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How resilient are coastal marine soft-bottom communities with high diversity?

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ABSTRACT

Based on the large amount of data accumulated over 50 years on soft-bottom communities mainly from the English Channel and the Mediterranean Sea, this study analyses the relationship between diversity (Taxonomic Richness TR, Shannon diversity H' , and Pielou evenness J') and abundance of taxa on diverse shallow benthic habitats ranging from muddy sand to gravel. Only samples with $H' > 4.0$ are selected for this analysis, making up a total of 379 data points. Communities with HDLA (High Diversity and Low Abundance) are common, while some samples show HDHA (High Diversity and High Abundance). Well-known significant correlations are found between H' , J' , TR and abundance. Moreover, temporal and spatial monitoring of oil spills, urban and industrial outfalls, harbour sediment dumping and salmon aquaculture tend to illustrate the high resilience of soft-bottom benthic communities after the cessation of a disturbance or with increasing distance from the source. Conversely, low resistance of benthic communities after an oil spill is linked to the abundance of sensitive species to hydrocarbons before the sediment pollution.

1. Introduction

Faced with the increase in marine human activities and pressures on ecosystems, particularly in estuarine and coastal areas, it is essential to measure the impacts of these anthropogenic activities (Halpern et al., 2008, 2015; Kappel et al., 2012; Borja et al., 2016; Korpinen and Andersen, 2016; Tamis et al., 2015; Gissi et al., 2021; Simeoni et al., 2023; JPI Oceans, 2024). The macrobenthos is among the biological compartments most affected by the degradation of the marine environment during trawler fishing, the extraction of aggregates, harbour sediment dredging and spoil deposition, hydrocarbon extraction or sediment dumping as well as the installation of offshore wind turbines throughout Europe, the United States and China (Currie and Isaacs, 2005; Jiao et al., 2015; Spagnolo et al., 2019; Dauvin et al., 2022a). To measure the impacts, it is mandatory in most cases to monitor the benthos affected by these activities.

The BACI (Before-After Control-Impact) approach is most often proposed to assess these impacts (Underwood, 1994; Aguado-Gimenez et al., 2012; Pezy et al., 2017; Methratta, 2020). An alternative approach, the Before-After-Gradient (BAG) design, can be used to sample along a gradient with increasing distance from the source of perturbation both before and after the human activity (Methratta, 2020). The following question arises: is it possible to detect the effect of

a human activity with the available indices? Under these conditions, it is often difficult to assess the resistance of a benthic ecosystem, i.e., its tendency to undergo little modification following an environmental disturbance, and the resilience, i.e., the capacity of an ecosystem to return to a state close to that observed before the disturbance (Carpenter et al., 2001, 2005; Brand, 2009; Newell et al., 1998; Elmqvist et al., 2003; Hughes et al., 2005; Dauvin et al., 2012; Allen et al., 2016; Sguotti et al., 2024; Dauvin, 2024). In fact, recolonization after a human perturbation takes place in several stages of ecological succession characterized by the obliteration of physical and biological impacts that vary greatly from one activity to another and from one site to another (Newell et al., 1998; Desprez, 2000; Desprez et al., 2010; Hawkins et al., 2002; Kaiser et al., 2006; Cooper et al., 2007; Elliott et al., 2007; Foden et al., 2009, 2010; Jones and Schmitz, 2009; Le Bot et al., 2010; Barrio-Froján et al., 2011; Lotze et al., 2011; Aguado-Gimenez et al., 2012; Duarte et al., 2015). Biological colonization after the cessation of a perturbation shows that marine soft-bottom benthic communities display an intrinsic resilience (Hawkins et al., 2002; Elliott et al., 2007; Lotze et al., 2011; Duarte et al., 2015; Dauvin et al., 2021a; Dauvin, 2023, 2024, in press) as in the case of most marine ecosystems (Duarte et al., 2015; Gattuso and Duarte, 2021). But do all benthic communities show such a capacity, and is this resilience favored by high biodiversity in some benthic ecosystems? Diversity is important because it helps

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buffer the environmental stresses on an ecosystem (Balvanera et al., 2006; Matthews and Whittaker, 2015; Hong et al., 2022). A diverse ecosystem should have a better chance of surviving rapid changes with minimal losses; and it is expected that diversity plays an important role in providing a variety of diets for the organisms in the ecosystem and increases the variety of responses to disturbance and the likelihood that species can compensate for one another (Bernhard and Leslie, 2013). Diverse ecosystems can sustain complex ecological interactions between biotic and abiotic components in an ecosystem (Frontier, 1985; Balvanera et al., 2006; Hong et al., 2022).

Several studies have pointed out that coastal soft-bottom benthic communities are characterized by high species richness with numerous species and few individuals (Ellingsen, 2001; Rumohr et al., 2001; Gray, 2002; Moritz et al., 2009; Bakalem et al., 2020). Such observations are rare in estuaries mostly characterized by low diversity and high abundance under permanent disturbance (Dauvin et al., 2017a, 2017b; Elliott and Quintino, 2007). Low abundance and high species richness are also observed for some taxonomic groups such as the isopods of the Antarctic (Zemko et al., 2017) and the cumaceans along the continental shelf and slope of the Gulf of Guinea (Stepien et al., 2021).

Moreover, these communities are also characterized by low abundances, and high numbers of rare species (Gray et al., 2005). High Diversity and Low Abundance could imply a better resistance to perturbations than other communities with low diversity and high abundance (Alison, 2004). Conversely, in low diversity communities, some species may show very high abundances. Often, such communities correspond to the pioneer stage of succession following a perturbation when few opportunist species are able to proliferate under stress conditions. Nevertheless, in constantly disturbed environments, such as estuarine areas with high river inflow, shallow depths, significant thermal fluctuations, communities, characterized by few species and high density, should not be regarded as pioneer since they can be practically considered “stable” due to their high resilience, according to the Paradox of Estuarine Quality (Dauvin, 2007; Elliott and Quintino, 2007).

Many authors have discussed the relationship between the species diversity of a community and the sampling effort (Gentil and Dauvin, 1988; Hawkins and Hartnoll, 1980; Gray, 2002; Ugland et al., 2003; Dauvin et al., 2013). It is clear that insufficient sampling surfaces hinder the satisfactory estimation of the alpha diversity of a station or a community (Dauvin et al., 2013). But large sampling surfaces cannot always be envisaged to estimate the real diversity of a station or a community (Gentil and Dauvin, 1988). In fact, for soft-bottom benthic communities, the surface sampled is a balance between the cost of the sampling effort and the quality and quantity of information needed to define species richness, and to estimate the abundance of each species or the total abundance of all the collected species. Cumulative species richness helps to define the minimum sampling effort required to obtain a good assessment of the species richness of a benthic area (Hawkins and Hartnoll, 1980; Ellingsen, 2001; Rumohr et al., 2001; Gray, 2002; Ugland et al., 2003).

This review is based on 50 years of workings on soft-bottom communities, mainly concerns benthic ecosystems from the English Channel (used as a model of a megatidal sea) and also the Mediterranean Sea (a microtidal sea). In this way, a great amount of data on species or taxa richness versus the abundance of species or taxa from diverse benthic habitats ranging from muddy sand to gravel have been accumulated. These habitats are mainly characterized by high species richness often linked with low abundances, but are sometimes associated with high abundances.

The main objective is that of resilience of benthic ecosystems. The re-analysis of these data permit also to demonstrate the correlation between species or taxa richness versus the species abundance. The present study illustrates different cases of communities with HDLA (High Diversity and Low Abundance) and HDHA (High Diversity and High Abundance), focusing on their resistance and resilience under diverse human

pressures.

2. Methods

2.1. Available data for soft-bottom macrobenthos

Only the sampling using a mesh size of 1-mm have been considered in the analyses, H' and J' are calculated after identifying the species or taxa and counting the refusal retained on the sieve. Only stations with a Shannon diversity >4.0 corresponding to diverse benthic communities are selected (Appendix A).

Along a gradient from fine to coarse sediments, the selected stations concern the following subtidal sites which are all in marine salinity conditions (> 30.00) (Fig. 1; Table 1):

- Sandy mud: English Channel, Bay of Morlaix (Dauvin, 2000) and Bay of Becquet, North Cotentin (Andres et al., 2020).
- Fine sand: Bay of Morlaix (Dauvin, 1998), Rade de Cherbourg (Baux et al., 2017); Galicia (Gomez Gesteira and Dauvin, 2005); Offshore Sfax, Gulf of Gabès.
- Muddy fine sand and sandy mud: Galicia (Gomez Gesteira et al., 2005), Bay of Seine (Dauvin et al., 2022a, 2022b).
- Medium sand from the MACHU dumping site in the Bay of Seine (Marmin, 2013); Dieppe-le-Tréport site (Pezy and Dauvin, 2021).
- Well-sorted fine sand: Mediterranean Sea (Dauvin et al., 2017b), Bay of Bou Ismail (Bakalem et al., 2020); Channel of the Gulf of Gabès (Dauvin et al., 2021b).
- Coarse sand: Bay of Morlaix (Dauvin, 1988); Bay of Saint-Brieuc (Ratsimbazafy, 1998), Cherbourg area (Andres et al., 2020); Bay of Skhira, Gulf of Gabès (Boudaya et al., 2019).
- Sandy gravel and gravely sand: offshore Bay of Seine (Lozach, 2011; Lozach and Dauvin, 2012; Dieppe-le-Tréport site (Pezy, 2017; Pezy and Dauvin, 2021); Channel of the Gulf of Gabès (Dauvin et al., 2021b).
- Gravel: offshore English Channel (Dauvin et al., 2022b); offshore Bay of Seine (Lozach, 2011; Lozach and Dauvin, 2012); Dieppe-le-Tréport site (Pezy and Dauvin, 2021).
- Pebble and gravel: high-energy hydrodynamic environment in the Alderney Race (Foveau and Dauvin, 2017).

2.2. Responses of benthic communities to anthropogenic pressures

Most of the coastal sites studied here have been affected by anthropogenic perturbations such as the “Amoco Cadiz” oil spill which occurred in March 1978 along the North Brittany coast in France (Dauvin, 1988, 1998, 2000; Poggiale and Dauvin, 2001) and the “Aegean Sea” oil spill in Galicia on December 1992, on the Atlantic coast of north-western Spain (Gomez Gesteira and Dauvin, 2005). Both oil spills correspond to an intensive short-term disturbance. The eastern part of the Bay of Seine is affected by permanent dumping of large amounts of sediment dredged from the harbours of Le Havre and Rouen for 70 years (Marmin, 2013; Pezy et al., 2017, 2018; Baux, 2018; Baux et al., 2020; Raoux et al., 2020; Dauvin et al., 2022a, 2022b). Recent data have been obtained by Chauvel et al. (2024) on the effects of low-intensity granulate extraction on the macrofauna from an offshore site in the Bay of Seine for ten years, while the impact of salmon aquaculture on the macrobenthic fauna has been studied in the Rade de Cherbourg after twenty years of exploitation (Dauvin et al., 2020). Mosbahi et al. (2022) has studied the short-term effects on the benthic fauna due to the cessation of trawling in the Gulf of Gabès, Tunisia, during the COVID-19 Pandemic lockdown. Boudaya et al. (2019) and Mosbahi et al. (2019) have assessed the effects of permanent multiple anthropogenic pressures on the offshore macrofauna in the Gulf of Gabès (Tunisia, central Mediterranean Sea).

All these cases illustrate the sensitivity, resistance or resilience of benthic communities to human activities and pressures.

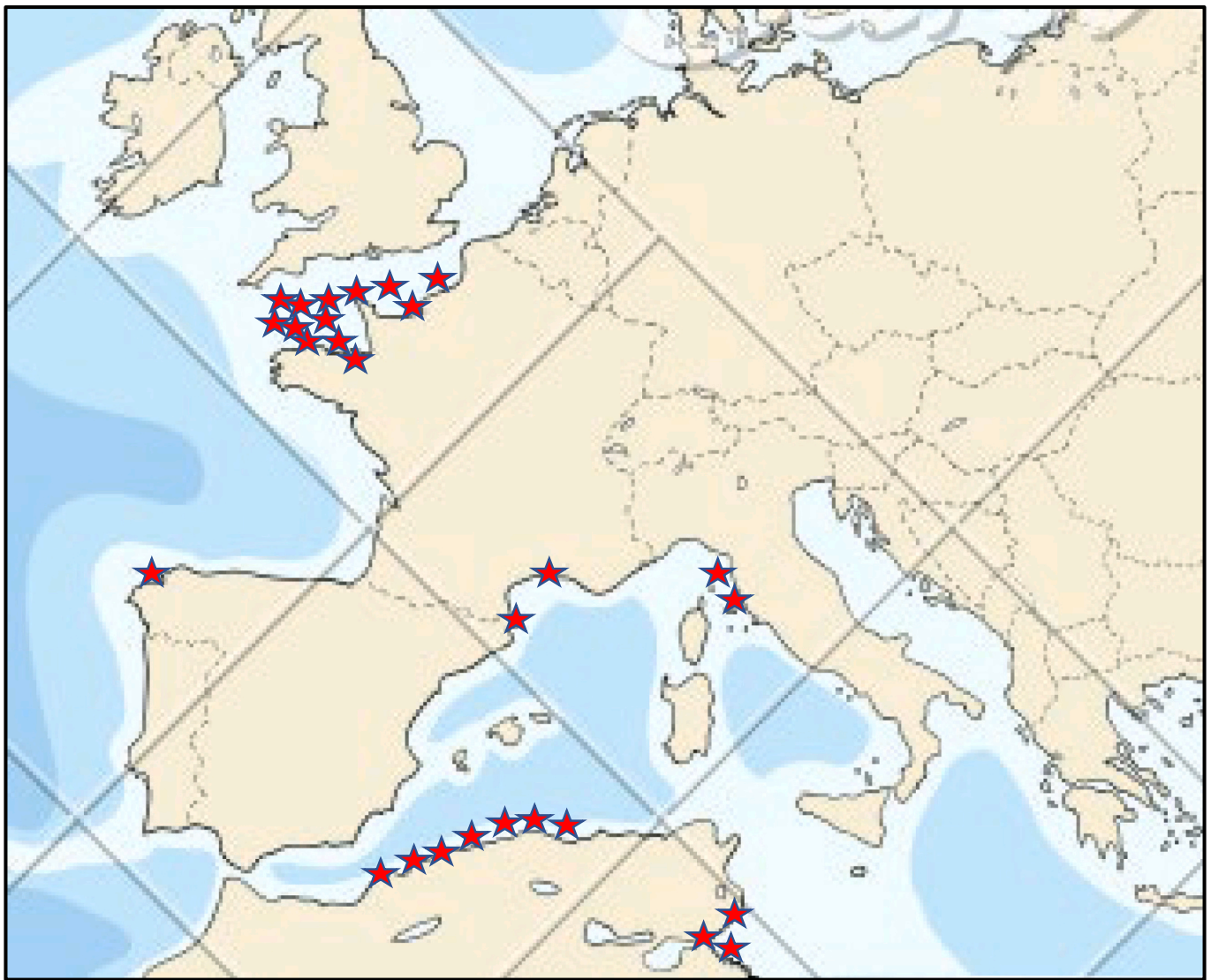


Fig. 1. Location of the sampling sites in the English Channel and North-Eastern Atlantic Ocean and western part of the Mediterranean Sea.

2.3. Univariate indices

The Taxonomic Richness corresponds to the number of taxa found in the total sampling surface which varies from 0.1 to 2.8 m² (Table 1). The abundance is the number of individuals found in the total sampling surface which varies from 0.1 to 2.8 m² (Table 1). Many indices have been proposed and used to assess the species diversity for soft-bottom communities. But the most widely used diversity index in the ecological literature is the Shannon diversity index (H') (Shannon, 1948), which corresponds to the information content of a system calculated using Log_2 (Frontier, 1985). It is often associated with Pielou's J' index of species evenness, which is related to the Shannon index but does not depend on the number of species in the sample (Pielou, 1975).

The Shannon diversity index varies from 0 to a maximum value occurring when all species have the same number of individuals: $\log_2 S$ (where S is the number of species). For the ecological diversity of water masses as stipulated by the European Framework Water Directive, Vincent et al. (2002) suggested the following Quality Status threshold values: Bad (0–1), Poor (1–2), Moderate (2–3) Good 3–4 and High >4. Frontier (1985) considered that a Shannon index $H' > 4.5$ corresponds to a highly diversified community. In this study, only values >4.0 have been arbitrary selected following the Vincent et al. (2002) threshold for high Quality Status of coastal water masses.

Evenness is a measure of the relative abundance of the different species in the same sample, community or an area. Pielou's J' index varies between 0 and 1. A value of 1 represents a community with perfect evenness, decreasing to zero when there is only one species in a sample, a community or an area. Dauvin et al. (2017a) has estimated the following thresholds for Ecological Status in terms of J' : Bad < 0.2, Poor 0.2–0.4, Moderate 0.4–0.6, Good 0.6–0.8 and High >0.8.

2.4. Statistical analyses

The linear correlations between univariate indices are estimated with Spearman's coefficient; p values are also estimated within the Spearman method. The numbers of individuals per taxon (abundance) are transformed in $\text{Log}_{10} N$.

The figures illustrate temporal changes or spatial gradient of univariate indices: Taxonomic Richness, Abundance, Shannon diversity H' and Pielou evenness J' from different sampling surfaces. A BACI (Before-After Control-Impact) approach is used for the dumping experimentation on MACHU site from the eastern part of the Bay of Seine and for the cessation of fishing activity during the COVID-19 Pandemic lockdown in the Gulf of Gabès.

Table 1
Location of sites, dates and sampling strategy.

Site	Station and depth	Sediment	Date	Sampling gear	Total sampling surface number of replicates	Reference
English Channel, Bay of Morlaix	Primel, 25 m	Coarse sand	1977–1980	Hamon grab	2.8 (10 replicates)	Dauvin, 1988
English Channel, Bay of Morlaix	Pierre Noire, 17 m	Fine sand	1977–1996	Smith-My Intyre	1.0 (10 replicates)	Dauvin, 1998
English Channel, Bay of Morlaix	Rivière de Morlaix, 10 m	Muddy sand	1977–1996	Smith-My Intyre	1.0 (10 replicates)	Dauvin, 2000
English Channel, Bay of St Brieuc	P2-P3, 25–30 m	Coarse sand	1992–1993	Hamon grab	1.0 (4 replicates)	Ratsimbazafy, 1998
English Channel, Alderney Race	Moul2, PT34, 60 m	Pebbles and gravel	April 2015	Dredge	–	Foveau and Dauvin, 2017
English Channel, Rade of Cherbourg	S21, 10 m	Mixed sediment	February 2014	Van Veen	0.3 (3 replicates)	Baux et al., 2017
English Channel, west Cherbourg	HV1, QU3, 10–20 m	Coarse sand	February 2018	Van Veen	0.3 (3 replicates)	Andres et al., 2020
English Channel, Bay of Becquet	B9, 20 m	Sandy mud	January 2016	Van Veen	0.3 (3 replicates)	Andres et al., 2020
English Channel, offshore Bay of Seine	1 station, 42 m	Gravel	April 2009	Hamon grab	0.5 (2 replicates)	Lozach and Dauvin, 2012
Offshore English Channel, west to 0°	Box 1 to box 13, 45–100 m	Coarse sand to gravel	2010–2011	Hamon grab	0.5 (2 replicates)	Dauvin et al., 2022a
English Channel, Bay of Seine	8 stations, 15–30 m	Muddy sand	2016–2017	Van Veen	0.3 (3 replicates)	Dauvin et al., 2022b
English Channel, Bay of Seine, MACHU	2 stations, 15–20 m	Medium sand	2010–2011	Van Veen	0.5 (5 replicates)	Marmin, 2013
English Channel, offshore Dieppe	6 stations, 12–25 m	Medium sand	2014–2016	Van Veen	0.5 (5 replicates)	Pezy and Dauvin, 2021
English Channel, offshore Dieppe	7 stations, 12–25 m	Sandy gravel	2014–2016	Van Veen	0.5 (5 replicates)	Pezy and Dauvin, 2021
English Channel, offshore Dieppe	12 stations, 12, 25 m	Gravelly sand	2014–2016	Van Veen	0.5 (5 replicates)	Pezy and Dauvin, 2021
North Spain, Galicia	X and Z, 10–15 m	Fine sand	1993–1996	Box corer	0.1 (3 replicates)	Gomez Gesteira and Dauvin, 2005
Mediterranean Sea	Western Basin, 2–25 m	Well Sorted Fine Sands	1967–2009	Mainly Van Veen	0.1–1 (1 to 10 replicates)	Dauvin et al., 2017a, b
Mediterranean Sea, Bay of Bou Ismail	98 stations, 3–135 m	Muddy sand-Gravelly sand	August 1988	Smith Mc Intyre	0.2 (2 replicates)	Bakalem et al., 2020
Mediterranean Sea, Gulf of Gabès	Offshore Sfax, 5–20 m	Fine sand	2015–2016	Van Veen	0.2 (2 replicates)	Mosbahi et al., 2019
Mediterranean Sea, Gulf of Gabès	Bay of Skhira, 1.5–24 m	Coarse sand	April 2010	Van Veen	0.2 (2 replicates)	Boudaya et al., 2019
Mediterranean Sea, Gulf of Gabès	Kneiss tidal Channel, 1.5–20 m	Fine sand to gravelly sand	2016–2017	Van Veen	0.4 (4 replicates)	Dauvin et al., 2021a, b

3. Results and targeted comments

3.1. General patterns of univariate indices

A total of 379 data points is available corresponding to samples yielding a Shannon H' diversity ≥ 4.0 (Appendix A). The maximum value is reported for one station of the Bay of Bou Ismail (Algeria), with 6.42 associated with a taxonomic richness (TR) of 138 and a number of individuals per 0.2 m^2 of 371 (i.e., a mean abundance of three individuals per taxon). Only four other H' values exceed 6.0, three in the Bay of Bou Ismail and one from the Pisan Riviera on the western coastline of Italy (6.31 associated with TR = 72 and 360 individuals per m^2) (Appendix A). Although the TR ranges up to 140, the values are in part a function of the sampling effort which varies strongly from one set of data to another (Table 1). But high values have been registered for a weak sampling surface such as in the Bay of Bou Ismail (Algeria) with 138 taxa for 0.2 m^2 while for 1 m^2 the RT is 140 on the fine sand community at Pierre Noire station along the French coast of the English Channel. The Pielou evenness index J' varies from a minimum value of 0.59 to a maximum of 0.99. Finally, the numbers of individuals per station varies strongly from 77 at a station in the Bay of Bou Ismail to 13190 at a station along the Pisan Riviera.

There is a significant positive correlation between H' values and TR (Fig. 2). H' tends to increase with the number of taxa. Conversely, J' decreases with increasing number of taxa, i.e.: the number of individuals per taxa tends to be dissimilar when the number of taxa increases

(Fig. 2). While no correlation exists between the number of individuals and H' , there is a strong significant negative decrease of J' with decreasing numbers of individuals (Fig. 2); again, J' tends to be higher when the number of individuals decreases. The numbers of individuals tend to show a significantly positive increase when the number of taxa increases (Fig. 2). Finally, there is a weak but significant positive correlation between H' and J' ; high values of H' correspond to high values of J' (Fig. 2).

3.2. Low resistance and high resilience after an oil spill

3.2.1. The Bay of Morlaix

Although benthic communities from two stations in the Bay of Morlaix (North Brittany coast, France) were strongly affected by the oil spill of the “Amoco Cadiz” in 1978, they show quite different responses to the hydrocarbon pollution (Dauvin, 1998, 2000). For the series of observations at these two stations over a period of 20 years (from 5 to 12 sampling dates per year), only data from August were selected for the present study.

In 1977, the amphipod *Ampelisca* populations dominated on a fine sand community at the Pierre Noire station (PN), but disappeared during the spring of 1978 due to their sensitivity to the toxicity produced by hydrocarbon pollution. This chemical perturbation is correlated with a sudden increase of the Shannon diversity H' from 2.31 in August 1977 to 3.84 in August 1978. This measure of diversity remained high (> 4.0) until August 1989, except during the summers of 1982 and 1984 when

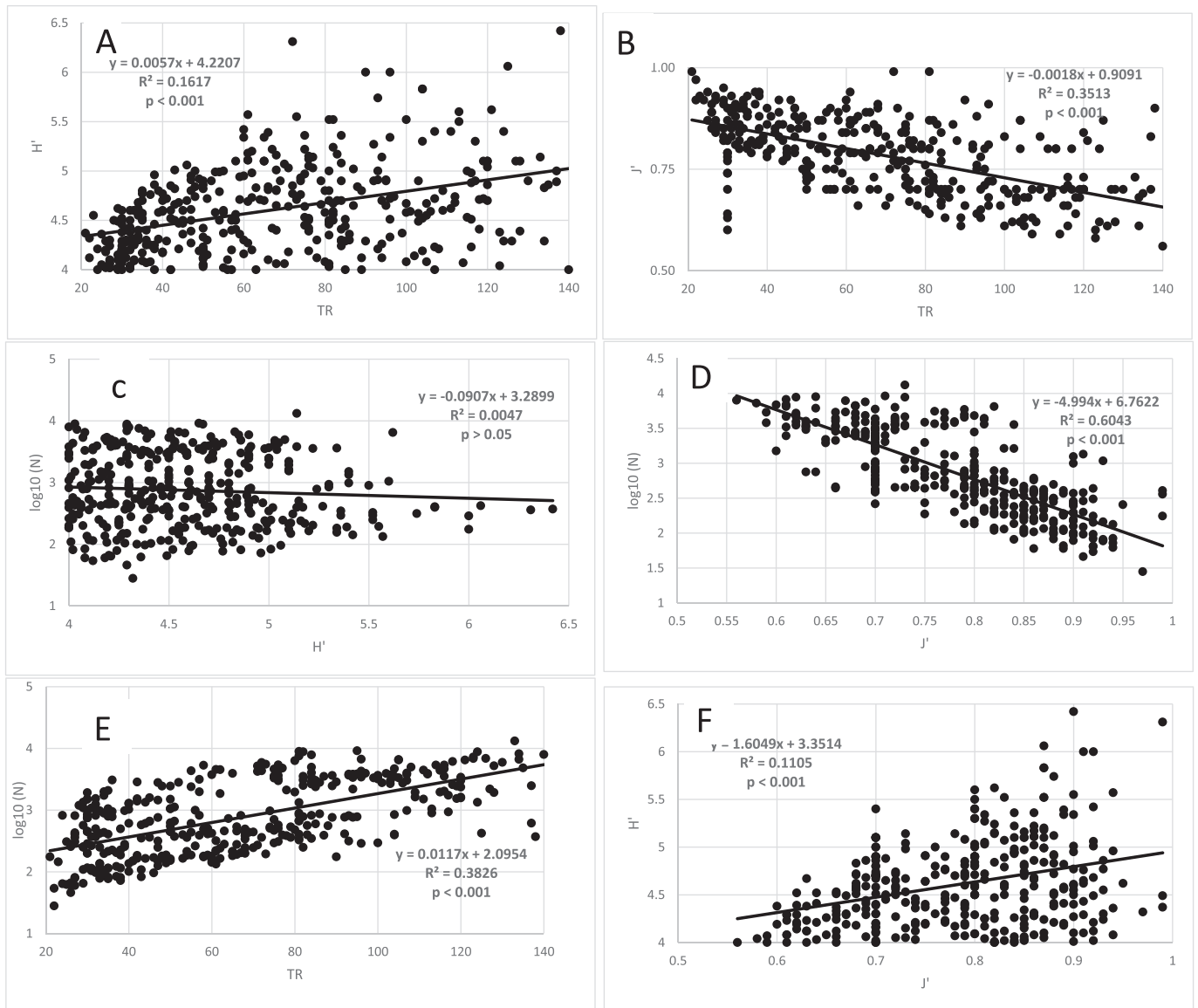


Fig. 2. Linear correlations between univariate indices estimated with Spearman's coefficient associated with p for all the values reported in Appendix A. The numbers of individuals are transformed in $\log_{10} N$. A) Shannon diversity H' versus Taxonomic Richness (TR); B) Pielou Evenness J' versus Taxonomic Richness (TR); C) Shannon diversity H' versus $\log_{10}(N)$; D) Pielou Evenness J' versus $\log_{10}(N)$; E) $\log_{10}(N)$ versus Taxonomic Richness (TR) and F) Shannon diversity H' versus Pielou Evenness J' .

there was a proliferation of the polychaete *Pseudopolydora pulchra* (Carazzi, 1983) (Fig. 3). During the recolonization of the benthic community by *Ampelisca* spp. and the increase in population density (abundance per m^2), H' showed values of around 3.0. By 1995, H' had returned to values similar to those observed in 1977 before the spill. This long-term survey illustrates the change from low H' to high H' in a diverse benthic community dominated by a group of organisms sensitive to hydrocarbon pollution. Ten years after the perturbation, there was a return to low H' and high abundances mainly due to the recovery of high abundances among the *Ampelisca* populations (Fig. 3). Apart from the evolution of the abundances and the Shannon diversity, TR showed an increase (with values often >130 per $1 m^2$ sampling) during the period of low abundance of *Ampelisca* spp. from 1980 to 1991. This was probably due to the available ecological niche liberated by the disappearance of dominant *Ampelisca* spp., which built up at the sediment surface and occupied large areas. Then, TR decreased towards the end of the survey in 1995 and 1996 and recovered levels similar to those observed in 1977 (Fig. 3). J' increased just after the oil spill and

decreased abruptly during the proliferation of *Pseudopolydora pulchra* in August 1982. Subsequently, the values obtained for J' fluctuated mainly between 0.4 and 0.6 throughout the rest of the observation series without showing any periodicity.

On a muddy-fine sand community at the Rivière de Morlaix station (RM) dominated by polychaetes such as *Chaetozone* spp. and *Melinna palmata* Grube, 1870, no notable changes of the structural indices were observed after the hydrocarbon pollution from the Amoco Cadiz (Fig. 3). Pollution-sensitive amphipods showed low abundances in this community dominated by opportunistic polychaeta living in an area naturally enriched in Organic Matter. H' remained low (< 4.0) throughout the study except in August 1992 when it reached 4.12. Most of the other values of H' were comprised between 2.0 and 3.34, while the two first values of the series in 1977 and 1978 were < 2 . TR remained always lower than values obtained at the neighbouring PN station, reaching a maximum of 81 ($1 m^2$ sampling) with values mainly ≤ 60 (Fig. 3). The abundances varied from 2100 to 6600 ind. m^2 , except in 1982 (proliferation of the polychaete *Pseudopolydora pulchra* as at PN) when the

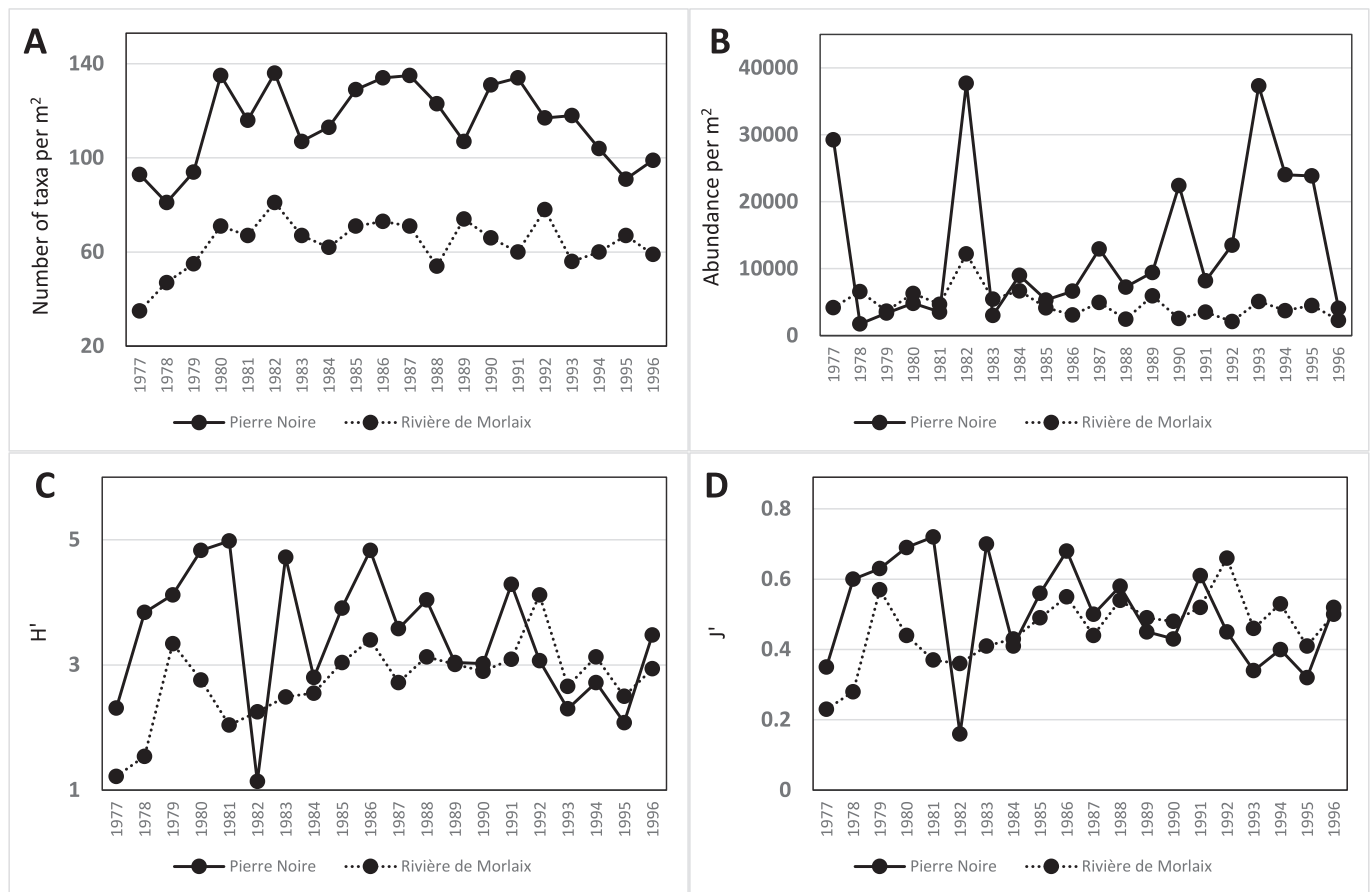


Fig. 3. Pierre Noire and Rivière de Morlaix stations in the Bay of Morlaix; A) Temporal changes in Taxonomic Richness, B) Temporal changes in abundances and C) Temporal changes in Shannon diversity H' , and D) Temporal changes in Pielou evenness J' . The Amoco Cadiz spill had affected the benthic community in March–April 1978.

values reached 12,223 ind. m^2 without any clear pattern. Finally, J' was low (0.2–0.25) at the beginning of the series and tended to increase through time to exceed 0.6 in August 1992 (Fig. 3). Moreover, along the time, the number of taxa of non-sensitive polychaetes species to the hydrocarbons at the station Rivière de Morlaix had increased, but in the same time the dominance of *Chaetozone* spp. had decreased between 1977 and 1980, and remained relatively stable after. On this station, the values of Number of taxa, H' and J' do not return to the pre-spill levels observed in 1977.

3.2.2. The Galician rias

Two sites (X and Z) in the sublittoral fine-sand macrobenthic community located in the central part of the Ares-Betanzos Ria were sampled over four years (December 1992–November 1996) after the oil spill from the wreck of the “Aegean Sea” on 3 December 1992 on the North Galician coast (Gomez Gesteira and Dauvin, 2005). Station X was more affected by the spill (low resistance to pollution) than station Z. TR increased from values <40 at both stations during the first year after the spill, then increased to >60 at the end of the survey in 1995–1996 (Fig. 4). H' showed a decrease at station X one year after the disturbance during the winter of 1993–1994, then increased to values near those observed at the beginning of the survey in 1993. At station Z, H' stayed at values >4.0 except in some dates between April 1993 and June 1994, and tended to increase regularly from August 1994 to the end of the survey in June 1996. At both stations, the abundances per m^2 were low during the first year after the spill, showing a seasonal pattern with maximum levels during the summer mainly at Z (Fig. 4) and a steep increase at X two years after the spill. In summary, the three indices exhibit an increase with time after the spill disturbance, illustrating the

resilience of these benthic soft-bottom communities after the disappearance of all trace of hydrocarbon pollution in the sediment.

3.3. Industrial contaminants in the Gulf of Gabès

The Gulf of Gabès, on the south-eastern coast of Tunisia, is affected by a number of industrial, urban and fishery activities which severely impact the benthic communities (Boudaya et al., 2019; Mosbahi et al., 2019).

The Bay of Skhira is subject to intensive anthropogenic pressures: soft bottom trawling, chemical pollution from phosphoric acid production, and shipping activity (Boudaya et al., 2019). In April 2010, 28 stations were sampled along four transects, including 21 stations on three transects (North, Centre, and South), each of which comprised 7 stations selected along an inshore-offshore gradient (3 to 12 km) extending from the phosphogypsum outfall (Fig. 5). The four structural indices (Shannon H' diversity, Pielou Evenness J' , TR and total abundances per $0.2 m^2$) show similar patterns: an increase with distance from the outfall, with H' increasing from 2.6 to 2.8 near the outfall to 3.9–4.3 at a distance of 12 km. J' increases from 0.64 to 0.67 near the outfall to >0.90 at 12 km offshore, while TR increases from <10 near the outfall to >30 offshore and the abundances increase from <1000 individuals per $0.2 m^2$ near the outfall to >5000 individuals per $0.2 m^2$ offshore (Fig. 5).

In the same sector of the Tunisian coast, near the Sfax industrial-harbour complex, Mosbahi et al. (2019) sampled 12 stations along four transects at distances from 600 m to 3900 m offshore from the harbour in 2015–2016 (April, July, October 2015 and January 2016) on $0.2 m^2$ surface. Again, there is a coastal-offshore gradient with an increase in the four structural indices; H' values increase from 1.86 to 2.13

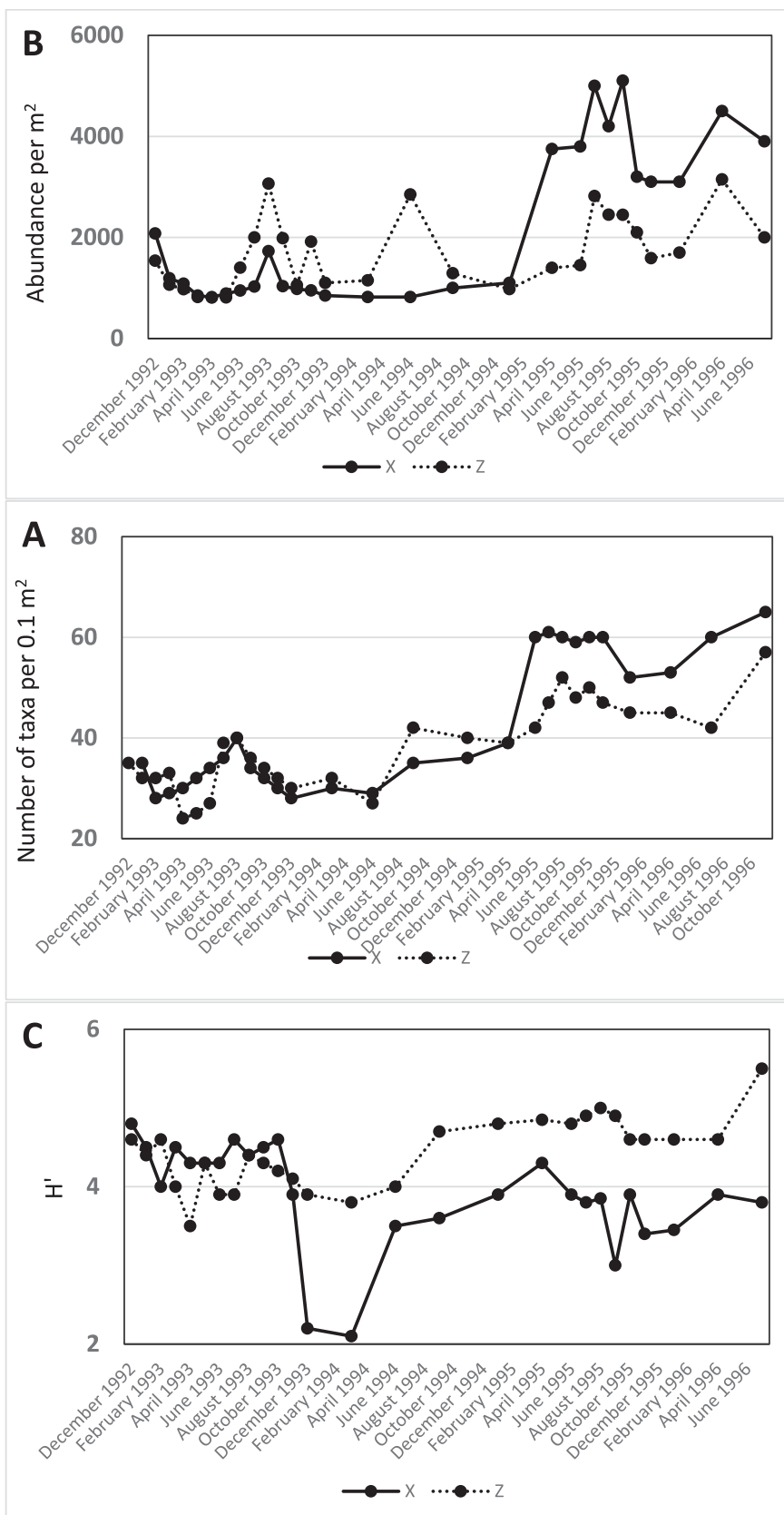


Fig. 4. Stations X and Z in the Galician rias. A) Temporal changes in Taxonomic Richness, B) Temporal changes in abundances and C) temporal changes in Shannon diversity H'.

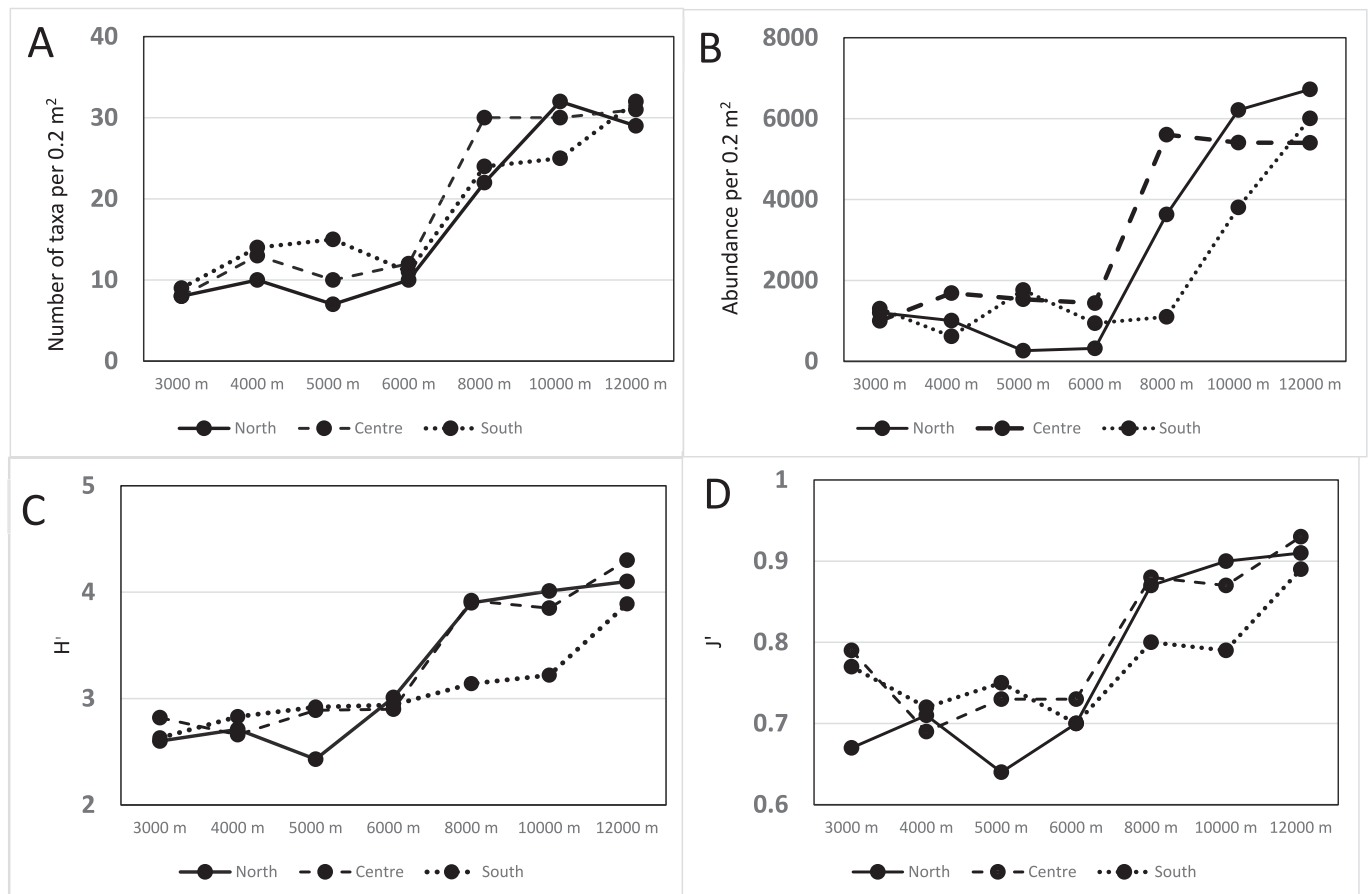


Fig. 5. Bay of Skhira in the Gulf of Gabès. Spatial gradient over a distance of 3000 to 12,000 m from the phosphogypsum outfall, covered by three transects in the North, Centre and South of the Bay. A) Taxonomic Richness, B) Abundances and C) Shannon diversity H' , and D) Pielou evenness J' .

near the outfall to 3.85–4.02 at 3900 m from the outfall. J' shows an increase from 0.41 to 0.45 to 0.85–0.91, TR from 7 to 19 to 26–29 and abundances range from 467 to 525 to 1223–1656 individuals per 0.2 m² (Fig. 6).

In summary, both studies illustrate that the benthic communities were impacted by the proximity of the source of disturbance and recovered high values of structural indices seaward of the pollution source.

3.4. Cessation of fishing activity during the COVID-19 pandemic lockdown

Mosbahi et al. (2022) have described for the first time the effects of bottom trawling on the macrobenthic fauna in tidal channels of the Kneiss Islands in the Gulf of Gabès, in comparison with a period when fishing activity was halted during the COVID-19 Pandemic lockdown in 2020. Following a BACI protocol, two control stations (protected by artificial reefs) and two trawled stations (impacted stations) were sampled during a period without bottom trawling activity from March to May 2020 and also during a trawled period. Five sampling campaigns were carried out: one during March before the lockdown period (T0), another at the end the lockdown period (total cessation of trawler fishing activity controlled by the coast guard and the Tunisian navy) (T1), and three after the lockdown period: T2 (two days after), T3 (two weeks after) and T4 (one month after).

The four univariate indices are lower for both impacted stations in comparison with the two non-Impacted stations (Fig. 7). Moreover, for the impacted stations, the indices increased rapidly during the lockdown (T1), and decreased rapidly just after the beginning of the trawling

activity (T2), returning to similar values at T4 than before the cessation of trawling (T0). At the non-Impacted stations, H' showed small changes, with values included between 3 and 4 (maximum 3.7) (Fig. 7). At the impacted stations, H' exceeds 3 only during the lockdown period (Fig. 7).

These results illustrate the negative effect of trawling activity in shallow waters and the high resilience of macrobenthic communities of the tidal ecosystem of the Kneiss Islands.

3.5. Harbour sediment dumping: the case of the Bay of Seine

3.5.1. Dumping experimentation on MACHU site

A BACI approach was adopted to assess the bio-sedimentary changes on two experimental MACHU dumping sites (MASED and MABIO) on the Bank of Seine by depths of 12–20 m in the eastern part of the Bay of Seine on a fine-to-medium sands (Marmin, 2013; Pezy et al., 2017, 2020). Sampling was carried out 14 times from 2010 to 2015 (Fig. 8): twice before dumping in April 2010 and November 2011, seven times during the overall dumping period (i.e., May, June, July, October and November 2012, and January and March 2013) and five times after dumping operations (May, August and November 2013, March 2014 and March 2015). Using this database to assess the impact of dumping about 1 million cubic meters at both sites (Fig. 8, Dauvin et al. (2018) proposed a Dredge Spoil Disposal (DSD) index based on the response of selected species to spoil disposal and a ratio between the abundance of each of these species at impacted and unimpacted stations. The DSD index varies from 10, when no selected species are observed at the impacted stations, to 0 when no selected species are observed at the unimpacted station. In October 2012, just after the end of a massive dumping operation (Fig. 8), the DSD index varied between 4 and 10. For

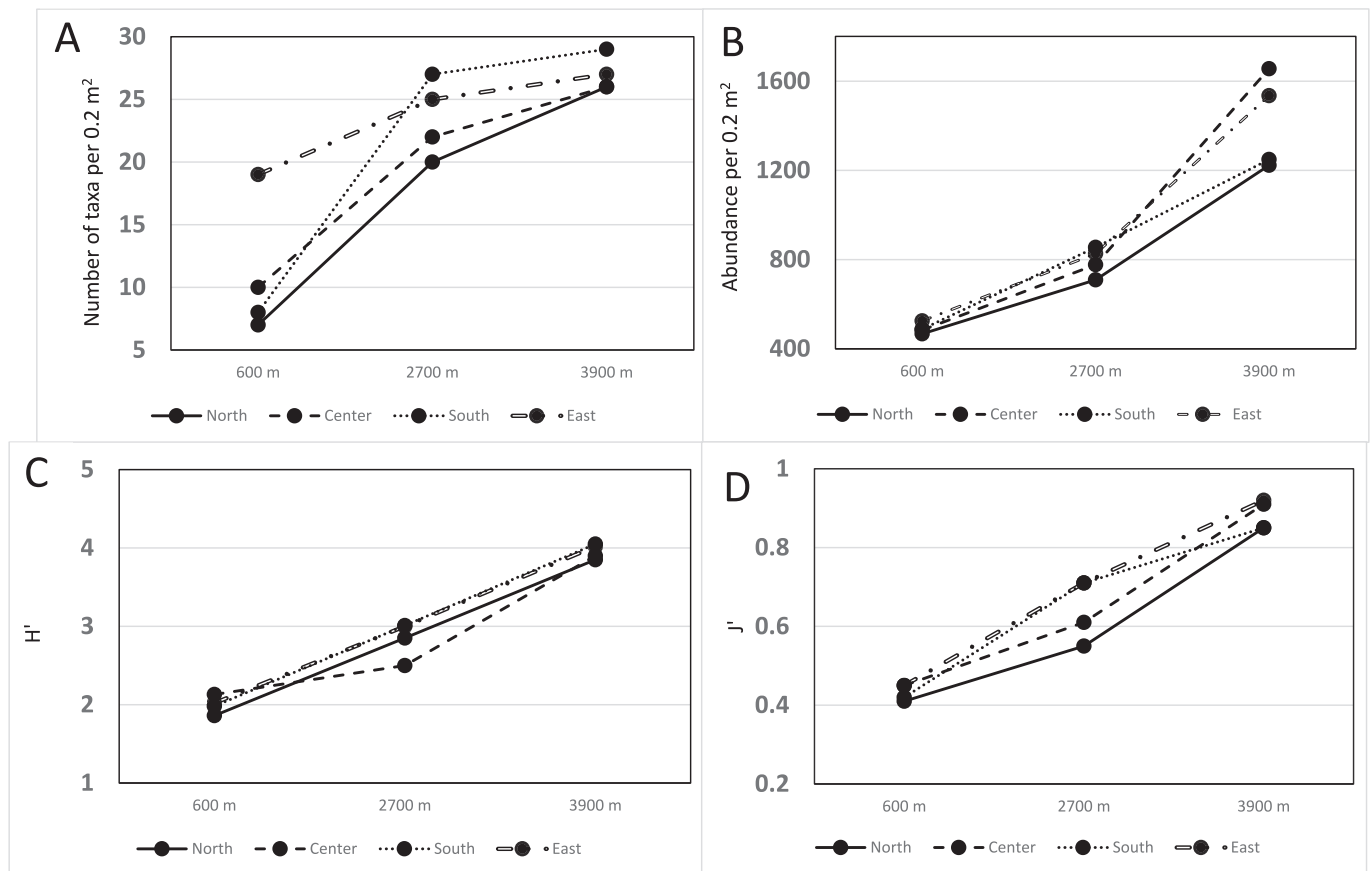


Fig. 6. Offshore Sfax harbour in the Gulf of Gabès. Spatial gradient over a distance of 600 to 3900 m from the urban outfall, covered by four transects in the North, Centre, East and South of the zone. A) Taxonomic Richness, B) Abundances, C) Shannon diversity H' , and D) Pielou evenness J' .

both the MASED and MABIO sites, the values increased just after the beginning of the dumping, remained high (impacted conditions) throughout the operation, then decreased rapidly just after the cessation of spoil disposal; similar values were obtained at the end of the observations in March 2015 compared with values measured at the two dates before dumping (Fig. 8).

These results show that, after the cessation of a perturbation (dredge spoil disposal) on a benthic habitat, the ecosystem recovered rapidly to the state observed before the disturbance, thus illustrating the high resilience of the eastern part of the bay of Seine (Dauvin et al., 2018, 2021a).

3.5.2. Spoil dumping experimentation at the Octeville site

Sediments dredged from Le Havre Harbour have been deposited on the Octeville disposal site since 1947 (Dauvin et al., 2022a). During an experimental period from August 2016 to September 2017, a study was set up to identify the spatio-temporal changes of the macrobenthos collected at ten stations and on six dates (T0: 17 August 2016, T1: 11 October 2016, T2: 19 December 2016, T3: 3 April 2017, T4: 19 June 2017 and T5: 18 September 2017): three impacted stations with different volumes of dumped sediments, two influenced stations located within the Octeville site and five stations outside the disposal site (north and south zones) (Dauvin et al., 2022a). Only variations in H' are reported here (Fig. 9). All the values are comprised between 2.7 and 4.46. The highest values correspond to the non-impacted stations, while the impacted stations show the lowest values, especially station HK at T3. The influenced stations show intermediate values, except at T4, when H' attained the highest value at station IL (Fig. 9).

A gradient of disturbance can be identified from the variations in H' , with mainly the lowest values at the impacted station and highest values

at the non-impacted stations.

3.6. Aggregate extraction

Chauvel et al. (2024) have assessed the ecological effects of low-intensity marine aggregate extraction based on two winter sampling campaigns in 2018 and 2023 in a coarse sediment high-energy hydrodynamic environment in the central part of the eastern basin of the English Channel (Lozach and Dauvin, 2012). In this area, values of Shannon H' reached 5.3 at a station sampled in 2018. In their comparison with unimpacted stations (references), they included secondary impact stations affected by an input of fine particles due to resuspension during granulate extraction and directly impacted stations corresponding to furrows created during the extraction. The impacted stations showed significantly lower values of H' in 2018 and 2023 compared to the unimpacted and secondary impact stations; similar patterns were observed for the Pielou J' index, abundance and TR. Thus, it is clear that aggregate extraction impacted the gravel-coarse sand community, mainly due to the absence of the large bivalve *Glycymeris* and the polychaete *Glycera lapidum*. There was also a negative impact on H' at impacted stations due to the colonization of polychaete opportunist species such as *Sabellaria spinulosa* and *Pista cristata*, as well as the decapod *Pilumnus hirtellus*, by r-selected species such as the polychaetes *Jasmineira elegans*, *Sabellaria spinulosa* and *Bispira fabricii* (all filter feeders).

3.7. Impact of salmon aquaculture in the Rade de Cherbourg

The Rade de Cherbourg in the north of the Cotentin peninsula hosts the only sea salmon farm on the French coast of the English Channel.

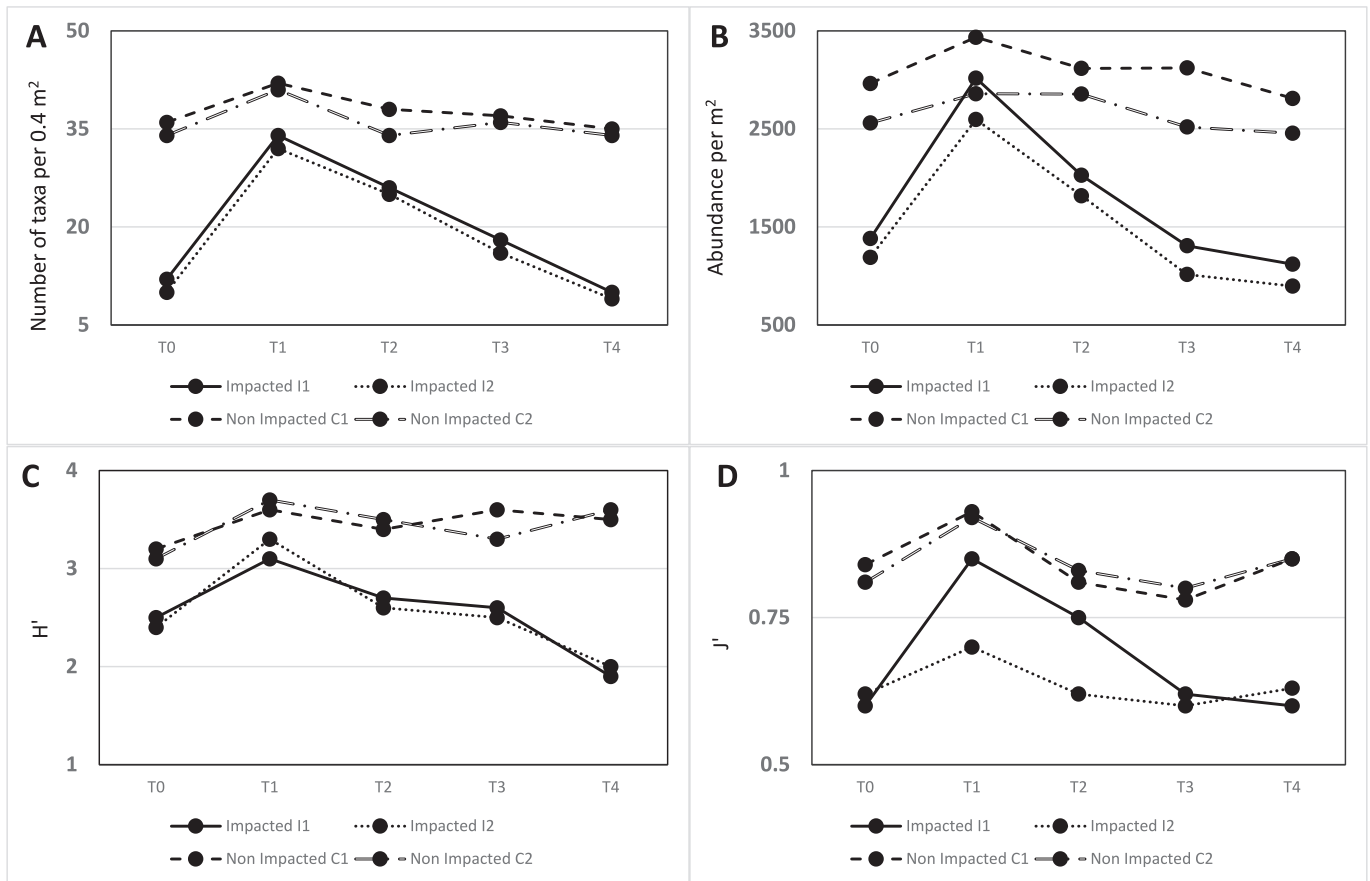


Fig. 7. Kneiss channel in the Gulf of Gabés. Temporal changes of the indices before, during and after the cessation of fishing activity during the COVID-19 Pandemic lockdown. A) Taxonomic Richness, B) Abundances, C) Shannon diversity H' , and D) Pielou evenness J' .

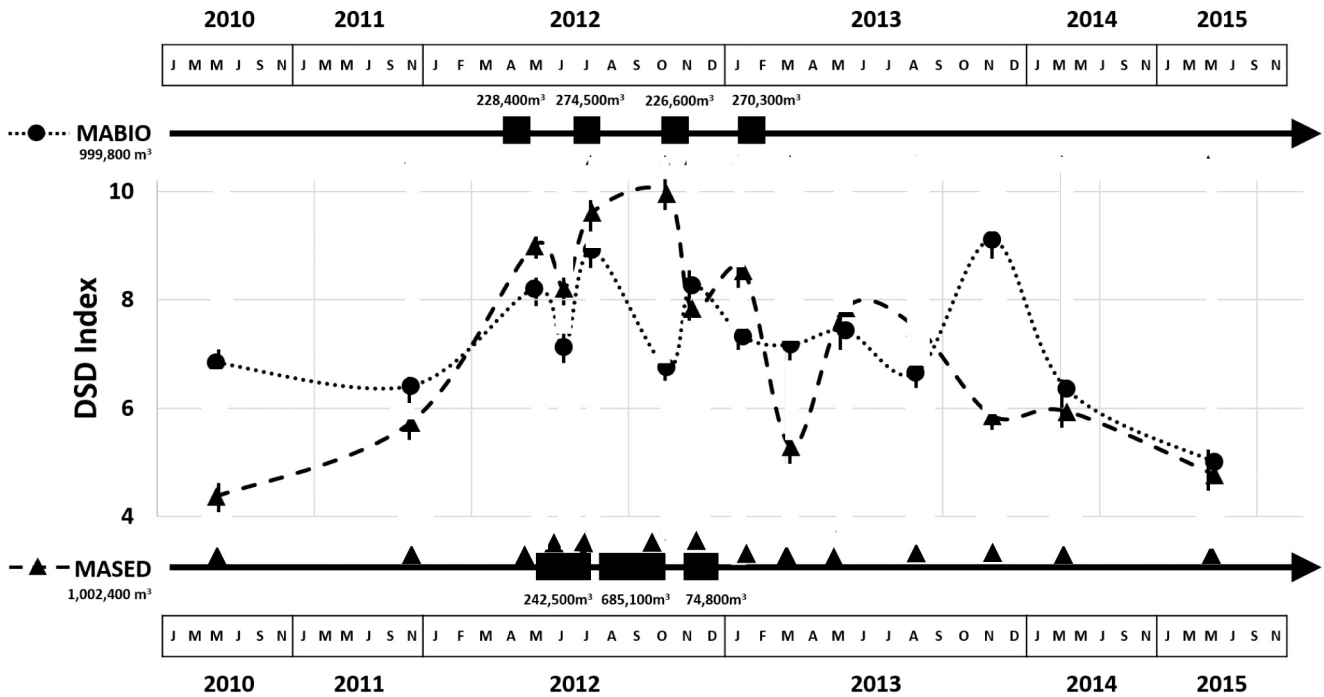


Fig. 8. Schedule of dumping operations at two experimental sites (MABIO and MASED) in the MACHU dredge spoil disposal zone in the eastern part of the Bay of Seine, with the corresponding accumulated dumped volumes at each site and dates of macrofauna sampling, values of the DSD Index and date of sampling from 2010 to 2015 (From Dauvin et al., 2018).

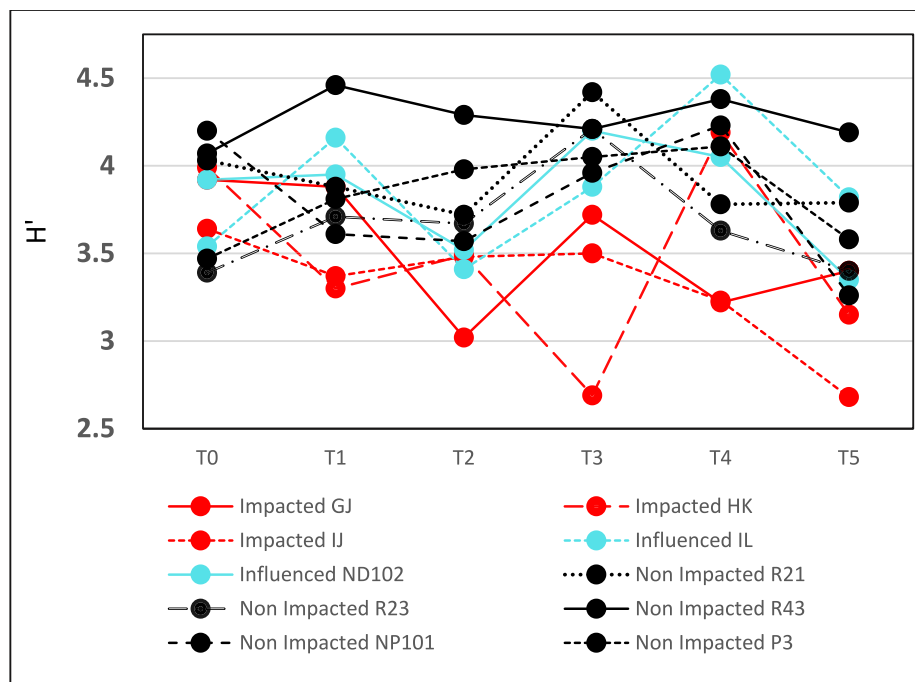


Fig. 9. Spatio-temporal changes of the Shannon diversity H' at ten stations (impacted, influenced and non-impacted) around the dredge spoil deposit site Octeville in the eastern part of the Bay of Seine and on six dates (T0: 17 August 2016, T1: 11 October 2016, T2: 19 December 2016, T3: 3 April 2017, T4: 19 June 2017 and T5: 18 September 2017) (From Dauvin et al., 2022a).

With a view to assessing the effect of this human activity on the macrobenthic communities, a sampling strategy was developed during an annual cycle in 2013–2014 (Dauvin et al., 2020). Following an East-West axis parallel to the north breakwater where the salmon cages were located, six benthic stations were sampled during five campaigns (T1: 31 October 2013, T2: 19 February 2014, T3: 8 April 2014, T4: 13 June 2014 and T5: 18 September 2014). One impacted station (CC8) was

located under a cage, two non-impacted stations (OR and ER) outside the fish farm (> 600 m from the central cages), and the three other influenced stations (OC8, EC8 and EC16) near the central cages (OC8: 50 m to the west; EC8: 50 m to the east; EC16: 500 m to the east). Apart from the results obtained for abundances and TR, the non-impacted stations yield very different values for H' and J' , mainly at the beginning of the study with the highest and the lowest values of H' (Fig. 10).

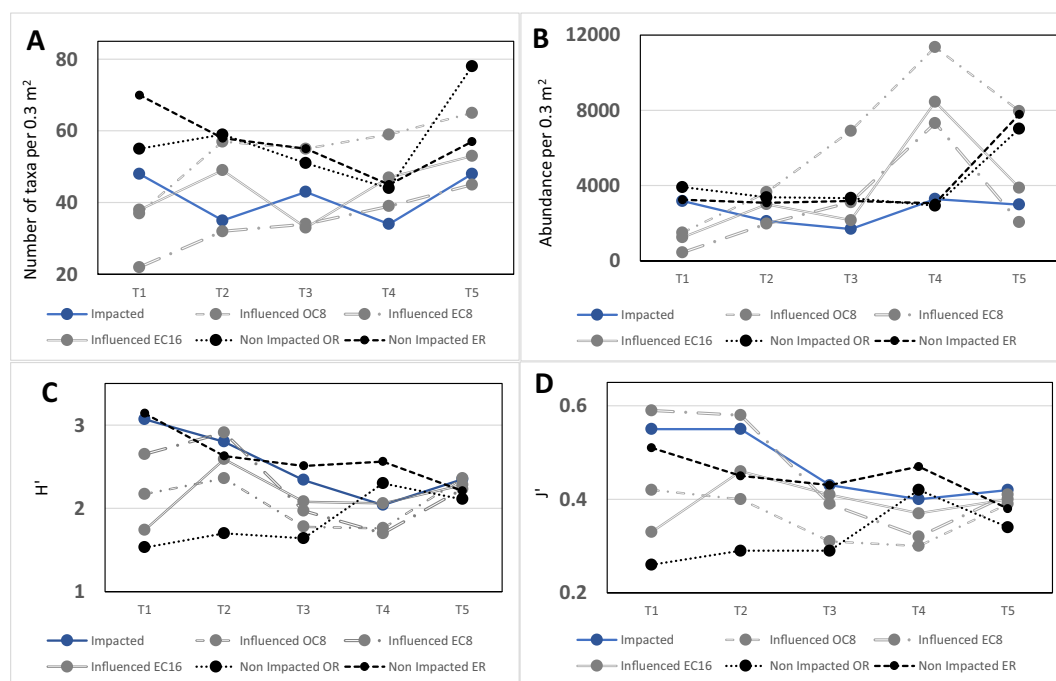


Fig. 10. Spatio-temporal changes of univariate indices at six stations (impacted, influenced and non-impacted) around the salmon cage in the Rade de Cherbourg and on five dates: T1: 31 October 2013, T2: 19 February 2014, T3: 8 April 2014, T4: 13 June 2014 and T5: 18 September 2014. A) Taxonomic Richness, B) Abundances and C) Shannon diversity H' , and D) Pielou evenness J' .

The impacted station shows similar patterns to the non-impacted ER station, except for TR which shows values always lower than the non-impacted stations. The three influenced stations show values intermediate between the impacted and non-impacted stations, except for the abundances where the highest values are observed at T3 and T4 (Fig. 10). Apart from the distance from the cages, the indices show temporal variations with a large range at T1 and a low range at T5 mainly for H' and J' (Fig. 10).

Furthermore, Dauvin et al. (2020) have demonstrated that sediment type, fine particles, Total Organic Carbon content, macrobenthos abundances and biotic indices all show that the impact of the fish farm has remained relatively low and local in this megatidal regime. This has prevented the accumulation of Organic Matter (OM) under the cages, while the resulting dispersion around the cages ensured a general enrichment of the northern part of the Rade de Cherbourg. This particularity means that it is difficult to use the responses of univariate indices to assess the real impact of salmon aquaculture in this high-energy hydrodynamic area.

4. General discussion

4.1. Diversity versus abundance

High values of Shannon diversity H' were obtained for most of the soft-bottom communities sampled from sandy mud to gravel and pebble substrates (Appendix A). Nevertheless, the highest values (H' > 5.0) were observed on coarse sand and gravel in the English Channel and on fine sand of the Mediterranean Sea mainly in the Algerian bays. High values of H' are common at non-impacted stations, but rare at impacted stations where opportunist species - mainly polychaetes - are currently observed in relation to an important amount of Organic Matter in the sediment. An exception is observed at the Pierre Noire station in the Bay of Morlaix (North Brittany, France) when H' increased suddenly after pollution of the sediment by the Amoco Cadiz oil spill in March 1978. As before the spill, the community was dominated by dominant sensitive amphipod populations (low H'). Their disappearance just after the pollution caused an increase of H', which ten years later at the end of the 1980' returned to values similar to those observed before the pollution.

High H' values in excess of 6.0 are very uncommon; out of the 379 data points (Appendix A), only 4 values reach this threshold and 10 values are higher than 5.5. According to the threshold of Frontier (1985), i.e., 4.5, >50% of the values reach this value, which indicates a highly diversified benthic community. The significant positive correlation between H' and TR (Fig. 2A) suggests that H' is not entirely independent of the species richness of a sample, which is itself in part linked to the sampling effort (i.e., the sampled surface). Nevertheless, TR values >120 were obtained with different sampling areas: 0.2 m² for the Bay of Bou Ismail or 1 m² for the Pierre Noire station in the Bay of Morlaix.

Conversely, J' decreases with increasing TR (Fig. 6B) and reaches 1.0 on some stations with low numbers of taxa (TR of about 20), but also for TR comprised between 70 and 80. Similar relative abundances of the different taxa in the same sample is more likely when associated with low TR and low abundances than with high TR and low abundances. Again, the significant negative correlation between J' and TR (Fig. 2B) suggests that the J' values are not entirely independent of TR in a sample, which is linked to the sampling effort.

There is no correlation between H' and abundance (Fig. 2C), while J' decreases significantly with the abundance (Fig. 2D); conversely, abundance is significantly and positively correlated with TR (Fig. 2E). Finally, there is a positive correlation between H' and J', the highest values of H' being associated with high values of J' (Fig. 2F).

High Diversity is commonly associated with Low abundances (HDLA) in shallow coastal or deeper soft-bottom communities where rare species (represented by one or two individuals in a sample) make up a high number of taxa (Ellingsen, 2001; Rumohr et al., 2001; Gray,

2002; Gray et al., 2005; Moritz et al., 2009). Gray et al. (2005) have proposed the following hypothesis: recruitment of rare species from outside their preferred sediment is probable because most marine invertebrates exhibit large populations on a wide geographical scale and are thought to be relatively more efficient at colonizing a wide range of benthic habitats by pelagic larval dispersion. In the same vein, Moritz et al. (2009) suggested that, under oligotrophic conditions in Mediterranean ecosystems characterized by low densities and biomasses, high TR is due to the presence of a mosaic of local habitats compared with other oceanic ecosystems.

HDLA assemblages are observed in the Bay of Bou Ismail (Algeria): 841 taxa (307 taxa were recorded only at one station and 126 taxa at two stations, i.e., > 51% of rare taxa) and 17,120 individuals were identified from a sampling area of <20 m² (98 sites × 0.2 m²) (Bakalem et al., 2020). TR per 0.2 m² varies from 8 to 138 taxa. >50% of the samples show TR > 50. Comparable characteristics (HDLA) have been observed during the three decades 1980–2009 in the shallow soft- mainly fine sand bottom communities along the Algerian coast (1180 km shoreline and 0–136 m depth) (Dauvin et al., 2013). During this period, 1642 macrobenthic taxa were recorded while the abundances remained moderate (<1000 ind. m²).

High Diversity (TR and H') is also associated with high abundances in a few cases of High Abundance at the Pierre Noire station (5370 ind. m², TR: 116 and H': 4.51 in July 1980) or along the Italian coast at the Pisa station (13190 ind.m², TR: 133 and H': 5.14) (Appendix A). Moreover, high Shannon diversity H' > 4.0 is linked in 60 % of cases with a number of individuals lower than 1000.

To compare the TR of soft-bottom communities, the use of a cumulative species curve has often been proposed as a surrogate of univariate indices such as H' and J' (Ellingsen, 2001; Rumohr et al., 2001; Gray, 2002; Ugland et al., 2003). Large databases demonstrate that high species diversity can be linked with many rare species and that it is difficult or even impossible to estimate the number of taxa in a rich community (Gentil and Dauvin, 1988). The increase of the sampling surface increases the possibility of collecting new taxa that have not been sampled before. This is related to the link between sampling effort and the increase in TR, but also H', while J' shows a decrease. Nevertheless, using the criterion H' > 4.0 selected in this study (High Quality Status according to the threshold of the Water Framework Directive), the link with sampling effort does not change the Quality Status.

4.2. Resistance and resilience of soft-bottom communities

The available temporal and spatial data for the examples presented here from shallow soft-bottom communities of the Atlantic coast and western Mediterranean Sea allow us to identify cases of low resistance and high resilience of these marine ecosystems. The low resistance of the Pierre Noire station in the Bay of Morlaix to hydrocarbon perturbation is correlated with the dominance of sensitive amphipod populations before the spill. This situation is uncommon in soft-bottom communities that are often dominated by polychaetes or bivalves less affected by hydrocarbons (Dauvin, 1998, 2000). Moreover, the *Ampelisca* populations show a high resilience, with the ability to reconstitute their populations in a decade in spite of the absence of a pelagic larval phase. To a lesser degree, after the "Aegean Sea" oil spill in North Galicia, one of the two studied stations (X) was more affected (low resistance) by the spill than station Z. This was probably due to the presence of sensitive amphipods including *Ampelisca* spp. before the spill, while polychaetes dominated at station Z (Gomez Gesteira and Dauvin, 2005).

The high resilience of such marine ecosystems is due to several factors:

- benthic communities in shallow coastal habitats are adapted to continuous natural stress (swell removing the surficial sediment, seasonal changes of temperature);
- a high Taxonomic Richness, linked to high Shannon Diversity H';

- an intrinsic ability to host a high number of species is favourable for the recovery of a high diversity after a disturbance; for example, the number of taxa remained high in spite of the pollution, i.e. 80 species per m² just after the Amoco Cadiz spill in August 1978 (Fig. 3);
- most of the dominant species in such soft-bottom communities have a benthic-pelagic life cycle and are able to produce numerous larvae which are widely dispersed by currents and which can thus rapidly colonize the benthic habitats after the cessation of a disturbance (Dauvin et al., 2021a).

The benthic fauna is more diverse than the pelagic fauna and show a strong capacity of resistance to human activities and a high resilience that allows a return to a condition close to that observed before the disturbance. This resilience appears to be an intrinsic property of benthic marine ecosystems. Hughes et al. (2005) have suggested that high species richness should confer greater resilience to marine ecosystems. In their review, Elliott et al. (2007) present concepts, understanding and experience of the restoration, recovery and human-mediated modification of estuarine coastal and marine ecosystems. Later, Bernhard and Leslie (2013) show that biological diversity from the genetic to the species to the seascape scale facilitates ecosystem functioning in a changing environment by increasing the range of biological responses and the possibilities that species can compensate for one another if some disappears. Such diverse communities possess an increased capacity for recovery following disturbance. Moreover, Duarte et al. (2015) have identified six paradigms of coastal and estuarine ecosystem recovery, i.e., 1) Recovery of marine ecosystems is idiosyncratic; 2) Ecosystem function is easier to recover than ecosystem structure; 3) Degradation is fully reversible; 4) Degradation and recovery follow similar, but opposite, trajectories; 5) Recovery depends on the characteristic of the pressures; and 6) Connectivity accelerates recovery. In a recent review, Dauvin (2024) reported that resilience is observed in all marine ecosystem types and at multiple locations worldwide. The factors most important for resilience include biogenic habitat, recruitment/connectivity, physical setting and management of local-scale stressors. In their review, Gissi et al. (2021) underline that climate change is a key, global driver of change of marine ecosystems, but at local and regional scales, human stressors interact with climatic change and modify its effects on marine ecosystems.

In many cases, soft-bottom macrobenthic communities respond in similar ways to diverse human pressures, showing an ecological recovery succession after a reduction or elimination of the stressor or with increasing distance from the perturbation source. The period of recovery can be long, a decade in the case of the Pierre Noire station, two years at the MACHU experimental site in the Bay of Seine, less than one month for the subtidal tidal channels in the Gulf of Gabès during the COVID-19 Lockdown (Mosbahi et al., 2022). Similarly, provided the impact of a given activity (sediment deposition, aquaculture cages, urban and industrial outfalls, granulate extraction) is local, it will not affect the entire surface of a benthic community, so at a certain distance (some kilometres) the impact will remain non-detectable.

As recovery is a long-term process such as in the case of benthic communities from oil spills, Hawkins et al. (2002) underlined that most of studies are often too short-lived to identify all the dynamic processes of a total recovery. Initiated, one year before the Amoco Cadiz spill, both stations of the Bay of Morlaix continue in 2025 to be sampled twice a year (near 50 years of long-term survey). Jones and Schmitz (2009) then Lotze et al. (2011) evoke evidence that most ecosystems globally recover from very major perturbations on timescales of decades to half-centuries.

Without denying the many negative effects of human activities on coastal ecosystems, particularly in semi-enclosed areas such as estuaries, ports, or bays with low-energy hydrodynamics, where accumulations of organic matter result in the proliferation of opportunistic species (and low diversity, TR and H'), it is important to emphasize that environmental damage can be reversed if the perturbation ceases. On the other

hand, estuarine, industrial-port or coastal developments, with the construction of dikes and land reclamation on the shallow seabed, are irreversible and must be limited, as in the Mediterranean (Meinesz et al., 1991). These shallow-water coastal environments are essential for the biological cycles of many species of fish which find indispensable conditions for their larval and juvenile stages. In a general point of view, Borja et al. (2016) promote to develop an Integrated Ecosystem Approach to evaluate the health status of marine ecosystems. This ecosystem approach incorporates knowledge of ecosystem function and services and can be used to track how management decisions change the health of marine ecosystems and their ability to recover after a disturbance. Recently, Solé Figueras et al. (2024) have reviewed the current scientific knowledge on how human drivers affect coastal marine ecosystem services. And find that understanding combined effects of different drivers and considering various time and space scales is still a pending issue.

In agreement with Gattuso and Duarte (2021) who have pointed out that the global ocean is surprisingly resilient, there are reasons to be optimistic about the future of shallow soft-bottom communities and their capacity of high resilience faced with the interaction between climate change and the continuous development of human activities in such continental shelf ecosystems (Korpinen and Andersen, 2016; Gissi et al., 2021; Simeoni et al., 2023).

CRedit authorship contribution statement

Jean-Claude Dauvin: Writing – review & editing, Writing – original draft, Methodology, Conceptualization.

Declaration of competing interest

No interest statement.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2025.117850>.

Data availability

Data will be made available on request.

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