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Disentangling trawling impact from natural variability on benthic communities

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Abstract

Various environmental parameters such as temperature, depth and currents influence the composition and distribution of benthic assemblages. However, the impact of trawling on benthic communities depends on their species composition since not all benthic species are equally sensitive to trawling. Moreover, trawling can have effects on benthic species similar to some natural disturbances, such as a local increase in turbidity. Thus, species adapted to these natural disturbances may be resistant to a certain level of trawling. This study evaluates the joint influence of environmental parameters and trawling pressure on four functional sensitivity indices in three environmentally contrasted areas: the English Channel, the Gulf of Lion and the eastern coast of Corsica, the two latter being located in the Mediterranean Sea. The different environmental parameters influencing the behaviour of these indices were identified in each of the study areas. These parameters were divided into two groups according to the type of influence they have on the benthic community. The first group of variables, used for modeling "Scope for Growth" (SfG), relates to the resilience of species, while the second, "Disturbance" (Dist), concerns their resistance to physical impacts. This work highlighted that the distribution of benthic species in the English Channel is mainly linked to physical disturbances and therefore to their resistance, whereas it is mainly parameters linked to the resilience of communities that influence the distribution of benthic fauna in the Mediterranean. The effect of abrasion could be distinguished from the natural environmental disturbances in the English Channel and Gulf of Lion where trawling was found to have a significant effect on functional sensitivity indices. The composition and distribution of benthic communities in Corsica, did not seem to be influenced by trawling pressure.

Keywords: Environmental factors, Trawling impact, Resilience, Resistance, Natural disturbance

1. Introduction

Physical disturbances generated by bottom trawl are known to induce changes such as reduced benthic habitat complexity (Watling and Norse 1998), increased local turbidity and enhanced release of the organic matter normally buried in the sediments (Palanques et al. 2001). Trawling also leads to mortality in benthic invertebrates and thus affect the structure and the functioning of benthic invertebrate communities (Collie et al. 2000; Rijnsdorp et al. 2018). Bottom impacting fishery activities (trawling or dredging) induce abrasion, which may be defined as a scraping of the substrate (e.g. by a trawl door or an anchor) without sediment removal, but eroding a surface over time. Abrasion may also result from natural processes but in the present study, this term was used solely to describe the impact of trawling on the seabed.

Benthic species have different degrees of sensitivity to trawling depending on their biological characteristics and in particular their recovery rates (Hiscock et al. 1999; Lambert et al. 2014; Foveau et al. 2017; Pitcher et al. 2022). Further studies have shown that opportunistic species such as polychaetes (Kaiser et al. 2006) were less affected by trawling while the abundance of some sessile, long-lived and filter-feeding species decreased after a certain level of trawling (Kenchington et al. 2001; Tillin et al. 2006). However, the response of benthic community to trawling depends on the pre-fished, initial composition of the community (Kaiser et al. 2002) which is likely to be directly linked to the local ambient environment condition.

This natural composition and the distribution of benthic assemblages may be strongly shaped by physico-chimical drivers (Hall et al. 1994) such as, for example, salinity or bottom-water temperature, depth (Rees et al. 1999), the amount of organic carbon (Eleftheriou and Basford 1989) or the chlorophyll a concentration (Heip et al. 1992) and the oxygen saturation (Diaz and Rosenberg 1995). Salinity has an influence on the distribution and diversity of benthic species since each species has a salinity preference (Gogina and Zettler 2010). Changes in salinity significantly affect different physiological processes such as active intracellular transport, feeding rate or absorption, respiration and excretion of nutrients (Schmidt-Nielsen 1997) and in particular osmoregulation (Kinne 1971). Variations in salinity lead to changes in the amount of energy allocated to different metabolic processes and individual production (Normant and Lamprecht 2006). Temperature can affect growth, reproduction, and abundance of benthic species and specifically of benthic suspension feeders (Boero and Fresis 1986). For example, seasonal increase in temperature can induce a temporary increase in the metabolic rate of some benthic species (Brockington and Clarke 2001) and even induce several episodic events of mass mortalities affecting species of cold-water affinity as it is reported in Mediterranean Sea from 1983 (Rivetti et al. 2014). Depth can have an influence on body size of some individuals of benthic macrofauna with a size increase along the depth gradient (Albertelli et al. 1999). Benthic animals are also organized structurally, numerically and by feeding mode in relation to food availability (Rosenberg 1995). In the Mediterranean Sea for example, Benthic suspension feeder’s dynamics are particularly influenced by the existence of a common energy shortage phenomenon mainly related to low food availability (Coma and Ribes 2003). Finally, oxygen saturation can have an effect on benthic community composition because there are large variations in tolerance to hypoxia and anoxia between different benthic species (Nilsson and Rosenberg 1994).

Hydrodynamic parameters such as shear bedstress [current and wave-generated bottom shear stress, (Thistle 1981)] and sediment grain size (Couce et al. 2020) are also known to strongly structure the distribution and composition of benthic assemblages. For example, in the English Channel, diversity hotspots of sessile epifauna are in gravel and pebbles sediments (Foveau et al. 2013). Natural disturbance, resulting from waves and current, has the potential to erode seabed sediment, causing resuspension of organic matter (Morris and Howarth 1998) and affecting settlement of new invertebrate recruits (Hunt and Scheibling 1997).

As trawling itself is known to have fairly similar consequences, species adapted to natural disturbances may also be resistant to trawling (Kaiser 1998). Many species in shallow tidal and wave-swept sandy habitats are well adapted to high rates of disturbance-induced mortality (Diesing et al. 2013) and therefore have greater resistance to additional fishing disturbance. Thus, several studies have focused on comparing the effect of natural disturbances and trawling in benthic habitats. Hiddink et al. (2006) have, for example, demonstrated that trawling impacts were greatest in areas with low levels of natural disturbance and limited in areas with high degree of natural disturbance. Van Denderen et al. (2015) observed a decrease in abundance of filter feeders and long-lived species with an increase of the fishing pressure or of the degree of natural disturbance. These different results suggest that the effect of trawling on benthic communities could potentially be intertwined with natural disturbances in areas where these are significant.

Process-driven seafloor habitat sensitivity (PDS) may be defined from the method developed by Kostylev and Hannah (2007), which takes into account physical disturbance and food availability as structuring factors of benthic communities. This conceptual framework is composed of two main axes which describe species biological traits and general metabolic expenses of adaptation to environmental properties.

The "Disturbance" axis reflects the magnitude of habitat change (destruction) (i.e. the stability of habitats over time), solely as a result of the natural processes that influence the seabed and are responsible for the selection of biological traits (Foveau et al. 2017). Several proxies of natural disturbances can be used such as bottom current velocity or wave height. It can be related to the potential natural resistance of the community to physical disturbance [i.e. the capacity of the benthic community to withstand the physical disturbance (Lake 2012)]. The "Scope for Growth" axis takes into account environmental stresses inducing a physiological cost to organisms and limiting their growth and reproductive potential. This axis estimates the remaining energy available for the species growth and reproduction [the energy spent on adapting itself to the environment being already taken into account; (Kostylev and Hannah 2007)]. The growth of benthic species is strongly influenced by the food supply but also by other parameters such as water temperature (Phillips 2005) or chlorophyll *a* concentration. It can be linked to the metabolic theory of ecology and the potential natural resilience of communities. The resilience can be defined as the capacity to recover from the disturbance even though the community and ecological processes have been diminished (Lake 2012). Following the model associated with this framework, maps of the physical environment may be converted into a map of benthic habitat types, each supporting communities of species with specific sensitivity to human pressures (which are here considered as potentially excessive additional stresses to natural processes). Although this last step is based on many assumptions and hypotheses that may lead to important uncertainty, the conceptual framework itself, classifying between environmental stresses shaping resistance or resilience, remains a very useful way to group and interpret the effect of several simultaneously investigated factors

When studying the effects of trawling induced abrasion, the environmental variables selected should best reflect the level of natural disturbance to benthic species. In habitats with low natural disturbance, surface sediments are little altered by natural processes (wave and tidal current). This allows the establishment of a high diversity of sessile and erect species that are known to be very sensitive to trawl abrasion (Foveau et al. 2017). Naturally undisturbed habitats where the cost to growth and reproduction of species is high are often composed of suspension feeders , have a long life span and slow growth and are therefore particularly sensitive to trawling (Bradshaw et al. 2003; Kostylev and Hannah 2007).

The implementation of the Marine Strategy Framework Directive (MFSD) requires tools able to detect and monitor the effects of anthropogenic impacts on benthic communities, such as sensitivity indices derived from specific biological traits describing species position in the sediment, feeding mode, mobility, adult size, fragility or longevity. Ideally, they should be insensitive to natural variability (Kröncke and Reiss 2010). However, since functional sensitivity indices are based on a set of biological traits known to be sensitive to trawling but also to most kind of natural physical disturbances (van Denderen et al. 2015), they are likely to respond equally to both pressure types. It seems necessary to try to dissociate the effect of fishing and natural disturbance on the behaviour of each of these indices but also to verify whether the influence of these parameters differs according to the habitats sampled, as suggested by the study of Diesing et al. (2013).

Aims of this study were to (a) identify the environmental forcing that influence the behaviour of the functional sensitivity indices in three different areas (English Channel, Gulf of Lion and Corsica) and (b) assess the joint influence of these environmental parameters and trawl disturbance on these indices.

2. Methods

2.1. Study areas

2.1.1. English Channel

The English Channel is a shallow strait located between France and England. This study area is characterized by shallow waters rarely exceeding 100 m and the presence of strong tide-induced currents (Larsonneur et al. 1982). The speed of these currents decreases towards the West, in the Celtic Sea but also in the bays.

2.1.2. Gulf of Lion

The Gulf of Lion, located in the north-western Mediterranean Sea, is the largest part of continental shelf in the North West Mediterranean basin. With an average depth of 90 meters, the Gulf of Lion ultimately extends into a steep slope cut by numerous canyons. This slope is located near the 160 m isobath and forms a border between the coastal zone and the abyssal plain. Due to the micro-tidal regime of the Mediterranean Sea, the circulation of water masses in the Gulf of Lion is strongly influenced by atmospheric conditions (mainly winds and heat flows), river inputs and the Liguro-Provençal Current (LPC). The swell, mainly generated by onshore winds in this area, is relatively frequent but, except during winter storms, of very low amplitude (Guizien 2009).

2.1.3. Corsica

Corsica is an island located in the north-east of the western Mediterranean Sea, off the coast of mainland France and Italy and in the north of the Tyrrhenian Sea. In this study, only the east coast of Corsica was studied. This area is characterized by a relatively narrow continental shelf, whose width varies between 5 km in the North and 25 km in the South and which slope is between 110 and 120 m depth (Bellaiche et al. 1994). The depth increases rapidly with distance from the coast and reaches about 900 m in the central area between Corsica and Italy. The current in this area runs northward along the Italian coast, a small part of which will cross the Corsican canal (located between Italy and Corsica). This East-Corsican current has a strong seasonal variability (Millot and Wald 1980; Crepon et al. 1982).

2.2. Environmental data

Based on previous studies (Vaz and Llapasset 2016; Foveau et al. 2017) and the framework developed in the Kostylev habitat approach, environmental parameters being known to influence the composition and resilience of benthic communities to physical pressures were considered in this study. In the present work, it was considered that benthic community composition is mainly linked to physical constraints (“Disturbance axis”) such as friction on the seabed due to tidal currents or stress induced by the waves. These parameters will mainly influence the composition of the community in epifauna/infauna and fragile/flexible species. The resilience of benthic community (“SfG” axis) depends mainly on metabolic constraints such as nutrition, osmotic, thermal or hyperbaric regulation. It will therefore be influenced by temperature (and in particular strong variations in temperature), depth or availability of food. The details on the data sources used for each variable in each sea basin may be found in Appendix A. The environmental layers were averaged or considered representative over a period of time similar to that of the biological observations used in this study.

2.2.1. English Channel

In the area considered in this work, there was no or very little stratification and the oxygen saturation was nearly maximal due to shallow depths and mixed waters masses (Foveau et al. 2017). As a result, surface hydrological variables were considered relevant to describe seabed environmental conditions. The following environmental factors were used to reflect the main ecological characteristics of the benthic habitats in the English Channel:

Variables related to the community resilience (or scope for growth)

Food availability: approximated by surface Particular Organic Carbon, considered as food for benthic fauna

Salinity: mean salinity at bottom was derived from an hydrodynamic model prediction over the study area (Foveau et al. 2017)

The growth rate of benthic species is related to temperature value and stability. Different temperature proxies were used in this study:

Sea Surface Temperature (SST): obtained from NOAA satellite data

Seasonal temperature variability (Ta): approximated by the standard deviation on average annual temperatures between years

Inter-annual temperature variability (Ti): approximated by the standard deviation of average annual temperatures between years

Variables related to the natural physical disturbance

Wave stress: data were obtained from a wave model and is expressed as a vertical pressure on the seabed in $N.m^{-2}$

Seabed stress: the friction of water masses on the bottom, due to the diurnal tide (Aldridge and Davies 1993) and is expressed as a vertical pressure on the seabed in $N.m^{-2}$.

Friction velocity: estimated using data of wave generated currents and seabed stress.

Depth: bathymetric data were obtained from digital terrain model (DTM) data (SHOM 2015) and depth mostly conditions the exposure to wave impact in the English Channel as it is a generally shallow area. The resolution was about 100 m and the DTM was vertically referenced to the sea mean level.

Sediments: sediments were categorized in 5 classes (Mud, Fine Sand, Coarse Sand, Pebbles, and Gravels) relative to the average mean grain size of superficial sediments (Larsonneur et al. 1982). Gulf of Lion and Corsica

Unlike in the English Channel, Mediterranean waters are often very stratified and much deeper. Salinity, hardly varying at the scale of this study, was not used in modelling Scope for growth.

However, oxygen saturation was considered here. The following environmental factors were used to reflect the main ecological characteristics of the benthic habitats in the Gulf of Lion and in Corsica:

Variables related to the community resilience (or Scope for Growth)

Different temperature proxies were therefore used in this study:

Temperature: average bottom temperature calculated from monthly hydrodynamic model predictions

Seasonal temperature variability (Ta): approximated by the standard deviation of bottom temperature between monthly averages

Inter-annual temperature variability (Ti): approximated by the standard deviation of bottom temperature between yearly averages

Chlorophyll *a* concentration: maximum concentration of surface chlorophyll obtained from monthly satellite observations Chlorophyll *a* concentration is used as a proxy of the primary production (Huot et al. 2007) and thus the energy available for the growth and development of the benthic fauna.

Depth: bathymetry is expressed as average water depth (EMODnet Bathymetry Consortium 2018). Unlike in the English Channel (where it was considered as an important contributor of physical disturbance), in the Mediterranean it is considered a good proxy of the benthic fauna growth and development as it is linked to the stratification, the food availability for benthic fauna and the temperature.

Stratification: average absolute difference between surface and 30 (± 5) m depth water density over 20 years. The Mediterranean Sea is characterized by a strong stratification of the water column in summer, due to high water column stability and high temperatures. This stratification is responsible for the exhaustion of dissolved surface nutrients.

Food availability:

To calculate the food availability, only surface chlorophyll *a* was available as a reliable proxy of primary production. However, both depth and stratification negative effect on food availability at bottom were accounted for following Kostylev and Hannah (2007).

Oxygen saturation: average percent of dissolved oxygen at bottom

Variables related to the natural physical disturbance

Seabed shear stress (SBS): values were estimated using hydrodynamic models (based on current data, wave significant height, peak frequency, peak direction and bathymetry) limited to the north-west Mediterranean and is expressed in $N.m^{-2}$.

Higher seabed shear stress in Mediterranean (although at much lower values than in the values than in the mega tidal English Channel) generates sediment resuspension which, in fine sediment areas as similar effect to trawling (Durrieu de Madron et al. 2005) and will likely benefit to species that are adapted to its impact.

Sediment gain size: A sediment map in the French Mediterranean waters (Garlan 2011) was used to derive average grain size in mm.

2.3. Abrasion data

Table 1: Abrasion and environmental variables ranges of the sampled stations in the three studied areas. The three abrasion values represent the minimum value, median and maximum value. *Food availability computation and units are different in the English Channel ($g.m^{-3}$) and the two other areas (no unit, see Appendix A for details)

	English Channel	Gulf of Lion	Corsica
Food availability*	154.80 - 204.30 - 338.80	0.70 - 0.72 - 0.77	0.65 - 0.67 - 0.71
Salinity (‰)	31.18 - 34.97 - 35.33	–	–
SST (°C)	11.70 - 13.41 - 13.99	–	–
Temperature (°C)	–	13.05 - 13.84 - 15.22	13.74 - 13.92 - 14.94
Ta (°C)	0.14 - 0.64 - 0.87	0.11 - 0.84 - 1.05	0.12 - 0.16 - 0.72
Ti (°C)	0.04 - 0.24 - 0.43	0.04 - 1.44 - 3.02	0.04 - 0.07 - 1.05
Wave stress ($N.m^{-2}$)	0.06 - 0.44 - 3.09	–	–
Friction velocity ($m.s^{-1}$)	0.10 - 0.29 - 0.56	–	–
Seabed stress ($N.m^{-2}$)	0.15 - 1.09 - 3.02	0.01 - 0.02 - 0.08	0.01 - 0.01 - 0.02
Depth (m)	7.00 - 34.00 - 121.43	31.45 - 92.90 - 132.72	67.43 - 90.81 - 149.13
Sediment average grain size (mm)	–	0.03 - 0.03 - 0.08	0.36 - 1.52 - 4.01
Oxygen saturation ratio	–	0.78 - 0.87 - 0.89	0.78 - 0.82 - 0.86
Chlorophyll *a* concentration	–	0.74 - 1.44 - 4.74	0.40 - 0.54 - 2.04
Stratification	–	0.12 - 0.21 - 0.53	0.27 - 0.29 - 0.29
Sampled abrasion range (y^{-1})	0.00 - 7.47 - 74.15	0.08 - 4.81 - 20.69	0.00 - 0.11 - 2.03

To determine the abrasion value at each sampled stations of the three studied areas (Table 1), maps of 90th inter-annual (from 2009 to 2017) percentile of swept surface area ratio per year [SAR(y^{-1})], based on VMS data (Eigaard et al. 2016) were used (method detailed in Jac et al. 2020a). Resolutions of these maps were different: 3'x3' (about 5.4 x 3.5 km resolution) in the English Channel (www.ospar.org) and 1'x1' (about 1.8 x 1.3 km resolution) in Mediterranean Sea (Jac and Vaz 2020). In both cases, all fishing vessels operating in these areas were included, whatever their country of origin In the English Channel, information concerning the type of commercial gear (beam trawl, dredge or bottom trawls) used was not available and the abrasion due to each type of gear could not be estimated in each study area.

2.4. Biological data

2.4.1. Surveys

The following benthic invertebrate by-catch data derived from scientific bottoms trawl surveys occurring in the English Channel and in French Mediterranean waters were used in this work: Channel Ground Fish Survey (CGFS, Coppin and Travers-trolet 1989) and CAMANOC (Travers-trolet and Verin 2014) in the English Channel and Mediterranean International Trawl Surveys (MEDITS, Jadaud et al. 1994) in the Gulf of Lion and in Corsica (Table 2; Figure 1).

In the Mediterranean areas (Gulf of Lion and Corsica), MEDITS occurs yearly in June. The sampling gear used is a four panels' bottom trawl with a 20 mm stretched mesh size at the cod-end. The sampling scheme is stratified by depth and evenly distributed over the whole study area. Hauls are carried out during daytime at 3 knots and are 30 min long above 200 m (MEDITS 2017).

In the English Channel, CGFS are conducted yearly in October and CAMANOC in September 2014. The sampling gear used is a Very High Vertical Opening bottom trawl with a 20 mm stretched mesh size at the cod-end. The sampling scheme was fixed following an initial randomly definition by depth and sediment type in the western English Channel, or evenly distributed over a regular grid in the eastern English Channel over the whole study area and hauls are carried out during daytime for 30 minutes at 4 knots (ICES 2015, 2017). Since the scientific gears and methodology used on each study site are standardized, the benthic catchability is assumed to be constant in our datasets. Benthic fauna, considered as by-catch, was sorted, identified, counted, and weighed.

Table 2: Number of stations sampled per year at the three study areas for which all environmental data were available

Years	English Channel	Gulf of Lion	Corsica
2008	89		
2009	84		
2010	85		
2011	92		
2012	78	48	10
2013	88	47	10
2014	121	48	10
2015	82	48	10
2016	70	48	10
2017	57	47	10
2018	94	47	10

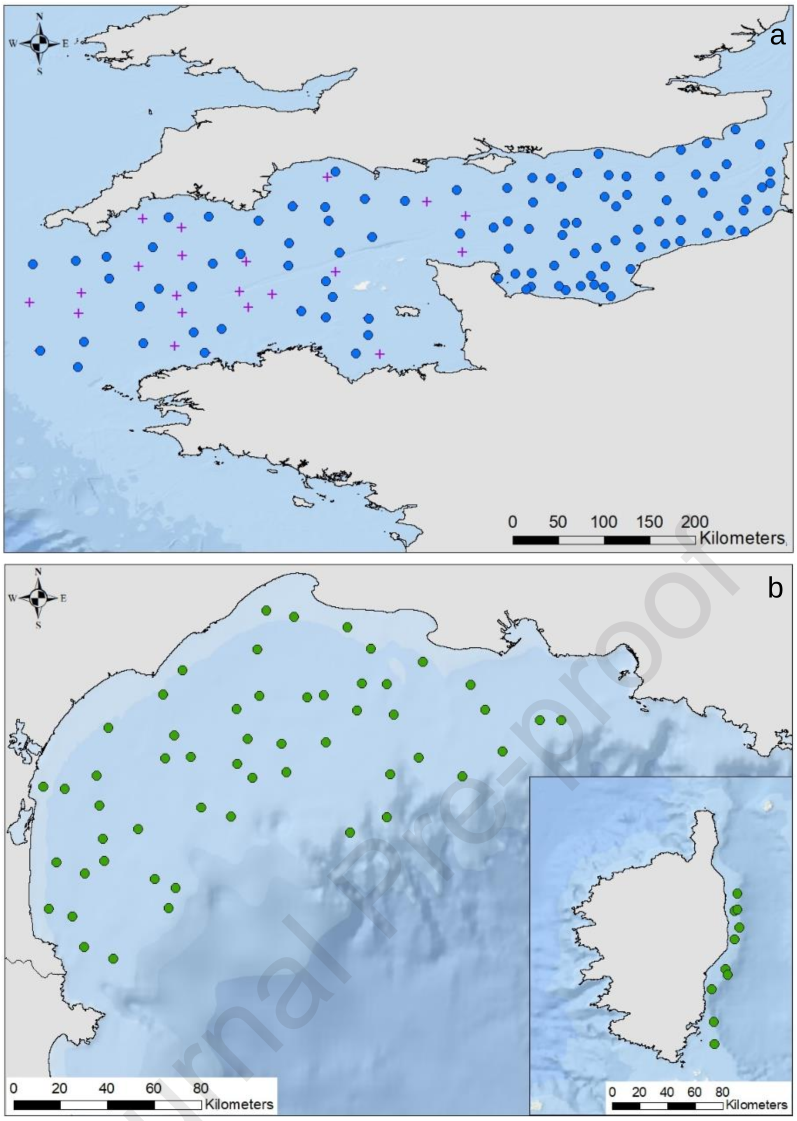

Figure 1: Location of sampled stations in the English Channel (a) and the Mediterranean Sea (b). The purple crosses correspond to the stations carried out during CAMANOC survey (2014), the blue dots during CGFS survey in 2018 and green dots during MEDITS survey in 2018.

2.4.2. Biotic indices

Biomass data were chosen over abundance data because abundance was not estimated for several colonial species such as hydroids or sponges. Data were standardized according to trawling swept area and expressed in $g.km^{-2}$. Commercial species (*Homarus gammarus, Crangon crangon, Maja brachydactyla, Pecten maximus, Aequipecten opercularis, Palaemon serratus, Nephrops norvegicus, Buccinum undatum, Cancer pagurus, Aristaeomorpha foliacea, Aristeus antennatus, Parapeneus longisrostris,* and *Bolinus brandaris*) and cephalopods have been removed from the datasets because the spatial pattern of abrasion is not independent of the presence of target species. To reduce misidentification errors, a procedure proposed by Foveau et al. (2017) to aggregate uncertain taxa at a higher identification level was applied. In order to be kept at its initial taxonomic level, a given species had to be observed in 90% of the sampled years, otherwise it was iteratively aggregated at higher taxonomic level (genus, family, order, class, phylum) until it fulfilled this criterion. If not, it was removed from the analysis.

In earlier studies, Jac et al. (2020a, b) demonstrated that functional sensitivity indices, based on biological traits characterizing potential responses of organisms to physical abrasion (position in the sediment, feeding mode, mobility, adult size, fragility), were the most suitable for monitoring the effect of trawling on benthic communities, particularly with scientific trawl data. For each taxon and each biological trait considered, the score assigned corresponded to the modality most frequently used by the species. Each of these traits were scored for each species and taxon composed of several species were checked in terms of biological trait homogeneity. Groups that were found too heterogeneous were dropped from the analysis and when the deleted taxon represented more than 25% of the total station's biomass, the station was removed from the dataset. A list of the taxon that were found in the different study areas is given in Appendix B. These species scores were combined in different ways depending on the chosen indices and weighted with relative biomass (preferred to account for differential gear efficiency over different sediment types). Only four indices [Trawl Disturbance Indicator (TDI), modified- Trawl Disturbance Indicator (mTDI), partial- Trawl Disturbance Indicator (pTDI) and modified sensitivity index (mT)] were used in this study as they were shown to be the most effective in earlier studies (Jac et al. 2020a, b). Traits scoring and calculation methods of each of these indices are fully detailed and developed in Appendix C.

2.5. Data analyses

Functional sensitivity indices that did not have a normal distribution were log- or square root transformed prior to analyses. To explore the relationship between the different explanatory variables, correlation matrices were produced (Appendix D).

2.5.1. Initial selection of environmental parameters

Since multicolinearity between the variables had to be avoided as much as possible for model construction, the calculation of the variance inflation factor (VIF) for each predictor variables was performed with the car R package 3.0-9 (Fox et al. 2019) after a generalized linear model (GLM). The lack of multicolinearity results in a small VIF and a VIF value that exceeds 10 indicates a problematic amount of colinearity (Lin 2008). The variables with too high VIF were iteratively removed, since the presence of multicolinearity implies that the information that this variable provides about the response is redundant in the presence of the other variables (Bruce and Bruce 2017).

2.5.2. Model of environmental influence on indices

To evaluate the influence of natural variability on functional sensitivity indices, generalized additive models (GAM) were used to investigate which environmental variables influenced the studied indices. As the available variables used to describe environmental conditions differed between the studied areas, separate models were developed for each study area. Since benthic community sampling was conducted over several years and benthic assemblages may change between years (independently of the environmental factors tested here), the "year" factor was also added in these models. The year effect was investigated as a structuring variable rather than a random effect to measure the amount of variance that could be explained by this effect and how much was shared and was therefore confounded with other structuring compartments. The lack of annual abrasion and environmental data did not allow for a full study of the year effect which was not the focus of the present work. Gaussian models with an identity link were built with a spline function and third degree of smoothing for all variables. For each GAM, the most significant variables were selected using forward procedure based on the Akaike Information Criterion (AIC; Akaike 1974) using the MASS package 7.3-51.5 (Ripley et al. 2019).

A variance partitioning procedure was used to distinguish the effect of inter-annual variation from the effect of variables related to resilience process and those related to disturbance impact using the model explained deviance and the adjusted coefficient of determination (adjusted R-squared) which is related to the amount of explained variance in a gaussian context. This procedure was used to quantify the marginal (when alone) contribution and conditional (when dropped) contribution of each type of process following the procedure described in Lehmann et al. (2002).

2.5.3. Study of abrasion influence on indices

Since the relationship between abrasion and functional sensitivity indices is not always linear over the entire abrasion range (Jac et al. 2020b), GAMs were produced to study the influence of abrasion on each of the indices in the three studied areas.

2.5.4. Natural variability vs. abrasion

In order to understand the influence that environmental conditions (and the inherent inter-annual variations) and abrasion can have, separately and jointly, on the functional sensitivity indices, additional GAMs were carried out. In the three studied areas, if it was found to be significant, abrasion was added to models previously developed for each index

For each index in each study area, percentages of deviance explained and adjusted R-squared for each of the three models (only environmental parameters, only abrasion, and all variables) were compared to determine whether natural variability (distinguishing disturbance from resilience variables) overlapped with the effect of abrasion (and thus trawling) on benthic communities.

3. Results

3.1. Environmental parameters selection

In the three studied areas, strong correlations were observed between several environmental parameters. Thus, in the Gulf of Lion, the different temperature parameters (SST, Ti, Ta) were highly correlated (> 0.81). Ti was also strongly positively correlated to oxygen concentration and negatively correlated with depth (Table D.1). A high positive correlation between chlorophyll a concentration and stratification was also observed in this area. In Corsica, only the temperature parameters (SST, Ti and Ta) were strongly correlated (Table D.2). In the English Channel, salinity and food availability were strongly correlated (> - 0.87) but were also highly correlated with depth and Ta (Table E.3).

3.1.1. English Channel

None of the environmental parameters studied in the English Channel had a variance inflation factor (VIF) greater than 10 (Table 3). Thus, all these environmental variables were retained for further analysis.

Table 1: Variance inflation factor (VIF) of each environmental co-variable in the English Channel.
SST = mean of the sea surface temperature ; Ta= standard deviation of monthly mean temperatures; Ti = standard deviation of average annual temperature between years

Environmental parameters	VIF
Food availability	7.68
Salinity	4.60
SST	1.87
Ta	4.43
Ti	1.91
Wave stress	3.03
Friction velocity	6.42
Seabed stress	1.05
Depth	6.74
Sediments	4.97
Year	1.26

3.1.2. Gulf of Lion

The majority of parameters had variance inflation factor (VIF) superior to 10 when all environmental variables were retained (Table 4). All environmental variables had a VIF< 10 after the iterative removal of Ti, stratification and oxygen saturation.

Table 2: Variance inflation factor (VIF) of each environmental co-variable in the Gulf of Lion and variable removal effect. Each VIF column represents a new iteration (from left to right)
Grey shading indicates parameters with VIF>10. Ta = standard deviation between monthly mean temperature within a year ; Ti = standard deviation of average annual temperature between years

Environmental parameters	VIF	VIF	VIF	VIF
Ti	28.33	-	-	-
Ta	16.41	11.10	10.24	4.83
Stratification	15.72	14.39	-	-
Depth	15.56	13.10	10.25	9.71
Oxygen saturation	14.21	14.11	11.70	-
Chlorophyll a concentration	11.09	9.63	4.49	1.82
Food availability	9.35	8.41	4.14	2.56
Temperature	5.86	4.43	4.38	4.05
Seabed stress	2.79	2.77	2.50	2.41
Sediment size	2.44	2.40	2.06	1.85

3.1.3. Corsica

The variance inflation factor was initially greater than 10 for almost all environmental variables (Table 5). All environmental variables had a VIF< 10 after the iterative suppression of the temperature, chlorophyll a concentration and intra-annual temperature variability (Ta) data.

Table 3: Variance inflation factor (VIF) of each environmental co-variable in Corsica and variable removal effect. Each VIF column represents a new iteration (from left to right)

Grey shading indicates parameters with VIF>10. Ta= standard deviation between monthly mean temperature within a year ; Ti = standard deviation of average annual temperature between years

Environmental parameters	VIF	VIF	VIF	VIF
Temperature	447.62	-	-	-
Ti	275.78	13.68	9.75	2.51
Ta	76.70	19.26	10.33	-
Chlorophyll a concentration	25.96	21.06	-	-
Food availability	23.98	19.75	5.35	3.73
Stratification	20.27	9.72	3.84	3.08
Oxygen saturation	13.29	13.27	5.29	4.98
Depth	14.16	9.27	8.71	5.11
Sediment size	1.44	1.30	1.19	1.13
Seabed stress	1.40	1.38	1.37	1.35
Year	1.31	1.26	1.23	1.22

3.2. Influence of environmental parameters on indices

3.2.1. English Channel

Over the eleven environmental variables studied in the English Channel, only the sea surface temperature (SST) was consistently removed from all tested models (Table 6). Food availability (Fa), salinity, annual variation of temperature (Ti), friction velocity (FV), seabed stress (SBS) and type of sediment (Sed) were retained in all GAMs developed. The year and wave stress parameters were also retained for two indices: TDI and pTDI. Overall, the models selected highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure E.1, E.2, E.3 & E.4). Linear trends over time were sometime observed in the regression coefficient value of the year factor and indices values were found to mostly increase over time in the English Channel (Figure E.1, E.2 & E.3).

Table 4: Model selected for each sensitivity index in the English Channel.

AdjR² = adjusted R-squared; Fa = Food availability ; Ta= standard deviation between monthly mean temperature within a year ; Ti = standard deviation of average annual temperature between years ; FV = Friction velocity ; SBS = Seabed stress ; Sed = sediment type. “s” correspond to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.25	27.1
mTDI	s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.23	23.8
pTDI	s(Fa, 3) + s(Salinity, 3) + s(Ta, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.32	33.4
mT	s(Fa, 3) + s(Salinity, 3) + s(Ti, 3) + s(FV, 3) + s(SBS, 3) + Sed	0.22	22.8

In the English Channel, the deviance proportion explained by “Scope for Growth” and “Disturbance” parameters was relatively similar across the different indices, with the exception of the pTDI, for which the explained deviance by SfG parameters was higher than for other indices. More precisely, the marginal and conditional effects of the Dist parameter were greater than those of the SfG parameter for all indices except pTDI. From 66 to 77% of the deviance of each index was left unexplained by the studied variables (Table 6; Figure 2).

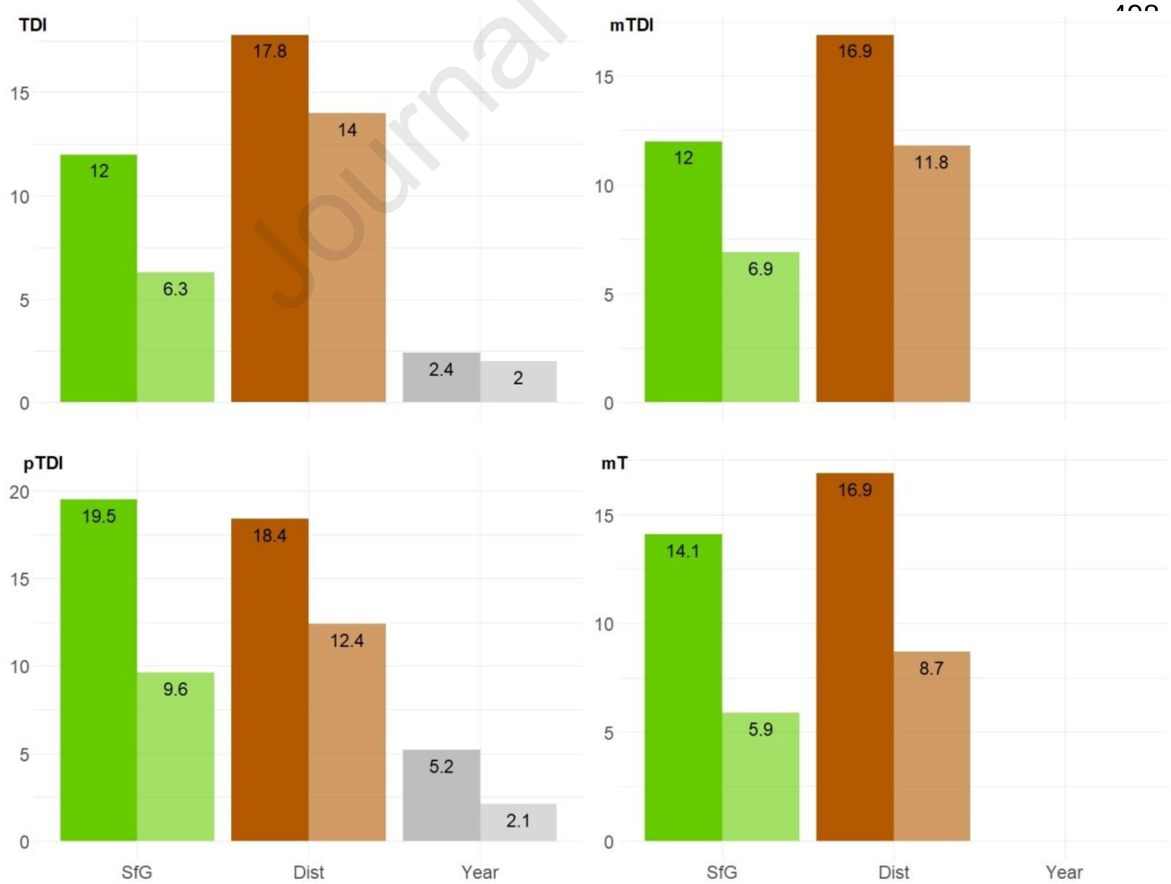

Figure 2: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in the English Channel. SfG = Scope for Growth; Dist= Disturbance. Colored bars= marginal effects; bars with transparency= conditional effects. Unexplained deviation for each of the indices (TDI: 72.9%, mTDI: 76.2%, pTDI: 66.6%, mT: 77.2%).

3.2.2. Gulf of Lion

Over the eight environmental variables studied in the Gulf of Lion, only depth was removed from all developed models (Table 7). The chlorophyll a concentration, the intra-annual variation of temperature (Ta) and the year parameter were retained in each GAM. SBS was also retained for all indices except the TDI. As in the English Channel, the models selected highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure E.5, E.6, E.7 & E.8). A decrease in the value of the model intercept over time could be observed for most indices but pTDI where it was increasing (Figure E.5, E.6 & E.7).

Table 5: Model selected for each sensitivity index in the Gulf of Lion.
AdjR² = adjusted R-squared; Chla = concentration in Chlorophyll a ; Ta= standard deviation between monthly mean temperature within a year ; SBS = Seabed stress ; Sed = sediment size; Temp= Temperature. "s" correspond to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Ta, 3) + Chla + s(Sed, 3) + Year	0.45	47.0
mTDI	s(Ta, 3) + s(Fa, 3) + Chla + s(Temp, 3) + SBS + s(Sed, 3) + Year	0.52	54.2
pTDI	Ta + Chla + s(Temp, 3) + s(SBS, 3) + Year	0.34	35.9
mT	s(Ta, 3) + Chla + s(Fa, 3) + SBS + s(Sed, 3) + Year	0.53	55.3

In the Gulf of Lion, the proportion of deviance explained by "Scope for Growth" and "Disturbance" parameters was high (>35%) and similar between the mTDI and the mT and even if values stayed relatively high, they were lower for TDI and pTDI (Figure 3; Table 7). In addition, for each index, the deviance explained by SfG parameter was always higher (for marginal and conditional effects) than the one explained by Dist parameter. Finally, overlap effects were very important in the gulf of Lion, because differences between marginal and conditional effect was high for each parameter.

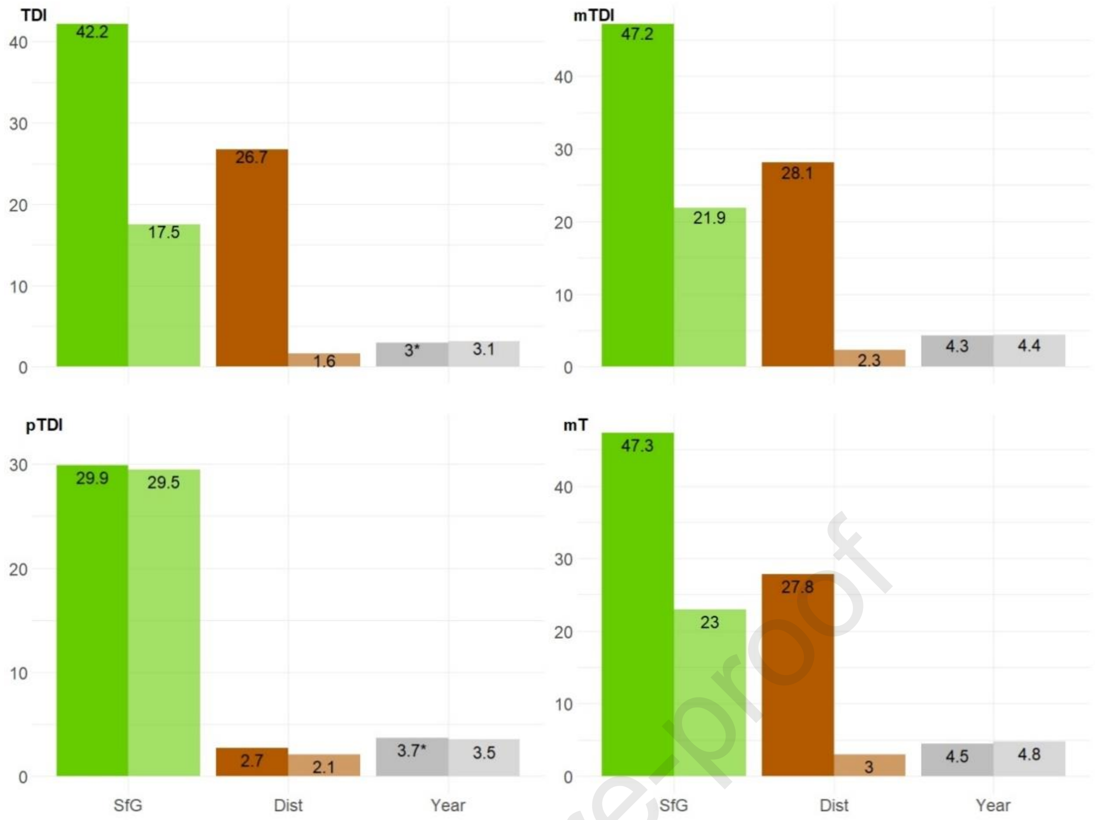

Figure 3: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in the Gulf of Lion. SfG = Scope for Growth; Dist= Disturbance. Colored bars= marginal effects; bars with transparency= conditional effects. * indicate that the effect of this variable alone was not significant. Unexplained deviation for each of the indices (TDI: 53%, mTDI: 45.8%, pTDI: 64.1%, mT: 44.7%)

3.2.3. Corsica

Over the eight environmental variables studied in Corsica, only the year parameter was removed from all models (Table 8). FA, SBS and the sediments grain size (Sed) were also retained for TDI derivatives and the mT. Stratification parameter was also retained for all indices except the mTDI. As before, the models selected highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure E.9, E.12, E.15 & E.18).

Table 6: Model selected for each sensitivity index in Corsica.

$AdjR^2$ = adjusted R-squared; Fa = Food availability; Ti = standard deviation of average annual temperature between years; stratif = Stratification; O_2 sat = oxygen saturation; SBS = Seabed stress; Sed = sediment size. “s” correspond to spline function.

Indices	**Selected explanatory variables**	**$AdjR^2$**	**Explained deviance (%)**
TDI	Fa + s(Ti, 3) + s(O_2 sat, 3) + s(stratif, 3) + s(SBS, 3) + s(Sed, 3)	0.33	43.1
mTDI	Fa + O_2 sat + s(SBS, 3) + Depth + s(Sed, 3)	0.37	42.7
pTDI	s(Fa, 3) + s(Ti, 3) + s(stratif, 3) + s(SBS, 3) + Depth + s(Sed, 3)	0.37	45.2
mT	s(stratif, 3) + Depth	0.31	33.5

The proportion of deviance explained by environmental variables was high (>33%) and relatively close for TDI and its derivatives. The value for mT was lower even though it remained relatively high (Table 8; Figure 4). As in the Gulf of Lion, for each index, the deviance explained by SfG parameter was always higher (for marginal and conditional effects) than the one explained by Dist parameter. Only the SfG parameter (stratification and depth) even seemed to have an influence on the mT. Over 55% of the deviance of each index was left unexplained by the environment. Moreover, the variables seemed to have a more structuring effect when they were all together in the general model than when the SfG and Dist variables were separated (conditional effects), where they explain less variance and some of them were no significant (Figure E.10, E.11, E.13, E.14, E.16 & E.17).

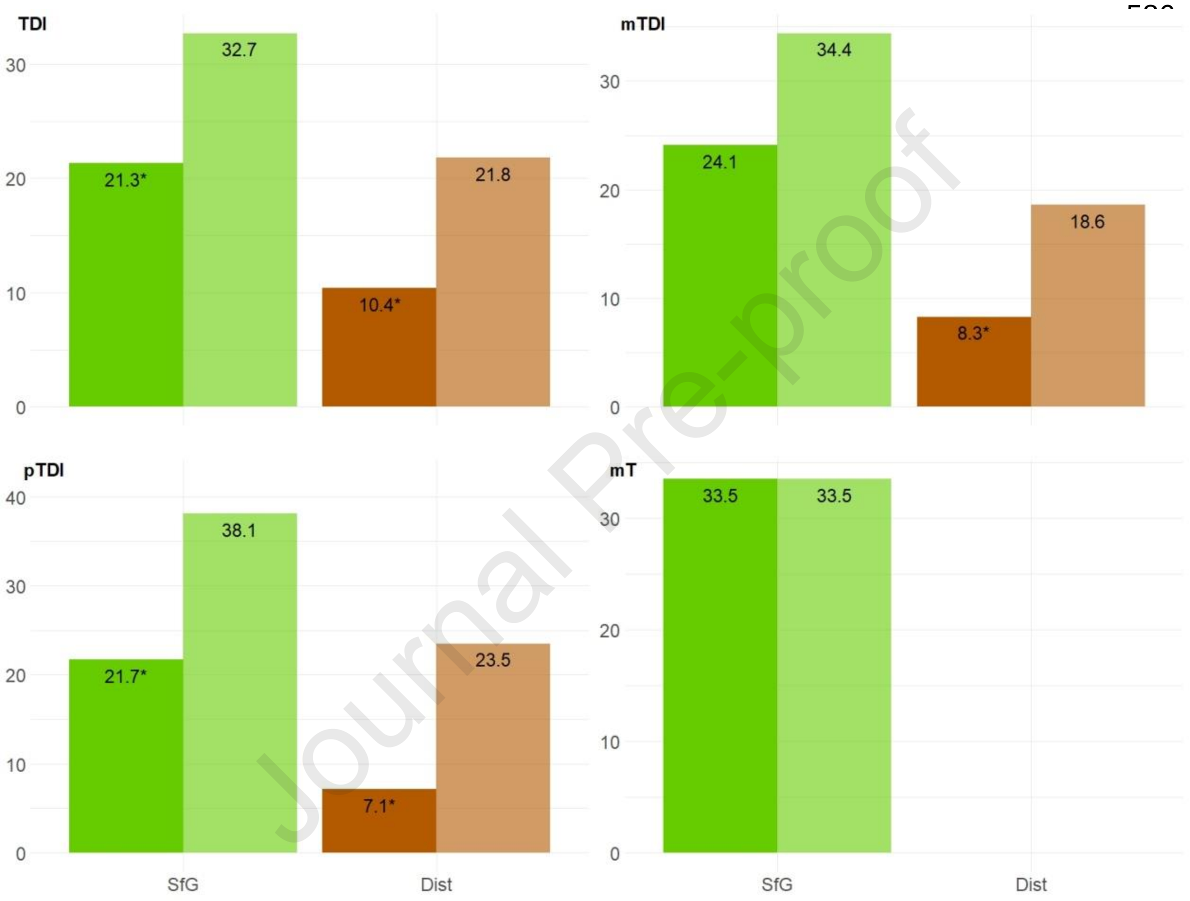

Figure 4: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in Corsica. SfG = Scope for Growth; Dist= Disturbance. Colored bars= marginal effects; bars with transparency= conditional effects. * indicate that the effect of this variable alone was not significant. Unexplained deviation for each of the indices (TDI: 56.9%, mTDI: 57.3%, pTDI: 54.8%, mT: 66.5%).

3.3. Abrasion influence on indices

In the English Channel, the proportion of deviance explained by abrasion was higher for pTDI than for the other indices (Table 9). In the Gulf of Lion, values of deviation explained by abrasion were very similar for TDI and mTDI, lower for pTDI and higher for mT (Table 9). The shape of relationship between abrasion and index, in both the English Channel (Figure 5), and the Gulf of Lion (Figure 6) was similar and generally decreasing with abrasion for the four sensitivity indices. In contrast, no significant relationship between abrasion and indices was observed in Corsica (Figure 7).

Table 7: Evaluation of the influence of abrasion (SAR.y^{-1}) on sensitivity indices in the three studied areas (AdjR² = adjusted R-squared)

Areas	Indices	AdjR²	Explained deviance (%)
English Channel	TDI	0.13	13.2
	mTDI	0.12	11.8
	pTDI	0.16	15.9
	mT	0.09	9.3
Gulf of Lion	TDI	0.16	16.7
	mTDI	0.16	16.6
	pTDI	0.12	12.5
	mT	0.18	18.9
Corsica	TDI	-	-
	mTDI	-	-
	pTDI	-	-
	mT	-	-

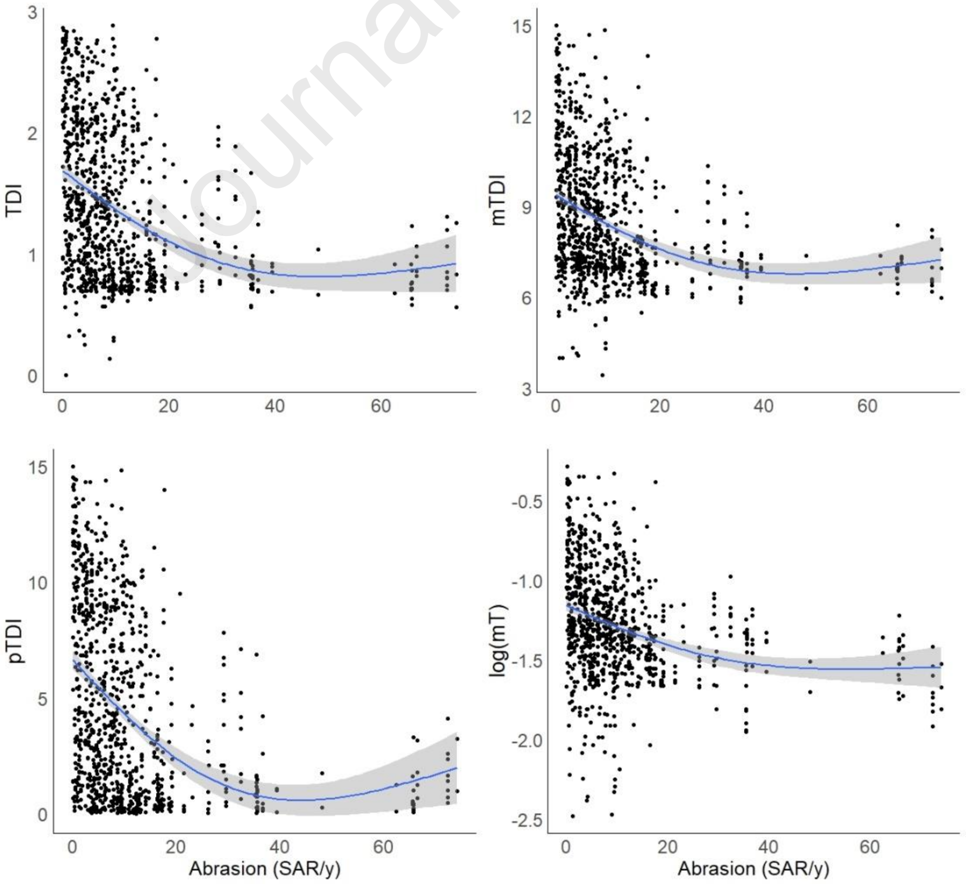

Figure 5: Relationship between abrasion (SAR.y^{-1}) and sensitivity indices in English Channel

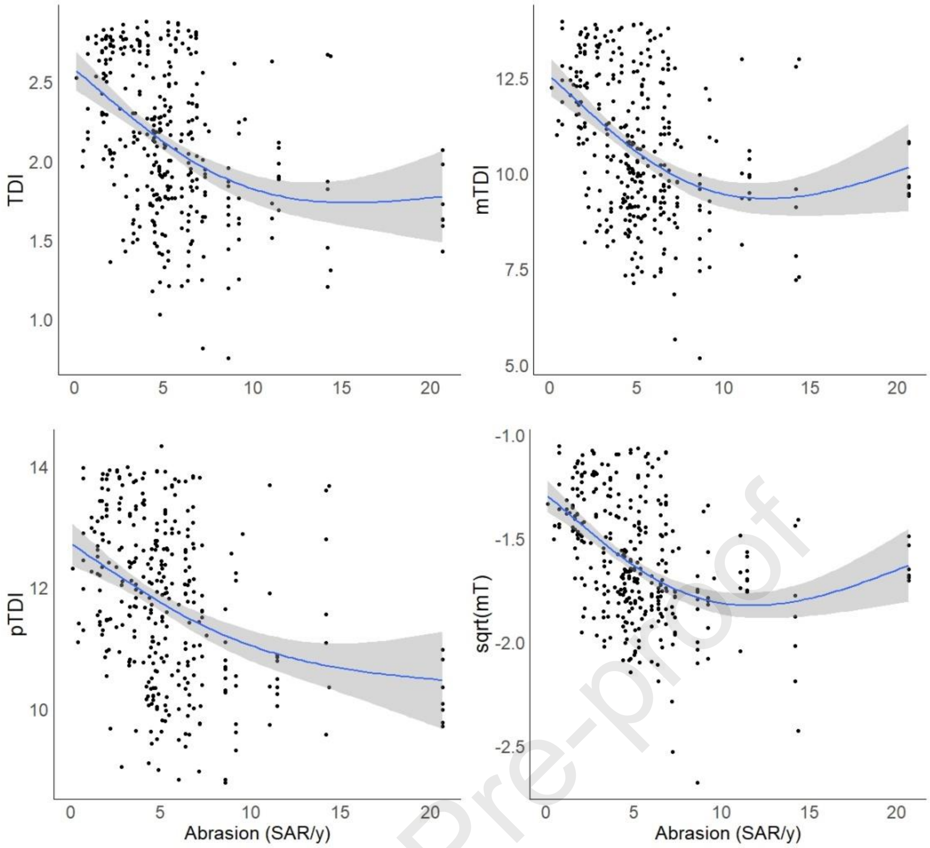

Figure 6: Relationship between abrasion (SAR.y^{-1}) and functional sensitivity indices in the Gulf of Lion

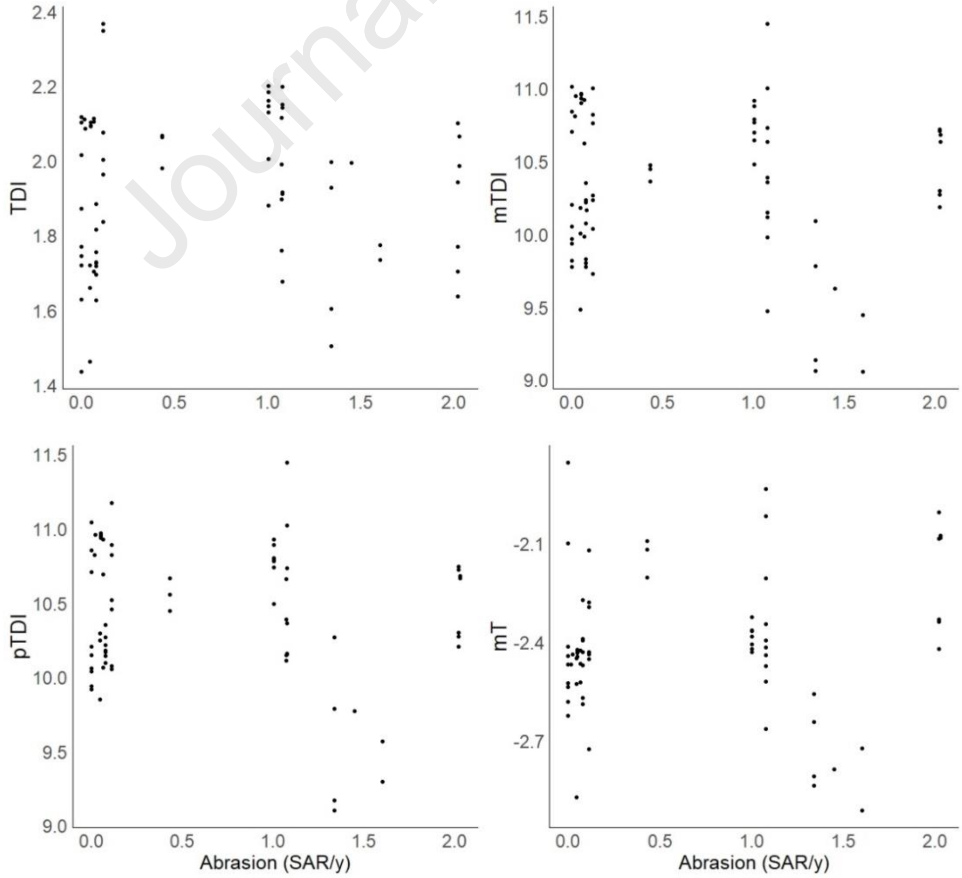

Figure 7: Absence of significant relationship between abrasion (SAR.y^{-1}) and functional sensitivity indices in Corsica

3.4. Natural variability vs. abrasion

In view of the results obtained for Corsica in the part 3.3, the analysis combining environment and abrasion effects was not relevant. These analyses were also carried out in the other two study areas.

3.4.1. English Channel

In the English Channel, the abrasion and several environmental variables were retained in all GAMs (Table 10). For all indices, environmental variables retained were the same that for model without abrasion (Table 6).

The deviance explained by environmental parameters and/or abrasion was higher for the pTDI than for the other indices (Figure 8). For each index, the deviance explained by abrasion alone was quite high (marginal effect > 9%) but very low when other variables were taken into account. In all cases, from 6.4 to 11.6% of the variation explained by abrasion was found to also overlap with the environment effect. Over 62% of the deviance of each index was left unexplained by the environment or the abrasion.

Table 8: Evaluation of the combined influence of previously selected environmental parameters and abrasion on sensitivity indices in the English Channel. AdjR² = adjusted R-squared; Fa = Food availability ; Ti = standard deviation of average annual temperature between years ; FV = Friction velocity ; SBS = Seabed stress. Sed= sediment type. "s" correspond to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Abrasion, 3) + Fa + s(Salinity, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.29	31.2
mTDI	s(Abrasion, 3)+ s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.26	27.5
pTDI	s(Abrasion, 3) + s(Fa, 3) + s(Salinity, 3) + s(Ta, 3) + Ti + s(Wave stress, 3) + s(FV, 3) + s(SBS, 3) + + Sed + Year	0.36	37.7
mT	s(Abrasion, 3) + Fa + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.24	25.5

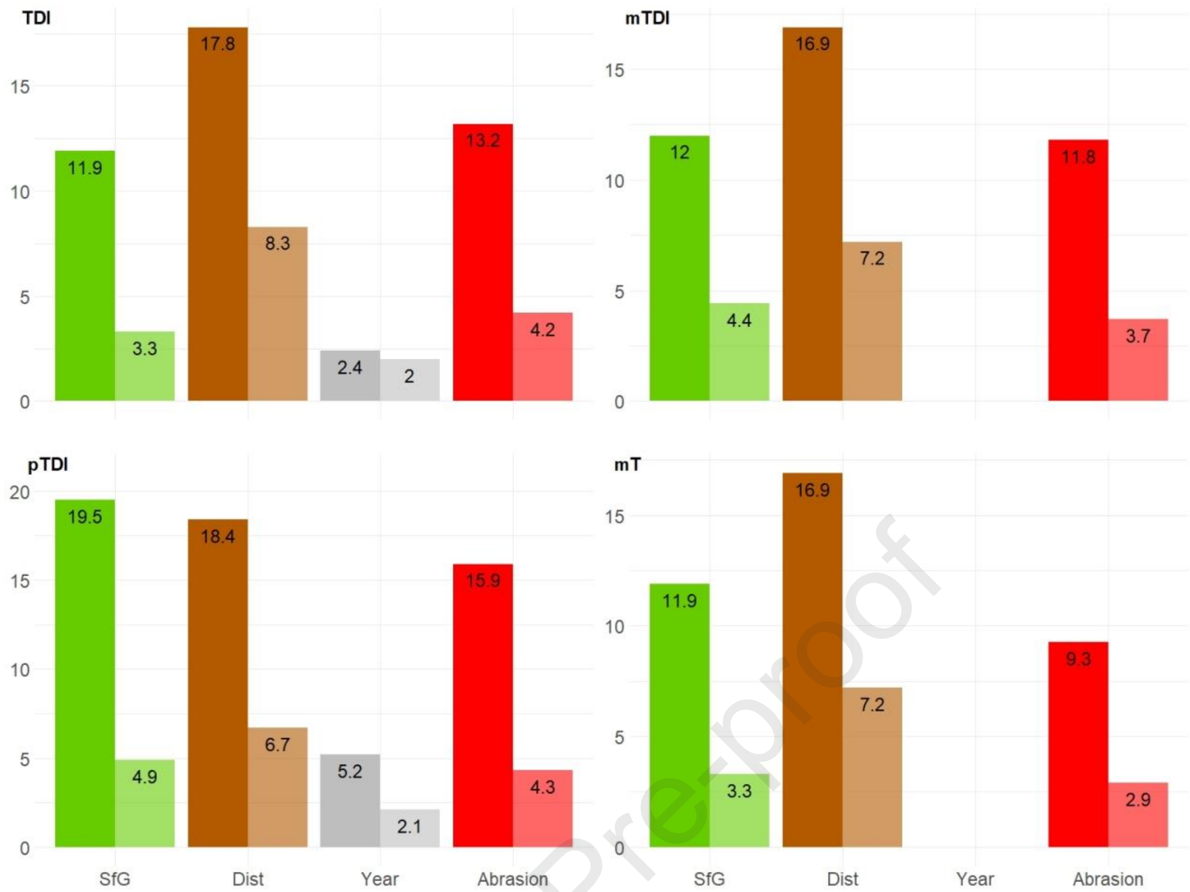

Figure 8: Percentage of deviance explained by each group of variables (SfG, Dist, Year or Abrasion) for each sensitivity index in the English Channel. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal effects; histogram with transparency= conditional effects. Unexplained deviation for each of the indices (TDI: 68.8%, mTDI: 72.5%, pTDI: 62.3%, mT: 74.5%).

3.4.2. Gulf of Lion

In the Gulf of Lion, abrasion was retained by the selection model procedure only for the pTDI (Table 11) and its addition added little explanatory value to the model (Figure 9). For other indices only the initial environmental parameters were retained. However, the percentage of deviance explained by environment and/or abrasion was relatively low for pTDI compared to the other indices. Around 50% of the deviance of each index was not explained by the studied parameters.

Table 9: Evaluation of the combined influence of previously selected environmental parameters and abrasion on sensitivity indices in the Gulf of Lion. AdjR² = adjusted R-squared; Chla = concentration in Chlorophyll a ; Ta= standard deviation between monthly mean temperature within a year ; SBS = Seabed stress ; Temp= Temperature ; Sed = sediment size. “s” correspond to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Ta, 3) + Chla + s(Sed, 3) + Year	0.45	47.0
mTDI	s(Ta, 3) + s(Fa, 3) + Chla + s(Temp, 3) + SBS + s(Sed, 3) + Year	0.52	54.2
pTDI	s(Abrasion, 3) + Ta + Chla + s(Temp, 3) + s(SBS, 3) + Year	0.35	37.7
mT	s(Ta, 3) + Chla + s(Fa, 3) + SBS + s(Sed, 3) + Year	0.53	55.3

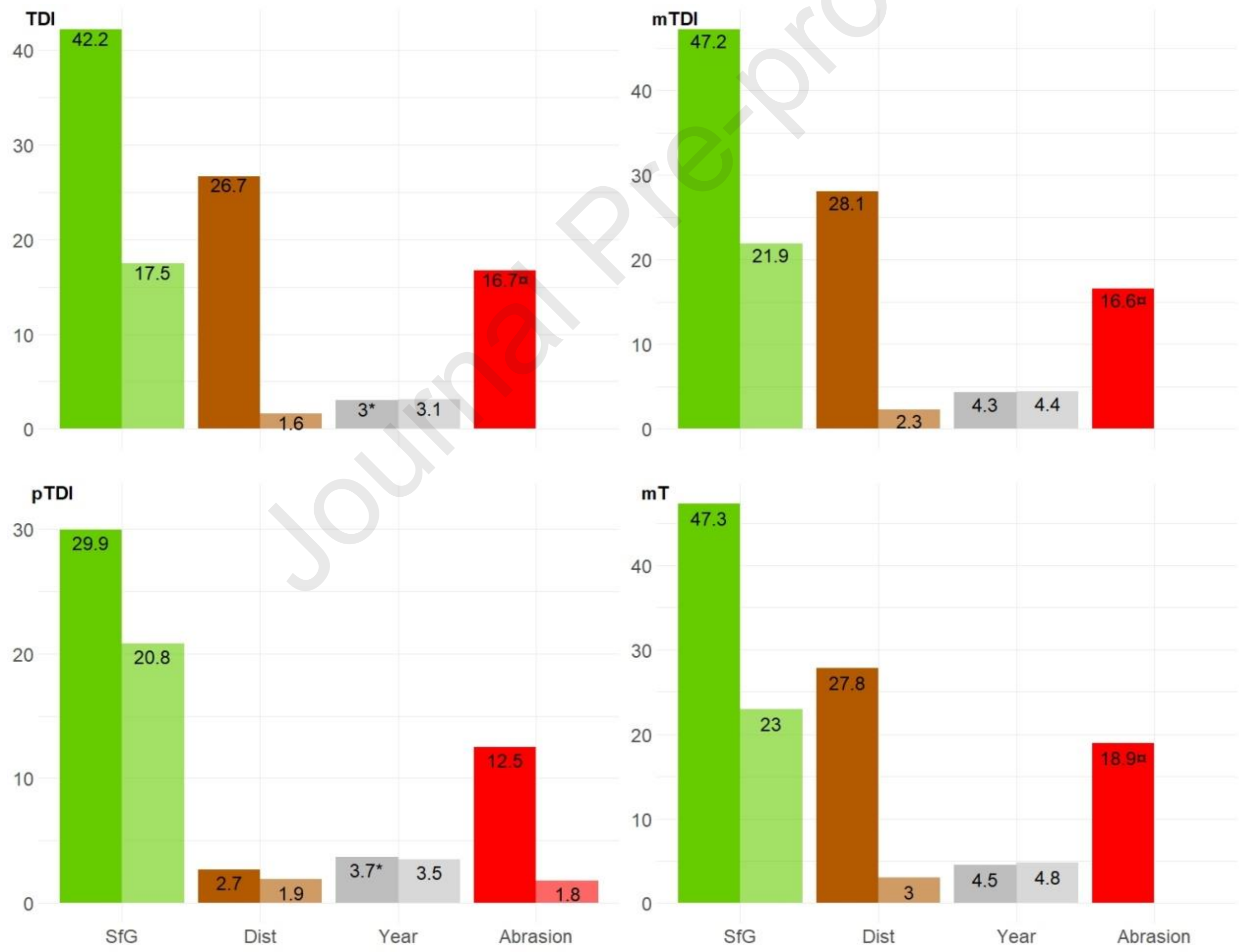

Figure 9: Percentage of deviance explained by each group of variables (SfG, Dist, Year or Abrasion) for each sensitivity index in the Gulf of Lion. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal effects; histogram with transparency= conditional effects. ¤ indicate that the effect of this variable alone was significant but not with the other variables in the model; * indicate that the effect of this variable alone was not significant. Unexplained deviation for each of the indices (TDI: 53%, mTDI: 45.8%, pTDI: 62.3%, mT: 44.7%).

4. Discussion

4.1. Which environmental parameters drive the composition of benthic communities?

Distribution and composition of benthic communities is known to be strongly influenced by environmental conditions (Hall et al. 1994). However, regional differences in nature and intensity of the forcing factors could be observed. Even if the environmental parameters studied here were, supposed, representing the same disturbance and resilience drivers in the different study areas, the composition of the different benthic communities seemed to be governed by different environmental processes. Differences in the variables chosen to compose the disturbance and SfG axes in the two areas, namely the inclusion of salinity only in the English Channel, or of Oxygen saturation only in the Mediterranean, or the different classification of depth (as a disturbance variable in the English Channel but a SfG variable in the Mediterranean) may partly explain these differences. Moreover, their number and quality by which they were measured or produced also differed in the two basins. Nevertheless, the strong ecological differences shaping the three study areas are more likely to explain these differences. In the English Channel, food availability, salinity, inter-annual temperature variation, friction velocity, seabed stress and sediment type were the main factors influencing the composition of benthic communities. Environmental variables related to "Disturbance" processes had a greater correlation than the others on the different indices tested. In this zone, the benthic communities seem to be particularly structured by their potential natural resistance to physical disturbance and in particular their ability to withstand wave and tidal currents (friction velocity, seabed stress). Bremner et al. (2006) found that “SfG axis” variables such as salinity and SST had the greatest influence on the biological traits of benthic species in the English Channel and Irish Sea. However, they did not study exactly the same environmental variables as in the present study and used a larger number of biological traits. More precisely, in the present work, index values tended to be positively correlated with the friction velocity or the seabed stress and negatively with the wave stress. These results, apparently counter-intuitive, may be explained as follow in the local context. Seabed stress is derived from tidal currents which shape the sediment types of the English Channel. As a result, coarser sediment, hosting more trawl-sensitive filter feeder species, may be found on areas with higher tidal stress. On the other hand, wave stress is more important on shallow coastal areas, where finer sediment communities, usually naturally adapted to disturbance, may also be found.

In the Gulf of Lion and Corsica, the main environmental parameters that influenced the benthic composition were different from those in the English Channel. Concentration of chlorophyll *a*, intra-annual temperature variations, food availability at bottom (FA), the seabed stress (SBS) and the sediment average grain size were retained for the Gulf of Lion and the depth, FA, stratification, oxygen saturation, inter-annual temperature, SBS and the sediment size, for Corsica. In both zones, despite a non-negligible influence of the different parameters related to the "Disturbance" axis, parameters related to the metabolism of benthic species (Chl *a* concentration, Ti, FA, depth) were more strongly correlated to the different indices. In these two areas, the distribution of benthic communities seemed to be mainly influenced by the availability of resources necessary for their growth and development than by physical processes. As the Mediterranean sea is a microtidal sea with relatively low swell amplitudes in the Gulf of Lion (Guizien 2009), these results seem to indicate that benthic communities are not naturally shaped by disturbance. In addition, regarding the oligotrophy of the Mediterranean sea (Rosenberg et al. 2003), the availability of food (and the chlorophyll a concentration in the Gulf of Lion) was logically found to be a factor limiting the growth and development of benthic communities. Even though the Gulf of the Lion and Corsica are relatively close, several factors influencing the composition of benthic communities were different, which confirms the usefulness of studying these two areas separately. These differences may reflect the different hydrodynamic and geomorphological conditions between the two areas. The Gulf of Lion is a continental shelf where the depth is relatively shallow (90m on average; SHOM 2015) and where the circulation of water masses is mainly linked to regional winds (Millot 1990). Conversely, east Corsica is composed of a relatively narrow continental shelf followed by a steep continental slope (the depth increases rapidly with distance to the coast; SHOM 2015) hence the marked effect of depth on the structure of benthic communities in this zone. Moreover, the Gulf of Lion is one of the most productive areas in the Mediterranean, much more so than Corsica. However, since the Mediterranean is an oligotrophic sea this factor may still be considered limiting in the Gulf of Lion, especially from spring to autumn when the waters are most strongly stratified (Cresson et al. 2020).

More surprisingly, within a same area, indices did not seem to be influenced by the same environmental variables. For example, in the English Channel, a significant influence of the wave stress and year factor was observed on TDI and pTDI, whereas this was not the case for the other indices. These results, although calculated on the same biological data and based on the same biological traits (Foveau et al. 2019), suggested that certain index calculation methods may mask the influence of some environmental variables. The deviance explained by these parameters differed between indices and was higher for pTDI than any other indices in all areas except in the Gulf of Lion. As this index only takes into account the species most sensitive to trawling (Jac et al. 2020a), these results suggested that the distribution of these species in the English Channel and in Corsica was particularly influenced by the environmental parameters studied here. In these two zones, the deviance explained by environmental parameters (conditional contribution) related to resilience (scope of growth) appeared to be greater for pTDI than for the other indices. In the Gulf of Lion, even if the deviance explained was lower for the pTDI than other indices, the deviance explained by SfG parameters (conditional contribution) was also higher for the pTDI than for other indices. This may suggest that the distribution of species considered sensitive to trawling is more dependent on factors related to resilience than other species of the benthic community which is coherent with ecological expectation of slow recovery rates of these species. Resilience capacity even appeared to be the main factor structuring the species sensitive to trawling in Corsica and the Gulf of Lion. In the present work, the species particularly sensitive to trawling were filter feeders, sessile, large, fragile and belonged to the epifauna. The availability of food is known to be, in certain areas, a factor limiting the development of filter feeders with low mobility such as *Amphiura filiformis* (Rosenberg 1995). Bremner et al. (2006) showed that there is a link between the flexibility of the species, their position in the sediment and a number of environmental factors such as salinity or temperature. Finally, the size of benthic species can also be related to productivity (Romero-Wetzel and Gerlach 1991).

Regardless of index type or study area, the majority of environmental variables appeared to have a complex and non-linear relationship with the indices. When all areas and indices are combined, only the Chlorophyll *a* concentration had a negative linear relationship with functional sensitivity indices. This may result from the fact that many species exhibit asymmetric responses (or, although less frequently, multimodal patterns) along environmental gradients (Anderson 2008). These results confirm the interest and even the need to use splines and generalized additive models (GAMs) in the present study, to better understand the effect of natural variables on the functional sensitivity indices studied.

Linear trend over time could sometime be observed in some of the indices. In the English Channel, this pattern may reflect a general improvement of the benthic habitat status (increased biomass of sensitive species). In the Gulf of Lion, the contradictory patterns between the indices may be explained by a relative decrease of middle range sensitive species biomass over time. In the absence of data allowing to link this pattern to other explanatory variables, we chose not to expand on this effect that may need further investigation in the future. This reflected however that the models' intercepts tended to increase or decrease linearly over time independently of the environmental characteristics encountered. As such this pattern is not expected to alter our conclusions concerning the overlapping effect between abrasion and environmental conditions.

4.2. Abrasion

It is generally accepted that trawling has an impact on benthic communities and that not all species are equally sensitive to it (Kaiser et al. 1998; Sanchez et al. 2000;   et al. 2006). Jac et al. 2020a showed that four functional sensitivity indices, based on biological traits known to respond to trawl disturbance (Bremner et al. 2006; Gray and Elliott 2009; Bolam et al. 2014), responded significantly and negatively along a gradient of abrasion intensity but behaved differently depending on the studied area. In the present study, all functional sensitivity indices were significantly influenced by abrasion, except in Corsica where no significant influence of the abrasion was observed. The trawler fleets operating in Corsica are very small (for both regulation and economic reasons) and the continental shelf suitable for this activity is relatively narrow. This may explain why the trawling fishing effort (and therefore the abrasion) is relatively low in this area and was probably always so. The explained deviance was quite low for all the indices (< 20%) and relatively different between some indices within the same studied area. The higher explained deviance did not result from the use of the same index in the three studied areas. In the English Channel, as for the environmental parameters, the abrasion explained a larger part of the pTDI variance than that of the other indices whereas in the Gulf of Lion, this index has the lowest value of explained deviance. These results showed that in the English Channel, the biomass of species sensitive to trawling is particularly influenced by the abrasion [whereas it does not seem to be the case in the Gulf of Lion (lower value of explained deviance for pTDI)]. Different spatial resolutions of fishing intensity data were available over each study area which may affect the absolute estimated value of the trawling intensity (see Amoroso et al. 2018). However, it is unlikely that overestimation or underestimation of the trawling intensity may affect the result as the absolute value of SAR were not compared between the two zones and only their relative variability and shape of relationship were explored. In the Gulf of Lion however, no null abrasion value area could be observed which may result in a reduced gradient of impact that limits the detection power of this study. Finally, among the various environmental parameters studied, those related to natural physical disturbance (Dist) had the greatest influence on indices. This suggests that, in the English Channel, benthic communities are essentially structured by physical disturbances. In the Gulf of Lion, physical disturbance and abrasion do not appear to be sources of significant stress for benthic communities and therefore do not appear as strongly structuring parameters.

In the Gulf of Lion, abrasion seemed to explain a larger part of the variance of mT than of the other functional sensitivity indices whereas the contrary has been observed in the English Channel. Compared to TDI and its derivatives, a factor has been added to the method of calculating mT: the protection status of the species (Jac et al. 2020a, Appendix C). The large difference in the influence of abrasion on mT and other indices could be related to this factor. This difference could also come from the method of combining the different biological traits used. In the calculation of the mT: a hierarchy is made between the different traits by separating primary and secondary factors and then, those having direct and indirect effect. The addition of the factor "protection status" in the calculation of TDI and its derivatives could allow the validation of one or the other of these hypotheses.

4.3. Natural variability vs. abrasion

4.3.1. English Channel, an area under multiple stressors

In some cases, where natural disturbances are very high, the effect of trawling on benthic communities may be very limited or even undetectable (Kaiser et al. 1998; van Denderen et al. 2015). In the English Channel, the addition of abrasion in the different GAMs did not result in removing the significant influence of one of the environmental variables. Abrasion itself seemed to have a significant influence on the index regardless of the index of functional sensitivity studied. The apparent effect of abrasion is not fully overlapping with that of the environmental variables. The deviance explained by models including both abrasion and the various environmental parameters is higher, whatever the index studied, than models containing only abrasion or only environmental factors. This indicates that, in the English Channel, contrary to what has been observed by Stokesbury and Harris (2006) in the Atlantic or by Sciberras et al. (2013) in Cardigan Bay (Wales), natural disturbances, although strong (large swell and strong tidal currents), do not fully mask the impact of trawling on benthic communities. The fact that, for each index, the value of the deviance explained in the final model was not equal to the sum of the deviance explained by the environment and that explained by fishing indicated that there was still an overlap between the effect of fishing and the effect of environmental parameters on benthic communities. As shown in Kaiser (1998), trawl disturbance seems to affect benthic communities in a similar way to natural disturbance but to also induce specific changes, such as reflected in biomass, that are not fully masked by that of the environmental parameters.

In summary, in the English Channel, the composition and distribution of benthic communities is governed by environmental conditions but also by fishing effort (or abrasion) and species most sensitive to trawling are the most suited to detect this effect. As a result, the pTDI index seemed to be the most appropriate to detect the specific effect of abrasion (independently of the environment) in this study area.

4.3.2. Gulf of Lion, too late to say?

In the absence of tidal currents, the Gulf of Lion is subjected to a calm hydrodynamic regime and is dominated mainly by fine sediments (Ferré et al. 2008). Thus, since the benthic communities are not subjected to major natural physical disturbances, their composition and distribution should be particularly affected by the abrasion induced by trawling (Kaiser 1998). Following this hypothesis, abrasion should have a significant influence on all indices, independently (or with little overlap) of environmental conditions. It appeared that in models combining abrasion and environmental parameters, abrasion specific effects could only be detected when using pTDI.

Two hypotheses may emerge from the absence of significant relationship between abrasion and the chosen indices when environmental parameters are taken into account. Firstly, the significant effect of abrasion observed on its own is entirely shared with one or several environmental variables. The correlation matrix indicated that abrasion was not fully correlated to one variable but slightly correlated (> 0.60) with several variables (the three proxies of temperature and depth). The effect of abrasion may not be distinguished from the effect of the combination of these variables. The second hypothesis is that the significance of the observed abrasion is in fact only resulting from its strong spatial correlation to the environment. Consequently, fishing has no longer effect on the benthic communities of the Gulf of Lion.

The use of the available *in situ* observations alone does not permit to confirm either of these hypotheses with certainty. A significant effect of abrasion on pTDI could be detected when food availability and sediment size variables were removed. This suggests that abrasion does have a significant effect on the distribution of trawl-sensitive species, but, when considering the entire benthic community, this effect is masked by variations in these environmental parameters. Given that trawling has been present in the area for a very long time and at extremely high intensities (Jac and Vaz 2020), it is conceivable that trawling has lead to long-term changes in both sediment characteristics' (Brown et al. 2005; Trimmer et al. 2005) and benthic assemblages. Original communities might have been replaced by benthic communities fully adapted to the fishery induced abrasion (Jac et al. 2020b). These semi-natural communities are therefore only shaped by local environmental variations.

In order to verify these hypotheses, it is necessary to monitor benthic communities along a wider abrasion gradient, containing in particular unfished areas. Since no untrawled areas are currently sampled within the framework of scientific bottom trawl surveys, cruises dedicated to monitoring the effect of trawling on benthic communities should be implemented. In the case where no unfished area may be left [as it seems to be the case in the Gulf of Lion (Jac and Vaz 2020)], a temporary closure of certain zones to fishing may allow to monitor the evolution of the environment (granulometry for example) and of the benthic communities, and observe (or not) a return to original communities.

The significant influence of the year on all the indices studied shows an inter-annual variability in the composition of benthic communities in the Gulf of Lion. This was also reported by Labrune et al. (2007), who suggested that these changes could be cyclic and potentially linked to regional climatic variations.

4.4. Corsica, too little to say?

Contrary to what has been observed in other study areas, no significant relationship between the four indices and the abrasion was observed in Corsica. This was suspected as abrasion values are relatively low over the whole Corsica (Jac and Vaz 2020; Jac et al. 2020a). Benthic communities were consistently sampled in areas with low levels of fishing. A previous study (Jac et al. 2020a) showed that the chosen indices did not appear to be able to detect the effect of trawling on benthic communities at such low levels of abrasion. An environmental effect, mainly related to the resilience of communities (SfG), was however detected by the indices. Moreover, the absence of a significant effect for most of the environmental variables when taken separately (marginal contribution), whereas they had a significant effect in the overall model, indicated either an overfitting of the model or important underlying interactions (antagonistic or synergistic effects) between environmental parameters related to unknown processes. The latter, often referred to as the Simpson's paradox, may result in drawing the wrong conclusions and requires complementary data to be solved (Pearl 2014). It is also important to highlight that the available data comprised of ten stations, observed over seven years (70 observations). These were analyzed within GAMs containing up to six explanatory variables which may be deemed arguable in terms of statistical robustness. In view of these results, no conclusion can be made on the relationship between functional sensitivity indices and the environment in this area. Finally, the absence of a significant effect of the year factor suggested that, contrary to what was observed in the two other study areas, the benthic communities sampled in Corsica were relatively similar over time, reflecting the little natural or anthropogenic variability present in Corsica.

4.5. What the future holds for the benthic communities of the European continental shelves?

When an ecosystem is affected by anthropogenic pressures, it may, if it has some capacity to resist to disturbance, initially show little response to increasing pressure. However, beyond a certain point, change can become rapid and lead to a radically different state of the ecosystem. Likewise, the importance of its resilience will condition its ability to recover after the pressure stops. Thus, depending on the combined capacities of resilience and resistance of these ecosystems, the decrease in pressure does not always lead to their return to their initial state, different recovery trajectories are possible (Andersen et al. 2009; Ducrotoy 2010; Fauchard 2010; Shade et al. 2012; Selkoe et al. 2015).

In the English Channel, the strong hydrodynamics (Larsonneur et al. 1982) shape naturally resistant benthic communities and allow them to withstand significant fishing pressure. Moreover, in this area of high productivity (https://www.emodnet.eu/en/map-week-chlorophyll-concentration), a decrease in physical disturbance induced by trawling could lead to a satisfactory recovery of the benthic communities with sufficient resilience. Processes related to the resilience of the community (SfG) have a lesser relationship to the observed assemblages and may not be limiting in the area. Although the results of this study do not allow to determine if the resilience of the communities will follow the same pattern as their disappearance or if a hysteresis phenomenon (delay of the recovery trajectory due to too low resilience) will be observed, it is likely that the community should be capable of some level of recovery. In the southern North Sea and western English Channel respectively, McLaverty et al. (2020) and Sheehan et al. (2013) have shown that trawling closures allowed sufficient recovery to the point that they may probably be used as reference areas to detect impact on benthic communities in other highly disturbed areas. However, in areas were natural disturbance and fishing effort are important, it may be impossible to distinguish between the two effects and benthic communities may appear to be fully adapted to the fishery pressure (Szostek et al. 2015)

In the Mediterranean Sea, the work carried out by Jac et al (2020a) did not highlight the existence of benthic habitats in good ecological status in the Gulf of Lion in areas where abrasion is low or intermediate. This seems to suggest a low resistance of benthic communities naturally undisturbed by regional hydrodynamics. Moreover, the benthic communities present in this area seem to be relatively structured by environmental variables related to resilience. The resilience capacity of the species therefore seems to be a limiting factor for these communities and the presence of a hysteresis phenomenon in the Gulf of Lion, durably preventing their recovery, seems plausible.

5. Conclusion

The present study attempted to disentangle the effect of bottom impacting fisheries from that of environmental processes shaping the resistance and resilience processes governing the benthic communities in contrasted regions. In the different study areas, benthic communities did not seem to be structured by the same environmental factors. In the English Channel, environmental parameters related to the resistance of species to natural physical disturbances were those which mainly influenced the benthic communities whereas in the Mediterranean, these were the parameters related to the resilience (scope for growth) of the communities. Abrasion also appeared as a variable structuring benthic community in the English Channel whereas this was not observed in Corsica. In the Gulf of Lion, only one index was able to differentiate between the abrasion effect and the various environmental variables. In the two zones where an abrasion effect could be detected, the pTDI index, focusing on the species the most sensitive to trawling, seems quite appropriate to evaluate the effect of abrasion independently of the environment, in particular parameters related to growth and resilience of benthic species.

However, in order to better understand and predict the recovery trajectories resulting from a reduction or a ban of bottom trawling and dredging pressures, direct observation of the evolution of communities in newly protected areas seems necessary. Such knowledge is required to rule on the reversibility of the impact of trawling in European waters and to set habitat specific pressure thresholds to return and maintain appropriate benthic ecosystem functioning, halt biodiversity erosion and develop truly sustainable fisheries.

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Highlights :

- The joint influence of environmental parameters and trawling pressure on four functional sensitivity indices in three environmentally contrasted areas (English Channel, Gulf of Lion, Corsica) was evaluated.
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- Environmental variables were classified in two groups according to the type of influence they have on the benthic community (resilience *vs*. resistance)
- The distribution of benthic species in the English Channel appear to be linked to physical disturbances and therefore to their resistance
- In the Mediterranean Sea, the distribution of benthic fauna seems to be due to parameters linked to the resilience of communities
- The effect of abrasion can be distinguished from the natural environmental disturbances in the English Channel and Gulf of Lion

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: