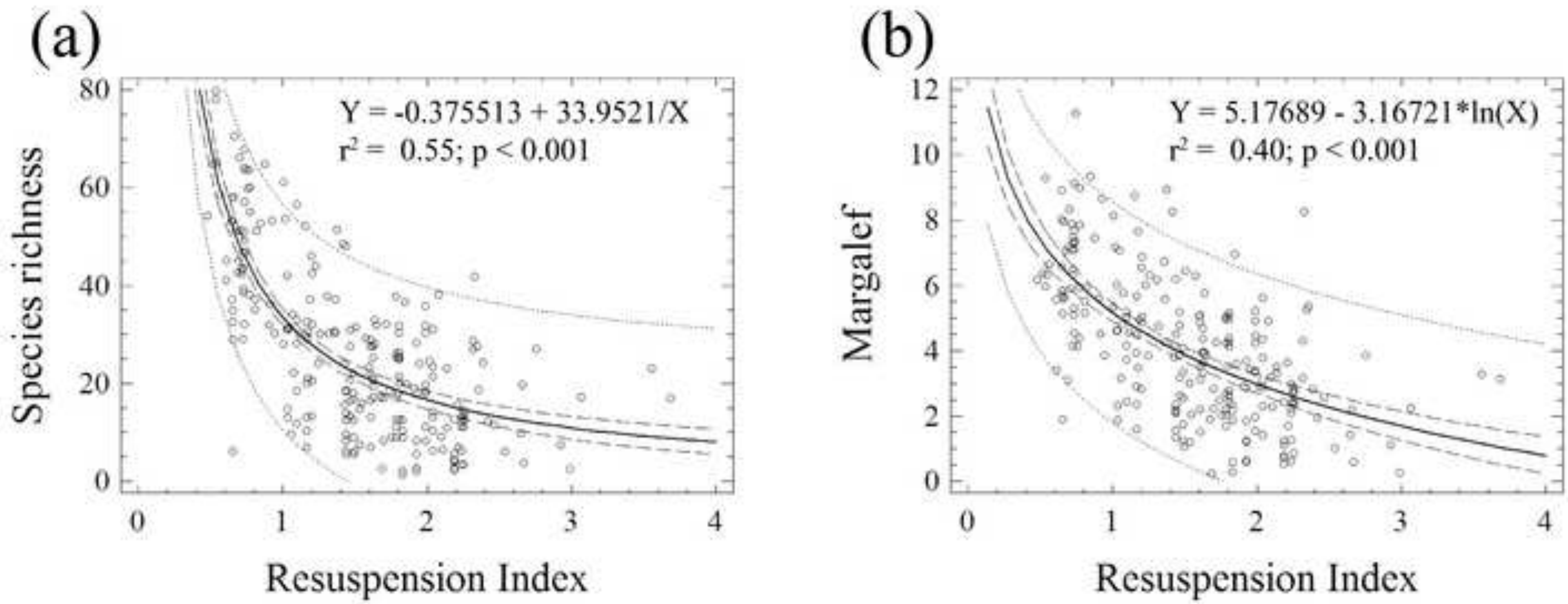

Figure6

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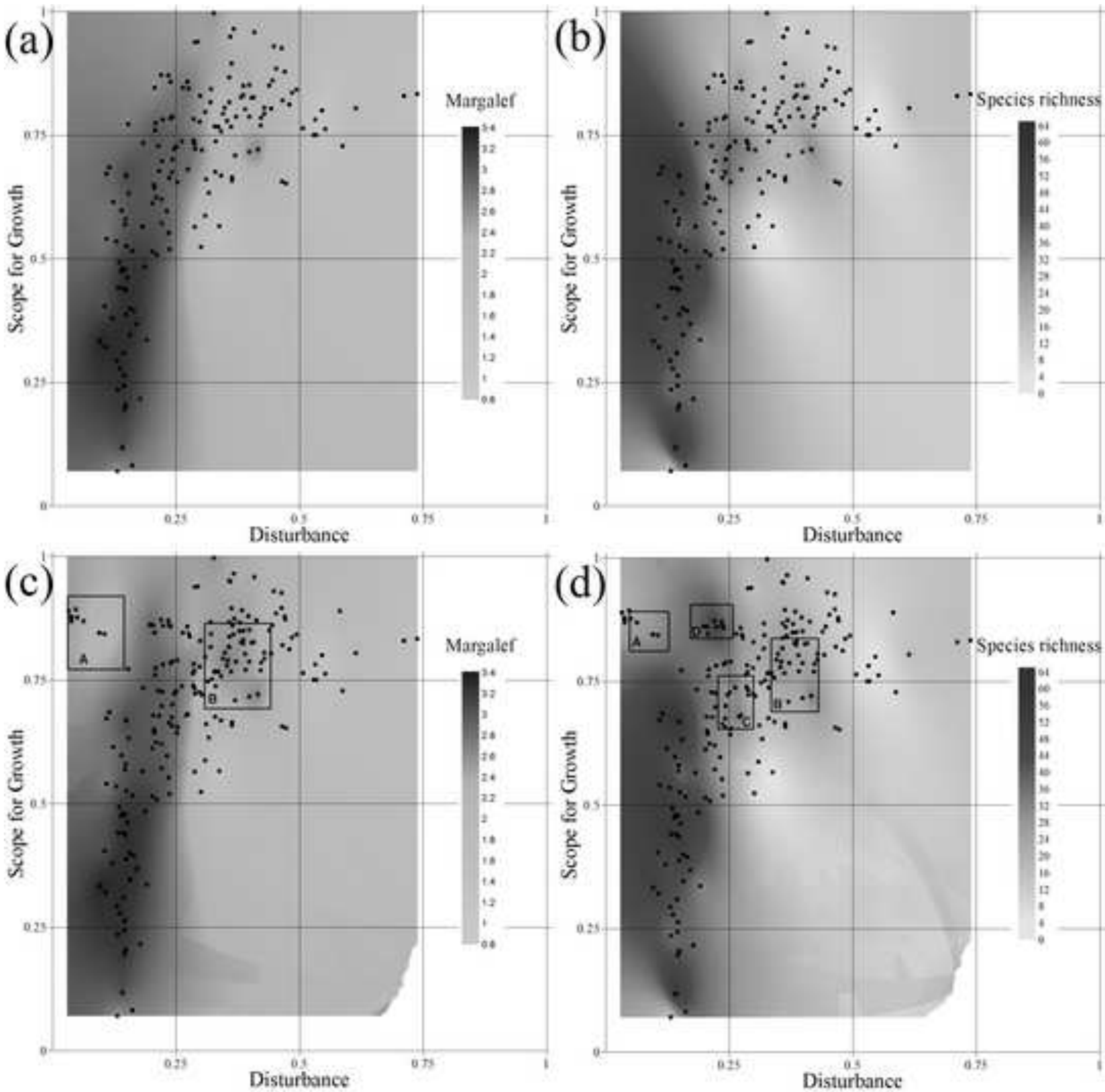

Figure7 Colour

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