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TRAIT-BASED INDICATORS DEVELOPMENT FOR ASSESSING THE IMPACT OF TRAWLING ACTIVITIES

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Chapter 1:

General Introduction

The escalating need to sustain global food security amidst rising population pressures necessitates innovative strategies to manage the Earth's natural resources sustainably. One critical area requiring urgent attention is the sustainable management of marine living resources, particularly fisheries, which are vital for food security and economic stability worldwide.

Marine fisheries provide a significant source of food in the global economy, and total fisheries production has expanded considerably over the past seven decades. This expansion has led to the depletion of fish stocks and adverse effects on habitats and non-target species. In the last two years, the world's fishery sector experienced a decline, primarily due to a decrease in capture fisheries, which fell by 4.5 percent in 2019 from the 2018 peak of 96 million tonnes, and then by a further 2.1 percent in 2020 [FAO, 2022]. This decline has catalyzed a shift toward methods that focus not only on managing target species but also on mitigating impacts on all ecosystem components to preserve their integrity and ensure sustainable extraction.

Trawling represents the fishing activity with the highest spatial distribution, characterized by significant aggregation along continental shelves worldwide [Amoroso et al. 2018], accounting for approximately 24% of global landings [FAO, 2017]. This non-selective capture method, operating primarily on the seafloor, has been considered one of the most destructive fishing methods for decades, with severe consequences for coastal system structures [Jones, 1992, Eigaard et al. 2017].

Bottom trawling involves dragging a cone-shaped net along the water column or seabed to catch slower-swimming species. The most commonly used gears for bottom trawling are beam trawls, otter trawls and dredges. Specifically, this PhD thesis refers to bottom otter trawling, which plays a significant role in the fishing sector of various European countries fishing in the Mediterranean [Sala et al. 2019].

The structure of a bottom otter trawl consists of a net bag designed in two wings ending in a narrow collector called a codend (Figure 1). The mesh size of the codend in most bottom trawl fisheries is regulated to achieve proper selectivity of the species fished. The net's entrance features a lower part, the footrope, loaded with weights to maintain contact with the seabed, and an upper part, the headrope, equipped with floats to maintain the cone shape during hauling. The net structure is held open by trawl doors linked through a series of cables called sweeps and bridles. These doors also maintain gear contact with the substrate and guide fish towards the net's entrance [He et al. 2021].

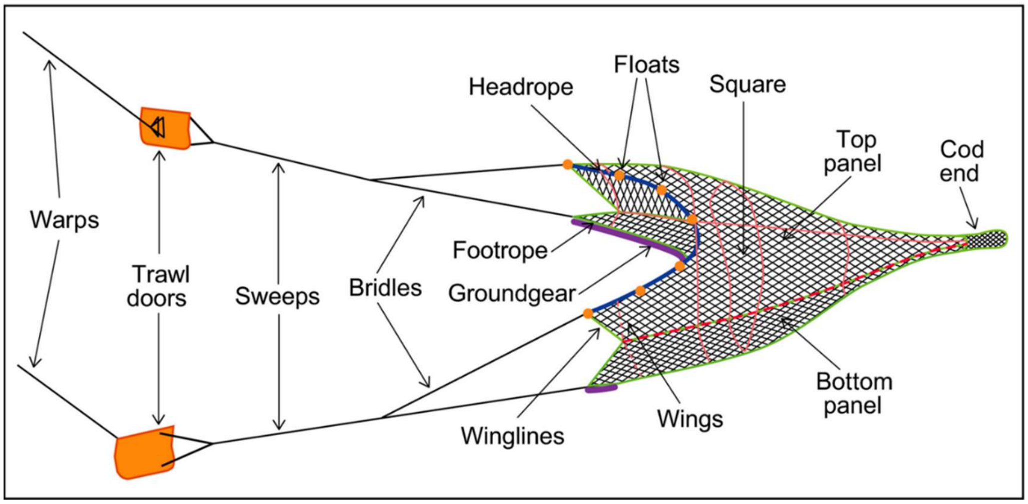

Figure 1 - Layout of a bottom otter trawl (from McConnaughey et al. 2020)

This fishing method notably impacts the sediment and the benthic organisms inhabiting it. These impacts involve geotechnical or hydrodynamic influences on the benthic environment [O'Neill and Ivanovi´c, 2016]. Geotechnical effects include contact drag, substrate penetration and piercing, lateral sediment displacement and pressure field transmission through the sediment. Hydrodynamic effects encompass hydrodynamic drag and sediment mobilization into the water column. Such effects primarily result from components of the gear that interact most with the seabed (ground components) such as otter doors, sweeps/bridles, ropes, ground gear, chains [Eigaard et al., 2016].

Trawl tracks create furrows that may persist over time, particularly in areas subjected to repeated – chronic – trawling, like the highly fished fishing grounds. A single otter trawl passage can penetrate up to 10 cm deep into the sediment, disturbing approximately 12 kg of sediment per meter of seabed trawled [Bradshaw et al. 2021]. This activity smoothens the seabed, reducing the heterogeneity essential for various species and simplifying community structures. Additionally, the turbulent flow from ground components can suspend about 9.5 kg of sediment per meter of trawl track [Bradshaw et al. 2021]. This resuspension may extend even to kilometers from the trawled point and it may stand even more than 20 hours after the trawling event [Depestele et al. 2016], releasing organic matter in the water column, inducing local hypoxia events [Breimann et al. 2022]. This may alter the microbial activity occurring in the sediments and the permanence of the organic matter that reside in the sediments, generating increasing water column turbidity and altering microbial activity in the sediments [Duplisea et al. 2001].

The effect that bottom trawling exerts on communities strongly depends on the environmental context that influences the community and the historical pattern of disturbance.

The presence of natural disturbances like substantial nutrient inputs and shear stress induced by waves and currents can select species with characteristics mainly belonging to organisms with an r-strategy: high rates of growth and reproduction, high fecundity, small body size, early maturity onset, short generation time and high ability to disperse offspring. Those characteristics make those species also highly resilient to fishing disturbance; therefore, such communities may mask the trawling effect as changes in trawling intensity in the long term may not be reflected in changes of community structure as the community remains in an alternative stable state [Van Denderen et al., 2015]. Sediment typology may also influence how towed gear exerts its impact. Finer sediments allow the bottom components to penetrate more deeply, leading to the depletion of a higher fraction of the biota associated with the seabed [Hiddink et al., 2017]. In contrast, coarser, rocky seabeds, although penetrated less by the gear, often host structuring species that enhance community biodiversity. Therefore, the removal of these species by trawl passage may more significantly hinder the state of the community.

Similarly, the presence of long fishing history patterns may lead to the presence of highly resilient communities that are hardly influenced by fishing gradients. Initial trawling impact is typically the most significant, resulting in average declines of approximately 15.5% in the biomass of benthic biota [Hiddink, 2006, Hiddink, 2017]. Even if successive towing activities are of lower intensity, they are sufficient to prevent the community from fully recovering from the impact status, reducing overall biomasses and promoting resilient species in the long term [Bremner et al., 2003, Kaiser et al., 2006]. Therefore, trawls cause a decline of large, sessile and low productive benthos, as these are most vulnerable to the direct passing of trawl gears and have slowest recovery rates. Short-lived, opportunistic benthos and scavengers/predators are less vulnerable or able to recover more rapidly, and such species usually dominate areas that are trawled frequently [Kaiser et al. 2006]. Furthermore, trawling selectively removes habitat-forming species, like corals and sponges, which play critical roles in creating and maintaining the structure of marine ecosystems. The loss of these species can lead to cascading effects on other marine life that rely on them for shelter and breeding grounds. Over time, the cumulative long-term selection could drastically alter community composition towards often leading to habitat biodiversity impoverishment [Bremner et al., 2003, de Juan et al., 2007, Mangano et al., 2013]. As a consequence, this process reduces the variation observed among trawled grounds, even in the presence of gradients [Neumann et al. 2016].

Effective management measures and regulation plans of trawling activities are crucial to mitigate its impacts on marine ecosystems. A large effort was made to focus the mitigation of the impact on commercially targeted stock with approaches that focused on controlling catching quotas and setting specific thresholds for the sustainable yield of singular species populations in regions of interest. Furthermore, seasonal closures, and restrictions on trawling in sensitive areas are essential to reduce the intensity and frequency of trawling impacts [McConnaughey et al. 2020]. Although effective for reducing the exploitation on specific resources, current policies push for the adoption of plans that involve the management of multiple species and the associated ecosystem components to reduce the side-effects of trawl fishing on the benthic and demersal ecosystem.

In Europe, the Marine Strategy Framework Directive (MSFD) mandates an ecosystem-based approach to fishery regulation, aiming to maintain seabed integrity by protecting certain benthic invertebrates and habitats. Achieving this requires a comprehensive understanding of the structural components of benthic communities, the impacts of trawling and the mechanisms regulating community responses and recovery [Rijnsdorp et al. 2016].

Ongoing monitoring of trawling areas and their ecological effects is essential for refining management strategies and ensuring their effectiveness in reducing environmental impacts. This effort increasingly requires methodological frameworks that use monitoring data to identify and describe impacts, estimate their spatial occurrence and extension, and evaluate vulnerability components. These frameworks benefit from the use of statistical models that relate the change in abundance of certain vulnerable components of the benthic systems with the effort distribution of trawling extracted from extensive satellite data. Furthermore, they constitute fertile ground for the development of impact indicators and the application of technologies such as acoustic and motion sensors embedded in fishing gear.

In recent years, benthic ecologists have delved into the use of biological trait approach to assess the impact of trawling activities on these communities [ICES 2017]. These approaches are founded on the theory that species expressing similar biological and life-history characteristics undergo similar selective pressures from environmental and anthropogenic gradients. Thus, such traits can serve as proxies for the main descriptors of an individual's fitness and performance: growth, reproduction, and survival [Violle et al., 2007]. This allows them to often be considered reliable indicators of habitat ecological integrity, as they can predict how ecosystem functions change under specific stresses by identifying the group of species that regulate or control particular processes, along with the traits they possess to withstand these stresses [Lavorel, 2013].

Thesis outline

The selection of traits to use in the development of indicators is a critical phase in the investigation and estimation of the impacts produced by trawling as it should be based on clear ecological hypotheses that link the trait to the disturbance and to the availability and quality of that information. Often it is guided by expert judgment or common knowledge from the literature, defining the direction in the response of different trait modalities and their scoring within the indicator model. It is therefore important to ensure a certain degree of objectivity in the inclusion of traits and the modalities they represent as well as the effects of trawling that are hypothesized to be associated with them.

For this purpose, the objective of this thesis was to examine whether the application of trait-based approaches is effective in estimating and describing the impacts generated by trawl fishing on benthic and demersal communities, particularly in areas where such activity is heavily stratified over time, a situation particularly common within the continental shelves in the Mediterranean Sea.

As a preliminary phase, in the introductory section 1.1, a literature review has been performed to assess which are the main traits associated with trawling disturbance, what are the direction of response commonly observed for such traits, and if trait selection and response could differ between different target species (benthic, demersal, or pelagic). Results of this activity allowed for the objective selection of which traits and modalities would be included in the analysis methodologies of the subsequent chapters.

The combination of taxonomic and trait analysis is potentially a useful approach to better understand the mechanism of interaction between anthropogenic and natural disturbance in shaping community structure, especially in chronically disturbed scenarios. To do this, in **chapter 2** the response of benthic and demersal communities has been examined in an intensely trawled ground using both taxon-based and functional indicators. The objective was to compare the two groups of indicators and see if functional responses could aid interpretation of the effect of trawling and to check the efficacy in such context of traditional trait-based multivariate techniques developed in the community ecology background [Legendre et al., 2014].

The effectiveness of impact assessment methodologies and frameworks necessitates validation to assess their generalization capacity, adaptability, consistency, and sensitivity in detecting changes in response to trawling pressures across diverse habitats and spatial scales. Therefore, case studies within regional-local contexts become crucial for testing and evaluating the performance of such approaches and their suitability in assessing adverse effects on seabed habitats. In **chapter 3**, the benthic impact assessment framework described in Rijnsdorp et al. [2020], known as Relative Benthic Status (RBS) has been applied to a local context in the Mediterranean Sea, specifically across the continental shelves area around Sicily (Italy, Central Mediterranean Sea). In **chapter 4**, the same approach was used to address a novel trait-based framework to assess the vulnerability of the benthic community to trawling. The aim was to develop a tool useful to meet the targets set by the MSFD and that follows the standard criteria submitted by expert working groups in the field of community analysis (ICES WGFBIT). A particular focus was set to provide feedback on the choices made during the development of the structure and to determine the main traits that contributed to the final scores. Results of chapter 3 were also fundamental to apply a recognized and published trait-based methodology that could have been compared to the results obtained from the novel indicator developed in chapter 4.

A final task of the project was to integrate the information obtained from the study of the interactions between the biological traits of marine communities and the fishing disturbance with an analysis in the application of motion tracking technologies in the field of marine species and human activities (i.e., bottom trawling). This activity was pursued in collaboration with the industrial company Turingsense EU Lab as part of the PON R&I 2014-2020, Axis I "Investments on Human Capital" - Action I.1 "Innovative PhDs with industrial characterization" fundings related to the project. Consequently, in **chapter 5**, we investigated how the inclination of trawl doors may affect the capture of demersal and benthic species in fine sediments of the continental shelf and how this can influence the interpretation of the impact based on the indicators applied in the previous chapters.

In **chapter 6**, an overview of the thesis findings is presented, pinpointing how the analysis of trait variation has supported the interpretation of the ecological effect of trawling on benthic communities, how developed methodologies can help to highlight impacts and quantify which components drive the vulnerability of the community other than provide support on which type of traits and indicators could be useful to assess the impacts in specific regional contexts and whether the dynamics of the gears could influence the catch composition of the benthic-demersal assemblage.

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Section 1.1:

Exploring Biological Traits selection associated to Trawling Disturbances: a literature review

In this section, we have examined published articles on biological and life-history traits pertinent to the impacts of trawling disturbances. We adopted a 'response-and-effect framework' to distinguish between traits that are sensitive to environmental gradients ('response traits') and those that influence ecosystem functions ('effect traits') [Lavorel & Garnier, 2002; Violle et al. 2007, Lavorel 2013]. This model facilitates an understanding of how disturbances may affect both population dynamics and ecosystem health as a whole [Díaz et al., 2013; Salguero-Gómez et al., 2018]. The composition of traits within a community influences its vulnerability to disturbances [McLean et al., 2019] as well as its capability to maintain ecosystem functions over time [Debouk et al. 2015].

The application of trait-based approaches to address the impact of trawling activities on marine communities is becoming standard practice [ICES 2017]. Nonetheless, the outcomes and insights derived from these analyses can be significantly affected by the selection and quantity of traits used in functional indices. Forming functional groups and applying trait-based methods to decode ecological dynamics prove beneficial only when the traits and groups selected are ecologically significant to the pertinent questions. Consequently, in applying the response-and-effect framework, it is essential to judiciously select which traits should be categorized as response or effect traits, ensuring there is robust mechanistic evidence connecting these traits with disturbances and ecological processes.

To support the decision on which traits to include in the trait-based approaches discussed in the thesis chapters, we have formulated several questions to investigate in the literature:

- Which are the main traits associated to trawling disturbance and why?
- Which of those traits could be classified as response traits and which as effect traits?
- Which trait represent resistance and which describe better resilience?
- Which traits show a clear pattern of response to trawling pressure?
- Does traits selection and response differ between different target species (e.g. benthic, demersal, pelagic)?

A comprehensive search of the literature was conducted using the Web of Science database.

We set a search string that has been run on the 6th of September 2023 using the following terms:

TS = (("beam trawl*" OR "bottom trawl*" OR "demersal otter trawl*" OR "otter trawl*" OR "trawl fisheries" OR "trawl*" OR "trawling") AND ("biological trait*" OR "ecological functional characteristic*" OR "ecological trait*" OR "effect trait*" OR "functional trait*" OR "life history characteristic*" OR "life history trait*" OR "life-history trait*" OR "performance trait*" OR "response trait*" OR "trait*" OR "trait* based" OR "trait*-based") AND ("marine" OR "sea" OR "benthic" OR "demersal" OR "pelagic"))

A total of 264 papers were initially found, to which we added an additional eight references extracted from citations within some of the researched papers that were considered relevant for our study. We included only papers associated with bottom trawling disturbance, which contained measurements of fishing intensity to assess effects on trait variation, and which accounted for one or more traits of marine species. The papers were first filtered by titles, then by abstracts, and finally by full text. Out of the total of 272 papers, only 33 met the criteria and were included in our review.

For each study, we extracted information about the habitat, with particular focus on the sediment type and depth range. Additionally, we considered the type of marine community investigated (benthic infauna, benthic epifauna, demersal or pelagic), the type of bottom fishing gear used, how fishing intensity was measured, the sampling technique used to assess the community, and whether variables other than fishing disturbance were considered in assessing the effects on trait response.

We evaluated the criteria used for the selection of traits, the type assigned to each trait (response or effect, *sensu* Violle et al. 2007), the expression mode of the trait (continuous, categorical, or interval), and the levels of these modes, including whether the trait is associated with a measure of species resistance or resilience. The assignment of response/effect or resistance/resilience traits was based on the information stated in the papers. For each mode, or for the entire trait if it is continuous, the direction of the relationship between the trait and the disturbance was also assessed (positive, negative, or neutral). This effect was associated to changes in the absolute or relative abundances of the trait modes, evaluated either along a fishing pressure gradient or by comparing areas of high pressure with those of low or no pressure. Additionally, secondary effects of other variables considered in the studies were extracted.

After compiling a complete list of traits, similar traits were grouped together to create a succinct selection of relevant traits. For instance, traits such as "maximum length," "maximum size," and "total length" were aggregated into a single trait category named "Size (length)." A similar approach was taken for trait modalities with similar but equivalent names. To further reduce the number of modalities falling into the same trait category and thus minimize the noise in the information, a re-coding of the modalities was also implemented to create a meaningful set of modalities for each extracted trait. This process was particularly useful for traits with several interval ranges that varied across different studies, such as size, lifespan, and sediment position.

The selected studies primarily accounted for benthic infauna and epifauna communities across sandy or muddy sediments (Figure 1). The main sampling techniques included box corers, grab dredges, trawl sampling, and video transects. Pelagic and demersal species were only involved in studies that utilized trawl or video sampling (Figure 2). For most studies, fishing intensity was assessed using satellite data (VMS or AIS) and logbook data, with a few studies employing video or acoustic technologies to evaluate trawled sites (e.g. use of sidescan sonar or towed cameras to provide an estimation of the trawling tracks).

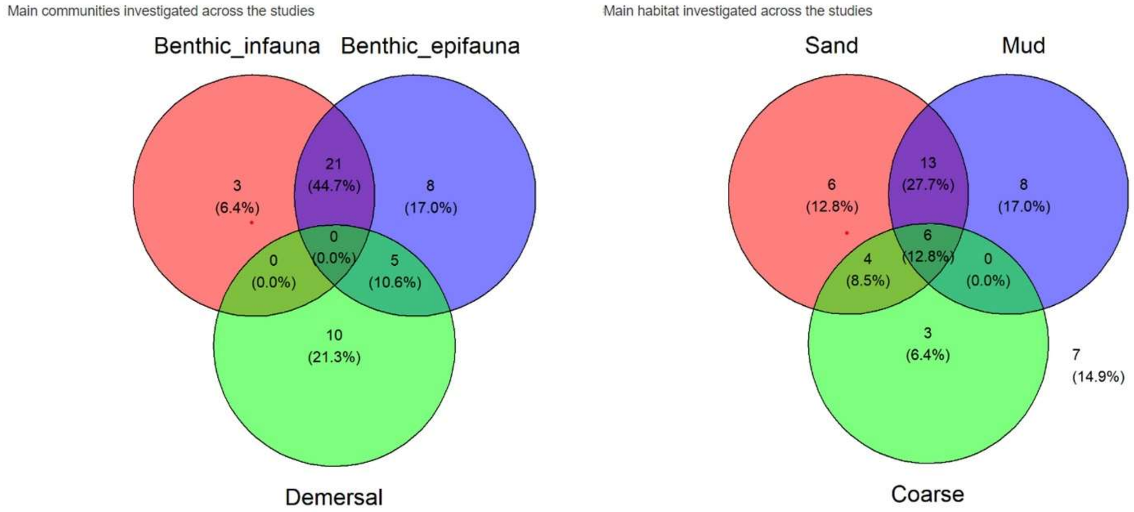

Figure 1 – Number of papers for each communities (benthic infauna, epifauna and demersal species) and habitat (sand, mud and coarse sediments) found in the review. To ensure the readability of the graphs, the only study that included pelagic species was not represented.

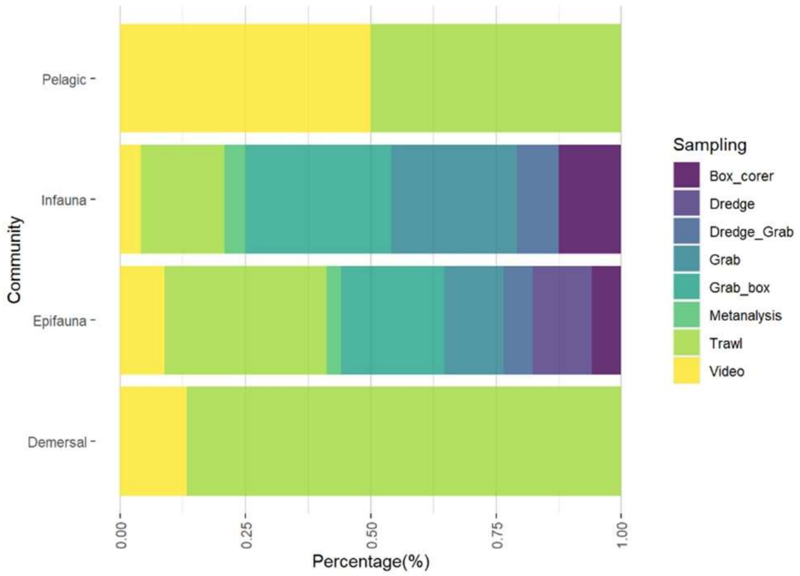

Figure 2 – Proportion of the main techniques used to sample the community across the investigated studies.

We identified a total of 38 traits linked to trawling disturbance (Figure 3). The selection of these traits in many studies was based on the best current knowledge of traits representing organisms' morphology, feeding patterns, and life histories, thus describing the functional structure of the community. Only 39% of these studies provided a clear rationale for the selection of traits and the hypothetical effects that fishing could have on their modalities (a summary of the rationale behind the main traits can be found in Table 1).

Of the 38 traits, all were considered at least once as a response trait in a study, while only 34% were also classified as effect traits (Figure 3). The most common effect traits included 'Bioturbation,' 'Feeding Mode,' 'Environmental Position,' and 'Mobility.'

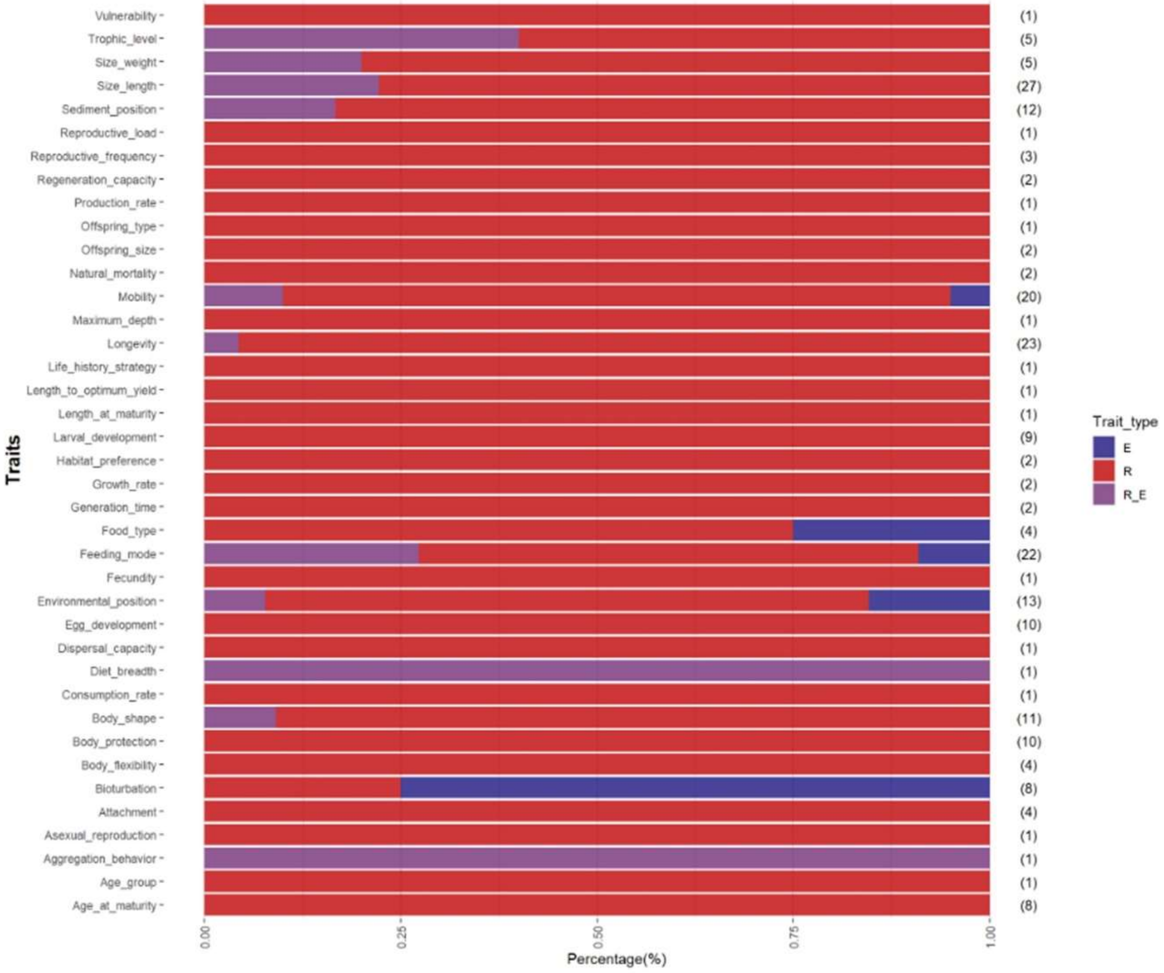

Figure 3 – Type of traits found across the investigated studies. E: effect traits (any trait which reflects the effects of a plant on environmental conditions; community or ecosystem properties, Violle et al. 2007), R= response trait (Any trait the attribute of which varies in response to changes in environmental conditions; Violle et al. 2007), R_E= traits considered both as a response and an effect trait in the study. The number between brackets indicates the number of observation found for that trait across the studies.

For only 17 traits, a classification between proxies of resistance and resilience was possible (Figure 4). Dissecting these traits into indicators of resistance or resilience, we noted that many traits related to reproduction (e.g., Offspring Type, Offspring Size, Larval Development, Egg Development, Age at Maturity) were considered proxies of resilience, while morphological characteristics (e.g., Body Shape, Body Protection, Body Flexibility) and spatial position (e.g., Sediment Position, Environmental Position, Attachment) accounted for resistance. Some traits, such as Size (both in length and weight), Mobility, and Longevity, were deemed representative of both aspects (Figure 4).

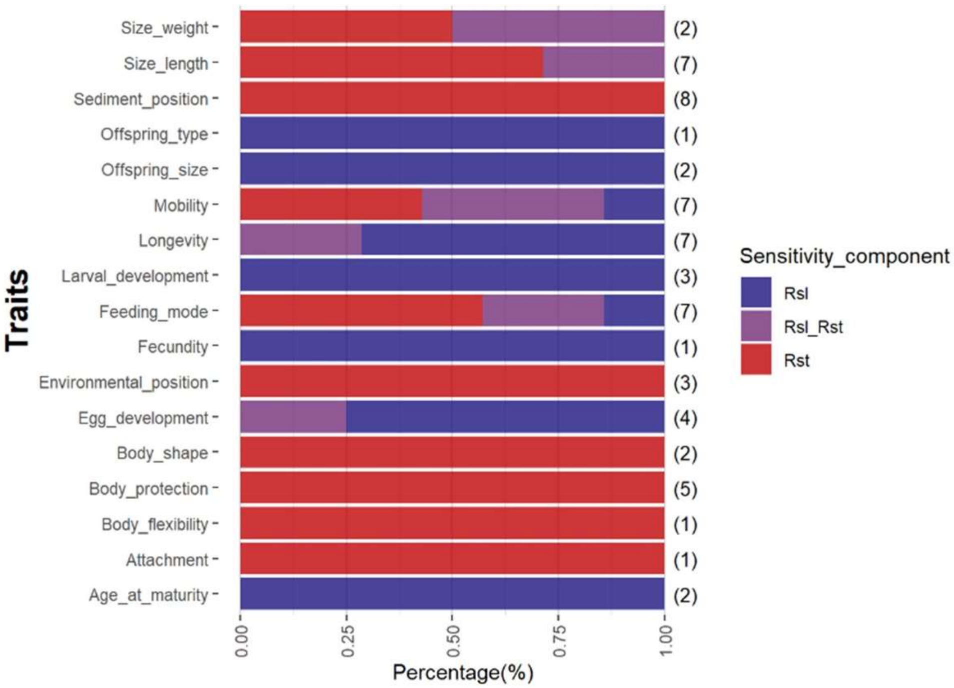

Figure 4 - Sensitivity components attributed to each trait across the investigated studies. Rsl = resilience (the rate of, or time taken for, recovery once the pressure has abated or been removed; MarESA 2023); Rst = resistance (the likelihood of damage due to a pressure MarESA 2023), Rsl_Rst = traits considered both as proxy of resilience and resistance in the study. The number between brackets indicates the number of observation found for that trait across the studies.

Exploring the effect of trawling on individual trait modalities, we observed that traits like 'Age at Maturity,' 'Longevity,' 'Mobility,' 'Sediment Position,' and 'Size Length' showed clear directional responses to the frequencies of positive or negative effects, with a substantial number of observations (Figure 5 and Supplementary Material M1). Specifically, 'Size Length' (27), 'Longevity' (23), 'Feeding Mode' (22), and 'Mobility' (20) were also the most commonly used traits for assessing fishing intensity effects on community trait composition.

The number of observations and directionality also changed according to the type of community investigated (Supplementary Material M2). While certain traits like 'Sediment Position,' 'Environmental Position,' and 'Attachment' were only relevant for benthic communities, other traits such as 'Trophic Level,' 'Maximum Depth,' 'Growth Rate,' and 'Generation Time' were relevant only for demersal and pelagic species. Due to the poor representation of these two groups in the studies, and therefore in the estimation of effects on the traits, we decided not to consider demersal and pelagic species in the conclusions of our trait selection.

Of the main traits we examined, we observed that for ‘Size Length’ an increase in the frequency of negative effects was present at larger size ranges. ‘Longevity’ followed a similar pattern, with species with longer lifespans more often negatively influenced than shorter-lived organisms. For ‘Mobility’ species with higher mobility were less likely to be negatively affected than sessile species, and for ‘Sediment Position’ we reported a higher frequency of negative effects for species living on the surface of the seabed compared to those living beneath it. (Figure 5).

Secondary traits like ‘Feeding Mode’ ‘Body Protection’ ‘Egg Development’ and ‘Larval Development’ were characterized by substantial observation but with a higher percentage of neutral effects compared to the aforementioned ones, obscuring the clarity of the response patterns in their modalities (Figure 6). Suspension feeders exhibited a higher frequency of negative effects compared to scavenger and predator species, although some positive effects were also reported. Species with high body protection (usually shelled) were the only modality to have a positive effect from trawling, although a good portion of neutral effects were also reported. For 'Egg Development,' we observed a higher frequency of negative effects for pelagic eggs and direct development for infauna and epifauna species, but controversial effects (either negative or positive) for organisms who can reproduce asexually. For 'Larval Development,' we instead observed a higher frequency of negative effects for planktotrophic larvae as well as for lecithotrophic larvae and those with direct development, although the percentages were minor. Although their pattern was not fully clear these traits could be useful in highlighting certain specific life-histories adaptations.

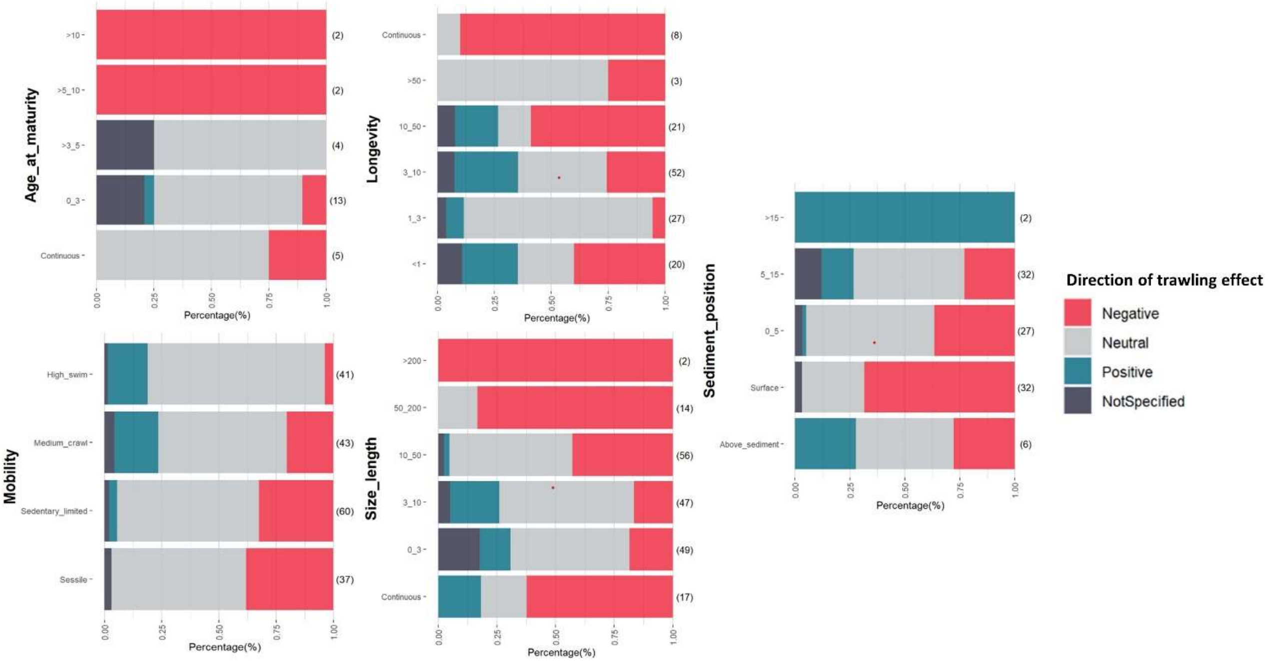

Figure 5 – Proportion of observations across the investigated papers linking the principal traits positively, negatively or without significance or not specified in the study to trawling disturbance. Unit of measure for ‘Age at maturity’ and ‘Longevity’ is years while for ‘Size length’ and ‘Sediment position’ is cm. The number between brackets indicates the number of observation found for that trait modality across the studies.

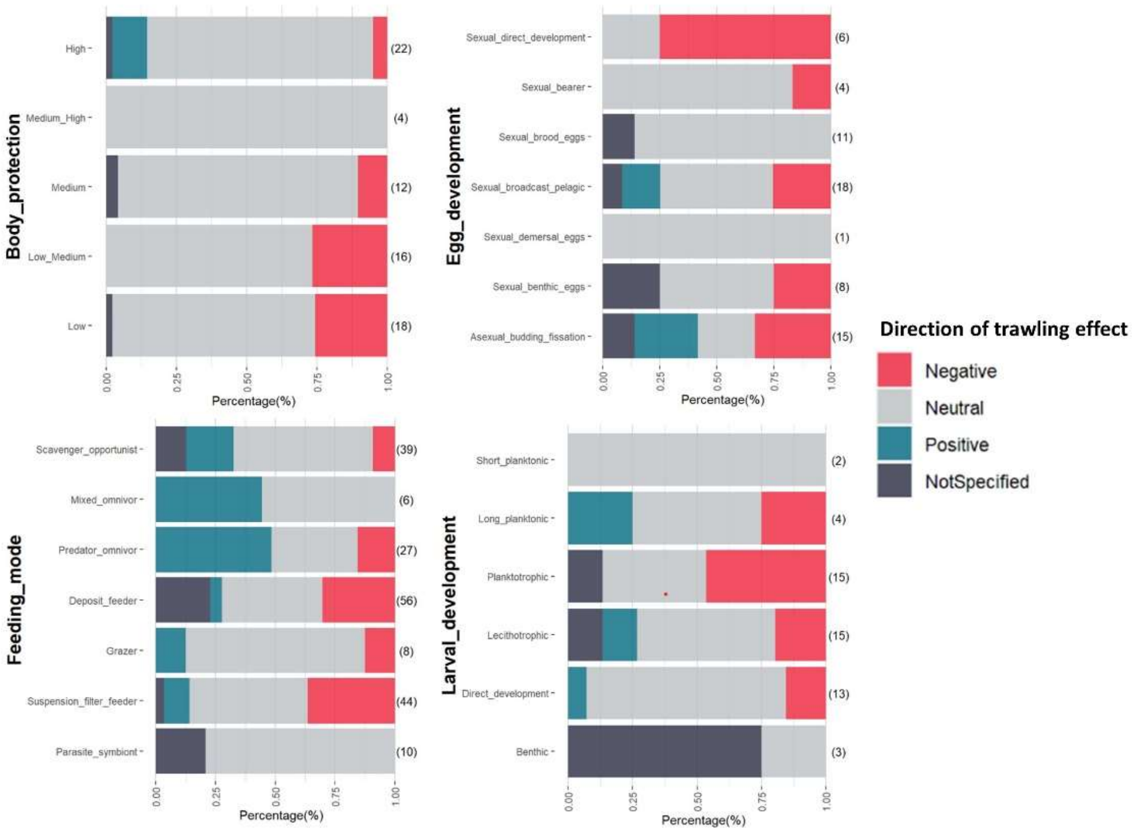

Figure 6 - Proportion of observations across the investigated papers linking the secondary traits positively, negatively or without significance or not specified in the study to trawling disturbance. The number between brackets indicates the number of observation found for that trait modality across the studies.

In conclusion, in light of these observations, we chose to consider these eight traits in our project as they are supported by the majority of observations found in the literature and have a clear rationale for the effects and criteria of selection (Table 1). Furthermore, quantitative assessments of the effect led by trawling were also possible to extract from some of the studies we accounted for, which were particularly useful to build an indicator within an impact assessment framework in Chapter 4.

Table 1: Biological and life-history traits selected to assess the sensitivity of the community to trawling pressure.

Trait	**Modality**	**Rationale for trait selection and hypothesized responses**
Body protection	Fragile/Unprotected Exoskeleton/tubiculous Shelled	Presence of hardened tissues can determine the likelihood of sustaining damage from a physical disturbance. Brittle and unprotected species are more prone to damage compared to species with durable skin or hard exoskeletons and shells.
Egg development	Asexual/budding Benthic eggs Brooded eggs Pelagic eggs	Pelagic eggs are generally safe from bottom-towed gears, while spawners may be fished but not the recruits. Eggs laid on the seabed or brooded are at risk of gear damage. However, trawling could aid species that reproduce through fragmentation or asexual means.
Feeding mode	Predators Scavengers Subsurface deposit feeder Surface deposit feeder Suspension/filter feeder	Trawling can have advantages for scavenging species, enhancing their energy intake and potentially accelerating growth and reproduction. Suspension feeders are more vulnerable as they require direct exposition to the surface and they also suffer from reduced filtration rates due to increased sediment resuspension. Conversely, deposit feeders may benefit from gear abrasion, which can make previously inaccessible food available again.
Larval development	Direct development Lecitotrhophic larvae	The potential for recovery from trawling relates to the type of larvae development and the extent of parental investment, as well as the susceptibility of nursery habitats to damage. Generally, species with direct benthic development and lecithotrophic larvae exhibit

	Planktotrophic larvae	greater parental investment compared to those with planktonic larvae or development through fission or fragmentation. Furthermore, direct benthic development may be directly impacted by trawling due to habitat disturbances.
Longevity	<1 year 1-3 years 3-10 years >10 years	Species with longer lifespans are less likely to withstand and recover from the effects of trawling. This is attributed to factors such as lower metabolic rates, delayed maturity, reduced annual reproductive output, and lower natural mortality.
Maximum length	0-3 cm 3-10 cm 10-50 cm >50 cm	Larger organisms typically exhibit slower growth rates, resulting in populations taking longer to recover from trawling impacts. Conversely, smaller organisms tend to grow faster, potentially leading to quicker population recovery. Additionally, larger organisms are more susceptible to capture by trawl gear.
Mobility	Crawler Sedentary/burrower Sessile Swimmer	Species with limited mobility face difficulties escaping from passing gear. Sedentary species have minimal escape opportunities, burrowers can seek refuge within sediments, providing them with some chance to evade contact with the gear.
Sediment position	Surface 0-5 cm depth 5-15 cm depth >15 cm depth	Species residing beneath the sediment have a reduced likelihood of being caught or damaged by trawl gear, whereas those dwelling on the sediment's surface are highly vulnerable.

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Chapter 2:

A functional trait-based approach to disentangle trawling disturbance onto bentho-demersal assemblage composition: evidence from a heavily exploited fishing ground (South-central Mediterranean Sea)

1 Introduction

Trawling is one of the fishing activities with the highest spatial distribution, characterized by a high spatial aggregation along the continental shelves worldwide [Amoroso et al. 2018]. The reported effects caused by this source of disturbance are various, affecting both directly and indirectly the benthic communities. Trawling alters the composition of the sediment with the direct action of the nets [Collie et al. 2000, Puig et al. 2012], affects the mortality rates of many species by reducing biomass and abundances (compared to conditions in which the disturbance is absent; [Hiddink et al. 2006] and - when chronic - can cause the alteration of the composition and structure of the community [de Juan et al. 2007, Howarth et al. 2018]. Opportunistic and scavenger species have been reported as increasing while detrimental effects have been reported on long-living species with important ecosystem functions, such as suspension-feeders and structuring species [Tillin et al. 2006, Mangano et al. 2013, Hiddink et al. 2019].

Understanding the effects of trawling disturbance on the bentho-demersal community is crucial to effectively manage the fishing sector [Eayrs et al. 2020, McConnaughey et al. 2020] and therefore maintain a state of sustainable exploitation of resources. Since the community response can vary according to the gear type, habitat and fishing pattern history [Sciberras et al. 2018], it is necessary to define clearly the relationships between the disturbance, the species involved and the surrounding environmental conditions. For this purpose, several case studies have been produced, however, in most cases, effects are estimated by comparing areas subject to frequent trawling activity with areas that are not as affected [Hiddink et al. 2017]. While this has allowed to observe a clear negative effect of fishing disturbance, many worldwide fishing grounds are characterized by disturbance gradients that follow a heterogeneous and a resulting patchiness distribution strongly dependent on the time and spatial scale of observation [Amoroso et al. 2018, Ferrà et al. 2018].

In the Mediterranean Sea specifically, the trawling activity affects mostly the continental shelf up to about 200 m and then decreasing proceeding offshore on the slope [Eigaard et al 2017, Ferrà et al. 2018]. In the entire basin, bottom trawlers are the main operating gears impacting conservation-priority species and causing the highest percentages of discard fraction [FAO 2020]. In particular, the Strait of Sicily, which proves to be an area of high biodiversity [Coll et al. 2012], hosts one of the largest fishing fleets in the Mediterranean Sea, the Mazara del Vallo fleet, with a history of exploitation at least thirty years, to which are added the fleets from Libya, Malta and Tunisia [Farrugio and Soldo 2014].

This scenario requires the implementation of multi-year management plans regarding bottom trawling, mostly encouraged by international organizations such as the General Fisheries Commission for the Mediterranean (GFCM) and implemented at national level [GSA 16

Management Plan 2018-2020] to safeguard the state demersal stocks with particular attention to the two main target species: deep-water rose shrimp (*Parapenaeus longirostris*, Lucas 1846) and european hake (*Merluccius merluccius*, Linnaeus 1758). From this point of view, several studies have been conducted to evaluate the effect of fishing disturbance on the state of bentho-demersal assemblages along the Strait of Sicily [Gristina et al. 2006, Dimech et al. 2012, Milisenda et al. 2017, Agnetta et al. 2019], however little information comes from the easternmost portion of the area, characterized by a rather extended continental shelf, the Malta bank.

The present study aims to explore the effect of fishing disturbance on the composition of bentho-demersal assemblages with data collected from fishing surveys conducted along the continental shelf area between the tip of Portopalo di Capo Passero (Sicily) and Malta. Other than evaluating the effects on species composition, it was considered important to evaluate also the effects of trawling and natural disturbance on functional components of the assemblage, using biological traits linked to community response to fishing impact. The combination of taxonomic and trait analysis is potentially a useful approach to better understand the mechanism of interaction between anthropogenic and natural disturbance in shaping community structure, especially in chronically disturbed scenarios like the one taken in account in this study.

2 Methods

2.1 Study area

The study area comprises the continental shelf of extending between Malta and the southernmost point of Sicily, Portopalo di Capo Passero (LAT 36.686111, LON 15.136111, CRS: WGS84), as a part of the Malta bank (Figure 1). This shelf is characterized by sand and muddy sediments and moderate to strong current kinetic energy (EMODnet data; [Martin Miguez et al. 2019]) hosting prevalently Mediterranean biocenosis of coastal and shelf edge detritic bottoms (A5.46, A5.47 of EUNIS classification). A small area on the north-east of Malta is characterized by Coralligenous habitat (A3). As a part of the Sicilian-Tunisian Platform, the seafloor bathymetry of the area varies very little ranging from 50m to 150-200m ca.

This area is crucial for trawling due to its high productivity and biodiversity [Coll et al. 2012]. Bottom trawlers show a high variability in the exploited fishing areas, which may change in the same day from the continental shelf to the middle slope, up to 700 m depth. Trawler landings are characterized by a high number of species of fish, crustaceans and molluscs, in various commercial categories. The area hosts Portopalo di Capo Passero fishing fleets which constitutes 4% of the gross tonnage of Sicilian ports [Popescu 2010], which are mainly focused on deep-water rose shrimp (*Parapeneus longirostris*) catches. These trawlers operate mainly on short-distance fishing trips, which range from 1 to 2 days at sea, with fishing taking place on the outer shelf and upper slope [Farrugio and Soldo 2014]. Moreover, this area, being located between the GFCM Geographical subarea (GSA) 15 and 16, is often overshadowed by information coming from the fleets operating in the Adventure Bank area (characterizing GSA 16) and from the fleets associated with the island of Malta (characterizing GSA 15). However, it is located near potential spawning and nursery sites of *P. longirostris* and *M. merluccius* and high-density distribution of demersal species of local interest such as *Mullus barbatus* (Linnaeus 1758), as well as being characterized by intense trawling near the coast [Farrugio and Soldo 2014, Fiorentino et al. 2017], further proving the importance of increasing ecological knowledge of the inhabiting benthic-demersal community.

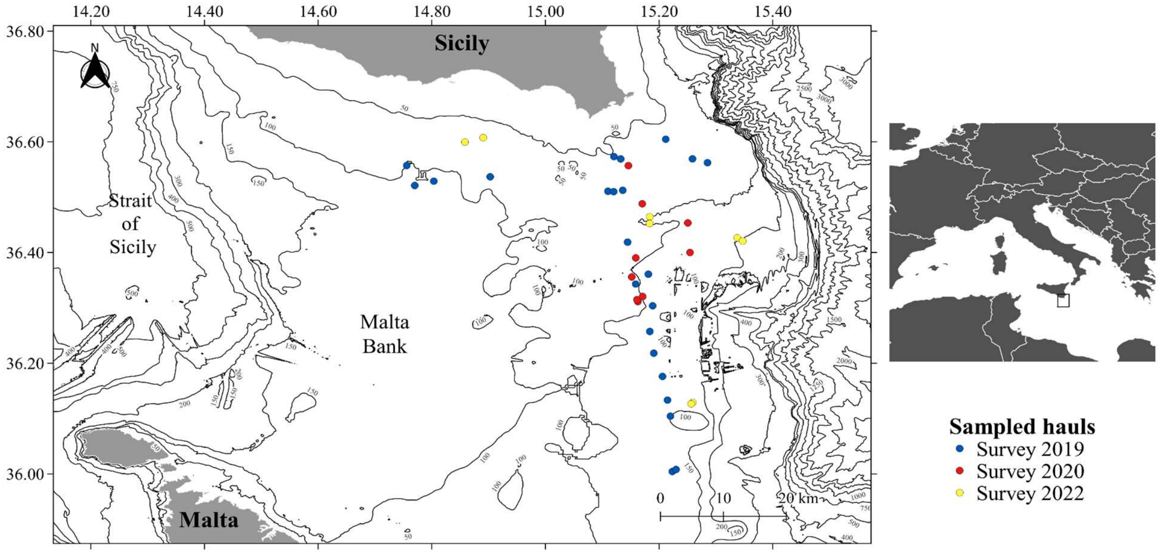

Figure 1 – Study area with main isobaths and sampling hauls done during the three fishing surveys. The dots shown are the average between the starting point and the ending point coordinates of each haul.

2.2 Fishing intensity and fishing survey

Fishing activity exerted by the trawling fleet around the area was estimated using the open source fishing effort AIS data at 100th degree resolution available from [Global Fishing Watch, 2022] for the period 2016-2020. The study area was divided into a raster grid of 1km^2 cell size on which Swept Area Ratio (SAR) was calculated and used as indicator of fishing intensity [Amoroso et al. 2018], representing the total area swept by trawl gear over a defined time period (usually 1 year) divided by the total seabed area at a defined spatial scale (the grid cell). First, aggregated satellite daily data was filtered to consider only signals linked to trawling activity and assigned to the corresponding cell. Due to the absence of information regarding vessel size and engine of each vessel signal, an average Mediterranean otter door width of 89.89 m and trawling speed of 2.9 knots was extracted from [Sala et al. 2019] and [Eigaard et al. 2016], respectively, and used in accordance to the number of signals per cell to calculate the swept areas per cell. Swept areas belonging to the same cell were summed and then divided by the area of the cell to obtain the ratio. An annual average raster of the period 2016-2020 was used to extract SAR information to link to the sampling hauls.

Bycatch data analyzed in this study was collected from three fishing surveys conducted along the study area in May 2019, July 2020 and July 2022 (named as HCP1, HCP2 and HCP3) falling within the actions conducted for the INTERREG Italy-Malta HARMONY and SenHAR projects. A 17.9 m long and 27 tonnage commercial otter trawler (distance across the mouth of the net 40m, head line height 1.7m, 20mm mesh diamond cod-end) was deployed for the sampling activity. The narrow mesh size was used to capture small fractions of the fishing assemblage. For every trawl, a standard vessel speed of 5.56 km/h (3knts) was selected.

A total of 40 trawls were carried out during the surveys along the bathymetry and fishing intensity gradients that proceed orthogonally from the coastline. Each trawl was assigned to a fishing intensity value through overlapping fishing routes to the average fishing intensity raster. First, the total distance for each single trawl was measured. For each of them, the distances of trawl passing through each raster cell were taken and converted into relative frequencies, dividing their value by the total distance of the corresponding trawl. Each relative frequency was then multiplied by the intensity value of each corresponding cell in order to obtain a weighted average, overall representing the average value of the area involved in each catch.

The bathymetry and coordinates of all the trawls were recorded on board and validated through QGIS and EMODnet DTM rasters. Trawls number 9, 10 trawls number 15, 16, 17 and trawls number 18, 19, 20 of the 2019 survey were merged together as there was high spatial correlation due to the minimal time interval between them. For each trawl, a subsample of the total catch was collected including commercial and by-catch species. Due to the well-known high presence (specifically more abundant in Sicilian trawled fishing grounds; [Milisenda et al. 2017] of the deep-water rose shrimp in all the catches, the species was removed from the analysis in order to avoid that occurrence dominance of this species masked and flattened the response of the remaining fraction of the assemblage. Once landed, the samples were frozen and transported to the Ecology Laboratory (University of Palermo, Italy) for taxonomic identification and measurement. The total wet weight and number of individuals of each species of the samples were estimated. To reduce possible bias, linked to the different durations and therefore different lengths of the hauls, and to reduce the effect of rare and dominant species in the dataset the reported, abundances were transformed with Hellinger transformation [Legendre & Legendre, 2012] prior to analysis. To discern what domain of the assemblage is more affected by trawling, each species was assigned to "demersal" or "benthic" category. The demersal category includes all fish species and mobile invertebrates that interact with the seabed and are often considered the primary targets of fishing activities. In contrast, the benthic category encompasses most invertebrates inhabiting the seabed with lower mobility, which are frequently treated as bycatch by fishermen.

2.3 Taxonomic and functional diversity measurement

After taxonomic identification of caught species, four different diversity indices (species richness, Shannon-Wiener's index, Simpson's index (1-D), Pielou's evenness; [Magurran, 2013] were computed using R package vegan for each sample (haul), to assess assemblage taxonomic biodiversity of the benthic and demersal domains.

A collection of five biological traits were selected to account for the possible effects of fishing activity and environmental variables on functional response of benthic-demersal assemblages (Table 1). Even though there are no objective criteria on selecting which are the most suitable response traits (sensu [Violle et al. 2007]) linked to fishing disturbance, the aforementioned traits are commonly used in literature to assess effects on marine benthic community [van Denderen et al. 2015, Bolam et al. 2017, Foveau et al. 2017, Ocaña et al. 2019, De Juan et al. 2020] and their information is easier to obtain in open-source online databases as FishBase, SeaLifeBase or BIOTIC. Each trait was divided into fuzzy coded modalities, spanning from 0 to a maximum sum of 1, according to the information found on the source databases to obtain a taxon-by-trait matrix (see Supplementary M2). According to this, each modality represents the proportion expressed by a species for that specific trait.

The obtained matrix was combined with Hellinger transformed species abundance-by-sites matrix in order to calculate the community weighted means (CWM) of each trait and a set of five functional diversity indices: Functional richness (F.Rich), Functional eveness (F.Eve), Functional divergence (F.Div), Functional dispersion (F.Dis) and Rao's index (Rao). CWMs for categorical traits data, as they are accounted in this study, represent the percentages of a given modality of the trait in a community, while the indices encompass three different components of functional diversity: richness, evenness and divergence [De Bello et al. 2021].

Table 1 – Biological traits and their modalities selected for the study.

Trait	**Modalities**
Maximum size	● <1 cm (L_1) ● 1-2 cm (L_1_2) ● 2-10 cm (L_2_10) ● 10-20 cm (L_10_20) ● 20-50 cm (L_20_50) ● >50 cm (L_50)
Longevity	● < 1 year (T_1) ● 1-3 years (T_1_3) ● 3-10 years (T_3_10) ● >10 years (T_10)
Egg development location	● Asexual/budding (edAsex)

	● Sexual – pelagic eggs (edPel) ● Sexual – benthic eggs (edBen) ● Sexual – brood eggs (edBrood)
Mobility	● Sessile (mSess) ● Swim (mSwim) ● Crawl/creep/climb (mCrawl) ● Burrowers (mBurrow)
Feeding mode	● Suspension (fSusp) ● Surface deposit (fSurf) ● Sub-surface deposit (fSubsurf) ● Scavenger/opportunist (fScav) ● Predator (fPred)

2.4 Statistical Analysis

Multivariate tests were used to test differences in measured species abundances (as number of individuals or biomass) and/or community weighted means (CWM) values between hauls of different fishing intensity values. To ensure the possibility of influence of other natural variables, we also reported and tested the effect of bathymetry (m), bottom temperature (°C), bottom dissolved oxygen (mmol/L), chlorophyll concentration at the sea bottom (mg/m3), seabed shear stress due to the currents (N/m2) and seabed slope (°C) assigned to each trawl (see SM1-S1; data was downloaded from Copernicus and EMODnet databases and assigned to each trawl with the same method applied for SAR).

Before the analysis, the correlation of the aforementioned variables was checked in combination with the spatial autocorrelation of hauls through Moran's I index [Moran 1984]. Furthermore, to highlight if hauls changed with the environmental variables, a k-means clusterization (number of clusters = 2) and a Principal Component Analysis (PCA) were applied. The distribution of total and single taxa abundances, CWMs, taxonomic diversity and functional diversity indices along the variables and in space, was visually inspected as well for both the domains. If the effect survey year was relevant on abundance composition, a PERMANOVA analysis was performed (using it as an explanatory factor).

Finally, the dominant species for each domain was individuated through Berger-Parker's dominance index [Magurran 2013]. These preliminary assessments were done to help to visualize similarities between samples and assist statistical result interpretation underlying which were covarying variables the most with assemblage structure.

In order to see if fishing intensity and the other variables affected catch assemblage (benthic and demersal) taxonomic composition, a redundancy analysis (RDA) was performed with Hellinger transformed data and standardized (mean equal to zero and s.d. equal to 1) environmental variables associated to the sampled hauls. Following the first RDA, a forward stepwise approach was applied to select the main variables leading the variability of the assemblage and reduce collinearity issues among them. The latter variables were then included in a partial RDA with latitude and longitude coordinates of the hauls as a conditioning factor, in order to isolate the effect of the variables from the effect accounted by the spatial distance of the samples. The same approach was also applied on computed benthic and demersal CWMs to check the effects on functional composition. Despite the analysis being applied both for biomass and count data, only the latter was reported on the paper due to having given better results.

The effects of variables on taxonomic and functional diversity indices and on total densities were explored with a linear regression model after checking the assumptions of normality of the residuals and homoscedasticity, through Shapiro-Wilk normality and Breusch-Pagan tests, respectively. When normality was violated, a linear model with permutation was applied, while in case of heteroscedasticity, the regression models were performed using heteroscedasticity-consistent standard errors through R package sandwich. Statistical analyses were conducted using the R package, Version R-4.2.0 [R Core Team, 2022].

3 Results

Fishing intensity around the study area showed a gradient from coastline to offshore with higher concentration along the eastern margin of the continental shelf (Figure 2). SAR values spanned from 0.36 to 37.37 with an average ± SD value of 9.86 (±7.60), confirming the area as a fishing ground particularly exposed to trawling activity. Due to the topographical structure of the area and to the sampling design, all considered variables showed a significant correlation with latitude variation, especially depth and fishing intensity (see SM1-S2). Specifically, it was found that, proceeding to lower latitudes (south direction), depth tends to increase (r = -0.76), while fishing intensity decreases (r = 0.76). Not only was depth negatively correlated with fishing intensity (r = -0.67), but this result was also displayed through the main environmental variables like temperature (r = -0.76), dissolved oxygen (r = -0.59) and chlorophyll concentration (r = -0.72). Those relations reflect the clusterization of sampled hauls obtained from k-means and PCA biplot (Figure 3), highlighting a cluster more in proximity of the coast with higher and more dispersed value of the mentioned variables and a deeper cluster with an inverse trend.

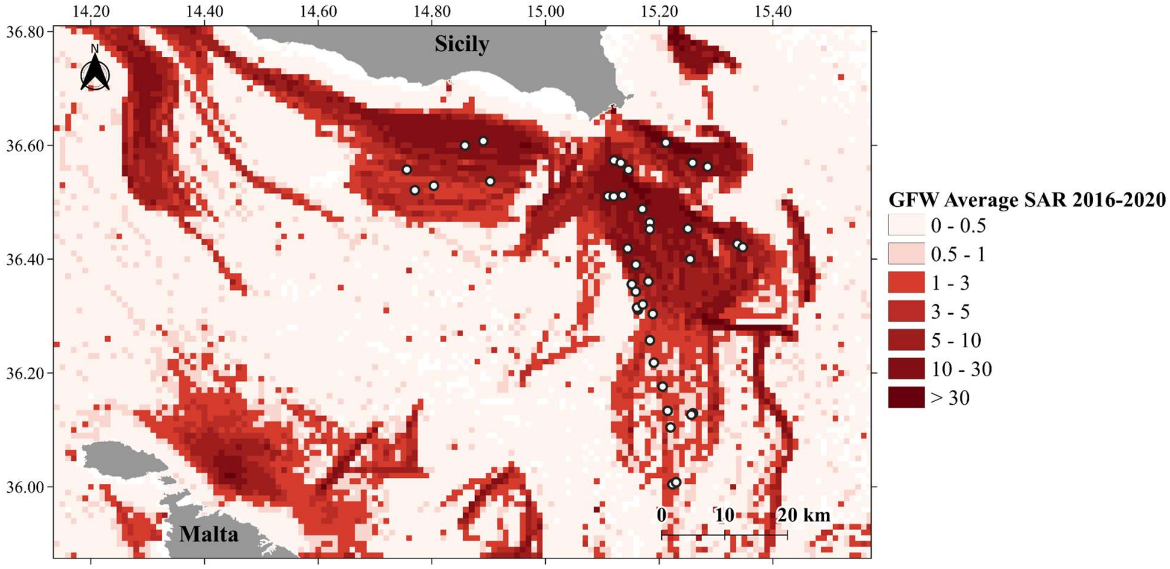

Figure 2 – Fishing intensity raster map expressed as Swept Area Ratio (SAR) of the study area obtained from analysis of Global Fishing Watch AIS data. Dots represents hauls sampled during the surveys.

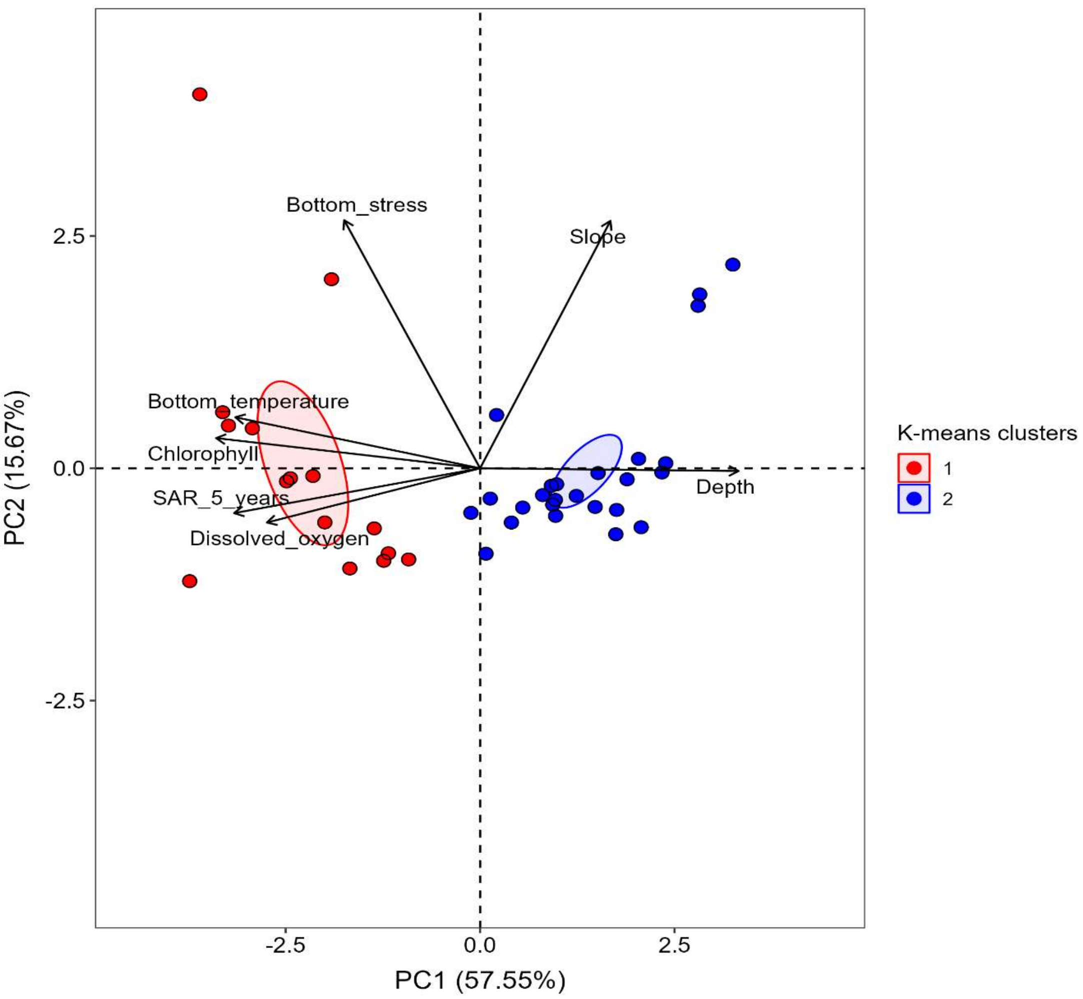

Figure 3 – PCA ordination plot of sampled hauls based on associated environmental variables and fishing intensity. Variables axes direction display environmental dependency while their length shows their relative importance. It can be seen a clustering tendency along PC1 axes mostly attributed to depth that is negatively correlated with bottom temperature, chlorophyll concentration, dissolved oxygen and fishing intensity. Color of the points represent the clusters obtained by k-means cluster algorithm with 2 groups that further underlines the tendency described in the ordination plot.

A total of 8,191 individuals (HCP1: 3,776; HCP2: 2,286; HCP3: 2,129), to an equal extent of 115.98 kg (HCP1: 60.76; HCP2: 35.70; HCP3: 19.52), were caught during the surveys. These individuals belonged to 103 species, of which 51 were demersal species (44 fishes, 5 species of cephalopods and 2 crustaceans) and 52 benthic (13 molluscs, 13 crustacean, 18 echinoderms species and 6 other taxa between cnidaria and porifera, SM1-S3). Demersal species were not present on two hauls (HCP1_M1 and HCP2_7) while benthic species were absent in four (HCP1_13, HCP1_14, HCP1_22, HCP1_23). Demersal domain accounted for the 70% (62% for biomass) of all individuals with an average total density per haul of 354 (±296 s.d.) individuals/km^2 and 4.87 (±3.39 s.d.) kg/km^2. Average ± SD benthic total density per haul were respectively 158 ±144 individuals/km^2 and 2.84 ±3.37 kg/km^2. Densities of demersal species, accounting biomass values, were negatively affected by fishing intensity, instead a positive effect of sea bottom temperature was observed if the total number of individuals were considered. Similarly, total counts of benthic domain were positively influenced by temperature while fishing intensity showed only a weak negative effect. Benthic biomass densities were positively related only to chlorophyll concentration (Table 2). Despite the trends shown on graphs (SM1-S4&S5) no significant effects of bathymetry were observed.

Assemblage taxonomic diversity seemed to not be influenced by fishing intensity. Chlorophyll concentration proved to be the main driver negatively affecting all indices associated to the demersal domain and positively influencing benthic species richness and Shannon's index. Secondarily, bottom shear stress had a significant positive effect on demersal Shannon, Simpson and Pielou's indices while a negative effect on Simpson (Table 2). Excluding *Parapenaeus longirostris* from the dataset, dominance scores were relatively low. The most dominant demersal species on average was *Trachurus trachurus* (15.3%) followed by *Arnoglossus laterna* (9.7%) and *Merluccius merluccius* (8.12%). Benthic domain was mainly dominated by the genera *Alcyonium* (27.63%) and *Munida rugosa* (16.83%) followed two species of Pennatulidae: *Pennatula phosphorea* (4.30%) and *Pteroides griseum* (4.08%). Demersal domain diversity tends to be higher than benthic one for all taxonomic indices used (Table 4).

Similarly, functional diversity indices didn't show effects led by fishing intensity variation. FRich of the demersal domain was positively related to bottom temperature variation while changes in chlorophyll concentration significantly reduced FDis and Rao. For the benthic domain only a positive effect of bottom shear stress to FRich was detected (Table 2). CWMs calculation highlighted an assemblage dominated by demersal organisms with maximum size between 10-20 cm (46.6%), a lifespan between 3-10 years (71.2%), pelagic eggs (80.3%), swimming through water (95.4%) and showing a predatory behavior (91.6%). Benthic domain was mainly characterized by organisms with maximum size between 2-10 cm (51.4%), a lifespan between 3-10 years (53.7%), releasing eggs in water column or brooding (36.1% and 39.4%), crawling on the seabed (54.5%) or staying attached to it (28.7%) and feeding on suspension organic matter (40.7%) or upon dead animals (24.0%). Mirroring those responses, the benthic domain showed a slightly higher functional evenness and functional divergence than the demersal domain (Table 4).

Table 2 – Results of linear regression models applied to demersal and benthic densities and to the four selected taxonomic diversity indices (Sp.Rich = species richness, H = Shannon's index, 1-D = Simpson's index, J = Pielou's eveness) in relation to fishing intensity and other environmental variables. Significant results are underlined, while empty spaces indicate that the corresponding variable was removed during the stepwise selection. SAR = fishing intensity expressed as swept area ratio, Depth = bathymetry expressed in meters, BTemp = seabottom temperature in Celsius, DO = dissolved oxygen concentration at the seabottom in mmol/L, Chl= chlorophyll concentration at the seabottom in mg/L, Stress = seabed shear stress expressed in N/m^2, Slope = slope of the seabottom in degree.

Variables		**Demersal**						**Benthic**					
		D.count	**D.biomass**	**Sp.Rich**	**H**	**1-D**	**J**	**D.count**	**D.biomass**	**Sp.Rich**	**H**	**1-D**	**J**
SAR	Slope	-17.21	-0.35					-6.49	-0.18	-0.181		0.007	0.008
	p	0.090	0.002					0.007	0.087	0.141		0.044	0.008
Depth	Slope				0.009	0.003	0.002			-0.064			
	p				0.009	0.002	0.019			0.029			
Btemp.	Slope	96.24	0.82	2.376	0.236	0.063	0.033	65.05			-1.256		
	p	0.023	0.120	0.003	0.001	0.001	0.110	0.009			0.162		
DO	Slope	17.62	0.20						0.29			-0.014	-0.025
	p	0.181	0.104						0.079			0.191	0.001
Chl	Slope			-94.834	-10.714	-2.728	-2.143		72.86	78.414	6.109		
	p			0.029	0.004	0.004	0.050		0.023	0.051	0.058		
Stress	Slope	-1018.21		-12.801	1.465	0.546	0.773					-0.701	-0.792
	p	0.130		0.079	0.043	0.004	0.001					0.007	0.003
Slope	Slope	97.21			-0.137	-0.028	-0.038				-0.137	-0.056	-0.039
	p	0.071			0.005	0.019	0.011				0.047	0.258	0.424
Adj R2		0.18	0.14	0.16	0.39	0.43	0.34	0.28	0.21	0.38	0.25	0.24	0.34

Table 3 – Results of linear regression models applied to the five selected functional diversity indices (F.Rich = functional richness, F.Eve = functional eveness, F.Div= functional divergence, F.Dis = functional dispersion, Rao = Rao’s index) in relation to fishing intensity and other environmental variables. Significant results are underlined, while empty spaces indicate that the corresponding variable was removed during the stepwise selection. SAR = fishing intensity expressed as swept area ratio, Depth = bathymetry expressed in meters, BTemp = seabottom temperature in Celsius, DO = dissolved oxygen concentration at the seabottom in mmol/L, Chl= chlorophyll concentration at the seabottom in mg/L, Stress = seabed shear stress expressed in N/m^2, Slope = slope of the seabottom in degree.

Variables		**Demersal**					**Benthic**				
		F.Rich	**F.Eve**	**F.Div**	**F.Dis**	**Rao**	**F.Rich**	**F.Eve**	**F.Div**	**F.Dis**	**Rao**
SAR	Slope	-0.012						0.006			-0.001
	p	0.101						0.221			0.156
Depth	Slope						0.005				
	p						0.056				
Btemp.	Slope	0.100			0.015	0.005	0.081			0.016	0.007
	p	0.001			0.001	0.001	0.048			0.009	0.036
DO	Slope						0.021		0.015		
	p						0.130		0.028		
Chl	Slope				-0.682	-0.190					
	p				0.015	0.019					
Stress	Slope	-0.793		-0.123			1.044				
	p	0.074		0.072			0.055				
Slope	Slope	-0.058	-0.019		-0.009	-0.002	-0.091				-0.007
	p	0.043	0.383		0.198	0.232	0.038				0.070
Adj R2		0.32	0.05	0.06	0.28	0.24	0.33	0.04	0.11	0.10	0.16

Table 4 – Summary (mean ±s.d.) of taxonomic (Sp.Rich = species richness, H = Shannon's index, 1-D = Simpson's index, J = Pielou's eveness) and functiona (F.Rich = functional richness, F.Eve = functional eveness, F.Div= functional divergence, F.Dis = functional dispersion, Rao = Rao's index)l diversity indices computed for demersal and benthic domains.

Domain	**Taxonomic**				**Functional**				
	Sp.Rich	**H**	**1-D**	**J**	**F.rich**	**F.Eve**	**F.Div**	**F.Dis**	**Rao**
Demersal	15.47 ±4.31	2.10 ±0.38	0.82 ±0.10	0.78 ±0.11	0.41 ±0.22	0.63 ±0.08	0.87 ±0.03	0.18 ±0.03	0.04 ±0.01
Benthic	9.15 ±4.02	1.46 ±0.46	0.64 ±0.17	0.70 ±0.17	0.54 ±0.26	0.72 ±0.11	0.81 ±0.07	0.26 ±0.06	0.07 ±0.02

Multivariate RDA analysis revealed that only a small portion of the variance (not higher than the 29%) observed in taxonomic and functional composition is explained by the variables included in this study. Variables accounted for approximately 10% variance more for the demersal domain than the benthic one and, in both cases, models applied to species count data showed a slightly better fit than ones applied to CWMs (Table 5). Most variation, in the demersal domain, was attributed to bathymetry, followed by bottom temperature, fishing intensity and to a lesser extent to seabed shear stress and slope if taxonomic composition is considered. Fishing intensity and slope showed to have a stronger effect when accounting functional composition. For the benthic domain fishing intensity, bottom temperature and bathymetry led the constrained variation explained by the RDA model with taxonomic data while temperature was removed when functional data were considered. Introducing spatial coordinates as a condition factor decreased, as expected, the variation explained by the model and by the variables, indicating not only an effect caused by the spatial proximity of the hauls but also by the combination of environmental, anthropogenic and spatial source of variability (SM1-S8). This aspect is amplified especially for the benthic domain, where the proportion of variance explained by latitude and longitude variation is similar if not higher than the portion accounted by fishing intensity and bathymetry (Table 5).

As a proof of these results, the ordination plots of the RDA models displayed a clustered data close to the center with only few species or trait modalities determining differences among the hauls (longer vectors). Although, in the ordination plot of CWMs some pattern of correlation of certain trait modalities with explanatory variables could be seen. For the demersal domain, trait modalities like fScav and edBen appeared to be more correlated to fishing intensity vector while modes like edPel and fPred were correlated more with bathymetry in opposite direction to the previous ones (Figure 4). Clusterizations of trait modalities is more evident for the benthic domain where modes like L_20_50, T_10, edAsex, edPel, mSess, fSusp are correlated and in opposite direction to modes like L_2_10, T_3_10, edBrood, mCrawl, fSurf and fScav even if correlation with constraining variables (bathymetry and fishing intensity) is less strong than the one with unconstrained axes (vectors oriented more along the PC1 than RDA1; Figure 5).

Table 5 – Summary table of the results obtained from Redundancy Analysis (RDA) applied to species cunt data (Taxonomic) and to CWMs (Functional) for both demersal and benthic domain (values between brackets represent the p-value obtained after permutations). Full RDA reports the results obtained from the model including stepwise selected variables while Partial RDA is referred to the model including the selected variables but removing the variance explained by spatial coordinates of the sampled hauls (expressed by Latitude and Longitude). Adj.R2 = adjusted R squared representing the variance explained by the RDA models.

% of intertia explained by	**Demersal**				**Benthic**			
	Taxonomic		**Functional**		**Taxonomic**		**Functional**	
	Full RDA	**Partial RDA**	**Full RDA**	**Partial RDA**	**Full RDA**	**Partial RDA**	**Full RDA**	**Partial RDA**
Constraining factors	40.26% (0.001)		31.85% (0.001)	26.93% (0.001)	24.91% (0.001)	19.36% (0.001)	19.61% (0.008)	12.50% (0.044)
Condition factors (Lat,Lon)		11.26%		8.21%		12.61%		16.92%
SAR	6.23% (0.001)	5.61% (0.003)	9.92% (0.003)	5.41% (0.037)	11.83% (0.001)	6.97% (0.002)	4.01% (0.185)	8.85% (0.027)
Depth	14.12% (0.001)	7.66% (0.001)	6.35% (0.032)	6.05% (0.027)	5.10% (0.026)	7.12% (0.002)	15.60% (0.008)	3.65% (0.191)
BTemp	7.04% (0.002)	7.09% (0.002)	6.92% (0.013)	7.68% (0.011)	7.99% (0.004)	5.27% (0.013)		
DO	4.58% (0.014)	4.14% (0.017)						
Chl								
Stress	3.48% (0.066)	3.51% (0.043)						

Slope	4.79% (0.008)	4.55% (0.009)	8.66% (0.006)	7.80% (0.013)				
Adj.R2	0.29	0.22	0.24	0.19	0.18	0.13	0.15	0.08

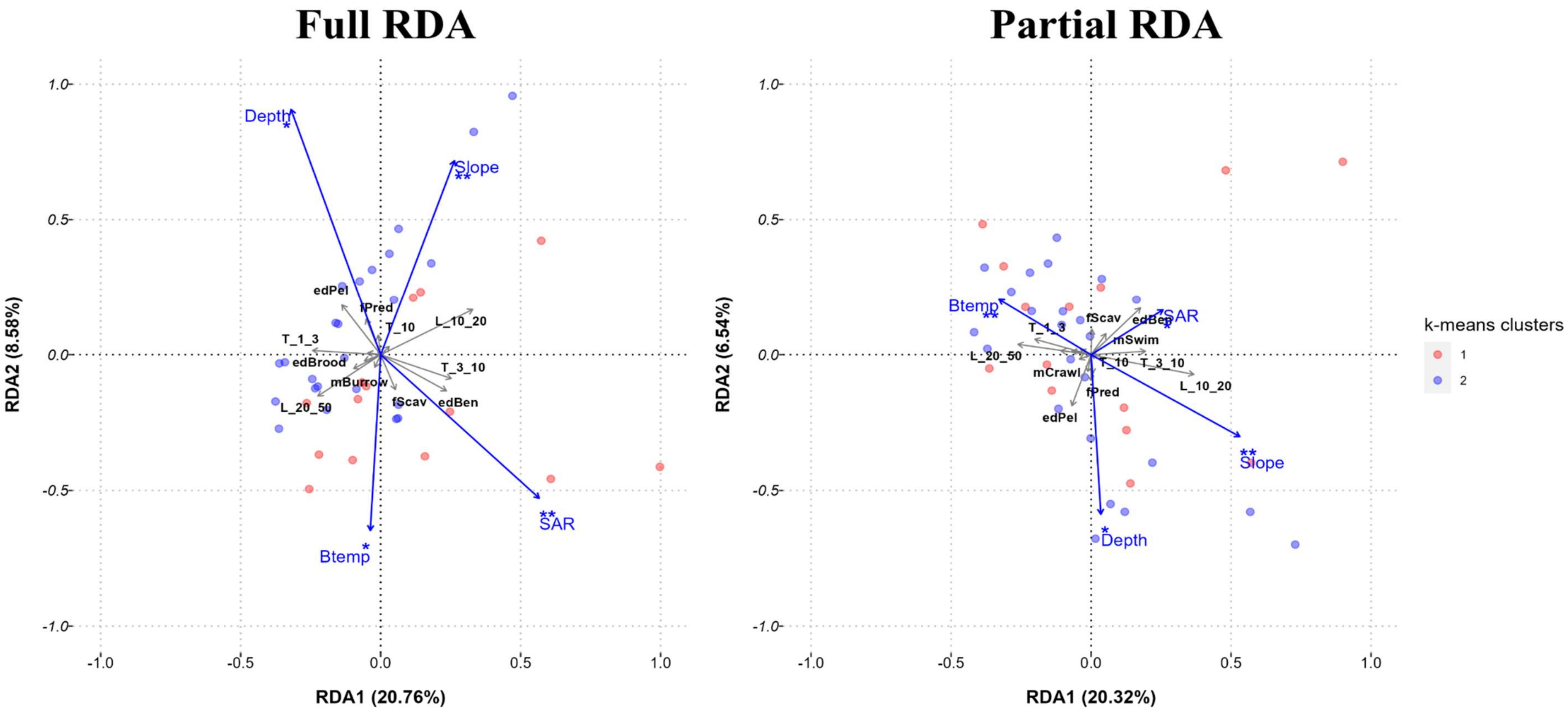

Figure 4 - Ordination of the all demersal CWMs of each traits modalities along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represents the clusters obtained from a k-means classification according the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, *** for p<0.001.

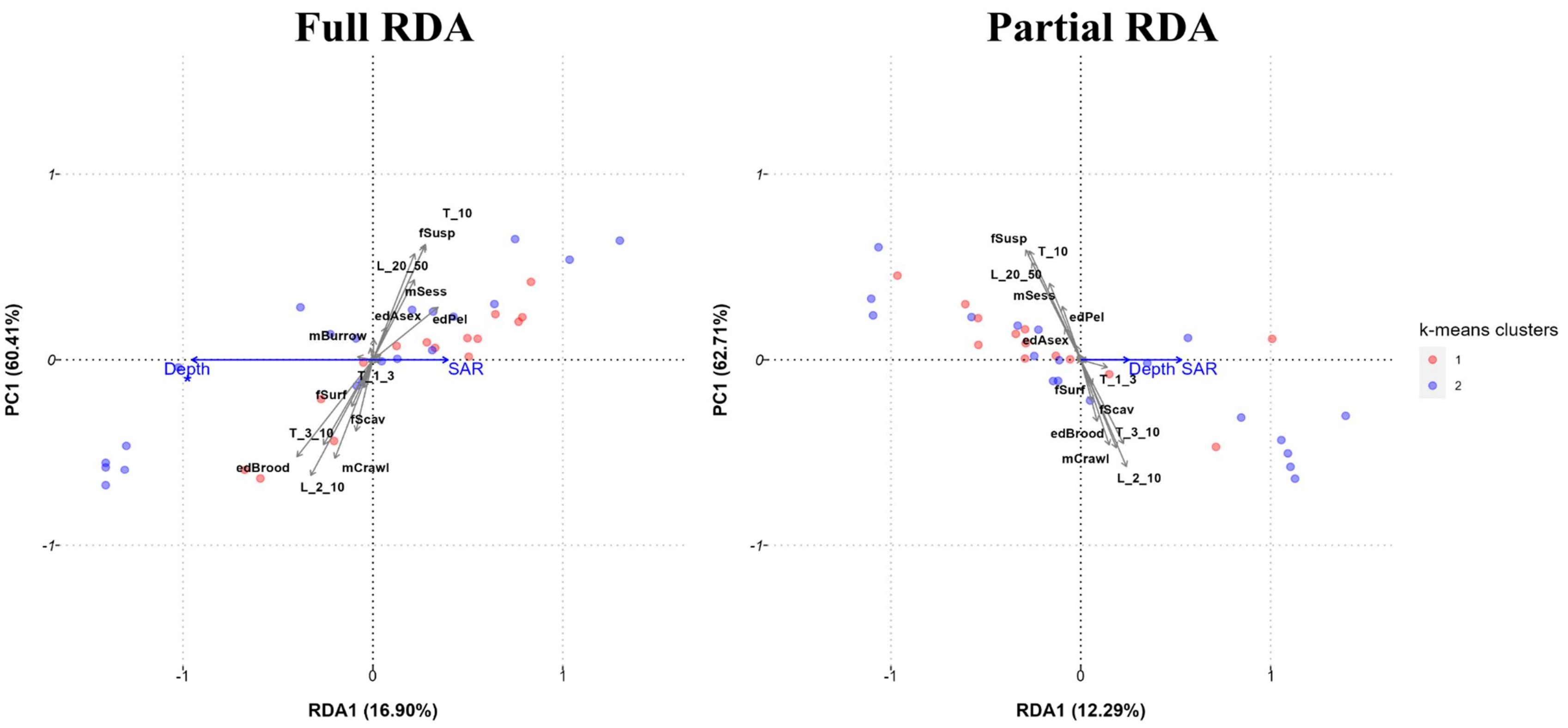

Figure 5 - Ordination of the all benthic CWMs of each traits modalities along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represents the clusters obtained from a k-means classification according the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, *** for p<0.001.

4 Discussion

The obtained results showed poor differences on bentho-demersal assemblage composition along the fishing intensity gradient observed across the continental shelf of the easternmost area of the Strait of Sicily. The described assemblage seems resulting from a combination of both chronic bottom trawling and bathymetric variation. Similar observations are found in the various fishing grounds spread along the continental shelf of the Strait of Sicily where trawling has been carried out for decades [Consoli et al. 2016, Terribile et al. 2016, Milisenda et al. 2017]. In such contexts the bathymetry is the main variable characterizing the community for two main reasons.

First, it is strongly correlated, as can also be seen in this study, with the spatial distribution of fishing activity [Eigaard et al. 2017, Amoroso et al. 2018, Metcalfe et al. 2018]: the annual intensity gradient showed a patchy spatial distribution with a strong reduction towards offshore. This is due to the fact that fishermen, following the limits imposed by the policies (Regulation (Eu) 2019/1241 of the European Parliament and of the Council), tend to carry out short trips in the same fishing grounds where they can maximize their revenues [Dimech et al. 2012], which correspond, in most cases, to the areas closest to the coast. The continuous removal activity given by the trawls causes the so-called "cultivation effect" [Mangano et al. 2013] which favors the selection of species with rapid reproductive cycles and reduced longevity and therefore better adapted to the latter disturbance, allowing them to become dominant with abundances and often also biomasses greater than areas in which fishing disturbance is absent. For example, this is observed in some fishing grounds of the Mediterranean Sea where communities are dominated by more opportunistic and resilient species such as *Parapenaeus longirostris* and *Aristeomorpha foliacea* [Dimech et al. 2012].

The second reason is given by the fact that, in a similar way to the fishing disturbance distribution, the spatial variation of the main environmental characteristics, such as temperature and sediment composition, follows a bathymetric gradient, with a strong heterogeneity of habitats and different ecotonal transitions along shallower seabeds that tend to gradually become more homogeneous as one proceeds towards greater depths, constituting a further element of differentiation of the community [Cartes et al. 2002, Cosentino and Giacobbe 2008, Dimech et al. 2008, Papiol et al. 2012]. However, since the area is characterized by a seabed that gradually degrades, there is no clear change in the composition of the community but rather a less accentuated transition. Furthermore, [Terribile et al. 2016] showed how the reduced variation could also be attributed to the long duration of the trawling activity which does not mirror well the small-scale habitat heterogeneity observable along the continental shelf of the central Mediterranean. Similarly, the high resolution of the fishing intensity, calculated in the study area, could be masked by the sampling technique based on the trawl survey, as each haul, following the disturbance gradient, covered areas with different intensity values. However, it needs to be considered that bottom otter trawling causes a minor impact on the benthic biota compared to other gears in combination with different substrata [Kaiser et al. 2006].

The strong correlation observed between bathymetry and other environmental variables, along with the clustering of sampled hauls, supports that relationship and underscores the significance of bathymetry and fishing intensity in explaining variation within both functional and taxonomic compositions. Despite only minor variations in assemblage composition being evident in RDAs, bathymetry and fishing intensity consistently account for a significant portion of the explained variation across both domains.

As depth increases, the community appears to become less influenced by environmental variations that could mask the impacts of fishing disturbance. Consequently, it becomes more sensitive to such disturbances, as highlighted by studies such as [Bolam et al. 2018] and [Sciberras et al. 2018]. Furthermore, the likelihood that the area is involved by frequent trawling events decreases. In fact, in the study the average fishing intensity values of the observed hauls belonging to the deeper cluster was half of the one reported for the shallower cluster. Comparative studies such as that of [Tillin et al. 2006] or [van Denderen et al. 2015] show that fishing disturbance has a greater effect in areas less prone to high levels of natural disturbance.

Looking at diversity indices and total densities, the greatest effects were associated to variables strictly linked to depth variation. Proceeding towards shallower areas, primary production showed an increment due to the continental runoff of nutrients and the increase of temperature. Those combined effects may shape the niches of the species that constitute the community, favoring species with higher thermal tolerance and that benefit for the increasing of productivity. Positive effects of seabed chlorophyll concentration on benthic biomass and diversity, as they can be seen in this study, were also reported in [Hiddink et al. 2006], where the infaunal biomass in the North Sea showed an increment as the chlorophyll content of the sediment increases until it reaches a plateau. Similarly, distribution of some dominant demersal species like *T. trachurus* and *A. laterna* is strictly linked to temperature changes and food limitation [Paulo-Martins et al. 2011, Leitão 2015, Punzòn et al. 2021], explaining the correlation of this species to the variation of this variables in the ordination plot (SM1- S8) and the positive trend in scatter plots of their abundances (SM1-S9).

As observed in [Bolam et al. 2017], bathymetry in conjunction with sediment characteristics explained the majority of trait variability toward the selection of sessile suspension feeders and burrowing surface-deposit feeder in deep muddy and coarse sediments while shallower coarse sediments are dominated by smaller scavenging and predator species. The obtained clusterization in partial RDA of the benthic community reflected a similar pattern with a differentiation between small crawling scavenger species with fast life cycles and sessile long-lived suspension feeder. Even though, the pattern was mostly explained by residuals of the model, it could be linked to the difference in properties of the sediment that was not possible to take in account in this study due to the low resolution of the habitat maps. Increase of homogeneity of sediment characteristics also occur in function of the stress caused by towed fishing gears, removing shell debris and coarser sediments that can sustain more complex communities [Handley et al. 2014].

Furthermore, the presence of correlation of species with opportunistic and scavenger behaviors (like *Spicara maena* for the demersal domain or *Stylocidaris affinis* for the benthic one) towards increases of fishing intensity is comparable to data observed in other studies led in shallower area most frequently subject to the latter disturbance [Demestre et al. 2000, Strain et al 2012, Mangano et al. 2013]. These organisms that normally feed on carrion and organic remains found on the bottom are particularly favored by the increase of organic contribution from both the resuspension of the sediment, caused by the physical action of the nets, and from the fraction of discard thrown back into the sea by fishermen. Due to their rapid recovery times and their motility, they are less vulnerable to fishing disturbance than more sessile species such as suspension feeders and grazers [de Juan et al. 2009]. However, while an increment of small benthic species relative abundance could be observed, an overall negative trend is frequently associated to trawling (Table 2, [Hinz et al. 2009, Kaiser et al. 2006].

The dominance reported, on this study, of sessile suspension feeders in the benthic domain even if apparently contradictory, was probably linked to two factors. First, despite that experimental design followed a pressure gradient, it is reasonable that the fishing disturbance involving the study area was as a remarkable driver having probably affected, in a long term, also the areas in which were observed low pressure values from the AIS data analysis. Several studies showed that even a low trawling frequency is sufficient to induce a shifting of the community from being characterized by the presence of large emergent sessile filters feeders and grazer to a community dominated by mobile scavenger, deposit feeders and predators [Tillin et al. 2006, Asch and Collie 2008, Strain et al. 2012, Handley et al. 2014, Eigaard et al. 2017]. This would mask the response of species with longer recovery times, such as Alcyonidae and Pennatulidae*,* as there would be no comparison with a pristine condition, while less vulnerable species with short recovery times more easily show a response as a function of the gradient [Sciberras et al. 2018]. In fact, note that although it is clearly demonstrated that trawling alters the structure and composition of the benthic-demersal communities, this response pattern is often found only by comparing areas in which this activity is exercised in a negligible manner with areas subject to a frequent disturbing activity [Hiddink et al. 2017]. The other reason could be linked instead to the distribution of those species along the environmental gradients. A moderate increase of hydrodynamic conditions and organic matter flows benefits those species and often their optimum could be found at relatively moderate depth between 40 and 60m [Ambroso et al. 2013]. So even though fishing intensity drives a clear reduction of abundances of this vulnerable species (SM1-S9), the effect is potentially masked from the positive effects induced by the increase of shear stress, chlorophyll concentration and bottom temperature of shallower areas.

Negative response of the demersal domain biomasses could be instead linked more to size selectivity and trophic shifts led by fishing activity. Benthivorous species, such as *Mullus sp*. appear to exhibit a high trophic plasticity directly linked on the food availability of the area, where higher physiological condition and trophic descriptors could be attributed to intermediate level of fishing disturbance

[Giacalone et al 2010, Mangano et al. 2017]. This direct relation is stronger especially with young and smaller fishes than adults that usually change their trophic behavior reducing the percentage of benthic invertebrates in their diet or exhibit higher selectivity [Machias and Labropoulou 2002, Eggleton et al. 2018]. Therefore, fishing activity through altering the structure of benthic community could lead to shift of fish diets between trawled and untrawled area [Fanelli et al. 2009] and contemporary select smaller individuals through direct effects of the characteristics of the deployed gear, like the mesh size [Sala et al. 2008]. However, relationships between unselective opportunists and benthic effect induced by trawling are not always clear [Eggleton et al. 2018] and some shifts could also be given by the ontogenetic characteristics of the species, as observed in *Mullus barbatus* which shows greater abundances of juveniles at depths between 50 and 150m with a summer spawning period between May and July [Machias and Labropoulou 2002].

The absence of a general influence of variables in the functional response of the two domains furthermore highlights the homogenization processes of the community that often are carried on by trawling [Tillin et al. 2006, De Juan et al. 2007, Handley et al. 2014]. Study area is an area subject to chronic fishing disturbance in which the community, already subjected for long time to trawling, has selected species with traits more compliant with this type of impact. Even if those species response differently to the stress, if many organisms share similar traits expression community, shows to be resilient to change in its structure due to fishing impact [Muntadas et al 2016]. This concept could be redirected to the low functional divergence measured of the analyzed assemblage and its relatively high functional evenness. It also can be noted that functional responses of community could often show non-linearity both to environmental variables and fishing impact [Lundquist et al. 2018], therefore small scales areas, as our fishing ground, could not be sufficient to examine relationship through different habitat responses across fishing gradients in order to show clear pattern of trait variation.

In conclusion, coupling taxonomic analysis with functional ones through Biological Trait Analysis and diversity indices, proved to be an excellent approach to increase the understanding and interpretation of community responses in chronically disturbed areas. As a matter of fact, the sole usage of normal indices of diversity applied to the taxonomic composition of assemblages may not correctly reflect the influence of the fishing disturbance compared to functional changes that last longer over time and allow to observe differences even in communities already adapted to such a condition [de Juan et al. 2007, Farriols et al. 2017, Sciberras et al. 2018].

Finally, the present study highlighted the influence of fishing around the southern seabed of the coasts of Cape Passero, an area that has been poorly studied compared to the neighboring fishing grounds of the Strait of Sicily, but that has an important economic value for the Sicilian fisheries [Popescu et al. 2010, Farrugio and Soldo 2014]. Despite the narrow investigation time window, the analysis conducted through the support of AIS data of the fishing fleets allowed the identification of exploitation trends comparable to those observed in other similar studies. Basing on our results, high trawled fishing ground are less prone to show clear trends of response in benthic and demersal communities where the scattered source of variation is most likely attributed to the different tolerances to the environmental gradients.

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Chapter 3: Estimating trawling impacts on benthic community: application of a quantitative and mechanistic framework on the Sicilian continental shelf (Central Mediterranean Sea)

1 Introduction

The regulation of human activities in marine systems has become an increasingly pressing concern in the light of recent sustainability policies [Fetting, 2020, Hermoso et al., 2022]. A significant recent endeavor in this regard has been the adoption of the Marine Strategy Framework Directive (MSFD) by European countries [Directive, 2008]. This comprehensive policy aims to attain a good environmental status for the European Union's marine waters and ensure the sustainable protection of the resource base upon which marine-related economic and social activities rely. To achieve this objective, the MSFD outlines several specific goals known as "Descriptors," which encompass crucial aspects that must be preserved in marine environments. Sea-floor integrity is Descriptor 6. This critical resource faces various threats, with 79% of the EU's coastal seabed considered to be physically disturbed [European Commission, 2020].

One of the primary human activities contributing to seafloor disturbance on a global scale is bottom trawling, prevalent in continental shelves, especially in European waters such as the North-east Atlantic and Mediterranean Sea, where an estimated proportion ranging between 50-90% of the entire soft sediments is trawled annually [Eigaard et al., 2017, Amoroso et al., 2018]. Trawling operations result in the removal of sensitive species and an alteration of the diversity within the marine bottom communities [Hiddink et al., 2006, Tillin et al., 2006, Howarth et al., 2018]. Moreover, the physical abrasion of the seafloor can cause sediment resuspension and alterations in its biogeochemical characteristics [O'Neill and Ivanovic, 2016, Oberle et al., 2016, Bradshaw et al., 2021]. These changes affect not only the habitat's structure but also the function of the communities residing within it [de Juan et al., 2007, Olsgard et al., 2008, Muntadas et al., 2016]. The impact on the seafloor may vary depending on habitat characteristics, the fishing gear used, and the resilience of species [Bolam, 2014, Sciberras et al., 2018]. Species with rapid recovery and specific behaviors such as burrowers and scavengers are more likely to survive or recover relatively quickly after trawling disturbance [Demestre et al., 2000b, de Juan et al., 2007].

This pressure could lead to a deterioration of seafloor integrity [Jac et al., 2020]. Monitoring is crucial to assess if the criteria established in Descriptor 6 of the MSFD are met. This involves assessing the extent of adverse effects on habitat type, including alterations to its biotic and abiotic structure and its functions. The development of indices and indicators to assess changes in benthic community state across different European shelf habitats has become a primary action to effectively implement the goals of the MSFD. Trait-based approaches have proven to be valuable tools for better understanding the effect of different human-induced pressures, especially those related to bottom trawling [de Juan and Demestre, 2012, Van Denderen et al., 2015, Rijnsdorp et al., 2018, Howarth et al., 2018, Hinz et al., 2021]. These approaches can be broadly categorized into qualitative methods, where experts assign scores to various features representing community structure and function, and quantitative methods, which establish mechanistic relationships between the impact and the traits [Pacifici et al., 2015]. While qualitative methods offer flexibility and a wide range of applications, quantitative methods are more objective and repeatable and can entail a rigorous statistical assessment of the relationship between the response and predictor variables.

The estimation of the relationship between benthic functional traits and trawling pressure remains an active area of research. Longevity, as the maximum lifespan recorded for a species, has demonstrated its effectiveness as an indicator of community change due to trawling [Rijnsdorp et al., 2018, Hiddink et al., 2019]. Species with higher lifespan correlate with a reduced likelihood of withstanding and recovering from the impact of trawling due to factors such as a lower metabolic rate, delayed maturity, diminished annual reproductive output, and decreased natural mortality. These factors collectively contribute to a slowed rate of increase and, consequently, a longer recovery period [Duplisea et al., 2002, Hiddink et al., 2019]. As a consequence, biological-trait methodologies based on longevity composition have been developed and integrated into quantitative indices to assess the impact of bottom trawling on the seafloor at regional scales [Rijnsdorp et al., 2020]. The effectiveness of these methodologies necessitates validation to assess their generalization capacity, adaptability, consistency, and sensitivity in detecting changes in response to trawling pressures across diverse habitats and spatial scales. Therefore, case studies within regional-local contexts become crucial for testing and evaluating the performance of such approaches and their suitability in assessing adverse effects on seabed habitats [Smith et al., 2023, Pierucci et al., 2023].

The primary objective of our study was to evaluate the current relative status of the benthic community on the Sicilian continental shelf in response to bottom trawling activities. Concurrently, our investigation focused on describing the longevity composition of the benthic community inhabiting the Sicilian continental shelf, utilizing by-catch samples collected during trawl surveys. We aimed to assess various factors that might influence the impact assessment approach, including spatial resolution, the average period over which the community could respond to the historical fishing pattern in the area and the incorporation of high fishing intensity samples for modeling the community composition in the absence of trawling.

2 Methods

The approach used in this study aims to quantify the benthic community's sensitivity to trawling. This is achieved by utilizing longevity as a proxy for sensitivity and constructing a model to depict the biomass distribution of longevity within the study area based on epifaunal trawl by-catch samples. Model outputs were applied to grid cells of 1x1 km of the study area. Subsequently, these distribution models are integrated with the spatial distribution of trawling intensity to accurately quantify the real impact exerted on the community.

2.1 Study Area and benthic samples

In this study, we have chosen to apply the benthic impact assessment framework described in [Rijnsdorp et al., 2020] to a local context in the Mediterranean Sea, specifically the continental shelf area around Sicily (Italy, Central Mediterranean Sea). The alternation between detritic uniform seabed and patches of sedimentary or volcanic rocky structures, combined with terrigenous nutrient inputs and seasonal upwelling processes influenced by current regimes, has facilitated high biological productivity near areas suitable for fishing activities [Consoli et al., 2016]. This, in turn, has fostered the expansion of the fishery sector in the region, particularly on the southern side known as the Strait of Sicily. The Sicilian fleet stands out as the largest regional fleet in Italy, both in terms of the number of vessels and total capacity [Popescu, 2010]. It is primarily characterized by set longlines, purse seines, and bottom otter trawls. The latter constitutes the highest percentage of the overall gross tonnage of the fleet, focusing on the majority of soft bottoms on the shelf for catching demersal species, notably the European hake (*Merluccius merluccius*) and the red mullet (*Mullus barbatus*), as well as the deep-water rose shrimp (*Parapenaeus longirostris*) [FAO, 2023]. Due to the widespread distribution of bottom trawlers, their activities are subject to regulation through various management plans, particularly in the Strait of Sicily. A key regulatory instrument in this context is Recommendation GFCM/45/2022/4 (repealing Recommendations GFCM/44/2021/12 and GFCM/42/2018/5), which establishes a multiannual management plan for the sustainable exploitation of demersal stocks in the Strait of Sicily. The management plan entails measures such as a freeze in fishing capacity/effort, the implementation of an effort regime for authorized vessels targeting European hake, catch limits for deep-water rose shrimp, and a temporal closure of 30 days between March and September. Additionally, Fishery Restrict Areas (FRAs) have been instituted to safeguard nursery areas and essential habitats crucial for European hake and deep-water rose shrimp stocks. Despite these regulatory plans, bottom trawling activities persist at high levels, posing a potential threat to the integrity of the seabed. This concern is particularly pronounced given the sustained high intensities over decades that have influenced and shaped the composition of both demersal and benthic assemblages [Gristina et al., 2006, Dimech et al., 2012, Mangano et al., 2013, Lauria et al., 2020, Good et al., 2022]. Such scenarios are particularly challenging due to the communities' adaptation to existing pressures, often making it difficult to detect changes associated with bottom trawling [de Juan et al., 2007, de Juan et al., 2009, Farriols et al., 2017].

This sub-region (Longitude: 11°36'E - 15°36'E, Latitude: 36°24'N - 38°24'N) falls within three General Fisheries Commission for the Mediterranean (GFCM) Geographical Subareas (GSAs): GSA10 GSA16 and GSA19 (Figure 1). GSA15 was excluded as no VMS fishing data were available.

To depict the longevity composition of the benthic community and assess its relative state trawl by-catch samples were used. This sampling approach primarily targets the epifauna and megafauna components of the benthic community. The samples were collected during three distinct fishing campaigns conducted along the Sicilian coast between 2010 and 2020 (2010-2013 data from Mangano et al. 2013; 2016-2020 data from ISPRA Italian National Monitoring Program campaign from 2016 to 2020 (ISPRA); 2019-2020 data from Interreg HARMONY Project provided by the Laboratory of Ecology, University of Palermo).

The surveys followed a protocol similar to the MEDITS campaign [MEDITS, 2017], employing a trawler with a 40-meter otter door spread and net with 10mm of mesh size. The net was towed for 30 minutes over the seabed shallower than 200 meters in depth and for 60 minutes over deeper seabed. The trawl speed was approximately 3 knots. UNIPA_HARMONY surveys used a commercial otter trawler with the same net characteristics, but the trawl duration was not fixed in the initial protocol design. Of the 173 samples that were collected on mud and sand sediments between 15 and 711 meters in depth, 82% were from the continental shelf, meaning they did not exceed a depth of 200 meters.

For the entire dataset 2010-2013 and the 2019-2020, both the total wet biomass and the number of individuals per species were available. For the remaining dataset 2016-2020, only the number of individuals was recorded. These counts were converted into total biomass by using the other data sets to estimate the average biomass per individual for each species. Biomass was chosen as the primary response variable, as it was initially validated in the published methodology. This selection was based also on its greater consistency in responding to fishing activity over time and its stronger association with trophic dynamics within the community compared to the number of individuals. Before analysis, we excluded all demersal species, encompassing Chordata and highly mobile invertebrates such as cephalopods and the deep-water rose shrimp. This exclusion was motivated by their unsuitability for impact assessment on a grid basis with high resolution, especially when compared to low-mobility species [Pierucci et al., 2022]. Many of these excluded species are targets of commercial fisheries, often displaying positive correlations between their biomass and swept-area ratio. These correlations may not accurately represent the broader effects of bottom trawling on benthic fauna. Due to the different trawl durations among the samples, biomasses were standardized by the surface area swept by each trawl and expressed as g/km2.

All benthic species were assigned to four longevity classes (<1, 1-3, 3-10, >10 years) through a fuzzy-coding method, as outlined in [Chevene et al., 1994]. Longevity estimates were extracted at the finest taxonomic level feasible from lists provided by [Bolam et al., 2014], [Beauchard and Troupin, 2018]. These fuzzy-coded biomasses were then aggregated by longevity classes and divided by the total biomass per trawl sample to determine the proportion of biomass in each longevity class.

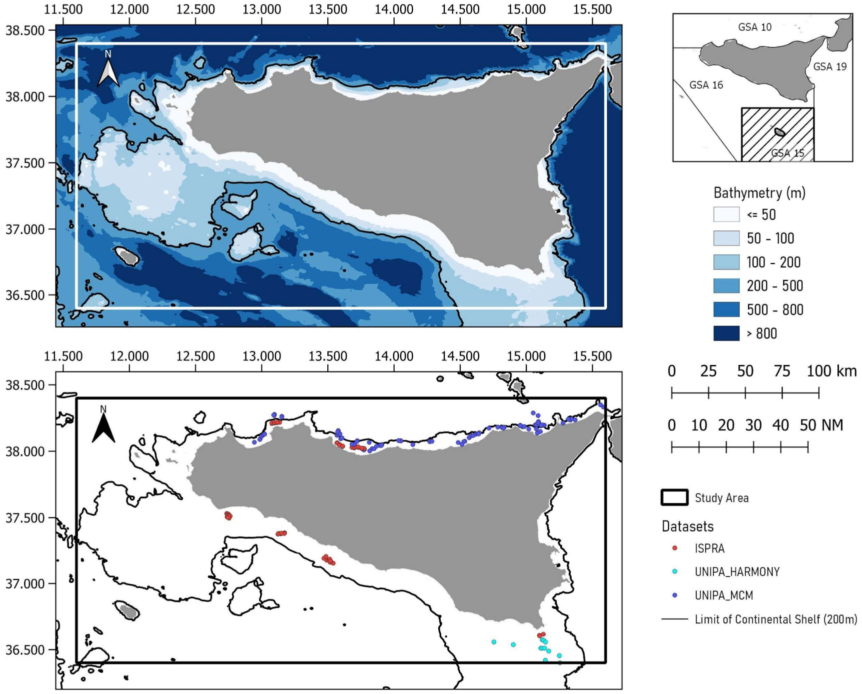

Figure 1: Selected study area and location of the trawl sampling points for each different dataset: Trawl survey campaign from Mangano et al. 2013 (blue points), ISPRA Italian National Monitoring Program campaign (red points) and Interreg HARMONY Project campaign (light blue points).

2.2 Fishing intensity and environmental variables

We used fishing intensity and six environmental factors to develop a model to predict the composition of the benthic community's longevity around the study area.

Fishing intensity was estimated using Vessel Monitoring System (VMS) data from bottom otter trawling vessels (with a length greater than 15m) available from 2007 to 2019 and expressed as the surface swept area ratio (SAR), which represents how many times a specific area is theoretically swept in one year [Eigaard et al., 2017]. SAR estimates were calculated at a spatial resolution of 1x1 km. No VMS signals were reported for depths shallower than 50m and areas within 3 nautical miles of the coastline, in compliance with the 2007 ban in the Mediterranean Sea (EU Council Regulation—EC No 1967/2006, 21 December 2006).

The environmental variables included in the models were sediment typology, depth, temperature, dissolved oxygen, primary production (expressed as mean chlorophyll concentration), and shear stress. We obtained the sediment Wentworth classification from the EUNIS habitat classification produced in [Vasquez et al., 2021] and depth information from the Digital Terrain Model (DTM) [Thierry et al., 2019]. Average temperature, primary production, and dissolved oxygen at the sea bottom were respectively extracted from [Simoncelli et al., 2014, European Union- Copernicus Marine Service, 2022] and [Teruzzi et al., 2021]. Shear stress due to waves and currents was extracted from [Rivier, 2010] as the 90th percentile, to account for events imposing strong constraints on the seabed while excluding extreme phenomena, over a period spanning from 2001, 2007 and 2009. The spatial distribution of environmental variables can be seen Figure 2, while the spatial and temporal variation of SAR is shown in Figure 3.

To obtain a single value per trawl sample, the midpoint of the trawl coordinates was used to assign a predictor value to each sample. We used fishing intensity values from an average of the three and five years before the sampling year when possible. We considered these two time periods because they can reflect the potential time for the response and/or recovery of the community [Hiddink et al., 2017]. Furthermore, we wanted to investigate if different spatial resolutions of fishing intensity would affect the estimation of the longevity composition of the community. To do it we considered using the original 1x1 km resolution of SAR and a downscaled version of 3x3 km resolution.

2.3 Longevity composition and impact assessment

Fishing impact assessments were conducted using three distinct approaches that were based on modeling the longevity composition of the benthic community, as described in [Rijnsdorp et al., 2020].

To begin, we converted the biomass proportion for each longevity class into a continuous scale by fitting a sigmoidal (logistic) function to the cumulative biomass, similar to the method de- scribed in the work by [Rijnsdorp et al., 2018]. This was done by applying a binomial generalized linear mixed model (GLMM) to the cumulative biomass proportions. We used the aforementioned environmental variables as predictors, along with fishing intensity. To account for potential spatial dependencies within the samples, we included Trawl ID as a random effect.

For the assessment, it was necessary to establish the longevity biomass relationship under untrawled conditions, so generally a cut-off criterion of SAR less than 0.1 is selected to detect reference samples representative of low exposure to fishing intensity [Bolam et al., 2017]. In regions where low fishing intensities are uncommon a cut-off criterium of 0.5 is recommended as a rule of thumb, instead of 0.1 otherwise it is possible to extrapolate the predicted longevity composition at an untrawled state adding fishing intensity to the model and setting it as zero [Pierucci et al., 2022]. To not lose information from sampled trawls, we considered it relevant to explore the usage of this higher cut-off point or to directly add fishing intensity in the model equation. Additionally, considering the limited representation of samples beyond the continental shelf, we examined whether excluding samples from depths greater than 200 meters would improve the model's fit. In total, we explored sixteen different conditions to model the longevity composition of our benthic community, taking into account the various factors and decisions mentioned above, including spatial resolution and time averaging of fishing intensity layers and cut-off points based on fishing intensity and depth (Table 1).

Table 1: Number of samples and summary of each predictor (mean ± standard deviation) for all the sixteen different conditions investigated to model the longevity composition of the benthic community. Incl/Excl = inclusion of SAR in the model or exclusion of samples with SAR =>0.5; 1km/3km = 1 x 1 km or 3 x 3 km resolution of the SAR layers; 3yrs/5yrs = 3 years or 5 years time period average for assigning fishing intensity to the samples; D/noD = exclusion of samples outside the continental shelf (> 200m) or inclusion of all the samples despite their depth. Unit of measure: Depth (m), Temperature (°C), Dissolved oxygen (µmol/l), Chlorophyll (mg/l),Shear stress (N/m2), SAR(1/year).

Condition	Sample size	N mud	N sand	N Granule-pebble	Depth	Temperature	Dissolved oxygen	Chlorophyll	Shear stress	SAR
Incl-1km-3yrs-NoD	173	76	83	14	136.1±136.2	15.0±1.2	207.6±9.7	0.14±0.05	0.012±0.026	2.65±4.30
Incl-1km-5yrs-NoD	173	76	83	14	136.1±136.2	15.0±1.2	207.6±9.7	0.14±0.05	0.012±0.026	2.25±3.52
Incl-3km-3yrs-NoD	173	76	83	14	136.1±136.2	15.0±1.2	207.6±9.7	0.14±0.05	0.012±0.026	2.41±3.82
Incl-3km-5yrs-NoD	173	76	83	14	136.1±136.2	15.0±1.2	207.6±9.7	0.14±0.05	0.012±0.026	2.06±3.10
Incl-1km-3yrs-D	143	49	80	14	83.4±39.2	15.2±1.2	209.7±9.1	0.15±0.05	0.014±0.028	2.55±4.45
Incl-1km-5yrs-D	143	49	80	14	83.4±39.2	15.2±1.2	209.7±9.1	0.15±0.05	0.014±0.028	2.17±3.67
Incl-3km-3yrs-D	143	49	80	14	83.4±39.2	15.2±1.2	209.7±9.1	0.15±0.05	0.014±0.028	2.41±4.06
Incl-3km-5yrs-D	143	49	80	14	83.4±39.2	15.2±1.2	209.7±9.1	0.15±0.05	0.014±0.028	2.05±3.29
Excl-1km-3yrs-NoD	87	45	37	5	94±61.7	14.9±1.1	206.6±10.6	0.15±0.05	0.005±0.020	0.06±0.11
Excl-1km-5yrs-NoD	92	45	37	10	98.8±63.2	14.9±1.1	206.9±10.4	0.14±0.05	0.004±0.020	0.08±0.13
Excl-3km-3yrs-NoD	88	48	35	5	96.8±62.4	14.8±0.88	206.7±10.4	0.14±0.05	0.003±0.008	0.08±0.12
Excl-3km-5yrs-NoD	88	48	35	5	96.8±62.4	14.8±0.88	206.7±10.4	0.14±0.05	0.003±0.008	0.08±0.11
Excl-1km-3yrs-D	80	38	37	5	79.4±37.7	14.9±1.1	207.6±10.4	0.15±0.05	0.005±0.021	0.05±0.10
Excl-1km-5yrs-D	85	38	37	10	85.4±43.9	14.9±1.1	207.9±10.2	0.15±0.05	0.005±0.021	0.07±0.14
Excl-3km-3yrs-D	80	40	35	5	81.0±38.1	14.8±0.9	207.6±10.3	0.15±0.05	0.003±0.009	0.08±0.12
Excl-3km-5yrs-D	80	40	35	5	81.0±38.1	14.8±0.9	207.6±10.3	0.15±0.05	0.003±0.009	0.08±0.12

When applying the SAR cut-off criterion, fishing intensity was excluded as a predictor, assuming that the sampled communities inherently reflected an untrawled state. Conversely, in models without the cut-off, SAR was included as a predictor in interaction with variables such as longevity, depth, and sediment type to detect its influence on biomass distribution. Therefore, the null model for the cut-off criterion included only longevity as a predictor, while the null model without the cut-off criterion included both longevity and SAR. This choice was driven by the necessity of estimating the biomass distribution of longevity classes in an untrawled state when using samples from various fishing intensities. Continuous predictors were natural log transformed to reduce the skewness of their distribution, especially fishing intensity, where a small value of 0.01 was also added to avoid taking the logarithm of zero.

We compared all possible model formulations for each of the sixteen conditions by employing the "dredge" function in the MuMIn R package [Barton, 2009] and selected the most parsimonious model after the null model using the Bayesian Information Criterion (BIC). BIC was preferred over the Akaike Information Criterion (AIC) due to its tendency to be more conservative in variable selection.

The selected models were subsequently used to assess which condition provided the most accurate estimation of community longevity composition. We compared each selected model to its corresponding null model to determine the percentage increase in explained deviation and its sig- nificance. The condition with the higher significant explained deviation was selected as the final model. This approach was chosen to facilitate a fair comparison of models, especially in cases where sample sizes differ significantly, as model selection criteria such as BIC or R2 would be biased.

To assess the impact, we applied three different approaches. The first method, known as the precautionary approach (L1), calculates the proportion of the community with longevity exceeding the reciprocal of trawling intensity in a specific area. It operates under the assumption that species may be impacted if trawled during their lifespan; thus, only species with longevity less than the average interval between two successive trawling events will not be affected. The estimation is derived by rearranging the logistic equation, with longevity set as 1/fishing intensity:

$$I_{L1} = \frac{\exp\left(\alpha + \beta_L * \ln\left(\frac{1}{S}\right) + \beta_H * H + \beta_S * \ln(S_0) + \beta_{LH} * \ln\left(\frac{1}{S}\right) * H + \beta_{HS} * \ln(S_0) * H + \beta_{LS} * \ln\left(\frac{1}{S}\right) * \ln(S_0)\right)}{1 + \exp\left(\alpha + \beta_L * \ln\left(\frac{1}{S}\right) + \beta_H * H + \beta_S * \ln(S_0) + \beta_{LH} * \ln\left(\frac{1}{S}\right) * H + \beta_{HS} * \ln(S_0) * H + \beta_{LS} * \ln\left(\frac{1}{S}\right) * \ln(S_0)\right)}$$

where α is the intercept of the model and β corresponds to the slopes associated with different predictors, where L stands for longevity, S for fishing intensity, and H for the environmental predictors. We set S_0 to 0.01 to prevent taking the logarithm of zero. It's important to note that the presence of interaction terms in the model may vary depending on the final model selection.

The second approach (L2) involves comparing the median longevity of the community at a specific trawling intensity to the value obtained under untrawled conditions. This method operates under the assumption that median longevity reflects the community's sensitivity to trawling. Therefore, an increase in fishing intensity results in a shift within the community toward shorter- lived species, leading to a decrease in median longevity. The equation for this approach is expressed as follows:

$$I_{L2} = 1 - \frac{M_S}{M_0}$$

where M_S and M_0 are, respectively, the median longevity at fishing intensity S and the median longevity of the untrawled community. Those are obtained from re-arranging the logistic equation as:

$$M_S = \exp(-\frac{\alpha+\beta_H*H+\beta_S*\ln(S)+\beta_{HS}*\ln(S)*H}{\beta_L+\beta_{HL}*H+\beta_{LS}*\ln(S)})$$

$$M_0 = \exp(-\frac{\alpha+\beta_H*H+\beta_S*\ln(S_0)+\beta_{HS}*\ln(S_0)*H}{\beta_L+\beta_{HL}*H+\beta_{LS}*\ln(S_0)})$$

Finally, we employed the population dynamic (PD) approach, as described in [Pitcher et al., 2017], which estimates the reduction in the community's biomass to its relative carrying capacity after trawling pressure occurs:

$$I_{PD} = \sum_{i=1}^{n} 1 - K_{Li} * (1 - S * \frac{d}{r})$$

whereK_{Li} is the biomass proportion of the longevity class i in the untrawled community, S is the fishing intensity, d is the depletion rate caused by the trawling gear and r is the recovery rate. Sediment-specific depletion rates resulting from bottom otter trawlers were obtained from [Pitcher et al., 2022], while the recovery rate was estimated with longevity using the equations derived from the meta-analysis in [Hiddink et al., 2019]. All three impact assessment methods were applied across the entire continental shelf surrounding Sicily using the parameters obtained from the model and the raster of the different predictors on a grid scale of 1 x 1 km. SAR values were extracted from the last year available in the VMS dataset (2019). To enhance the description of the impact assessment, a summary was provided for each sediment typology and GSA.

Statistical analyses were conducted using the R package, Version R-4.2.0 [R Core Team, 2023].

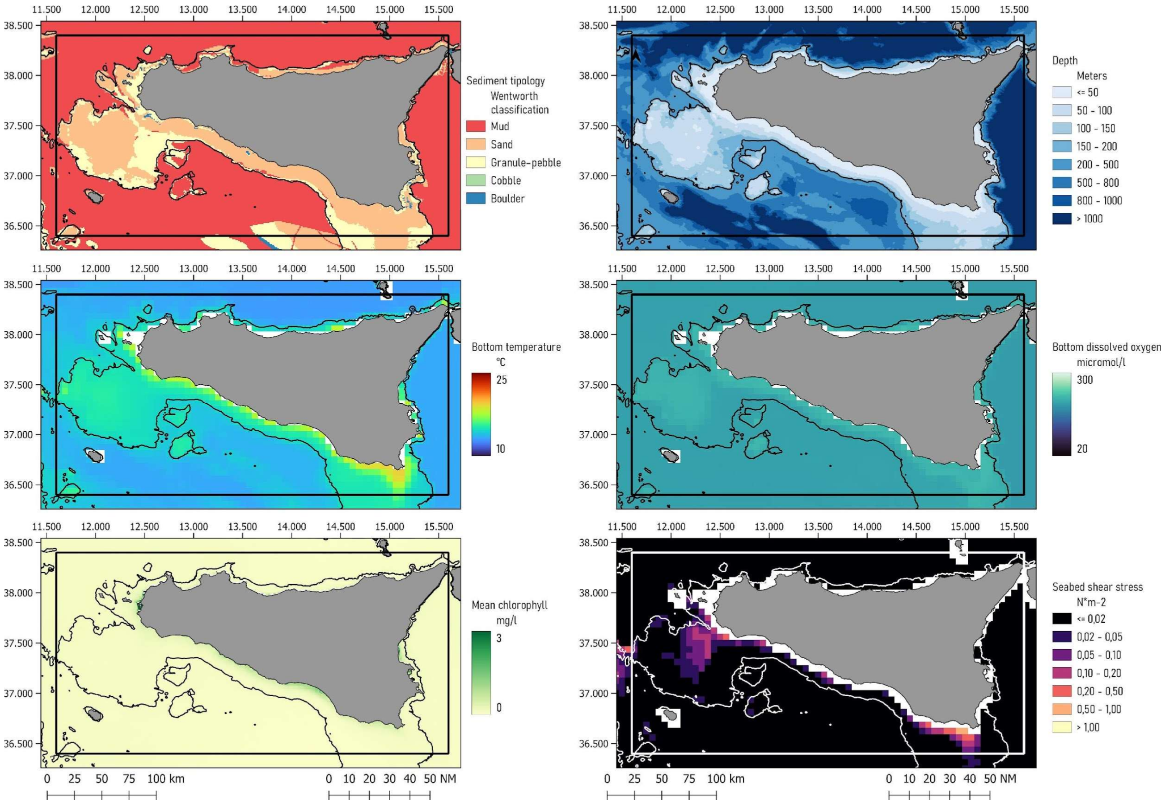

Figure 2: Spatial distribution of the six different environmental variables selected for estimating the longevity composition: sediment typology (Wentworth classification), depth (m), average annual bottom temperature (°C), average annual bottom dissolved oxygen concentration (µmol/l), annual bottom average chlorophyll concentration in the water column (mg/l) and seabed shear stress due to waves and currents (N/m2).

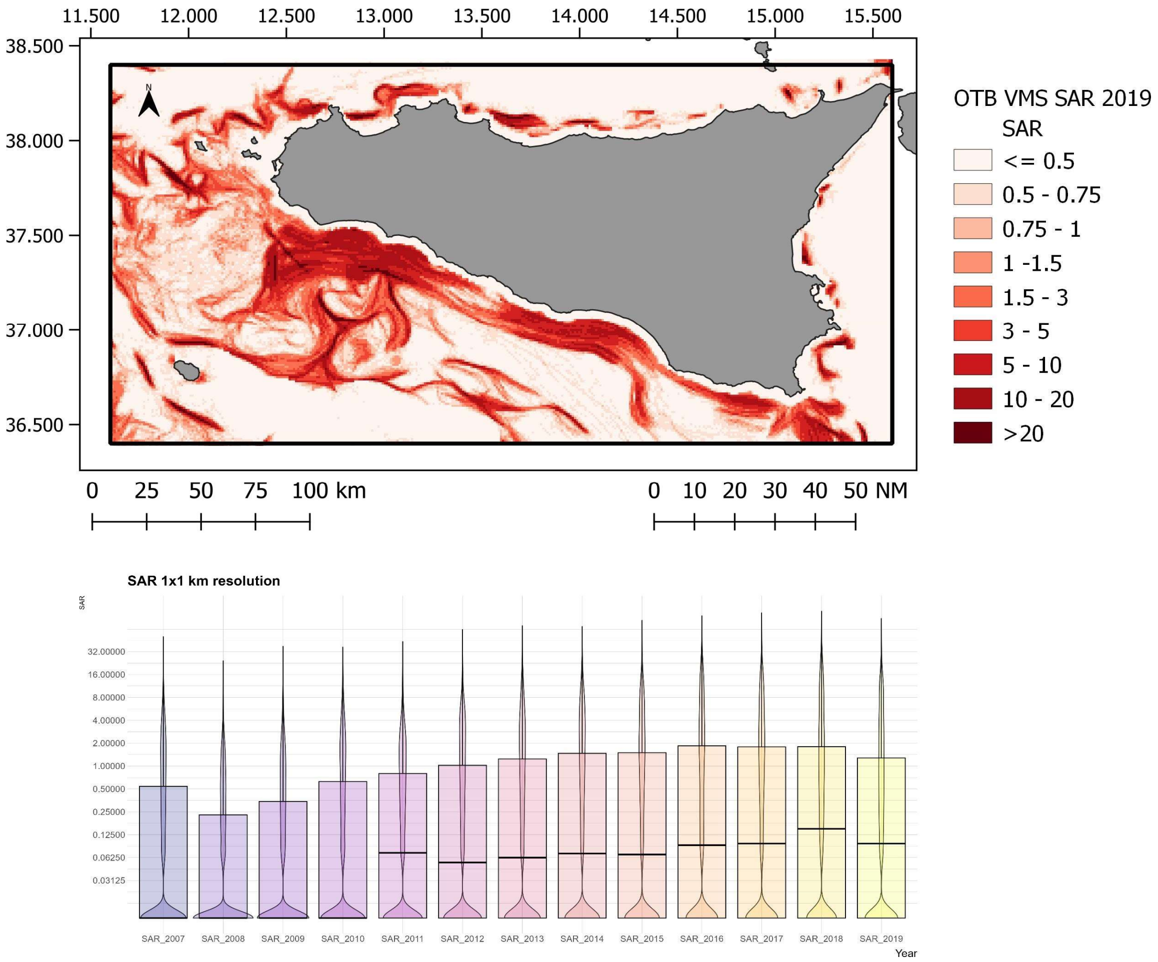

Figure 3: Spatial distribution of otter bottom trawling swept surface ratio (SAR) around the study area obtained from the analysis of VMS data. Below are the temporal distributions of the SAR values for each year starting from 2007 until 2019. SAR values were log-transformed, adding a small value of 0.01 to reduce the positive skewness and better visualize the distribution. The peaks at the bottom of the distribution correspond to values of SAR equal to zero.

3 Results

The Sicilian continental shelf primarily comprises sandy sediments (53.62%) in shallower regions, while mud (15.97%) and granule-pebble (29.92%) seabeds are prevalent in areas near the shelf edge. About 75% of the total area recorded SAR values exceeding 0, with an average of 2.36 ±3.55 years−1. The fraction with SAR >0.5 constituted 49%, with values greater than 5 years−1, predominantly spread across the shelf area of the Strait of Sicily and in proximity to the shelf edge throughout the region. Lower values are primarily observed below 50 meters depth and on the western side of the Adventure Bank and Hibleyan plateau (Strait of Sicily), as depicted in Figure 3. Sediment types exhibited similar trawling intensity values, although coarser sediments displayed a higher average (4.21 years−1) compared to sandy (2.94 years−1) and muddy (1.97 years−1) sediments.

3.1 Model selection

For the majority of conditions, null models were consistently found to be significant, with the lowest BIC. This is further emphasized by their high values of R2 and the low proportion of deviance explained by the different selected models compared to their null counterparts. Nevertheless, Depth proved to be the second most important predictor influencing the composition of longevity, in conjunction with fishing intensity. Only in four conditions, the selected model showed a BIC score lower than the null model and a significant increase of deviation explained (Table 2). Models at a coarser resolution (3x3 km) not only omitted the interaction term between depth and fishing intensity but also demonstrated a poorer fit compared to models that accounted for fishing intensity at a finer resolution (explaining a smaller portion of the deviance). Averaging fishing intensity over 3 and 5 years did not produce any noteworthy difference in model estimates.

These selected models were related to finer SAR resolution and a 3-year average period despite setting or not a SAR threshold for including samples in the model (see Table S2 and Table S3). We preferred to consider as the final model Model number 1 because models with a SAR cut-off criterion (number 13 and 14) led to halving the original sample size. According to the selected model, at greater depths, the proportion of long-lived species tends to increase. This relationship is slightly altered when the interaction term is introduced in the equation. Therefore, at greater depths (typically exceeding 100 meters), fishing intensity shifts the community towards species with shorter lifespans, whereas at shallower depths (less than 100 meters), higher fishing intensity tends to increase the proportion of long-lived species (Figure 4).

Table 2: Resulting models obtained through a stepwise selection procedure using the ’dredge’ function for each condition. Deviation explained is expressed as a percentage increase relative to the null model, while the p-value represents the significance of the difference between the deviance explained by the null model and the one explained by the selected model. For conditions using the SAR cut-off criteria, the null model considered only longevity as a predictor. In contrast, for the conditions without the cut-off, the null model considered both longevity and fishing intensity. Asterisks indicate the significance of the predictor’s slope coefficient inside the logistic function: * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$.

Model No.	Condition	N samples	(Intercept)	Depth	ll	SAR	Depth:SAR	df	BIC	R2	Deviation explained	p-value
1	**Incl-1km-3yrs-NoD**	**173**	**-6.5391**	**0.2194**	**2.5824*** **	**-0.907** **	**0.2037** **	**6**	**144.959**	**0.778**	**7.71%**	**0.0121**
2	**Incl-1km-5yrs-NoD**	**173**	**-6.5762**	**0.2306**	**2.5802*** **	**-0.9085** **	**0.2043** **	**6**	**145.3**	**0.777**	**7.50%**	**0.0135**
3	Incl-3km-3yrs-NoD	173	-4.2454	-0.1803	2.0678***	-0.0033		5	154.6	0.6761	0.76%	0.3352
4	Incl-3km-5yrs-NoD	173	-4.2234	-0.1842	2.0678***	-0.0007		5	154.6	0.6761	0.79%	0.3239
5	Incl-1km-3yrs-D	143	-6.3979	0.1675	2.6031***	-0.8967*	0.2003	6	118.6	0.7794	5.12%	0.1139
6	Incl-1km-5yrs-D	143	-6.4845	0.1896	2.6021***	-0.9127*	0.2044	6	118.7	0.7792	5.16%	0.1113
7	Incl-3km-3yrs-D	143	-3.3783	-0.4306	2.1365***	-0.0016		5	122.7	0.6905	1.84%	0.1913
8	Incl-3km-5yrs-D	143	-3.3541	-0.4352	2.1365***	0.0007		5	122.7	0.6905	1.89%	0.1858
9	Excl-1km-3yrs-NoD	87	-2.6148	-0.6059	2.5583***			4	80.9	0.7742	5.35%	0.0714
10	Excl-1km-5yrs-NoD	92	-2.9556	-0.5004	2.5177***			4	87	0.7682	3.81%	0.1128
11	Excl-3km-3yrs-NoD	88	-3.7751	-0.2988	2.0798***			4	84.6	0.6794	1.48%	0.3381
12	Excl-3km-5yrs-NoD	88	-3.7751	-0.2988	2.0798***			4	84.6	0.6794	1.48%	0.3381
13	**Excl-1km-3yrs-D**	**80**	**-0.9896**	**-0.9994***	**2.5515*** **			**4**	**73.3**	**0.775**	**9.79%**	**0.0195**
14	**Excl-1km-5yrs-D**	**85**	**-1.9412**	**-0.7358**	**2.4941*** **			**4**	**80.3**	**0.766**	**6.15%**	**0.0531**
15	Excl-3km-3yrs-D	80	-2.1173	-0.6972	2.0669***			4	75	0.6778	5.58%	0.0799
16	Excl-3km-5yrs-D	80	-2.1173	-0.6972	2.0669***			4	75	0.6778	5.57%	0.0799

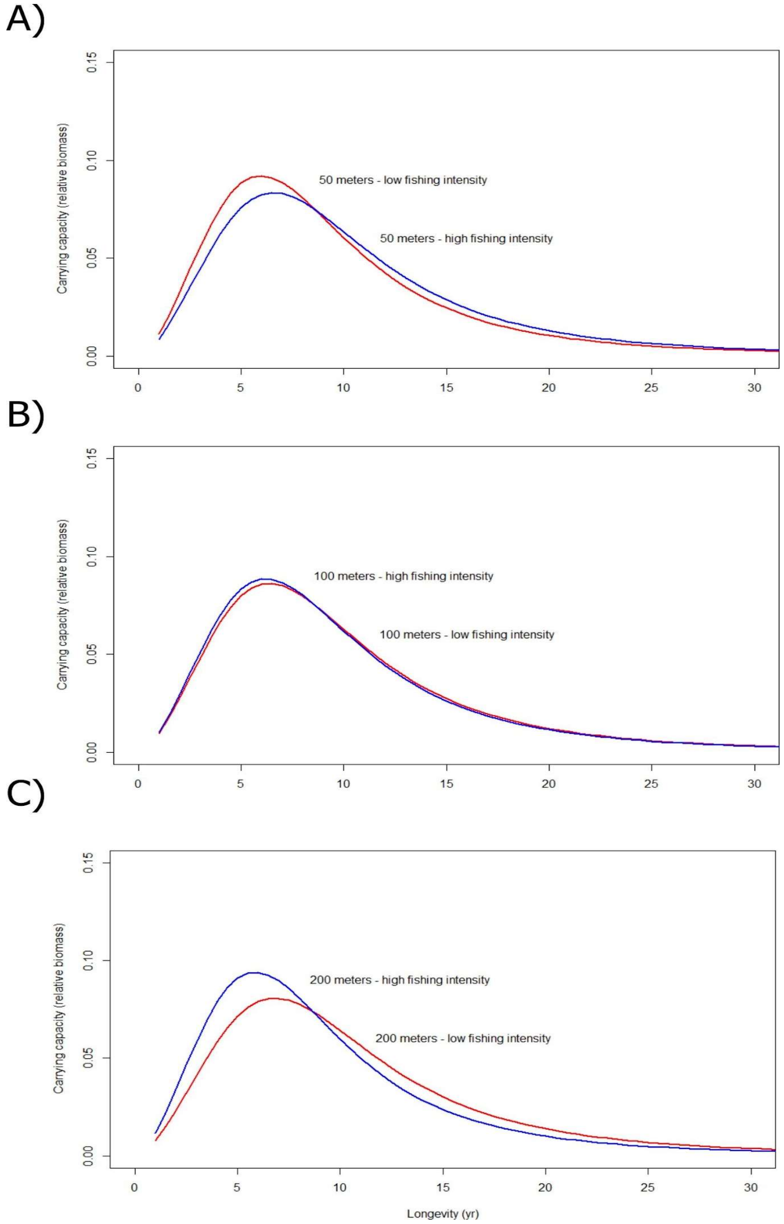

Figure 4: Longevity relative biomass curve distributions obtained from the final selected model (no cut-off SAR criteria, 1x1 km SAR resolution, 3 years average with no depth limit) at different depths (A = 50m, B = 100m and C = 200m) and fishing intensities (low SAR (red) = 0.1 and high SAR (blue) = 1).

3.2 Impact assessment

The median longevity estimates of all models exhibit a high correlation, as represented in Figure S1. While the distribution of these estimates within the continental shelf remains consistent across the models, there are slight variations, as illustrated in Figures S1, S2, S3, and S4. The community is predominantly characterized by species with medium to long lifespans, with a median longevity of approximately 8 years (7.5±1.8 considering the cut-off model and 8±2.1 without it). Lower median longevities are observed near the coast, with a gradient that increases as it moves towards greater depths, as previously indicated (see Figure 5).

A summary of the overall estimates of the three different approaches and for each sediment typology is presented in Table S4.

3.2.1 Precautionary approach L1

The L1 approach estimation revealed that, overall, 63% of the continental shelf exhibited values greater than 0.8. This indicates that in more than half of the area, at least 80% of the community would be impacted by trawling. This situation arises from a community primarily comprised of species with medium to high longevities and fishing intensities generally exceeding 0.5-1 year−1, resulting in significant impacts on any species with a longevity surpassing 1-2 years (see Figure 6). This phenomenon is particularly pronounced in GSA16, where median values are consistently close to 1 across different types of seabeds, as depicted in Figure 7.

3.2.2 Statistical-impact approach L2

Reflecting the spatial distribution of longevity, estimates for the L2 approach generally indicate a low impact, with only 10% of the total area demonstrating a reduction in median longevity of more than 20%. This is particularly noticeable in the Graham Bank, situated in GSA16 in the central part of the Sicily channel, and in the offshore bottoms south of Capo Passero (Hyblean plateau), as depicted in Figure 6.

Due to the presence of the interaction term between fishing intensity and depth, the median longevity of the untrawled community was found to be lower within the depth range of 50 to 100 meters, resulting in negative values (approximately 28% of the total area), indicating higher median longevity in comparison to the untrawled state. Higher values are concentrated in muddy sediments of GSA19 and granule-pebble sediments of GSA 16 (see Figure 7, Table S4).

3.2.3 PD approach

The average impact estimated for the PD approach is 0.16 ±0.17, and, overall, 66% of the shelf has a value less than 0.2, displaying a positively skewed distribution mirroring the trawling distribution. These values suggest that the continental shelf is in relatively good condition, particularly along the coasts of the north side, except for areas within GSA16 near the mentioned fishing grounds (Figure 6). High impacts are observed at the very edge of the shelf and the beginning of the continental slope in GSA10, likely due to the steeper bathymetric gradient and the spread of fishing pressure to deeper bottoms. GSA16 appears to have a relatively higher impact compared to the other two subareas, with muddy and granule-pebble sediments being more adversely affected than sandy ones, owing to the different depletion exerted by bottom trawl gear (see Figure 7, Figure S6, Table S4).

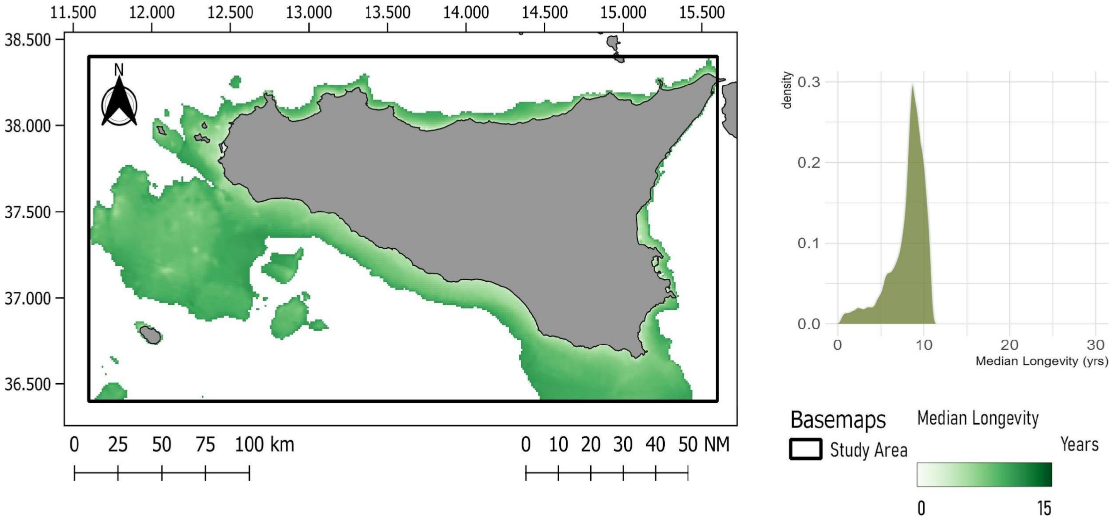

Figure 5: Median longevity distribution across the area based on the selected final model (no cut-off SAR criteria, 1x1 km SAR resolution, 3 years average with no depth limit). On the right, a density plot illustrates the distribution of scores across the map.

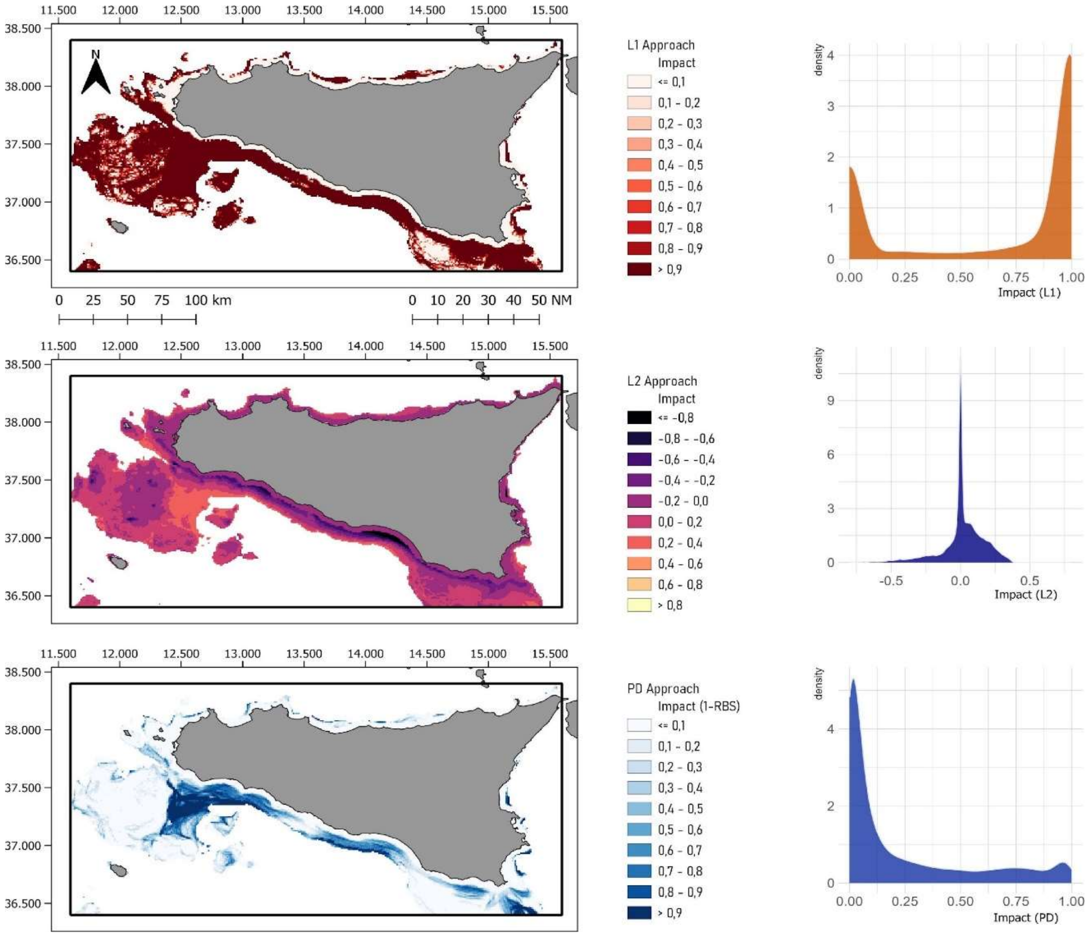

Figure 6: L1 (up), L2 (middle) and PD (bottom) impact assessments across the area based on the selected final model (no cut-off SAR criteria, 1x1 km SAR resolution, 3 years average with no depth limit). On the right, density plots illustrate the distribution of scores across the map.

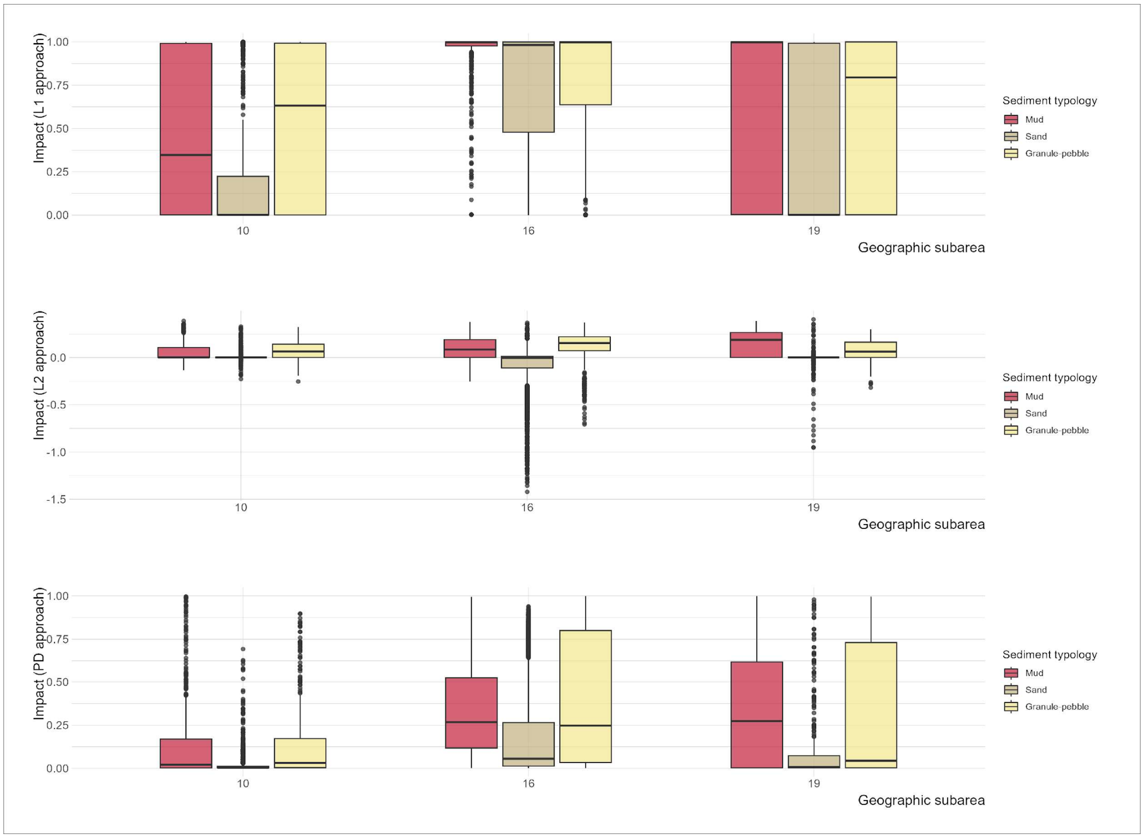

Figure 7: Summary boxplots of the three different impact assessment approaches for each GFCM Geographic Subarea and sediment typology inside the continental shelf of the study area.

4 Discussion

The epifaunal community around the Sicilian continental shelf features species with medium to high lifespans, ranging from 3 to 10 years or more. The median longevity, influenced by depth, fishing intensity, and their interaction, remains at 8 to 9 years across models. Among the impact assessment methods, the L1 approach shows low spatial variation due to high SAR values and the overall high median longevity. However, it still indicates notable impact. The L2 approach reveals a substantial 20% decrease in median longevity on the eastern side of the Adventure Bank in GSA 16 and the offshore bottoms south of Capo Passero (Hyblean plateau), widely recognized as critical areas for trawling activities owing to their high productivity. Despite that, the L2 approach yields negative scores inside trawled areas between 50 and 100 meters depth due to the significant interaction term found in the longevity models.

The PD approach is the clearest, detecting hotspot areas of impact corresponding to peaks in trawling intensity distribution. This is attributed to its exclusive reliance on estimating longevity composition in an untrawled state. Furthermore, it consistently produces a similar distribution of output values, irrespective of the conditions used in the models. In hotspot areas marked by the PD approach, the benthic community is diminished by nearly 100% of its relative carrying capacity, indicating significant impact.

4.1 Effect of depth and fishing intensity on longevity

Variations in demersal and benthic community responses to depth and fishing disturbance are not only reported in this study but also in various areas across the Mediterranean Sea [Labropoulou and Papaconstantinou, 2000, Demestre et al., 2000a, Dimech et al., 2008, Mangano et al., 2013, Dominguez-Carri´o et al., 2022, Jac et al., 2022].

Depth is inherently linked to gradients of variables like temperature, primary production, nutrient concentration, sediment characteristics, and current patterns, potentially limiting species distribution. Consequently, it may emerge as the primary driver of community distribution.

In our study, at low fishing intensities, the community's median longevity increases with depth. Deeper areas are more homogeneous and less prone to terrigenous inputs compared to coastal environments [Micheli et al., 2013]. This results in environmental gradients that become more homogeneous in deeper environments, as observed in the spatial distribution of the environmental predictors used in our models.

Homogeneous and stable conditions favor species with life histories that invest more in somatic maintenance, producing fewer but high-probability-of-survival offspring, optimizing resources, and ensuring reproductive success [Reznick et al., 2000]. These life histories, associated with later maturity, lower annual reproductive output, and lower natural mortality, lead to larger sizes and longer lifespans due to compensatory adjustments in individual energy budgets [Healy et al., 2014]. In shallow habitats, fast-growing species with shorter lifespans have a better chance of surviving high-disturbance environments and increased competition in high-energy settings [Van Denderen et al., 2015]. Consequently, deeper areas are generally more sensitive to trawling [Hiddink et al., 2006].

Our models also suggest that in middle-outer shelf areas (more than 100m depth), an increase in fishing intensity shifts the community to species with shorter lifespans. This behavior is consistent with literature findings and forms the basis of using longevity as an indicator of trawl sensitivity. Longer-lived species, connected to lower growth and reproduction rates, require longer recovery times to restore pre-disturbance biomass levels. Therefore, in scenarios where fishing intensity remains high and constant for extended periods, species with shorter lifespans are progressively selected as they can grow and reproduce in the time window between trawl passages or rapidly recolonize trawled areas.

Moving towards the inner part of the shelves (depth less than 100m), an increase in fishing intensity slightly increases the average lifespan of the community. Although unexpected, as it contradicts normal assumptions about the negative effects of trawling on longevity composition, this response may be linked to different depletions caused by sediment characteristics and the local response of certain species influencing model results.

Our community appeared relatively homogeneous, with approximately 30% of the recorded species always present along the sampled fishing intensity gradient. These persistent species account for the majority of the community biomass and are commonly found in the Mediterranean Sea on shelf areas [Colloca et al., 2003; Massutı and Renones, 2005; Mangano et al., 2013; Terribile et al., 2016]. Some of these species, including scavenger starfish of the *Astropecten* genera, decapods like *Aegaeon lacazei*, *Calappa granulata*, *Dardanus arrosor*, *Liocarcinus depurator*, *Polycheles typhlops*, *Medorippe lanata*, as well as deposit feeders like certain sea urchins such as *Diadema setosum* and *Echinus melo*, and holothurians like *Parastichopus regalis* and *Paraleptopentacta elongata*. Their opportunistic behavior allows them to have greater trophic plasticity, feeding on both live and dead organic matter. This, combined with rapid growth rates, enables them to compensate for the removal effect caused by trawling, potentially leading to increased abundances after trawling events [Tillin et al., 2006; Hinz et al., 2009; Mangano et al., 2013]. However, despite this adaptability, these epifaunal species demonstrate medium to high longevity, typically ranging from 3 to 10 years. We also frequently observed suspension feeders with lifespans exceeding 10 years in our samples, including sea pens (*Pennatula phosphorea*, *Pennatula rubra*, and *Pteroeides spinosum*), crinoids (*Antedon mediterranea* and *Leptometra phalangium*), ophiuroids like *Astrospartus mediterraneus*, and soft corals of the genera *Alcyonium*.

Unlike sessile hard corals, soft species like *A. palmatum* could be more resilient due to their relatively higher reproduction capacity, linked to planktonic larvae stages that can disperse for kilometers from the spawning point and relatively faster settlement periods [Kaiser et al., 2018]. Some of these species can retract beneath the sediment in response to physical pressure, such as towing activities [Chimienti et al., 2018]. In [Rijnsdorp et al., 2018], it is observed that for epifaunal taxa and suspension feeders, trawling shifted the community toward longer-lived taxa.

These observations suggest that these species, although highly vulnerable, may be found in trawled areas. So even though chronic trawling has reduced their biomasses, their distribution is probably no longer shaped by trawling but by other environmental constraints or due to the turnover of species distribution along the depth gradient [Ambroso et al., 2013, Pierdomenico et al., 2018]. As a consequence, intermediate depths in our study would show an increase in the median longevity of the community further enforced by the presence of scavenger species that mostly belong to intermediate-long lifespan categories.

Sediment composition may also play a role because sandy sediment, prevalent in the shallower part of our study area, creates greater resistance to the penetration of fishing gear compared to muddy sediments, thereby reducing the fraction of biomass extracted in a single pass [Pitcher et al., 2022]. Similar to findings in [Handley et al., 2014, Bolam et al., 2014, Rijnsdorp et al., 2018, Rijnsdorp et al., 2020], our muddy sediments tend to be more impacted than coarser sandy ones. Therefore, although sediment typology is not among the final predictors guiding longevity composition, it cannot be excluded that they may influence the mortality rate of certain species. Observing the behavior of individual species such as *A. palmatum* in the collected samples, it is noted that in deeper environments, it responds negatively to the increase in fishing intensity, whereas in shallower environments, this trend is not observable, precisely because in muddy sediments, trawling can induce higher mortality rates. This response is further complemented by the presence of environmental conditions favorable to these species, as shelf areas around Sicily could potentially generate high-energy zones where upwelling can occur [Pinazo et al., 1996; Beranger et al., 2004]. This, combined with terrigenous nutrient input and favorable seabed slope and granulometry, can create suitable habitat conditions, which, even though they do not directly reduce the negative effect of trawling, can facilitate the settlement and growth of new individuals [Dominguez-Carrio et al., 2022].

As a consequence, depletion and recovery of these species may locally exhibit rates different than those assumed by the models and solely based on the longevity of the species.

It is essential to note that, despite the influence of depth and fishing intensity, the models generally explained only a small portion of the deviance compared to their null model. This suggests that the predictors investigated provide a limited explanation for the longevity composition within the study area and community variation may be linked to random noise. In the Strait of Sicily, fishermen consistently exploit the same core fishing grounds for extended periods, and several studies have reported intense seabed exploitation on the continental shelf and slope across the study area [Gristina et al., 2006, Fiorentino et al., 2008, Knittweis et al., 2013]. These findings support the high and stable over time SAR values we measured. As a result, a shift in fishing intensity within the sampled fishing grounds leads to less variation compared to more sensitive areas. While the initial trawling impact is typically the most significant [Hiddink et al., 2017], subsequent towing activities protracted over time in the same area promotes resilient species in the long term, resulting in less variation observed among trawled grounds, even in the presence of gradients [Neumann et al., 2016].

4.2 Uncertainity and limitations

Trawl samples, due to their large area sampled, could underestimate changes in habitat characteristics at small scales. A single trawl pass can encompass various sediment types, leading to a mixed assemblage [Terribile et al., 2016]. For example, in GSA 16, the presence of banks and volcanic areas could form heterogeneous environmental gradients that the sampling design and satellite data may not capture [Spatola et al., 2018]. This may mask the contribution of certain variables in the models, such as sediment composition. This scale effect is demonstrated by the lack of interaction between depth and fishing intensity at larger spatial scales, suggesting that higher resolutions would be more sensitive in detecting changes in the community. Nonetheless, investigating through different data conditions to estimate the longevity composition, as we did in this study, is a useful approach for better understanding the dynamics that shape the functional space of the community.

The sampled assemblage is derived from trawl samples, which predominantly depict species with longer lifespans. In contrast, grab samples primarily collect short-lived infaunal species. This may lead to an underrepresentation of the latter group, with the effect of overestimating impact basing community sensitivity only on the long-lived portion of the community but also reducing the overall variability that the community may exhibit over environmental and anthropogenic gradients in the study area. Combining grab and trawl samples can offer a more comprehensive picture of the community's longevity composition, as suggested in similar studies [Rijnsdorp et al., 2018, Rijnsdorp et al., 2020, Pierucci et al., 2023].

In addition to the uncertainty stemming from estimating longevity composition, parameter selection for different approaches also introduces uncertainty into the final estimations. Local species responses, influenced by environmental context and life-history adaptation, may not align with assumed depletion and recovery rates, leading to deviations in impact estimates, as observed in the L2 approach. Single-trait response approaches, as mentioned in [Beauchard et al., 2021], may fail to detect community changes due to anthropogenic disturbances. While lifespan may not always be the most responsive trait to trawling pressure, it is strongly linked to key functional aspects of a species. Additionally, the capacity of the benthic community to recover following trawling impact as a function of lifespan is supported by results found in the literature [Hiddink et al., 2019].

4.3 Management implications and conclusions

Mapping regional trawling impact and benthic status may help informing policymakers in identifying sensitive or high-risk areas and then address more effective spatial management measures. The assessment, using PD and L2 metrics, revealed a negative response near shelf-edge areas, notably the eastern side of Adventure Bank and northwestern side of Malta Bank, critical nursery grounds for various commercial species [Farrugio and Soldo, 2014]. Despite those specific zones are not primary trawling grounds, we measured SAR values exceeding 10 year-1, causing an 80-100% reduction in benthic biomass, posing a significant threat to community recovery. This threat is more concerning within the RFA of the Adventure Bank, where trawling has been banned since 2016 (REC.CM-GFCM/40/2016/4) and our estimated impact in this area are supported by recent reports of illegal fishing activities detected through the VMS data in these areas [Alvarez et al., 2021].

Numerous studies in the Mediterranean have demonstrated that demersal assemblages, which encompass many commercial species, are intrinsically linked to the structure of macro-epibenthic communities [Colloca et al., 2003, Massutı and Renones, 2005]. Benthic community decline affects demersal species' productivity, reducing catches and potentially harm the livelihoods of the fishery sector. Prioritizing bottom-up processes to rehabilitate the benthic community benefits long-term demersal productivity and promotes spillover to adjacent trawling grounds.

Impact assessment methodologies, such as the one used in this study, will help in identify high-risk areas and the mechanisms regulating such occurrences. Operating through quantitative models allows exploring the setting of impact thresholds to preserve and manage areas of interest. In our study context, for example, it is possible to use the relationships found in the models as a basis to estimate different impact scenarios with changing spatial distributions of fishing intensity. Consequently, it would aid in monitoring the conditions within the existing Restricted Fishing Areas (RFA) to ensure strict adherence to the trawl ban. Furthermore, as suggested by the results of this study, reconsidering spatial boundaries for restrictions may be warranted to encompass the recovery of the benthic community and amplify protective effects on the overall community within the area. This extension of benefits would undoubtedly have a positive impact on the fisheries sector as well.

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Chapter 4: Trait-based framework to assess the vulnerability of marine communities to bottom trawling activities

1 Introduction

The marine environment is strongly influenced by human activities, with more than 90% affected by anthropogenic stressors [Halpern et al., 2015]. Despite the ecosystem services these environments offer to humanity, human activities exert different pressures on ecosystems, compromising the services from which we benefit [Schröter et al., 2005, Menegon et al., 2018]. In response, the management and conservation of these resources are necessary to ensure that human activities occur efficiently, safely, and sustainably. Tools such as Maritime Spatial Planning (MSP) are increasingly used in the planning of marine activities to reduce conflicts among anthropogenic activities, and enhance the sustainability and reduce environmental impacts of maritime operations [Douvere, 2008, Tuda et al., 2014]. This is achieved through environmental protection measures, such as assigning protected areas, and identifying opportunities for multiple uses of space through the use of the best available data, which requires assessments of the impacts of human activities on ecosystems. Spatially explicit vulnerability assessments that link information on the sensitivity of the environment to the occurrence of a pressure are fundamental to the implementation of spatial management [Metzger and Schröter, 2006]. Ecological vulnerability is characterized by: the exposure of the system to disturbance, depending on the characteristics of the disturbance (type, intensity, frequency, duration, etc.); the sensitivity of the system to disturbance, i.e., the degree to which the disturbance affects the system, positively or negatively, based on its characteristics; and its capacity to adapt and recover from it [Adger, 2006, Mumby et al., 2014, Pacifici et al., 2015]. Methodological frameworks for assessing the vulnerability of marine communities to multiple pressures have been developed [Halpern et al., 2008, Stelzenmüller et al., 2010, Patrick et al., 2010, Depestele et al., 2014, Ocaňa et al., 2019], with many of them using trait-based approaches (TBAs) [Certain et al., 2015, Jones and Cheung, 2018, Gonzàlez-Irusta et al., 2018, De Juan et al., 2020, Beauchard et al., 2021].

TBAs are founded on the theory that species expressing similar biological and life-history characteristics undergo similar selective pressures from environmental and anthropogenic gradients. Thus, such traits can serve as proxies for the main descriptors of an individual's fitness: growth, reproduction, and survival [Violle et al., 2007]. This allows them to often be considered reliable indicators of habitat ecological integrity, as they can predict how ecosystem functions change under specific stresses by identifying the group of species that regulate or control particular processes, along with the traits they possess to withstand these stresses [Lavorel, 2013]. In this study, we develop a trait-based framework to assess the vulnerability of the benthic community to bottom trawling impact. Trawling is one of the main human impacts affecting continental shelves worldwide [Amoroso et al., 2018], causing direct abrasion and resuspension of the seabed [O'Neill and Summerbell, 2011] and increasing species mortality. Furthermore, it generates indirect effects, including the alteration of food web dynamics through the introduction of discarded bycatch and selective removal of species [Queiròs et al., 2006, Hiddink et al., 2017, Eggleton et al., 2018] and the alteration of biogeochemical processes occurring in the sediments [Bradshaw et al., 2021]. This activity, over the long term, changes the community structure by selecting species less vulnerable [Tillin et al., 2006, Mangano et al., 2013]. The relative abundances of species with such ecological and biological characteristics can therefore be used to detect the impact of trawling on communities across different gradients and habitats. Therefore, we can develop trait-based ecological indicators for the assessment of the vulnerability of biological assemblages to trawling activities on a large scale to underpin management decisions.

In recent years, benthic ecologists have delved into the application of TBAs, focusing on assessing the impact of trawling activities on these communities [ICES 2017]. Various approaches follow a qualitative "susceptibility-resilience" framework, where different traits are selected based on the prior assumption that they respond to abrasion [Foveau et al. 2017, Gonzàlez-Irusta et al., 2018, Ocaňa et al., 2019, de Juan et al., 2020, Beauchard et al., 2021, Hinz et al., 2021]. The selection process is guided by expert judgment or common knowledge from the literature, defining the direction in the response of different trait modalities and their scoring within the indicator model.

One advantage of these approaches is their flexibility, allowing for relatively rapid assessments across multiple species, which can aid in prioritizing conservation planning and implementing adaptation schemes [Beauchard et al., 2021]. Moreover, they are often considered user-friendly, as they do not require complex modeling techniques and can utilize open-source information on species characteristics. However, these approaches are highly sensitive to the selected pool of traits, and precise vulnerability scores associated with each trait are often unknown, leading to the need for arbitrary, relative thresholds for trait modalities [Pacifici et al., 2015]. Furthermore, despite recent spatial applications of such indicators [Gonzàlez-Irusta et al., 2018, Ocaňa et al., 2019], few incorporate this feature, reducing their capacity to describe the magnitude of fisheries impacts and the requirements for measures to meet management objectives.

On the other hand, other indicators rely on mechanistic relationships linking population dynamics to the removal caused by trawling on the seabed [Duplisea et al 2002, Zhou et al. 2008, Pitcher 2014, Pitcher et al. 2017, Hiddink et al., 2019]. These approaches often directly model species populations or focus on a single trait, such as species lifespan, to derive specific parameters required for the indicator model, using it as a proxy for modeling, as an example, the recovery capacity of species when disturbance conditions change [Hiddink et al., 2019]. These approaches have the advantage of quantitatively defining the impact caused by trawling and often produce spatial estimates of impact and the state of the associated community. However, they typically require a larger amount of information and sufficient data to develop the models on which the indicator parameters are based [Pacifici et al., 2015]., although some of these approaches have been developed to require less data [Pitcher et al. 2022]. Additionally, they may lose effectiveness if other traits within the community better capture the variation induced by trawling, especially if long-term impacts have already pre-selected the trait modalities on which the indicator is based [Beauchard et al., 2017].

In light of this, the objective of our study was to develop a vulnerability framework based on multiple traits associated with trawling disturbance, aiming to provide a semi-quantitative tool capable of spatially mapping the vulnerability of benthic communities based on the fishing intensity of a given area of interest. In this framework, particular attention was paid to the selection and parameterization of traits within the indicator, leveraging effect sizes obtained from meta-analyses and empirical studies to reduce the subjectivity in assigning the effects of trawling on the response of selected trait modalities. These effects are then linked to spatial distribution models of these traits to create a map of the sensitivity of the studied community, which can be associated with the degree of exposure to pressure determined by the intensity and spatial distribution of trawling. Consequently, the approach can provide a quantitative and spatially explicit estimate of the potential change in the community due to trawling.

Furthermore, a sensitivity analysis was conducted to verify the contribution of each trait within the indicator in order to understand which characteristics of the community primarily define its sensitivity. This approach allows for a more rigorous guidance in the inclusion of certain traits in indicator development and provides negative feedback on how to improve the overall approach and where efforts should be focused to assess the impact on the community.

The entire framework was applied to benthic epifaunal communities in a heavily fished scenario in the Central Mediterranean Sea. This decision was made to test the framework in a realistic setting where a vulnerability assessment could help identify key target areas for management action. Additionally, it allows for comparison of the results with other impact assessment approaches applied in the same area, thereby aiding in result interpretation and validating their reliability.

2 Methods

This section describes the development and application of a methodological approach to estimate the benthic community's vulnerability to trawling activity. This approach is based on the use of the biological traits of the species that make up the community to define their response to the variation in fishing intensity. The first part focuses on defining the rationale of the approach and the criteria for selecting traits that describe the community's sensitivity to trawling. Subsequently, equations are presented that combine the sensitivity of each species into a single measure of the overall sensitivity of the sampled community, as well as one that integrates sensitivity with the actual distribution of trawling disturbance. In the second part of the methods, the entire framework is applied to a regional context as a community response indicator of vulnerability/impact to assess its performance and to compare the results obtained with those produced by the application of other trawling impact assessment approaches, such as the population dynamic (PD) approach [Pitcher et al., 2017].

2.1 Vulnerability framework

Our approach aligns with the criteria established for the Marine Evidence-based Sensitivity Assessment (MarESA) methodology, developed by the Marine Life Information Network (MarLIN) team [Tyler-Walters et al., 2023]. Sensitivity, as defined in this methodology, refers to the likelihood of change when an impact caused by an activity (pressure) is applied to a feature (receptor). This likelihood is dependent on the feature's ability to tolerate or resist change (resistance) and its capacity to recover from the impact (resilience). The pressure acts with a certain extent, magnitude, and duration, thereby defining its exposure. Vulnerability is defined as the likelihood of a feature's exposure to a pressure to which it is sensitive.

Bottom trawling is associated with the abrasion/ disturbance effect on the seabed surface and the removal of species. To discern the sensitivity of the community in our study to this pressure, we used species-level ecological characteristics and life history traits. Exposure to the impact of bottom trawling is determined by its spatial distribution, expressed as the Swept Area Ratio (SAR). SAR represents the number of times an area is swept over a time period, taking into account the number of passages and the width of the gear employed. This metric has proven to be reliable in describing and mapping trawling effort across continental shelves worldwide [Eigaard et al., 2017, Amoroso et al., 2018].

The target of the application is epifaunal species found in trawl catch assemblages (although the entire framework could be expanded to a wider range of species once trait information and effect sizes become available) and the final output represents the expected change in the community's abundance as a function of bottom trawling intensity level.

2.2 Trait selection and index parametrization

The traits considered are derived from a literature review aimed at identifying the most responsive traits related to trawling impact. The review encompassed studies that used any biological or life- history-related characteristics as response traits to trawling, accounting for both gradient studies and before-after impact designs. It reported the proportion of positive, negative, or neutral effects of trawling for each modality of the selected traits (see Section1.1 for more details about the method and results). Based on the observed patterns found in the review, the traits were selected and divided into primary and secondary traits. Primary traits are longevity, mobility, sediment position, and size (expressed as maximum length); secondary traits include feeding mode, body protection, egg development, and larval development (Table 1). Primary traits are considered those that showed higher proportion of studies indicating negative or positive directional pattern of response along fishing intensity gradients, while secondary traits are those with a response pattern not as well-defined as the primary ones due to the higher number of studies reporting neutral effect of fishing in the trait modalities but that can help account for certain variations in life-history strategies of the species within the community as a response to trawling. Furthermore, the considered traits are only those for which a quantitative change, as a function of trawling intensity, could be associated with information derived from empirical studies and meta-analysis extracted from the pool of the review.

To differentiate the contributions of the traits in the indicator, we relied on results gathered from our literature review regarding the frequency of directional versus neutral effects of fishing intensity on the modalities of the selected traits. To underscore their significance in determining the final sensitivity of the community, we assigned a weighting factor (Wf) to both primary and secondary traits. The weighting factor for the primary traits was set arbitrarily to a value of 1 in order to fully account the variations led by those traits, while for the secondary trait, it was set to 0.5.

Quantitative information was extracted from two meta-analysis results [Bolam, 2014, Hiddink et al., 2019] and five empirical studies [Tillin et al., 2006, Lambert et al., 2014, Van Denderen et al., 2015, Gonzàlez-Irusta et al., 2018, McLaverty et al., 2021]. We specifically focused on studies related to direct estimates of fishing intensity associated with bottom trawling, which considered benthic species (both infauna and epifauna) with comparable bathymetric ranges and habitat types across them. These studies examined variations in species abundance with specific trait modalities between fished and unfished areas or across a trawling pressure gradient (see Table S1). To quantify the effect size of the observed variations in these studies, we calculated a response ratio between the abundances of a certain trait modality at low (L) and high (H) trawl intensity scenarios, following the equation:

$$Eff.size = \ln(\frac{Abundance_H}{Abundance_L})$$

As a result, those effect size express the expected change in the abundance proportion of a trait modality with a unitary variation in fishing intensity.

Fishing intensity in all studies was reported as swept area ratio (SAR). For studies considering the effect of fishing intensity as a continuous gradient we used the provided model coefficient to predict the trait modality abundances at low trawl intensity by setting SAR values equal to 0 against those with SAR equal to 1 in order to calculate the effect size. The value of 1 was set to observe the change with a unitary variation of the variable. Once obtained, the effect sizes were pooled together across the studies for each trait modality running a linear mixed model between the effect sizes and trait modalities with study as a random effect to account observations coming from the same study and obtain the confidence intervals for each pooled effect size.

Table 1: Biological and life-history traits used to assess the sensitivity of the community to trawling pressure. The weight represents the relevance of the trait in showing a trend in response to the impact (1 for primary traits and 0.5 for secondary traits).

Trait	**Modality**	**Rationale for trait selection and hypothesized responses**	**Weight**
Body protection	Fragile/Unprotected Exoskeleton/tubiculous Shelled	Presence of hardened tissues can determine the likelihood of sustaining damage from a physical disturbance. Brittle and unprotected species are more prone to damage compared to species with durable skin or hard exoskeletons and shells.	0.5
Egg development	Asexual/budding Benthic eggs Brooded eggs Pelagic eggs	Pelagic eggs are generally safe from bottom-towed gears, while spawners may be fished but not the recruits. Eggs laid on the seabed or brooded are at risk of gear damage. However, trawling could aid species that reproduce through fragmentation or asexual means.	0.5
Feeding mode	Predators Scavengers Subsurface deposit feeder Surface deposit feeder Suspension/filter feeder	Trawling can have advantages for scavenging species, enhancing their energy intake and potentially accelerating growth and reproduction. Suspension feeders are more vulnerable as they require direct exposition to the surface and they also suffer from reduced filtration rates due to increased sediment resuspension. Conversely, deposit feeders may benefit from gear abrasion, which can make previously inaccessible food available again.	0.5
Larval development	Direct development Lecitotrhophic larvae Planktotrophic larvae	The potential for recovery from trawling relates to the type of larvae development and the extent of parental investment, as well as the susceptibility of nursery habitats to damage. Generally, species with direct benthic development and lecithotrophic larvae exhibit greater parental investment compared to those with planktonic larvae or development through fission or fragmentation. Furthermore, direct benthic development may be directly impacted by trawling due to habitat disturbances.	0.5
Longevity	<1 year 1-3 years 3-10 years	Species with longer lifespans are less likely to withstand and recover from the effects of trawling. This is attributed to factors such as lower metabolic rates, delayed maturity,	1

	>10 years	reduced annual reproductive output, and lower natural mortality.	
Maximum length	0-3 cm 3-10 cm 10-50 cm >50 cm	Larger organisms typically exhibit slower growth rates, resulting in populations taking longer to recover from trawling impacts. Conversely, smaller organisms tend to grow faster, potentially leading to quicker population recovery. Additionally, larger organisms are more susceptible to capture by trawl gear.	1
Mobility	Crawler Sedentary/burrower Sessile Swimmer	Species with limited mobility face difficulties escaping from passing gear. Sedentary species have minimal escape opportunities, burrowers can seek refuge within sediments, providing them with some chance to evade contact with the gear.	1
Sediment position	Surface 0-5 cm depth 5-15 cm depth >15 cm depth	Species residing beneath the sediment have a reduced likelihood of being caught or damaged by trawl gear, whereas those dwelling on the sediment's surface are highly vulnerable.	1

2.3 Sensitivity and Vulnerability estimation

Following the methodology of many trait-based approaches [De Bello et al., 2021], trait information were collected at the species level and compiled in a matrix. Trait modalities are then assigned using a fuzzy-coding approach, where fuzzy scores ranging between 0 and 1 are assigned based on the species' affinity to a specific modality. Fuzzy scores must sum up to 1 within each trait, ecologically representing the likelihood of a species manifesting different life strategies and the uncertainty of assigning this information. For continuous traits like size, when only numerical inputs were available for a species, without fuzzy categorical information, membership functions were crafted from boolean categories to derive fuzzy scores for each modality of those traits. A 50% overlap between categories was established, employing a trapezoidal function for the outermost categories and triangular functions for the inner ones [Cheung et al., 2005]. This approach served the dual purpose of defining the categorical aspects required by the index and addressing the uncertainty inherent in partitioning the continuous variable into categories. To calculate the community-level sensitivity to trawling, species biomasses are aggregated by trait modalities, first multiplying each species biomass by the fuzzy-coded trait categories, and then summing up these weighted biomasses per trait modality. Absolute biomasses per trait modality are then converted into relative biomasses per trait. This process yields proportions of modalities for each trait within the community, similar to what is obtained for community-weighted means applied to categorical traits [De Bello et al., 2021]. These community-weighted means were subsequently multiplied by the respective effect sizes extracted from the literature and the corrispective trait weighting factor.

The sensitivity of the community is then obtained following the equation:

$$S = \frac{\sum_{j=1}^{m} \sum_{i=1}^{n} B_{T_{jM_i}} * Eff.size_{T_{jM_i}} * Wf_{T_{jM_i}}}{\sum_{j=1}^{m} \sum_{i=1}^{n} B_{T_{jM_i}}}$$

Where *m* are the number of selected traits (*T*) (eight), *n* is the number of the modalities (*M*) for each trait,, $B_{T_{jM_i}}$ is the relative biomass of the modality i of Trait j, $Eff.size_{T\,ai}$ is the effect size related to the modality i of Trait j and $Wf_{T_{jM_i}}$ is the weighting factor related to the modality i of Trait j (1 for primary traits and 0.5 for secondary traits).

To better interpret the results, the pooled effect size representing the community sensitivity can be converted into a measure of expected percent change using the following equation:

$$S_{\%} = (\exp(S) - 1) * 100$$

therefore, a negative or positive value represents the expected percentage decrease or increase in the community's abundance with a unitary increase in fishing intensity.

Vulnerability is then calculated by multiplying community sensitivity with fishing pressure distribution, expressed as SAR.

The final equation for the vulnerability index was:

$$V = S * SAR$$

$$V_{\%} = S_{\%} * SAR$$

2.4 Application of the vulnerability approach

We applied the whole vulnerability approach to the continental shelf area around Sicily (Italy, Central Mediterranean Sea). This region encompasses highly productive zones, particularly on the southern side known as the Strait of Sicily, and boasts the largest regional fleet in Italy, both in terms of the number of vessels and total capacity [Popescu, 2010]. Among the fleet tonnage, bottom trawlers constitute the most substantial portion. Due to the spread and history of exploitation by the fishery sectors, this area can be an ideal area to assess vulnerability to trawling of the benthic community and is suitable for comparison with other applied impact assessments (see Chapter 2). The selected area, defined by Longitude: 11°36'E - 15°36'E and Latitude: 36°24'N - 38°24'N, falls within three General Fisheries Commission for the Mediterranean (GFCM) Geographical Subareas (GSAs): GSA10, GSA16, and GSA19. GSA15 was excluded due to the unavailability of VMS fishing data. Epifaunal catch samples from otter-trawl surveys were collected in this area from 2010 to 2020 (see Table S3 for details). Sampling was conducted using a trawler equipped with a 40-meter otter door spread and a net with a mesh size of 40mm. The net was towed for 30 minutes over seabeds shallower than 200 meters and for

60 minutes over deeper seabeds, maintaining a trawl speed of approximately 3 knots. The UNIPA HARMONY surveys utilized a commercial otter trawler with the same net characteristics; however, the trawl duration was not fixed in the initial protocol design. Out of the 173 samples collected on mud and sand sediments, ranging from 15 to 711 meters in depth, 82% were from depths not exceeding 200 meters.

The total wet biomasses per species, measured on board at individual level and aggregated during the surveys, were compiled into matrices for each trawl sample. Subsequently, the biomasses of the species were extracted and assigned to the selected eight traits using a fuzzy-coding method.[Chevene et al., 1994]. Species trait information was sourced from various published open-source databases: [MarLIN, 2006, Bolam, 2014, Beauchard et al., 2017, Gonzàlez-Irusta et al., 2018, De Juan et al., 2020, de la Torriente et al., 2020], CEFAS trait database available in [Pierucci et al., 2022] and [Palomares and Pauly, 2023]. Where information was unavailable in databases, we conducted searches in scientific literature, or where this was not succesful, assigned the trait modality associated with the nearest taxonomic rank for which information was available. Demersal species, such as Chordata, and highly mobile invertebrates, were excluded because effect sizes found in the literature were primarily associated with less mobile infaunal and epifaunal invertebrates. Additionally, these findings did not account the dilution effect on the species response caused by their greater spatial mobility. To account for the varying trawl duration among the samples, biomasses were standardized by the surface area swept by each trawl and expressed as g/km^2. Swept area was calculated by multiplying the average trawl width reported during the surveys (40 meters) by the haul duration in hours and the average fishing speed reported for the otter trawling vessels (3 knots = 5,556 km/h).

2.5 Trait distribution models and vulnerability assessment

We implemented the framework across the entire study area, dividing it into a grid with a resolution of 1 x 1 km mirroring the resolution of the fishing intensity layer. Utilizing the trawl catch assemblages mentioned earlier, we estimated the distribution of trait modalities biomass at the grid level. Generalized Additive Models (GAM) were employed using the ”mgcv” R package [Wood, 2011] to create distribution maps for the various modalities of the selected traits, essential as input for the vulnerability approach. The selection of these models was driven by the need for flexibility in capturing non-linear interactions between trait distribution and associated predictors. Following the acquisition of the fuzzy-coded trait biomass matrix, the aggregated absolute biomasses of each trait modality were used singularly as the response variable in the models.

Six environmental variables (sediment typology, depth, seabed slope, seabed shear stress, dis- solved oxygen, and average chlorophyll a concentration) and fishing intensity were chosen to model the variation in trait modality. As variation in shear stress and depth may influence the effect of fishing intensity in community response [Mangano et al., 2013, Lambert et al., 2014, Van Denderen et al., 2015], we decided to add an interaction term between these predictors and fishing intensity in our equations.

SAR scores were calculated using a bottom otter trawling Vessel Monitoring System (VMS) dataset for the period 2007-2019. No VMS signals were reported for depths shallower than 50m and areas within 3 nautical miles of the coastline, in compliance with the 2007 ban in the Mediterranean Sea (EU Council Regulation—EC No 1967/2006, 21 December 2006). SAR estimates were calculated at a spatial resolution of 1x1 km and assigned to each trawl coordinates as an average of the three years before the sampling year.

Sediment typology (Wentworth classification) was estimated from the EUNIS habitat classification produced in [Vasquez et al., 2021], depth and seabed slope information from the Digital Terrain Model (DTM) [Thierry et al., 2019]. Average temperature, primary production, and dis- solved oxygen at the sea bottom were respectively extracted from [Simoncelli et al., 2014, European Union-Copernicus Marine Service, 2022] and [Teruzzi et al., 2021]. Shear stress due to waves and currents was extracted from [Rivier, 2010] as the 90th percentile, to account for events imposing strong constraints on the seabed while excluding extreme phenomena, over a period spanning from 2001, 2007 and 2009.

To handle absences (zeros) in species by-catch data even when aggregated by trait modality, we adopted a delta GAM approach [Grüss et al., 2014]. This involved fitting two independent models: one estimating the influence of predictors on the presence/absence of trait modality, and the other estimating the magnitude of abundance where present. For the abundance models, a quasipoisson or Tweedie GAM with a log link function was used to deal with positive data with zeros, while for presence/absence data, a binomial GAM with logit as the link function was selected [Zuur et al., 2009]. Before initiating the analysis, we assessed correlations between explanatory variables for collinearity using Spearman rank correlations and Variance Inflation Factors (VIFs) [Zuur et al., 2009]. Predictors were removed from models if they exhibited Spearman rank correlation values above 0.5 and VIF values above 3. To account for potential spatial effects resulting from unmeasured drivers that might cause spatial auto-correlation in the residuals, the model included the location of each trawl (longitude and latitude). The predictors SAR, depth, seabed slope, dissolved oxygen, primary production and shear stress were log-transformed to reduce the skewness of their distribution. Predictors for each model were selected by comparing three variants: the full model (including all variables and the interaction between x and y), a reduced model with non-significant variables removed ($p\text{-value} > 0.05$), and an autoselected model incorporating an additional penalty in smooth terms to diminish the impact of non-significant predictors [Marra and Wood, 2011]. In the autoselected model a smooth penalization process is applied which penalizes only functions in the null space of the original penalty, allowing the complete removal of a predictor from the equation when the smoothing parameter equals zero. This process acts similarly to what is obtained from a stepwise selection in linear regressions and helps to identify and remove not relevant predictors in the model. As the final model, the one maximizing deviance explained and adjusted R^2 was chosen. Spatial autocorrelation in model residuals was assessed using the Moran I index.

Due to the limited data size, validation of the delta GAMs fitted for various trait modalities was performed using the same dataset employed for their development. Therefore, a comparison between observed and predicted biomasses, obtained by multiplying the presence/absence model with the abundance model, was done. To achieve this, we generated 1000 bootstrap matrices by resampling with replacement within the range of observed and predicted biomasses obtained for each trait modality. Subsequently, Spearman's correlation coefficients and confidence intervals were calculated between the bootstrapped predicted biomass values from the delta GAMs and the observed in the original datasets. A significance test was employed to test if correlations were different from zero [Vaz et al., 2006, Grüss et al., 2014].

The biomasses of different modalities at the grid level were estimated from raster maps of the selected predictors. Fishing intensity was intentionally set at zero to estimate the distribution of the single trait modality biomasses in an untrawled state. This step was necessary to combine community sensitivity with different gradients of trawling intensities. Each trait's modalities were then converted into biomass proportions within each grid cell by dividing them by the sum of the absolute biomasses associated with the same trait. This conversion was crucial to obtain the relative biomass proportions of the modalities within a trait required for applying the sensitivity equation and to ensure that each modality add up to 1 for the same trait. In the vulnerability equation, SAR values were selected from the most recent available layer (year 2019). Sensitivity and Vulnerability equations were applied to each cell of the study area grid.

2.6 Sensitivity analysis on the final outputs

To distinguish each trait's contribution to the variation in community sensitivity distribution and, consequently, the final vulnerability score, a sensitivity analysis on the sensitivity scores was con- ducted. To do this, the Species x Traits matrix was randomly permuted by randomizing the fuzzy coding within one trait and assigning random fuzzy coding for another species from the list. The number of permutations was set at 100, and for each permutation, the entire delta GAM approach was applied, resulting in different maps of Sensitivity scores. This method enables us to evaluate whether isolating a single trait and randomly assigning fuzzy codes to the measured biomasses of sampled species substantially alters the contribution of those modalities. If many species within the community exhibit similar modalities for a trait, the randomization process would result in minimal variation, indicating lower sensitivity to changes. Conversely, if the distribution of modalities for a trait varies significantly among the considered species, that trait would have a greater impact on sensitivity score variation, as it reflects an actual difference in biomass distribution among the modalities for that trait.6The Mean Absolute Error (MAE) served as a measure of dispersion between the sensitivity layer produced from the permutations and the reference one. The average MAE, along with upper and lower confidence intervals, was calculated for each trait. These values were then compared to assess the trait leading to the highest dispersion in the sensitivity scores, thereby identifying its significant impact on the overall vulnerability score.

2.7 Comparison with other impact approaches

To assess the performance of the index in detecting differences or changes in the benthic fauna community concerning trawling pressure, the obtained results were compared with those derived from another approach estimating the impact of trawling in the same study region. This approach, known as the PD approach or Relative Benthic State (RBS), as stated in [Pitcher et al., 2017], is a quantitative method designed to evaluate the risks to benthic habitats caused by towed bottom fishing gears. It relies on the logistic population growth equation, which is solved at the equilibrium state to derive the proportion of community biomass relative to its carrying capacity (K). The corresponding equation is as follows:

$$RBS = 1 - F * \frac{d}{r}$$

where F is the fishing intensity, d is the depletion caused by the trawling gear and r is the recovery rate of the community.

The recovery rate (r) is linked to the community's longevity composition based on the meta- analysis findings in [Hiddink et al., 2019]. Therefore, the approach focuses on a single trait serving as a proxy for community sensitivity to trawling. An impact measure can be calculated by taking the complement of the RBS (i.e., 1-RBS); thus, a value equal to 0 indicates low impact, with impact increasing as it approaches 1. Additionally, a sensitivity measure can be obtained by considering the median longevity of the community, where lower longevity suggests lower sensitivity to trawling. The dataset description and methodology for applying the entire PD approach framework on the Sicilian continental shelf are detailed in Chapter 3. Median longevity and PD impact maps were compared with Sensitivity and Vulnerability layers, respectively.

To assess concordance in their scores, Spearman's correlations were calculated between different indices. Correlations with predictors used in the trait distribution models were also evaluated to identify the main variables related to sensitivity and the risk of community impact. Visual investigations included scatterplots between indices and key predictors such as fishing intensity, depth, and sediment typology. The spatial distribution of impact approaches (Vulnerability and PD impact) was examined to determine if differences could be attributed to variations in score magnitude (quantity disagree- ment) or spatial pattern (allocation disagreement). This was calculated by normalizing the scores through the min/max method and applying the method proposed in [Pontius et al., 2008] to compute quantity disagreement (D_Q) and allocation disagreement (D_A). Quantity disagreement is derived by calculating the absolute value of the mean error between the two layers, while allocation disagreement is obtained by subtracting quantity disagreement from the mean absolute error between the two layers:

$$D_Q = \left| \frac{\sum_{i=1}^{n} V_i - I_i}{n} \right|$$

$$D_A = \frac{\sum_{i=1}^{n} |V_i - I_i|}{n} - D_Q$$

where V_i is the vulnerability score of the grid cell i, I_i is the PD impact score of the grid cell i and n is the total number of grid cells.

3 Results

3.1 Effect sizes of trait modalities

Average effect sizes and confidence intervals obtained from linear mixed models are presented in Table 2. The qualitative assessment of the review was consistent with the estimated effect sizes, demonstrating response trends among primary traits. However, confidence intervals overlapped with zero for all traits except longevity exceeding 10 years, signaling significant uncertainty in the estimates. Observing the average scores, species characterized by long life spans (> 10 years), larger sizes (> 50 cm), and low mobility (sessile and crawling) residing in the upper sediment layers (Surface and 0-5 cm) exhibited the highest percentage of decrease following trawling impact. Considering secondary traits, both filter feeders and deposit feeders displayed negative responses. Similarly, species with asexual or pelagic egg reproduction and direct or planktotrophic larval development also exhibited adverse effects. On the other hand, predators, scavengers, and species with benthic eggs and lecithotrophic development showed a positive response to trawling. A trend was observed in body protection, wherein more fragile species responded more negatively compared to their more resistant counterparts.

3.2 Distribution of environmental variables and fishing intensity

The Sicilian continental shelf is characterized by sandy sediments (53.62%) in shallower regions, with mud (15.97%) and granule-pebble (29.92%) seabeds prevalent near the shelf edge. Approximately 75% of the total area shows SAR values exceeding 0, with an average value of 2.36 ±3.55 S.D. year⁻1. Nearly half (49%) of the area has SAR values greater than 0.5 year⁻1, with values exceeding 5 year⁻1 concentrated in the Strait of Sicily and near the shelf edge. Lower SAR values are observed shallower than 50 meters' depth and on the western side of the Adventure Bank and Hibleyan plateau in the Strait of Sicily. Trawling intensity values are similar among sediment types, with coarser sediments showing a higher average (4.21 years⁻1) compared to sandy (2.94 years⁻1) and muddy (1.97 years⁻1) sediments.

3.3 Trait distribution models

Among the predictors used for modeling trait modalities biomass distribution, depth emerged as one of the most commonly selected variables with significant relative importance (see Table 3 and 4). This variable is frequently associated with fishing intensity and their interaction is relatively important for traits such as egg development, maximum length, mobility, and sediment position. Furthermore, this interaction predominates in the presence/absence models for all considered traits. Traits such as body protection, egg development, feeding mode, and longevity were also influenced by the interaction between fishing intensity and shear stress. Fishing intensity alone was not notably significant except for its weak negative influence on deposit feeders and predators, stronger for species with direct larval development and a slightly positive effect on high mobility species. Spatial effects (longitude and latitude of the hauls) were consistently included in all models and exhibited a high contribution to the explained deviance across several modalities.

Table 2: Pooled effect sizes and confidence intervals (CI) for each trait modality obtained from quantitative assessments of fishing intensity effects on trait modality abundances. Effect sizes are expressed as the logarithm of the response ratio between trait modality abundances at low and high trawl intensity. The pooled effect sizes are also represented as percent changes between low and high fishing intensity.

Trait	**Modality**	**Effect size**	**Lower CI**	**Upper CI**	**Percent change**
Body protection	Fragile	-0.23	-1.03	0.57	-20.35
Body protection	Exoskeleton	-0.04	-1.61	1.53	-3.98
Body protection	Shelled	0.11	-1.01	1.22	11.34
Egg development	Asexual	-0.23	-1.34	0.88	-20.76
Egg development	Benthic eggs	0.18	-0.53	0.89	19.99
Egg development	Brooded eggs	0.15	-0.57	0.86	15.69
Egg development	Pelagic eggs	-0.13	-0.74	0.48	-11.98
Feeding mode	Predator	0.30	-0.35	0.95	35.38
Feeding mode	Scavenger	0.15	-0.46	0.75	16.03
Feeding mode	Subsurface deposit feeder	-0.13	-1.70	1.44	-12.14
Feeding mode	Surface deposit feeder	-0.04	-1.15	1.07	-3.60
Feeding mode	Suspension/filter feeder	-0.45	-0.99	0.09	-36.22
Larval development	Direct	-0.09	-1.66	1.48	-8.55
Larval development	Lecithotrophic	0.24	-0.42	0.90	26.90
Larval development	Planktotrophic	-0.18	-0.84	0.48	-16.33
Longevity	<1 years	0.04	-1.07	1.15	4.25
Longevity	1-3 years	0.36	-0.25	0.96	43.00
Longevity	3-10 years	0.12	-0.48	0.73	13.30
Longevity	> 10 years	-0.76	-1.33	-0.19	-53.15
Maximum length	0-3 cm	0.18	-0.43	0.78	19.66
Maximum length	3-10 cm	0.00	-0.65	0.65	0.41
Maximum length	10-50 cm	0.18	-0.27	0.64	20.11
Maximum length	>50 cm	-0.44	-1.35	0.47	-35.77
Mobility	Crawler	-0.27	-1.38	0.84	-23.60
Mobility	Sedentary/burrower	0.38	-0.33	1.10	46.68
Mobility	Sessile	-0.20	-0.81	0.41	-18.44
Mobility	Swimmer	0.27	-0.44	0.98	30.86
Sediment position	Surface	-0.07	-0.68	0.54	-6.84
Sediment position	0-5 cm depth	-0.11	-0.68	0.46	-10.38

Sediment position	5-15 c depthm	0.25	-0.36	0.86	28.90
Sediment position	>15 cm depth	-0.11	-0.82	0.60	-10.66

Correlations between observed and predicted biomasses from bootstrap resampling were all significant and positive for all the trait modalities (see Table 5). Higher correlations (greater than 0.6) were observed for modalities such as medium body protection, pelagic egg development, asexual reproduction, suspension/filter feeding, direct larval development, high longevity (> 10 years), high maximum length (>50 cm), and sessile species, while lower correlations (less than or equal to 0.3) were found for low longevity (1-3 years), benthic egg development, and crawling.

The models obtained were combined with the raster data of the environmental predictors under untrawled conditions to produce raster maps depicting the relative biomass distribution of the different modalities (from Figure S2 to S9). At SAR equal to zero, inner shelf areas (between 0 and 100m depth) host higher proportions of crawling species with scavenging or suspension feeding behavior. In these areas, reproduction is mainly associated with the production of pelagic eggs or asexual reproduction, the latter primarily occurring along the southeast coasts in relation to suspension feeding. The inner shelf is also characterized by a higher concentration of species with high body protection in the northwest areas and low-body protection moving towards the southwest. Species with medium lifespans (3-10 years) are particularly found in the inner shelf, while as we proceed towards the edges of the continental shelf, the proportion of longer-lived species (> 10 years) increases, especially in southern areas such as the Adventure Bank and the Hibleyan plateau (between Sicily and Malta).

Deeper areas are characterized by higher proportions of sessile species, even though crawlers are still present. Moving from the inner to the outer shelf (100-200m), smaller sizes (3-10 cm) tend to be replaced by greater concentrations of larger sizes (10-50 cm and > 50 cm), especially in the northwest, while in the outer shelf of the southwest, there is a concentration of very small- sized species (0-3 cm). The outer shelf is also characterized by a higher concentration of predators and species with intermediate body protection, which produce benthic eggs, especially in the southernmost areas. A higher proportion of benthic egg producers is also present in the inner shelf of the southeastern areas of the Strait of Sicily.

Shelf edges mainly host species with sedentary/burrowing behavior or sessile characteristics, long lifespans, suspension/filter feeding, or surface deposit feeding. Additionally, there are peaks in the concentration of brooders and species with lecithotrophic larvae (only on the west side) or direct development; modalities that are generally less common throughout the entire area.

Modalities that prove to be ubiquitous and with high concentrations are species that live on the surface and develop planktotrophic larvae, while modalities such as swimming, low lifespan (< 1 year and 1-3 years), and subsurface deposit feeding are almost absent in the study area. This condition is dictated by the use of epifaunal samples derived from trawling to characterize the composition of the benthic community.

3.4 Sensitivity and Vulnerability assessment

On average, the overall community sensitivity across the study area is -6.43% (±2.74 S.D.), representing the average expected change at a unitary increase of fishing intensity (SAR = 0). Areas exhibiting higher community sensitivity are predominantly situated in the Strait of Sicily near the Adventure Bank (southwest of GSA16) and the Hibelyan plateau (southeast of GSA16). On the northern side, sensitivity increases closer to the shelf edge (see Figure 1). In total, 98% of the entire study area shows negative effect sizes, not exceeding an expected change of -20% of community abundance. Positive or neutral pooled effect sizes are only observed in areas near the coast, not exceeding 50 meters in depth.

Considering habitat types, the average community sensitivity remains consistent across sand (6.63% ±2.88), mud (6.74% ±2.99), and granule-pebble (5.93% ±2.25) sediments. Communities on the inner shelf exhibit slightly lower sensitivity (6.03% ±3.14) compared to those on the outer shelf (6.89% ±2.09).

Sensitivity scores demonstrate a weak yet significant negative correlation with depth ($\rho = 0.26$) and fishing intensity ($\rho = 0.23$), indicating that in our study area, deeper areas with higher fishing intensity happen to have higher sensitivity resulting from the trait composition of the community. It is important to note that this correlation does not imply an effect of fishing intensity on the sensitivity scores as they are estimated at SAR = 0. Despite their significance, other environmental variables showed little to no correlation.

The results from sensitivity analysis on sensitivity scores revealed an overall low degree of dispersion (average MAE obtained from random permutation close to zero) for all traits, indicating that overall many species exhibit similar trait expression and few traits actually influence the final sensitivity scores (Table 6).

Table 3: Relative importance, expressed as deviance proportional difference, of the predictive variables used in the GAM abundance models (where higher values indicate greater importance of the variable in the model). Significant terms are highlighted in bold. Asterisks denote the significance of the predictor's smooth terms in the model: * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. The overall deviance explained by the model and the adjusted R2 are also reported.

Trait	Modality	Sediment	SAR	Depth	SAR x Depth	Slope	Stress	DO	Prod	SAR x Stress	Spatial	Adj R2	Deviance explained
Body protection	Fragile	-1.20	0.00	**6.92*****	1.35	1.75	0.00	0.00	**1.85***	**5.71****	**1.79***	0.32	52.80
	Exoskeleton	0.27	3.62	**16.74****	2.41	0.71	0.73	0.11	1.48	1.09	1.36	0.21	41.20
	Shelled	-2.32	**0.44***	1.85	0.00	**7.39*****	0.00	0.00	0.00	**9.21****	4.36	0.33	37.50
Egg development	Asexual			**18.33*****	**12.94****	4.83			0.07		0.61	0.33	55.50
	Benthic eggs	0.91	0.20	0.00	**3.20*****	0.00	**4.17*****	0.00	0.00	**3.51*****	**14.08*****	0.86	82.60
	Pelagic eggs			**24.28*****	1.33	2.30			**4.85***	**1.76***	**6.77****	0.24	42.90
	Brooded eggs			**3.41*****	**12.92*****		**1.93*****	**2.57****	**10.76*****	**5.99*****	**2.85*****	0.59	67.20
Feeding mode	Surface deposit feeder	-1.17	**3.49*****	0.00	**0.56****	**3.32*****	**0.46***	0.00	0.00	**3.41*****	**10.45*****	0.89	81.90
	Subsurface deposit feeder	1.06	0.00	**7.69*****	0.00	**5.36****	0.00	0.00	0.00	**5.08*****	**12.30*****	0.04	41.40
	Predator		3.96	**20.00*****			**2.69***		1.63	3.33	0.17	0.22	35.50
	Scavenger					**-3.00****			-0.97	-0.22	**-6.08*****	0.14	21.00
	Suspension/filter feeder	**-0.42*****	0.00	**11.67*****	**3.76*****	0.00	0.00	0.00	**5.84*****	**4.63*****	**5.07*****	0.25	51.10
Larval development	Direct	**4.00*****	**7.26***	**2.23****	**2.82****	0.86	**1.38***	**1.39***	**1.33****	0.64	**1.13**	0.21	47.20
	Lecithotrophic	**7.60*****		**14.23*****			0.59	0.03	**9.02*****	**2.99***	2.83	0.04	50.70
	Planktotrophic	-1.20	0.00	**20.68*****	0.00	0.00	**1.45***	0.00	1.61	0.00	3.82	0.26	38.00
Longevity	<1 year	0.81	0.64	0.07	0.16	0.97	0.10	0.81	-0.01	**3.12***	**31.33****	0.53	60.80
	1-3 years	**0.33****	0.99	0.00	5.60	**2.02***	0.00	2.35	0.00	1.80	1.17	0.09	36.70
	3-10 years	-0.37	0.00	**9.53*****	0.96	**5.25****	0.00	0.00	**1.52***	0.00	**6.93****	0.33	47.10
	>10 years	1.86	0.75	**17.96*****	**3.23****	**4.11***	**2.03***	0.00	**6.90*****	**2.95****	**1.69***	0.35	54.40
Maximum length	0-3 cm	1.70	0.05	1.68	4.26	2.82	1.21	1.95	0.32	2.50	3.87	0.10	17.70
	3-10 cm			**18.29****	**5.88****		0.52				1.59	0.10	22.00
	10-50 cm		0.13	**27.51*****		4.20		**2.46***	**2.23****	**4.12****	3.53	0.35	52.90
	>50 cm	1.18	**0.20****	**3.18****	**4.54*****	0.00	0.00	**2.91***	0.00	1.52	**11.46*****	0.31	51.10
Mobility	Sessile	0.48	0.00	**14.10*****	**2.90***	0.37	0.00	0.00	**4.14****	**2.08***	**4.28****	0.29	53.20
	Sedentary/burrower	0.39	0.00	1.29	0.00	1.07	0.48	0.00	0.00	0.93	**15.18****	0.15	31.90
	Crawler	0.11	0.00	1.46	0.83	0.00	-0.03	0.00	0.00	1.36	**19.39*****	0.31	41.00
	Swimmer	0.52	**5.74*****	**11.90*****	**4.46****	**9.60*****	0.00	0.58	**3.35****	**3.25***	0.08	0.70	69.10
Sediment position	Surface	-1.04	0.00	**15.76*****	0.00	0.00	0.00	0.58	**1.62***	1.92	**6.12***	0.28	41.80
	0-5 cm depth	1.94	0.00	**10.54****	0.00	**3.55****	3.91	3.31	3.27	0.35	3.75	0.19	28.30
	5-15 cm depth	0.15	0.00	0.00	**7.48*****	1.26	0.00	0.81	0.00	**5.37****	**26.32*****	0.07	53.80
	>15 cm depth	0.95	0.00	1.95	**8.09*****	3.22	0.00	0.00	0.00	0.00	0.00	0.12	26.20

Table 4: Relative importance, expressed as deviance proportional difference, of the predictive variables used in the GAM presence/absence models (where higher values indicate greater importanceof the variable in the model). Significant terms are highlighted in bold. Asterisks denote the significance of the predictor's smooth terms in the model: * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. The overall deviance explained by the model and the adjusted R2 are also reported.

Trait	Modality	Sediment	SAR	Depth	SAR x Depth	Slope	Stress	DO	Prod	SAR x Stress	Spatial	Adj R2	Deviance explained
Body protection	Fragile	3.13	0.17	1.72	**12.13****	0.43	0.07	0.16	1.22	0.00	2.95	0.23	27.50
Body protection	Exoskeleton		11.15	0.63		1.57	5.91	1.61		11.29	85.63	0.99	96.00
Body protection	Shelled	2.64	0.00	**4.05****	6.01	0.29	0.00	1.08	0.00	0.00	0.00	0.14	22.40
Egg development	Asexual	0.74			**10.72*****		0.25	3.32			**11.29****	0.47	39.90
Egg development	Benthic eggs	-6.33	11.32	11.32	8.80	**11.27***	8.14	6.47	6.47	9.32	**15.02****	0.25	26.50
Egg development	Pelagic eggs	**5.13***	**21.83***	25.45	27.49	17.73	17.73	**17.73****	**13.69***	**18.08***	13.69	0.62	72.70
Egg development	Brooded eggs		**6.68***	**6.12****			0.93		1.59		0.84	0.08	11.40
Feeding mode	Surface deposit feeder	2.35			**2.47***	1.13		1.76			1.42	0.05	7.99
Feeding mode	Subsurface deposit feeder				**6.59***	**2.26***				6.06	9.69	0.20	23.50
Feeding mode	Predator	0.59	0.00	11.55	0.00	**15.11***	0.00	0.00	0.00	4.09	5.46	0.35	56.10
Feeding mode	Scavenger	3.70	**10.32***	0.00	1.44	**7.21****	0.00	**5.99***	0.00	**8.27***	0.00	0.24	30.50
Feeding mode	Suspension/filter feeder	-0.94	0.00	0.00	**8.91****	0.00	0.78	**8.02****	0.90	1.42	**22.29*****	0.59	64.10
Larval development	Direct	1.18			**8.27****	1.42	**2.93****	**1.94***		4.11	**5.80****	0.26	24.60
Larval development	Lecithotrophic	0.54	0.00	3.78	0.00	0.11	0.00	0.00	0.00	**6.18****	**7.80*****	0.23	23.00
Larval development	Planktotrophic	-9.23	0.00	0.00	9.52	0.00	0.00	**34.24***	10.41	0.00	0.00	0.37	59.50
Longevity	<1 year	-1.90	0.00	0.00	**14.64***	**4.63***	0.00	0.00	0.00	3.35	**6.74***	0.29	37.40
Longevity	1-3 years	3.93	**2.97***	0.00	**17.83***	0.00	**6.89****	0.00	**10.62****	**23.27*****	4.68	0.64	69.60
Longevity	3-10 years				5.94	1.48	4.21	**7.26***		**8.28***	3.21	0.10	27.50
Longevity	>10 years		1.91	1.33	**7.79****			**10.55****			8.73	0.36	37.10
Maximum length	0-3 cm			**4.16***	2.73	**3.27***	**6.36***		2.00	2.94	**18.77****	0.35	35.20
Maximum length	3-10 cm	0.73	0.00	0.00	0.00	**24.97***	0.00	**11.87***	0.00	**49.23***	0.00	0.81	83.80
Maximum length	10-50 cm	10.79	0.00	0.00	4.76	0.00	0.00	0.00	0.00	3.47	0.00	0.02	12.50
Maximum length	>50 cm	**2.05***	0.00	**3.27****	**7.92****	**1.37***	0.00	**7.07*****	0.11	0.00	**7.24*****	0.39	38.30
Mobility	Sessile				**2.44***	0.80		**12.74****	1.40		**11.63*****	0.51	48.00
Mobility	Sedentary/burrower	2.16	0.00	**2.10***	0.00	1.55	0.00	**4.72****	0.00	3.16	**3.55***	0.17	20.70
Mobility	Crawler			4.43						**10.15***	8.02	0.03	13.10
Mobility	Swimmer			0.89		1.74	1.34	**5.06****		**9.99****	1.57	0.21	18.90
Sediment position	Surface												
Sediment position	0-5 cm depth		0.06			2.53		**9.37****		2.53	1.99	0.16	19.90
Sediment position	5-15 cm depth	0.06	0.00	0.00	**17.02*****	0.00	0.00	0.00	0.00	**7.18****	**8.82****	0.31	32.70
Sediment position	>15 cm depth		0.38		**13.55****		0.75				1.34	0.16	16.70

Table 5: Spearman's correlation coefficients and confidence intervals (CI) obtained comparing the abundance values predicted by the delta GAM to observed abundance values of the different trait modalities in the samples. Confidence intervals and p-values are produced through a bootstrapping resampling method.

Trait	Modality	Spearman's ρ	Lower CI	Upper CI	p value
Body protection	Fragile	0.57	0.44	0.67	4.77E-16
	Exoskeleton	0.62	0.51	0.72	2.20E-16
	Shelled	0.58	0.46	0.69	2.20E-16
Egg development	Asexual	0.68	0.57	0.77	2.20E-16
	Benthic eggs	0.27	0.11	0.41	0.000374
	Pelagic eggs	0.63	0.53	0.73	2.20E-16
	Brooded eggs	0.55	0.43	0.66	6.15E-15
Feeding mode	Surface deposit feeder	0.32	0.17	0.46	2.42E-05
	Subsurface deposit feeder	0.32	0.19	0.45	1.34E-05
	Predator	0.47	0.32	0.59	4.68E-11
	Scavenger	0.46	0.34	0.58	1.69E-10
	Suspension/filter feeder	0.69	0.59	0.78	2.20E-16
Larval development	Direct	0.61	0.49	0.70	2.20E-16
	Lecithotrophic	0.44	0.33	0.55	1.24E-09
	Planktotrophic	0.47	0.33	0.59	4.23E-11
Longevity	<1 year	0.42	0.29	0.53	1.04E-08
	1-3 years	0.21	0.06	0.35	0.004506
	3-10 years	0.40	0.25	0.53	6.06E-08
	>10 years	0.65	0.54	0.74	2.20E-16
Maximum length	0-3 cm	0.45	0.32	0.57	3.94E-10
	3-10 cm	0.40	0.26	0.54	4.12E-08
	10-50 cm	0.60	0.48	0.70	2.20E-16
	>50 cm	0.65	0.55	0.74	2.20E-16
Mobility	Sessile	0.67	0.56	0.77	2.20E-16
	Sedentary/burrower	0.40	0.27	0.54	3.66E-08
	Crawler	0.31	0.16	0.45	3.57E-05
	Swimmer	0.55	0.42	0.67	3.16E-15
Sediment position	Surface	0.49	0.36	0.61	4.94E-12
	0-5 cm depth	0.40	0.26	0.53	4.82E-08
	5-15 cm depth	0.56	0.47	0.65	5.70E-16
	>15 cm depth	0.37	0.24	0.50	3.77E-07

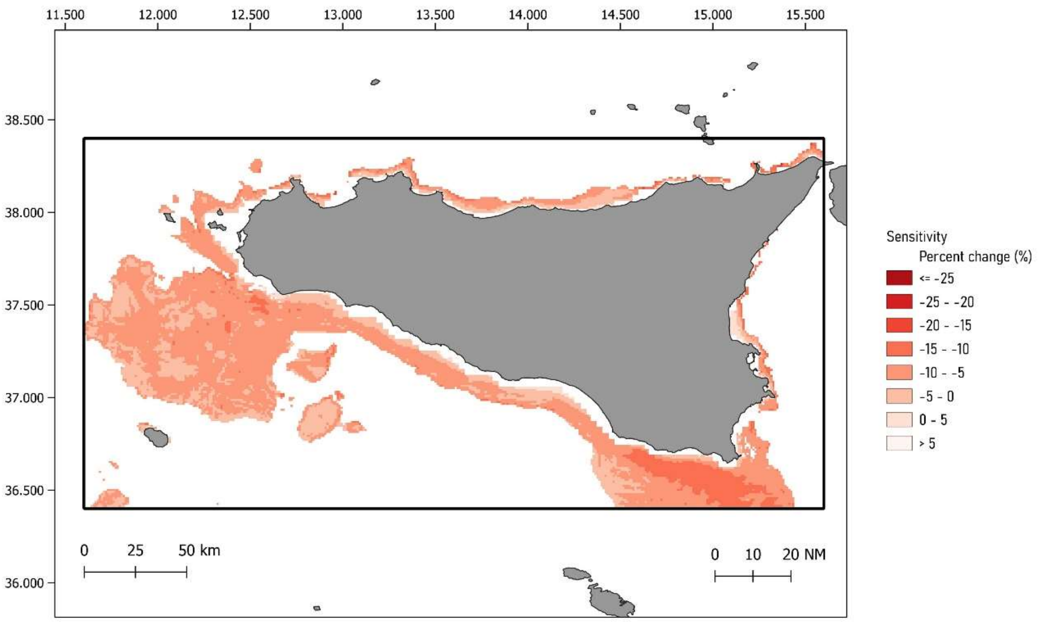

Figure 1: Distribution maps of the sensitivity scores across the study area; darker colors indicate higher sensitivities (more negative scores).

Only some traits exhibited an average MAE one order of magnitude higher or more than the variation observed due to permutations in other traits. Specifically, longevity and mobility emerged as such traits, suggesting that they influence sensitivity scores more significantly than others.

The vulnerability scores for the study area are illustrated in the Figure 2. By multiplying community sensitivity and fishing intensity, we observed an overall low vulnerability status of the community across the study area (-7.19%). However, there are noticeable hotspots of high vulnerability that contribute to increased variability in the estimate (standard deviation of 11.56). Overall, the 84% of the entire area shows vulnerability values below 0, only about 9.3% of the study area indicates a relative reduction of more than 50% in community abundance based on the current distribution of fishing effort compared to the state setting SAR = 0. These areas are primarily concentrated in the Strait of Sicily, reflecting locations where the community displays high sensitivity values and experiences peaks in trawling intensity exceeding 10 years−1. Positive values correspond to only 0.4% of the area and are confined solely to shallow areas less than 50m along the southern coasts where higher proportion of predator, scavenger and species with high body protection is observed (Supplementary Figure S2 and S4), while values equal to 0 are more prevalent in the northern part of the study area. Using only the two traits we found particularly significant in the sensitivity analysis (longevity and mobility), the vulnerability assessment consistently identified the same main vulnerable area in the Strait of Sicily, although the extent of areas with higher vulnerability appears to be broader, with an overall average value more negative (-27.56%) (Supplementary Figure S10).

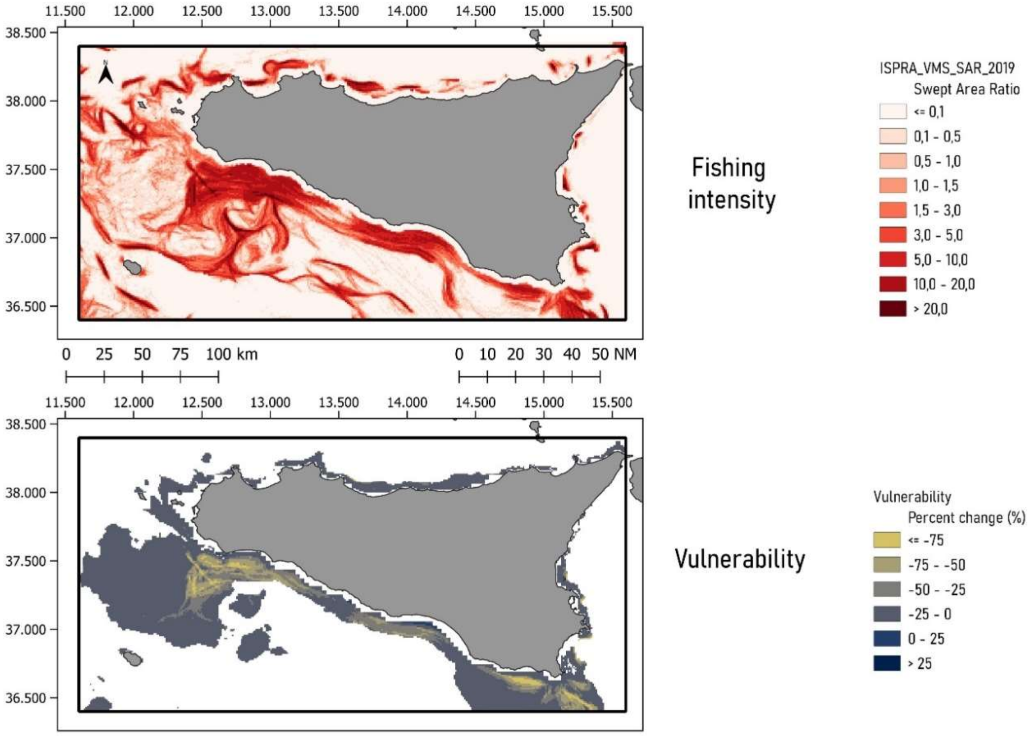

Figure 2: Distribution maps of the SAR raster and of the vulnerability estimates obtained from the application of the framework.

Table 6: The average mean absolute errors (MAE) and confidence intervals (CI) derived from 100 random permutations in the trait-per-species matrix for each trait, which were utilized to evaluate community sensitivity. The MAE were calculated between the reference sensitivity raster and the one obtained from the permutation and then averaged across all permutations.

Trait	MAE	Lower CI	Upper CI
Sediment position	0.000624	0.000618	0.00063
Larval development	0.003066	0.003062	0.003071
Egg development	0.003377	0.003377	0.003377
Body protection	0.005257	0.005125	0.005389
Feeding mode	0.007074	0.006683	0.007466
Maximum length	0.008937	0.008573	0.009302
Mobility	0.013827	0.013691	0.013962
Longevity	0.059333	0.059325	0.059341

3.5 Comparison with other impact assessment estimates

The comparison between sensitivity scores and median longevity from the two different frameworks revealed only a weak negative correlation (-0.26, p-value < 0.001). This suggests that as we examine species with longer lifespans, sensitivity scores tend to assume more negative values. Decomposing observations based on sediment typology, it becomes evident that estimates derived from sand and mud sediments exhibit stronger correlations (respectively, -0.44 and -0.73) than granule-pebble ones (-0.07), as illustrated in Supplementary Figure S1. Upon examining the difference in correlation between the inner and outer shelf, a significant negative correlation is observed only at shallower depths (-0.44), whereas no correlation (0.05) is present at greater depths.

Similarly, the impact assessment from the PD approach revealed a significant negative correlation with the vulnerability scores (-0.94, p-value < 0.001), indicating that higher impact levels correspond to greater reductions expected in the community (manifested as negative vulnerability values). Decomposing the vulnerability scores among sediment and depth classes did not noticeably alter this correlation or its significance. However, it is noteworthy that in sandier sediments, the relationship between the impact scores derived from the PD approach and the vulnerability scores appears more linear (see Figure 3). The distribution pattern between the PD impact assessment and vulnerability was consistent, with higher scores concentrated in the Strait of Sicily. This similarity is further supported by the comparison of normalized indices, which indicates a minor difference in the distributions of the two indices (MAE = 0.13). This discrepancy is primarily attributed to allocation disagreements, accounting for approximately 77% of the dispersion, rather than differences in the magnitude of the scores. The variation in spatial distribution may be attributed to the absence of negative values in certain shelf-edge areas in the vulnerability assessments, whereas the PD approach detects a certain degree of impact instead.

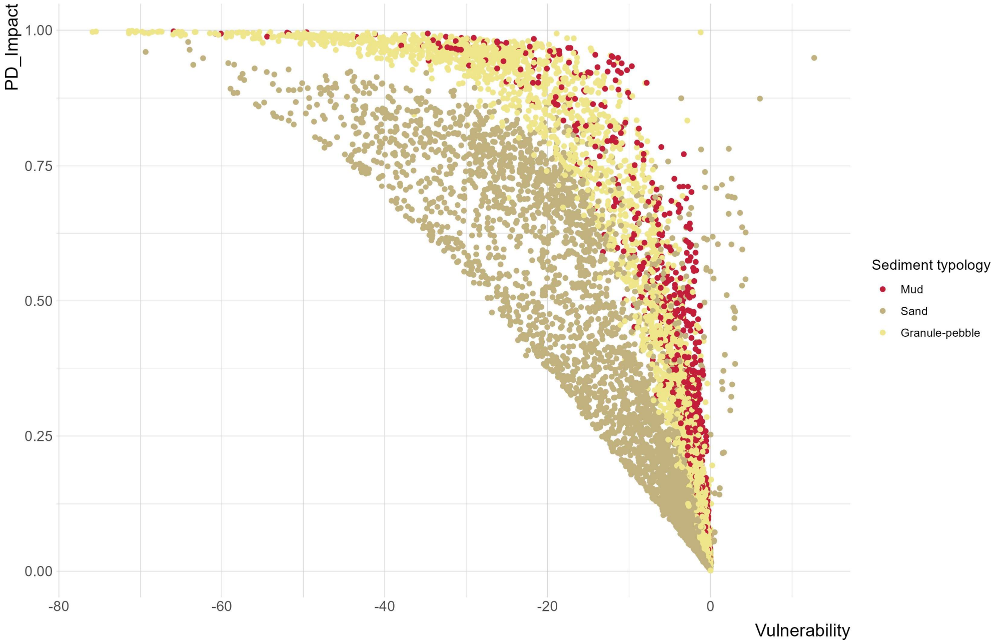

Figure 3: Scatterplot comparing estimates obtained from the vulnerability framework with those derived from the PD approach, with points distinguished by different sediment typologies.

4 Discussion

In our study, we developed and applied a trait-based framework to estimate the vulnerability status of benthic communities to trawling activity. This framework aims to define an indicator of the community's potential state and is structured following the principles of risk assessment, allowing us to describe the distribution of community sensitivity and its effective integration with the current disturbance state.

The choice to establish such a framework arose from the desire to employ more objective criteria in selecting the parameters and factors to include in the model, as well as the opportunity to evaluate the effects of these choices and their repercussions on the final estimation of vulnerability.

Utilizing effect sizes modeled from literature data was pivotal in attempting to introduce objectivity in assigning trait response to trawling pressure. These effect sizes accounted for multiple observations from different studies in similar habitat conditions and across comparable fishing intensity gradients, providing a generalizable estimate of the response that a modality could exhibit after trawling pressure. Although local responses can certainly help in interpreting certain trait-response associations, the use of such estimates in applications at a regional level covering larger areas allows for comparing different areas with varying levels of impact. It must be considered that the range of application of these relationships remains limited to the environmental context of the studies considered, primarily associated with responses of infauna and epifauna species on mobile sediments of the continental shelf/slope; this context is among the most common where trawling activity occurs and where most information on its effects is available.

We observed some directionality of response in the effect size scores and which modalities exhibited more sensitivity; for instance, species with high lifespans showed a clear negative effect between untrawled and trawled conditions. However, the directionality of certain effects should be approached with caution due to a high degree of uncertainty observed in the estimates extracted (confidence intervals overlapping with zero). A future systematic review and meta-analysis of faunal trait modalities abundance across quantified gradients in trawling intensity may enhance the accuracy of the estimates and provide coefficients that mechanistically describe the effect of fishing intensity on the variation of those modalities. Despite room for improvement, this preliminary application allows the use of information derived from statistical analysis based on observations published in the literature, justifying the assignment of certain scores and directions regarding the effect that trawling gradients apply on the abundance distribution of certain functional traits.

The use of spatial distribution models within the framework, such as GAMs, provides a flexible tool to describe and identify where certain modalities are expressed and which are the main variables guiding their distribution. For example, in our application, we found that depth is the main factor driving the variation of many trait modalities inside the community, shaping their relative proportion. Therefore, consideration of the influence of this factor should be given, as it is also related to the fishing disturbance gradient, and its effect proved to be significant in interaction with it. This suggests that a stratified approach for depth ranges in estimating fishing impacts may allow for the identification of communities with different sensitivity degrees, as this factor influences their functional composition.

The choice to conduct a sensitivity analysis on the sensitivity scores was also driven by the intention to identify the meaningful component of the indicator and provide feedback on the selection of certain traits and the assignment of their influence on the estimates. By conducting sensitivity analyses, we aimed to identify secondary traits that contributed less to community sensitivity. We found that traits like sediment position, larval and egg development displayed the same modalities almost across all the sampled community, therefore their influence on the variation of sensitivity scores was minimal and not relevant as other traits like mobility and longevity.

In our study, we still hold some degree of subjectivity, especially regarding the influence of certain traits over another, assigning a different weighting between primary and secondary traits. We based the choice by the frequency of negative and positive effects observed between trawling and the expression of those traits in the community, as observed in studies across the published literature. These choices are frequently adopted in the development of such indices and are supported by the current best available knowledge and mechanistic understanding about trawling effects on the selected properties, as well as by a process of validation of these choices and how they affect the indicator itself [de Juan and Demestre

2012, Bolam et al. 2014, Foveau et al. 2017, Gonzàlez-Irusta et al. 2018, de Juan et al. 2020, Hinz et al. 2021]. However, reducing subjectivity in the development of such methodologies must be a constant drive to ensure greater robustness of the choices and parameters assigned to the various components of the indicator, as well as to add greater transparency in the structure and aggregation of the characteristics assigned to the traits and the relationships that exist between them and the disturbance. In our case, we have tried to maintain a certain degree of objectivity in the choice of traits to consider and the assignment of parameters associated with the response of each trait. These relationships have been guided by an in-depth literature search, albeit in qualitative terms, which has allowed us to identify which traits to consider in the study and why these traits may be associated with trawling.

Future efforts could be directed towards refining the assigned weightings based, for example, on the results obtained from the aforementioned sensitivity analysis. Traits that drive less dispersion in sensitivity could be considered secondary or irrelevant to detect changes in community sensitivity. This process may help guide which traits can be considered more important than others, but instead of removing them from the equation and thus losing some information about the trait composition, it can assign a different degree of influence based on direct observation of the investigated community.

Our analysis of trait response distribution revealed a community with low sensitivity characterized by epifauna with low mobility or sessile habits, small size, medium to high longevity, opportunistic species, and predators or filter feeders. Variations in the expression of these traits are particularly evident in areas around the Strait of Sicily, where higher sensitivity traits such as sessile species and suspension feeders are observed, especially near the Adventure Bank and the southern coast of Capo Passero.

The Adventure Bank and Capo Passero host a diverse ecosystem comprising sessile and crawling species. Sessile species, which were present in our samples at higher depths, are mainly suspension feeders like soft corals of the genera *Alcyonium* and predators like some *Actinidae* species, reproducing through asexual or pelagic eggs, and have medium to high longevity. On the other hand, crawlers, though still present, are more common at shallower depths. They are predominantly predators and scavengers or deposit feeders, with medium longevity like seastars of the genera *Astropecten* or other echinoderms like *Parastichopus regalis*. The prevalence of those traits according to the depth gradient contributes to higher community sensitivity and vulnerability, especially when combined with observed fishing intensities. Trawling intensity, particularly around the Adventure Bank, often exceeds SAR values of 1, further impacting the ecosystem. The vulnerability estimates obtained reflect the integration of these two pieces of information, describing a study area predominantly with low vulnerability but with peaks of high vulnerability concentrated in fishing ground areas.

These high-sensitivity and high-fishing-intensity zones are renowned for their high productivity, stemming from a more heterogeneous habitat system due to the presence of canyons [Würtz and Rovere, 2015] and upwelling areas resulting from current exchanges between the Eastern and Western

Mediterranean basins. These resources provide excellent nursery areas and spillover conditions, creating ideal environments for the presence of particularly vulnerable species [Di Lorenzo et al., 2018]. For instance, discrete patches with varying densities of soft corals are commonly found at shelf edges, where moderate to strong bottom currents prevail [Ambroso et al., 2013, Dominguez- Carrìo et al., 2022]. Such conditions also attract high fishing effort from one of the biggest fleets operating in the Mediterranean [Russo et al., 2014, FAO, 2023]. Therefore, in these areas, less affected habitats unsuitable for trawling could play an important role as a natural reserve by sustaining populations of sensitive invertebrates that maintain their presence at lower densities in the most disturbed areas due to some spillover effect [Goode et al., 2020, Maiorano et al., 2022] but at the same time explains the high potential vulnerability of the community even though the decrease in the relative biomass of sensitive species does not reach 100%. In contrast, in northern areas, fishing intensities tend to concentrate at greater depths than the one considered in our study. Therefore, although the community composition may be similar [Di Lorenzo et al., 2018, Massi et al., 2021], albeit with more abrupt variations dictated by the strong bathymetric gradient, high vulnerabilities are not recorded in our application.

The vulnerability maps successfully identified similar risk areas as those identified by the PD approach. As observed, vulnerability estimates generated by the framework correlate with values obtained using an established approach commonly employed to detect trawling impacts on benthic communities [Rijnsdorp et al., 2020, Pierucci et al., 2023]. This correlation should not be viewed as redundancy but rather as evidence of how different approaches can complement each other, enhancing our understanding of which components determine community responses. The usage of a framework that could help to assess community sensitivity and provide a feedback on what are the main traits that are leading the variation in response could guide the selection of certain other indicators and which could be more optimal for the assessment at local or regional level. For instance, in our sensitivity analysis within the case study, we found that variations in community sensitivity were primarily attributed to two traits: mobility and longevity. Longevity, in particular, is the core trait influencing community response in the PD approach. This elucidates the high correlation between the two indices, as both the integration of SAR distribution in both approaches and longevity play a significant role in shaping the final score of both indices. However, this correlation weakens in less sandy and deeper sediments, where the community begins to exhibit a more homogeneous composition in terms of longevity (with a higher concentration of longer-living species), and variations are determined by other traits such as mobility due to the increased presence of sessile and sedentary species which, respectively, influence positively and negatively the overall sensitivity.

The developed vulnerability framework attempts to fulfill several criteria outlined in the literature for effectively assessing benthic habitats and seafloor integrity [ICES, 2022]. The availability of trawl samples, commonly utilized across various marine ecoregions for monitoring purposes [Bertrand et al., 2000], ensures a consistent flow of data crucial for maintaining the repeatability of the framework. While collecting samples may require significant effort and cost, leveraging already published open-source data and maps of fishing effort could mitigate these challenges. Additionally, as illustrated in the case study, the framework can evaluate a substantial portion of MSFD habitats with higher spatial resolution by combining adequate maps of fishing pressure derived from satellite data with the spatial coverage of epifaunal data from trawling surveys. Although initially designed to assess vulnerability to specific trawl methods, the conceptual framework can be expanded to other fishing types and sampling methodologies after obtaining new effect sizes that determine community sensitivity.

From a management perspective, the current framework could be relevant for MSFD purposes, such as identifying the extension of potential threats to benthic communities caused by trawling at the habitat scale and studying the integration of different management scenarios, especially those related to changes in trawling effort and its spatial distribution, to estimate fluctuations in community vulnerability in target MSFD areas. Different scenarios of effort distribution also allow an understanding of how the community's state may change in response to possible future fishing scenarios, providing an early warning tool for community change (a process of validation in such cases is always required). Even though a threshold was not set in this study, it is possible to adopt a fixed percentage change (for example, all cells exceeding a decrease of 50%) to estimate a determined footprint that could aid in highlighting high-risk areas, similarly to how it was done with trawling footprint in [Eigaard et al., 2017]. Moreover, the fact that the framework adopts a structure based on well-defined criteria of sensitivity and risk analysis [Brooks, 2003, Hiscock and Tyler-Walters, 2006, Tyler-Walters et al., 2023] helps in understanding how the different components of the methodology interact, although they are based on a more complex scientific theoretical background.

Based only on the effect sizes, expressed as response ratios, the integration with SAR assumes a linear relationship of the community response across the trawling gradient. This could mask some nonlinear effects of response to fishing on certain trait expressions of the community, especially at very low or high intensities. If overall community sensitivity is positive or neutral, a negative response at very high intensity would not be detected as the positive change does not reach a plateau. Although this constitutes a current limitation of the index formula, common gradients observed in fishing grounds such as the one we selected in this study did not produce anomalous behavior in the index's scores, as the overall sensitivity of the community appeared always negative or neutral in areas exposed to high fishing pressures. Furthermore, even though specific trait or species' responses could diverge from a linear response [de Juan et al., 2007], the cumulative response of the community could show a more homogeneous trend of response across a trawl gradient [Beauchard et al., 2021, Hinz et al., 2021, McLaverty et al., 2021]. Nonetheless, more sophisticated relationships with trawling intensity could be assessed in future to model the expected change of trait modalities as a function of the fishing intensity gradient.

Variation in community response as a function of the sediment type is nonetheless an important aspect to consider, as depletion rate could be influenced by it [Lambert et al., 2014, Hiddink et al., 2017, Sciberras et al., 2018, Pitcher et al., 2022]. For example, sandy sediments are less exposed to trawl effects than muddy bottoms, as the gear penetrates less [O'Neill and Ivanovic, 2016], causing lower abrasion and removal of species. In the current state, we did not have sufficient information to modulate the influence of fishing effort at different habitat level, although in our models only few trait modalities like 1-3 years lifespan, >50 cm in maximum size, direct and lecithotrophic larval development and suspension feeding were significantly influenced by sediment classification. Nonetheless including high resolution information about sediment characteristics and a weighting factor that could represent the different penetration that gear exert between coarse and fine sediments could improve the index performance.

Pooled trait response at the moment is assumed to be cumulative as they are pooled together with a weighted average of their effects. Trait modalities, when classified as assigning a species a certain degree of sensitivity when examined alone (in comparison to the distribution of other species possessing this trait), might provide responses in combination with other traits that constitute a meaningful way that ensures fitness through a life strategy. Although this simplification is made due to the lack of information about quantitative assessments of the interactions that may occur between trait modalities when selecting certain life strategies, it's important to acknowledge its limitations.

The establishment of the Marine Strategy Framework Directive (MSFD) by the European Union in 2008 necessitated the development of indicators for assessing and monitoring the impact of human pressures on the marine environment. Given that trawling is recognized as one of the most significant pressures on the seabed, it became imperative to develop indices to study its impact. Our framework follows a step-by-step approach that allows for the representation and spatial description of the community vulnerability to fishing impact. The process aimed to evaluate the inclusion of selected traits derived from literature information and to provide feedback on the relevance of those traits in the final score. Obtained results can be used to further improve the overall index as well as to guide the selection of the traits that can be used as an input for other methodologies for assessing the community's status [Jac et al., 2020a, Jac et al., 2020b]. Currently, the application of the framework is limited to assessing the response of benthic infauna-epifauna to trawling, which is expressed and linked to a linear response of the community to trawling distribution. In the future, employing meta-analysis and regression techniques on faunal trait abundance variations across quantified gradients in trawling intensity could help estimate non-linear effects in the response of different trait modalities. Regression techniques on effect sizes of trait modalities according to fishing intensity also offer a means to determine coefficients that more effectively integrate the exposure component with the intrinsic sensitivity of the community. This expansion of scope could broaden the framework's applicability to a wider range of species. For instance, incorporating studies that consider more mobile species like fishes and cephalopods (often targeted by commercial activities) and decomposing responses at different habitat levels could extend the framework's applicability to better describe the vulnerability not only of the benthic portion of the community but also other potentially impacted components.

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Chapter 5: Integration of assemblage indicators and measurement of otter door inclination to identify pattern of impact associated with trawling gear

1 Introduction

Bottom trawling, a fishing technique that captures fish and invertebrate species living close to or on the seabed, accounts for approximately 24% of global landings [FAO, 2017]. Consequently, trawling activities are globally significant for providing food to billions of people worldwide. Despite this importance, trawling's contact with the seafloor produces several impacts that may affect both the physical characteristics of the seabed and the structure of the communities inhabiting it [Kaiser, 2019].

These impacts involve geotechnical or hydrodynamic influences on the benthic environment [O'Neill and Ivanovìc', 2016]. Geotechnical effects include contact drag, substrate penetration and piercing, lateral sediment displacement, and pressure field transmission through the sediment. Hydrodynamic effects encompass hydrodynamic drag and sediment mobilization into the water column. Such effects primarily result from components of the gear that interact most with the seabed, such as otter doors, sweeps/bridles, ropes, ground gear, chains, among the others [Eigaard et al., 2016]. In addition to these physical effects, a single trawl passage may cause a reduction in total biomass of 15-29% [Hiddink et al., 2006, Hinz et al., 2009], and over time, the cumulative long-term effect could drastically alter community composition towards species more resilient to such pressure, usually characterized by more opportunistic feeding behavior, fast growth and reproduction rate, often leading to habitat biodiversity impoverishment [Bremner et al., 2003, de Juan et al., 2007, Mangano et al., 2013].

The combination of these processes results in direct and indirect effects that, if chronic, can lead to habitat damage, reduced seabed feature complexity, benthic mortality, species selection, and alteration of biogeochemical processes in the sediment through nutrient release and resuspension [Kaiser, 2019].

Therefore, understanding the mechanisms underlying the interaction between the seabed and fishing gear and developing predictive methodologies to assess and quantify the ecological and environmental impact of such fishing activity are crucial, and mandatory in a context of decarbonization of fishing sector.

Researchers have attempted to implement mechanistic models with experimental trials to find relations governing several parameters linked to gear behavior, such as drag and lift forces generated, otter board spread, net surface and volume covered, angles of attack of different towed components, net height, cable tension, penetration depth, sediment displacement, and volume re-suspended [Park, 2007, Prat et al., 2008, Ivanovìc' et al., 2011, O'Neill and Summerbell, 2011, Sala et al., 2013, Esmaeili and Ivanovìc', 2014, Bradshaw et al., 2021]. Advanced technology tools, such as software for three-dimensional models [Ivanovìc' and O'Neill, 2015, Xu et al., 2017] and acoustic [Park, 2007, Prat et al., 2008], optical [O'Neill et al., 2009], and inertial technologies [Engaas et al., 2001, O'Neill et al., 2018], are often employed to obtain these parameters. These applications also provide fertile ground for developing novel approaches not only to detect and describe the dynamics between the gear and the seabed but also to optimize performance and construct or use protocols that aim to reduce impacts and consumption without excessively compromising catch performance [Sala et al., 2013, Adam et al., 2019, McConnaughey et al., 2020].

On the other hand, efforts have been directed towards assessing the effects of fishing pressure on community response and monitoring the health or status of benthic habitats using indicators capable of capturing changes in the structure and functioning of benthic ecosystems. Such studies aim to estimate the depletion and recovery rates induced by bottom trawling activity [Hiddink et al., 2017, Sciberras et al., 2018], how community structure changes over short and long periods after exposure to disturbance [Hiddink et al., 2006, Hinz et al., 2009, Lambert et al., 2014], and which components better describe these changes from a quantitative and functional perspective [Tillin et al., 2006, Bolam et al., 2014, Sciberras et al., 2018, Beauchard et al., 2023]. These studies often involve research across fishing gradients, where data are collected from similar habitats with different levels of fishing effort [Hinz et al., 2009, Mangano et al., 2013, Farriols et al., 2017], or through Before-After Control-Impact (BACI) type experiments, comparing data collected before and after an impact with an undisturbed control site [Pitcher et al., 2009, Strain et al., 2012, Vigo et al., 2023].

Many recent applications have incorporated the concept of biological traits [Howarth et al., 2018, Jac et al., 2020a, Hinz et al., 2021, Beauchard et al., 2023]. Species' biological attributes describing aspects of their morphology and behavior are used to approximate their ecological role and identify characteristics crucial for withstanding stress [Lavorel, 2013]. Additionally, Trait- Based Approaches (TBA) allow for a relatively rapid assessment of multiple species compared to stock assessment metrics, aiding in prioritizing conservation planning and implementing adaptation schemes [Bremner et al., 2003].

However, few studies have attempted to investigate how gear dynamics affect species selection and caught assemblages, and how these dynamics influence the estimation of the impact caused by such activity, both taxonomically and functionally [Teal et al., 2014, Rijnsdorp et al., 2017, Rijnsdorp et al., 2020, Tiano et al., 2020]. The use of mixed approaches that integrate the study of net dynamics on catch performance with methodologies for estimating fishing impact allows for the adoption of methodological frameworks potentially helpful in interpreting the ecological response of affected communities [Adam et al., 2019], particularly those subject to long fishing pattern histories where trawling effects are difficult to detect [Foveau et al., 2017, Jac et al., 2020b]. Furthermore, the use of fishing surveys to assess fishing status and impact is widespread due to its extensive coverage and continuity for stock assessment purposes of various commercial species [Bertrand et al., 2007, ICES, 2015, Terribile et al., 2016]. Bycatch of non-target species accidentally caught produced during such campaigns is often used to estimate the effects of trawling on benthic communities [Jac et al., 2020a]. Evaluating the capture effectiveness of this component and how net components influence captured biomasses helps understand the effectiveness of such monitoring techniques and their potential influence on impact estimates.

In our study, we investigated how the inclination of trawl doors may affect the capture of demersal and benthic species in fine sediments across the continental shelf. Additionally, we applied measures of diversity and sensitivity to fishing pressure of the captured benthic assemblages based on functional traits associated with this disturbance.

Trawling doors serve a crucial function in maintaining the spread of the net but they also exert a significant impact on the seabed. They contribute substantially to the total drag of the trawl system, accounting for about 24% of it, and are responsible for roughly 16% of the total fuel consumption during trawling operations [Misund et al., 2002]. Consequently, their presence leaves distinct furrows that can be observed from acoustic recordings of the seabed [Depestele et al., 2016, Bradshaw et al., 2021]. Moreover, the distance between trawl doors determines the surface area covered during fishing activities.

The attitude of trawl doors during towing is not solely determined by the angle between the towing direction and the longitudinal axis of the door (names angle of attack) but also by factors like pitch and heel angle [SeaFish, 1993]. Pitch describes deviations from the horizontal running condition along the seabed, either upward or downward, at the forward end (warp attachment). Meanwhile, the heel (or roll) angle refers to the natural inclination of the board to lean inward or outward during trawling, considering the warp attachment. The ideal scenario of efficiency is when trawl doors maintain an angle of attack around 30-45° (as a function of their shape) and their surface its vertical respect to the seabed. Variation from this optimum reduce the catch efficiency of the net and its overall stability during the towing operation, with consequential alterations on the physical impact generated but also on the correct estimation of assemblage when sampling with this tool [Valdemarsen et al., 2007, Weinberg and Kotwicki, 2015].

Using gyroscope and accelerometer sensors attached to otter doors during an set of experimental otter trawl surveys, here we investigated whether and how the biomass composition of caught assemblage changes as a function of otter door dynamics described by its inertial variation. Our analysis also aims to investigate if the inertial response of the doors may detect different clusters of towing activity and which variables related to the seabed could explain these responses. Additionally, we analyzed the effect on taxonomic and functional diversity and sensitivity indices to identify a minimum set of indicators that provide a good representation of changes in assemblages, taking into account the main environmental and fishing pressure gradients affecting the community in the study area. We then used the results from the effects of inertial response of the doors to support the interpretation of impact assessment of the community across the trawling gradient.

2 Methods

2.1 Study site and data collection

Sampling was conducted on the NW Sicilian coast within the Gulf of Castellammare in the South Tyrrhenian Sea (Central Mediterranean Sea), covering approximately from 38°04’N to 38°16’N and from 12°79’E to 13°05’E. Torre dell’Uzzo mark the western boundary of the gulf, while Cape Rama marks the eastern boundary (Figure 1). The shelf extends parallel to the coastline for about 8 km offshore before sloping into a shelf break at around 140m depth [Iacono et al., 2014]. The continental slope is approximately 11° steep down to 500 m water depth, gradually decreasing to around 1.5° at a depth of 1300 m [Iacono et al., 2014]. Up to 14 narrow submarine canyons incise the slope, breaching the shelf break and extending into the outer shelf up to a depth of 110 m [Iacono et al., 2014]. These canyons are primarily distributed in the eastern sector of the Gulf and converge into the Castellammare Canyon at a depth of approximately 970 m. In the western sector of the Gulf, canyons are less incised and exhibit a smoother morphology, suggesting potentially lower activity of sediment transport dynamics within them.

Trawling is banned over a broad area (covering over 200 km2) that includes the entire shelf of this region, as established in 1990 (L.R. 25/90). However, high trawling intensities are recorded in the western sector of the slope, between 500 m and 700 m depth, near the offshore boundary of the no-trawl zone. Trawlers operate parallel to the isobaths and cease fishing on the eastern slope before crossing the more incised Castellammare Canyon. Within the no-trawl area, small-scale fisheries operate with 97 vessels distributed among 4 harbors [Co.Ge.P.A Golfo di Castellammare, 2016]. This scenario is beneficial to test community response to trawling gradients, as fishing effort decreases as we proceed inside the restricted area.

The data collection was part of the project actions of the Po Feamp Sicilia 2014-2020 “Rete 3 Golfi” project, aimed at informing spatial management plans for Sicilian fishing areas. Two commercial trawl vessels were employed in the study area to collect representative samples of the benthic and demersal communities. These vessels were 20.37 meters and 17.8 meters in length, with engine powers of 104.5 kW and 132 kW, respectively. Square mesh nets with a mesh size of 50mm were deployed for trawling. Trawling activities involved monthly data collection over a period of 12 months, starting from October 2022 and concluding in November 2023 (excluding August and October 2023). Sampling activities followed a random stratified sampling approach along depth strata, with three different ranges: 0-100m, 100-200m, and 200-500m, similar to trawl sampling protocols established by MEDITS [Bertrand et al., 2007]. Trawl duration was set at 1.5 hours, with an average speed of 2.5 knots (4.63 km/h).

All the collected specimens from each trawl were onboard sorted. Due to the high sampling effort and logistical constraints, approximately 70% of the captured species were frozen in storage boxes and transported to the laboratory for taxonomic identification and weight measurements. The remaining specimens were identified onboard and weighed before being discarded, allowing for the determination of the total biomass of the catch and the actual composition of the assemblage.

An Inertial Measurement Unit (IMU) was attached to the otter boards of the vessels to measure the acceleration forces acting during fishing operations and the inclination of the gear. Otter boards are crucial components that enable the trawl to spread adequately as the vessel tows along the seabed. They generate a lifting force and help channel the majority of the captured species toward the cod-end for capture. The IMU was positioned in alignment with the longitudinal side of the otter board, secured with a watertight lid (Figure 2). The IMU unit comprised a three-axial accelerometer and gyroscope, with its Z-axis aligned with the longitudinal side of the door (from tail to head direction), its X-axis oriented vertically (downward to upward for the right door, upward to downward for the left one), and its Y-axis perpendicular to the surface (from outward to inward direction). IMU was activated 30 minutes before the starting of the haul and associated with a specific boat protocol to retrieve the average towing speed and the timing and coordinates of the principal phases of the fishing activity (see sub-chapter 4.1). Raw acceleration (g units) and gyroscope data (rad/sec) were stored in an SD card and retrieved once survey daily operations were concluded. A total of 23 trawls have been selected from the collated dataset, the trawl successfully registered in their entirety by the sensor, along with the species captured during the trawling activity.

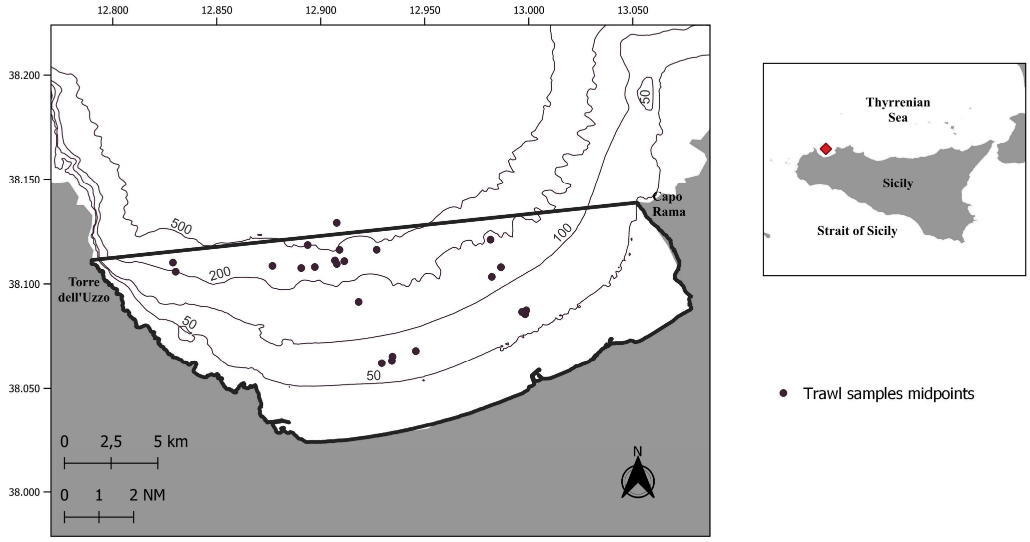


Figure 1: Selected study area and location of the midpoint of the trawl sampled during the survey. Solid black lines indicate the main isobaths expressed in meters, the black line in bold define the area closed to trawling activities since ’90. Black dots represent the trawl samples midpoint.

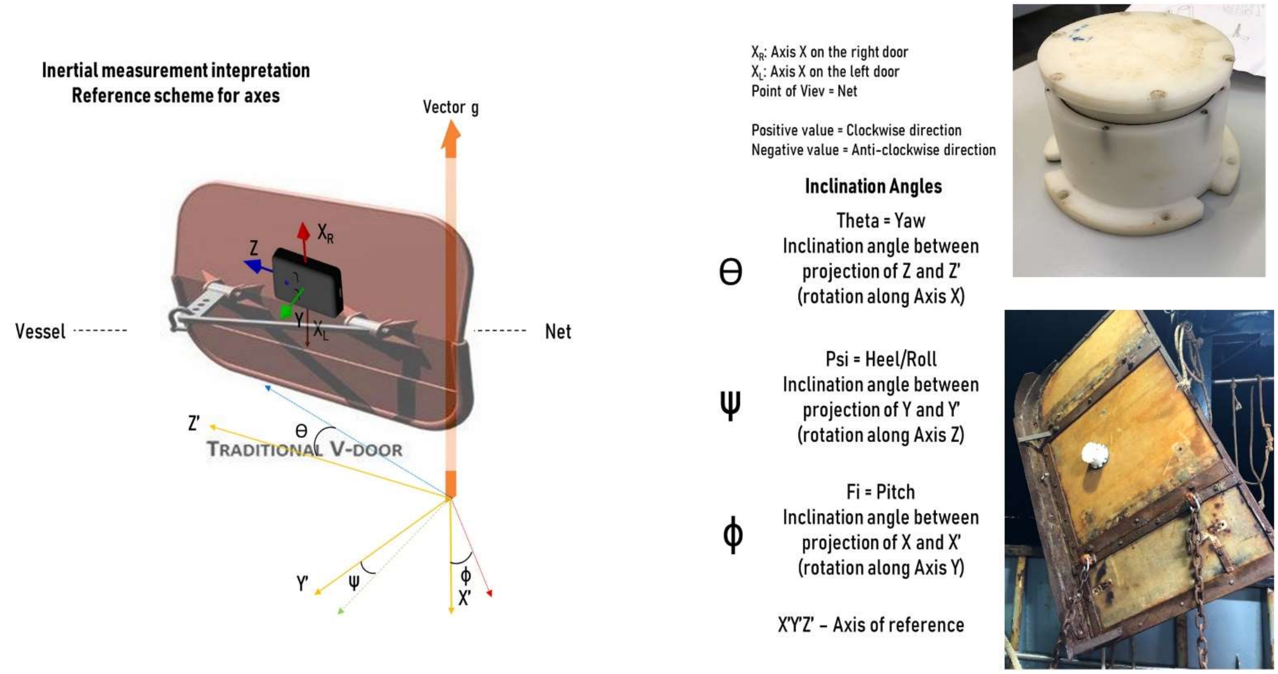
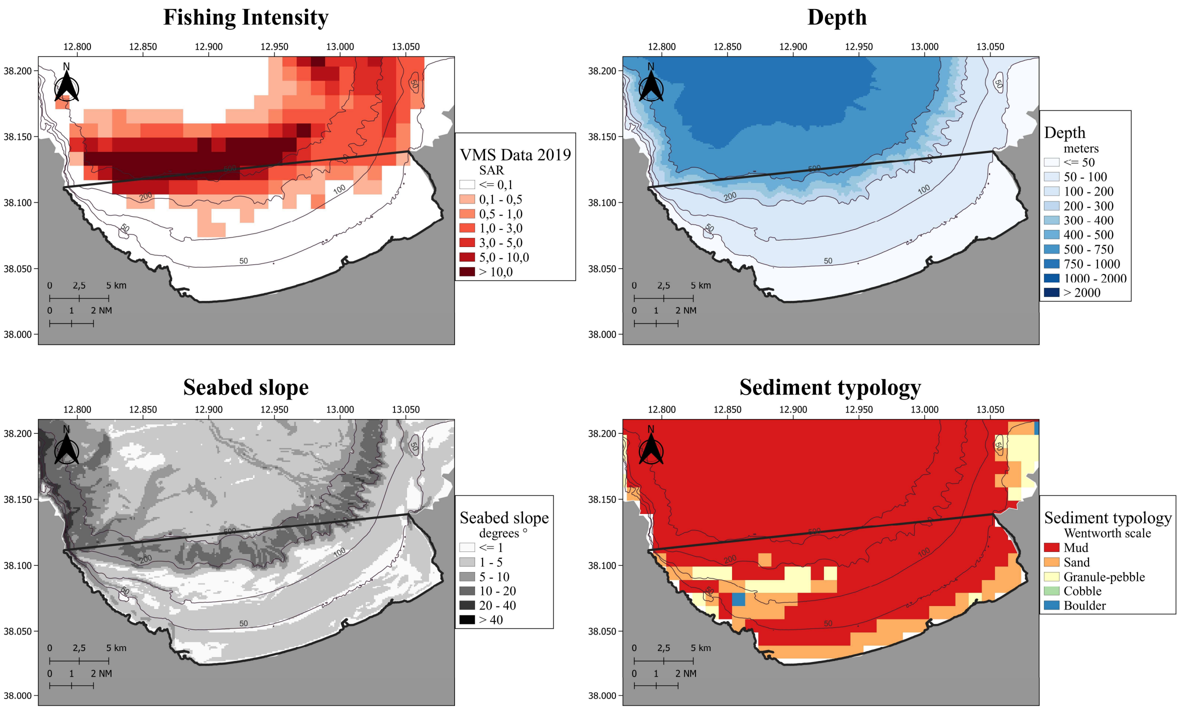


Figure 2: Reference scheme for Inertial Measurement Unit (IMU) displacement on the surface of the otter board and interpretation of inclination angles (Φ, Ψ and Θ) across the three main axis of the gravity vector g. On the right side the pictures of the watertight lid used to secure the sensor to the door's surface and the final configuration once attached. IMU unit contained a three-axial accelerometer and gyroscope used to measure the main acceleration forces and changes in angular velocity and estimate the inclination of the otter board during towing activity.



Fishing Intensity

Depth

Seabed slope

Sediment typology

Figure 3: Spatial distribution in the study area of the variables selected to investigate otter door inertial response and variation in assemblage composition and sensitivity to fishing pressure.

2.2 Environmental predictors and fishing intensity

To compute the abrasion induced by fishery activities on the seabed, expressed as the swept surface area ratio (SAR) per year, we utilized fishing trajectories and gear types aggregated yearly on a 1km x 1km grid of the study area. This approach follows the methodology outlined by [Eigaard et al., 2016] using a Vessel Monitoring System (VMS) dataset. Notably, no VMS signals were reported for depths shallower than 50m and areas within 3 nautical miles of the coastline, in compliance with the 2007 ban in the Mediterranean Sea (EU Council Regulation—EC No 1967/2006, 21 December 2006). We utilized 2019 data as they were the most recent available. Although they did not align with the actual year of the samples, the obtained fishing intensity layer could be considered an adequate representation of trawling effort distribution around the area, as trawling tends to be spatially homogeneous over the years [Piet and Quirijns, 2009, Amoroso et al., 2018].

In addition to abrasion, we selected depth, seabed slope and sediment typology as potential explanatory variables in the models. These variables were chosen to account for the inertial response of the doors, as they are all related to the state of the seabed, and to examine their effects on community composition. The sediment Wentworth classification was obtained from the EUNIS habitat classification produced in [Vasquez et al., 2021], while depth information was sourced from the Digital Terrain Model (DTM) [Thierry et al., 2019]. The slope of the seabed was calculated using QGIS.

The spatial distribution of environmental variables and fishing intensity can be observed in Figure 3.

2.3 Assessment of trawl performance

We aimed to evaluate trawl performance by initially investigating whether the inertial variation of the trawl could differentiate between different trawl dynamic patterns, and identifying seabed and gear-related variables that could explain such clusters.

To achieve this, we conducted a time series cluster analysis of the hauling series extracted from each trawl. Initially, raw acceleration and gyroscope data were filtered and segmented to isolate the portion related to the hauling phase (as detailed in sub-chapter 4.1). We applied a moving average filtering technique to the raw measurements to reduce noise and enhance signal clarity. Additionally, acceleration was normalized by gravitational acceleration (9.81 m/s2), and gyroscope data were converted to degrees per second for better interpretation. Inclination angles were derived from the acceleration data using equations outlined in [Fisher, 2010]. Specifically, Φ, Ψ, and Θ represented the angles of inclination concerning the projection onto the X, Y, and Z axes of the gravity vector and could be interpreted as descriptors of the pitch, roll and yaw of the object of interest (Figure 2). Considering the high correlation between inclination angles and acceleration data, we opted to focus solely on inclination data, as they provide information about the absolute orientation of the otter door during towing activities. Additionally, gyroscope data were retained as they can detect abrupt changes in rotation along the three main directional axes of the gear.

Hauling similarity was assessed using a multivariate distance-based method known as Dynamic Time Warping (DTW). DTW allows for the comparison of series of values by locally stretching or compressing them to maximize similarity [Zhang et al., 2017]. This approach is advantageous when dealing with time-series data of varying lengths or when focusing on shape rather than absolute values.

We applied the DTW algorithm to the six inertial variables obtained from the IMU (inclination and gyroscope data from X Y and Z axes) and used the resulting distance measure of similarity as input data for clustering techniques [Aghabozorgi et al., 2015]. Before applying the DTW algorithm, data were downscaled to 75% of the original size through interpolation due to computational constraints. Subsequently, we applied the DTW-PAM algorithm, grouping distances through Partition Around Medoids (PAM) cluster algorithm, with different K groups ranging from 2 to a maximum of 7. The optimal number of clusters was determined using various indices, such as the silhouette index, which evaluates the “goodness” of K selection.

Summary variables and centroids of the different clusters were calculated to compare the principal differences among inertial responses of the different groups. To identify variables that could explain the clustering of the sampled trawls, a discriminant analysis was conducted. Explanatory variables included those directly linked to trawl dynamics, such as average haul speed, seabed slope, depth, sediment typology and fishing intensity. Linear Discriminant Analysis (LDA) was employed to divide a response matrix into groups based on a factor, maximizing among-group dispersion versus within-group dispersion. This analysis helped determine how well an independent set of variables explained an a priori grouping, potentially obtained from previous clustering analyses [Borcard et al., 2011].

Additionally, we employed multivariate regression trees (MRT) to understand if explanatory variables could describe local structures of the inertial data and interactions among predictors. The MRT split the data into clusters based on environmental value thresholds, facilitating a deeper understanding of the relationship between environmental variables and inertial responses [De'Ath, 2002].

Furthermore, we ran generalized linear models (GLM) to assess the effect of otter door dynamics on the total caught biomass and the aggregated biomass of benthic or demersal species. Models were fitted with a Gaussian residual distribution with a log-link function for biomass variables. We considered adding second-degree polynomial variables to all potential explanatory inertial variables. This decision was prompted by our observation of scatterplots showing biomasses against the six inertial variables and vessel velocity. Therefore, we hypothesized a potential unimodal response of biomass to changes in the inclination of the otter boards, which could relate to a reduction in catch efficiency.

Finally, to explore whether inertial measurements of the otter door could explain variation beyond that explained by environmental variables in the community's biomass composition, a partial Redundancy Analysis (RDA) was conducted [Legendre and Legendre, 2012]. Individual wet biomasses for each trawl were summed up at the species level, and a Hellinger transformation was applied to the data. Predictors variables were standardized, and a partial RDA was performed with inertial measurements as conditioning factors. This process was conducted for the entire assemblage, as well as dividing the assemblage between mobile species, accounting fishes and demersal invertebrates like shrimps (hereafter accounted as "demersal" portion), and benthic epifaunal invertebrates (hereafter accounted as "benthic" portion).

2.4 Assessment of community sensitivity to trawling

To examine how the functional composition of caught assemblages changes across fishing intensity gradients, we analyzed a set of functional diversity indices alongside a sensitivity indicator developed in Chapter 3.

Initially, we identified eight biological traits capable of characterizing potential individual responses to physical abrasion: body protection, egg development, feeding mode, longevity, larval development, maximum length, mobility, and sediment position. These traits were selected objectively through a literature review focusing on trait responses to trawling gradients. We prioritized traits demonstrating the clearest trends in previous studies (see General Introduction chapter).

Data on these traits for benthic species were collected from various open-source databases [MarLIN, 2006, Bolam, 2014, Beauchard et al., 2017, Gonzàlez-Irusta et al., 2018, De Juan et al., 2020, de la Torriente et al., 2020], CEFAS trait database available in [Pierucci et al., 2022], and [Palomares and Pauly, 2023]. We then compiled a species-per-trait matrix, utilizing a fuzzy coding approach [Chevene et al., 1994] to assign trait modalities for different species.

The demersal portion of the assemblage, including all Chordata and highly mobile invertebrates, was excluded from the functional analysis. This decision was based on two primary considerations: the selection of traits and sensitivity effect parameters, which were tailored specifically for benthic infauna and epifauna invertebrate species. Additionally, the mobility of demersal species could dilute their response to trawling due to their broader distribution range and higher colonization potential.

Functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) were assessed using the species-traits matrix. These indices were chosen for their ability to highlight variations in specific functions among benthic communities [Villèger et al., 2008]. To accommodate categorical trait data, a Gower dissimilarity matrix was utilized to obtain the species-species distance matrix. Principal coordinates analysis (PCoA) was then performed on this matrix, with the resulting PCoA axes serving as the new ’traits’ for computing the three indices [Villèger et al., 2008, Lalibertè and Legendre, 2010, De Bello et al., 2021].

A functional sensitivity index was employed to detect specific impacts on communities. Unlike functional diversity indices, which assign equal weight to each trait level, semi-quantitative trait scoring indicates the potential sensitivity of the community to a given pressure.

The sensitivity indicator was assessed following the framework developed in Chapter 3 and based on effect sizes of trait modality response to trawling gradients found in metanalyses and empirical observations. Community sensitivity was calculated using the equation:

$$S = \frac{\sum_{j=1}^{m} \sum_{i=1}^{n} B_{T_{jM_i}} * Eff.size_{T_{jM_i}} * Wf_{T_{jM_i}}}{\sum_{j=1}^{m} \sum_{i=1}^{n} B_{T_{jM_i}}}$$

where *m* are the number of selected traits (*T*) (eight), *n* is the number of the modalities (*M*) for each trait,, $B_{T_{jM_i}}$ is the relative biomass of the modality *i* of Trait *j*, $Eff.size_{T\,ai}$ is the effect size related to the modality *i* of Trait *j* and $Wf_{T_{jM_i}}$ is the weighting factor related to the modality *i* of Trait *j* (1 for primary traits and 0.5 for secondary traits).

The relative biomasses of different trait modalities, commonly referred to as Community Weighted Means (CWM), were estimated for each trawl by multiplying the total biomass of each species by the fuzzy-coded trait matrix and summing up the biomasses within the same trait modality.

The final sensitivity score is then converted in percentage change, expressing the expected proportionate change of the sampled community between a untrawled state (SAR = 0) and a fishing intensity equal to 1 years−1 based on its pooled trait composition.

Diversity and sensitivity indicators were computed for each trawl and utilized as response variables. The response of these indicators to environmental and fishing gradients was tested using linear regression.

Additionally, we employed a multivariate approach to assess the influence of predictors on the functional composition of the caught assemblages. This involved conducting a partial RDA on the CWM scores calculated for each trawl with their associated environmental and fishing intensity values. Partial RDA was utilized to isolate and examine the effect of fishing intensity on the distribution of different trait modalities within the assemblages [Legendre and Legendre, 2012].

For all the linear regressions, assumptions of the model were checked through visual inspection of residual distribution. Any deviations from normality were corrected via permutation, and het- erogeneity of variance was addressed using heteroscedasticity-consistent standard errors. Stepwise forward selection of the listed predictors was conducted for both the linear regression and RDA analysis. All statistical analyses were performed using the R package, Version R-4.2.0 [R Core Team, 2023].

3 Results

The seabed typology of the Gulf of Castellammare samples was primarily characterized by muddy sediments. Therefore, this variable was excluded from the analysis, as all the trawls fell into the same category. The average trawl depth recorded was 218.4 meters (S.D. 153) spanning from a minimum of 64 meters to a maximum of 577 meters depth, with the seabed slope gradually increasing along the bathymetric gradient (mean slope of 5.0 with a standard deviation of 4.2) and exhibiting a strong positive correlation ($\rho = 0.75$). Trawls conducted at shallower depths generally encountered sediments with less steep and more uniform surfaces.

The intensity of fishing activity displayed a positive correlation with depth ($\rho = 0.63$). This relationship is mainly attributed to the influence of the trawl ban area that drives a high con- centration of fishing activity (exceeding 10 years−1) in the offshore western region, just beyond the outer edge of the protected area at depths around 400-500 meters. Lower values, typically below 0.1 years−1, were observed inside the Gulf, gradually increasing towards the borders of the ban area. The average swept surface area ratio (SAR) score among the sampled trawls was 4.17 years−1 (with a standard deviation of 12.60), ranging from a minimum of 0 years−1 for trawls at depths less than 100 meters to a maximum of 64.75 years−1 for trawls at depths greater than 400 meters outside the ban area. The average trawl speed recorded during the trawls was 4.5 km/h with a standard deviation of ±0.18.

3.1 Influence on trawl door dynamics

The DTW-PAM clusterization identified two optimal solutions with two or seven different clusters (see Supplementary Table S1). Despite uneven data pairing among these clusters, approximately 80% of the sampled trawls were grouped into a single one, almost 6% into another, and less than 3% (equivalent to a single trawl) into the remaining clusters (Supplementary Figure S1 and Table 1). Similar observations were made for the two-cluster scenario, where only two trawls belonged to one cluster and the rest to the other.

Table 1: Summary of the gyroscope measurements (angular velocity expressed in deg/sec along Axis X (GyrX) Y (GyrY) and Z (GyrZ)) and inclination, expressed in degrees (°) along Axis X, Y and Z of the seven DTW clusters. Data were reported as average and standard deviation values. Furthermore, the average values of the investigated variables related to the seabed-gear interaction were reported.

Cluster	GyrX	GyrY	GyrZ	Φ	Ψ	Θ	Depth	Speed	Slope	SAR
1	0.036 ±0	0.13 ±0.00	-0.01 ±0.00	-58.93 ±0.00	15.50 ±0.00	20.01 ±0.00	372.57	4.26	10.34	2.17
2	-0.11 ±0.04	0.16 ±0.06	-0.08 ±0.14	-68.85 ±0.01	20.89 ±0.23	1.11 ±0.20	134.52	4.44	4.32	0.47
3	0.25 ±0.00	-0.13 ±0.00	0.03 ±0.00	-60.60 ±0.00	29.05 ±0.00	-2.03 ±0.00	260.84	4.78	9.57	1.96
4	-0.18 ±0.00	0.04 ±0.00	0.05 ±0.00	-65.39 ±0.00	24.48 ±0.00	-0.01 ±0.00	127.79	4.48	0.86	0.04
5	-0.01 ±0.00	0.07 ±0.00	-0.06 ±0.00	-55.17 ±0.00	31.50 ±0.00	-0.27 ±0.00	476.57	4.54	6.63	17.73
6	-0.18 ±0.00	0.03 ±0.00	-0.05 ±0.00	-70.20 ±0.00	-8.71 ±0.00	15.35 ±0.00	114.48	4.26	0.96	0.197
7	-0.28 ±0.88	-0.04 ±3.70	-0.04 ±5.21	-58.61 ±4.92	18.98 ±5.72	4.01 ±4.44	222.57	4.53	5.92	3.68

Among the seven clusters, gyroscope data were consistent, particularly along axis Z, with values closely approaching zero. However, cluster 3 displayed positive angular velocity around axis X and negative values around axis Y, unlike the other clusters, which showed the opposite sign. Regarding inclination data, cluster 6 exhibited significantly more negative values for the angle Φ compared to the other clusters and negative values for the angle Ψ, in contrast to the positive values observed in the other clusters. Higher positive values of the Ψ angle were observed in clusters 3 and 5. Cluster 7, containing the majority of sampled hauls, was characterized by a pitch close to -60° (Φ), a positive roll around 20° (Ψ), and a slightly positive yaw angle around 5° (Θ). Cluster 2, 4 and 6 were the ones containing trawl in the shallower range with an average depth around 100 meters and with low average values of seabed slope and fishing intensity. Cluster 3 was the one with the highest averaged vessel velocity.

Discriminant analysis yielded an overall accuracy of 0.8529 (95% Confidence Interval: 0.6894, 0.9505), albeit lower than the proportion of the majority cluster (no information rate). It correctly classified all observations present in clusters 7, 6, and 3, using the corresponding average value of the four environmental predictors. However, the remaining clusters were erroneously classified into cluster 7, as the variation was not sufficient to distinguish them accurately from the most numerous clusters. Among the environmental predictors, average trawl speed proved to be the most effective variable in distinguishing between the different clusters, followed by fishing intensity, seabed slope, and depth (Supplementary Figure S2).

The multivariate regression tree, overall, explained only a small portion (18.6%) of the variance observed in the average measurements of the inertial variables among trawls. The data were primarily partitioned based on a fishing intensity threshold of SAR (3.81 years−1; Supplementary Figure S3).

3.2 Influence of trawl door dynamics on catch composition

The results of the evaluation of the effect of the inertial variables on total, demersal, and benthic biomasses are presented in the Table 2.

Overall, models incorporating the six inertial variables were able to explain between 46% and 70% of the observed variation. The rotational speed of the otter door did not yield any significant effects on the accounted biomasses and was often discarded during the stepwise selection process. The effects of velocity and inclination data proved to be nonlinear, except for benthic biomasses. The total caught biomass tends to decrease nonlinearly as the pitch (Φ) angle assumes more positive values, while the opposite can be stated for the roll (Ψ) angle. That is, as the otter board inclines inward, caught biomass increases until a breakpoint is reached. No significant effect was observed for yaw inclination, as the (Θ angle) was discarded during the stepwise selection.

Demersal biomasses are significantly influenced by the two angles, exhibiting the same directional trend reported for total biomass, although the significance and magnitude of the effects are slightly higher. Additionally, vessel velocity was shown to affect the caught biomass negatively. For benthic biomasses, the regression coefficients showed a significant negative influence of the roll angle, albeit with a lesser magnitude. Conversely, vessel velocity showed a strong nonlinear negative effect, considered significant by the model.

Table 2: Summary table of generalized linear regression models applied to total, demersal and benthic biomasses with the six inertial variables related to trawl dynamics: gyroscope measurement (GyrX,GyrY,GyrZ; deg/sec) and inclination data (Φ, Ψ, Θ; °) along axis X, Y and Z of the trawl door in conjunction with average vessel velocity. To account for not linear effect of velocity and inclination two-degree order polynomial terms were investigated in the GLM. Models used a gaussian distribution with a log link. The significance of the linear coefficients is highlighted with asterisk symbols: < 0.001 '***' < 0.01 '**' < 0.05 '*'.

Inertial Predictor	**Polynomial degree**	**Total Biomass**	**Demersal Biomass**	**Benthic Biomass**
Intercept		5.81	5.92	-2.36
GyrX	1°		1.81	
GyrY	1°			18.07
GyrZ	1°	-3.50		23.89
Φ	1°	-6.90 **	-7.31 ***	
	2°	-2.68 *	-1.97 *	
Ψ	1°	3.65 *	5.01 ***	-0.16 *
	2°	2.54 *	2.17 *	
Θ	1°			-0.15
	2°			
Velocity	1°	-1.05	-2.53 *	-71.75 *
	2°	-1.70	-0.22	-39.69 *
Adj. R2		0.46	0.62	0.70

The environmental and inertial variables included in the RDA analysis collectively explained 34.97% (df= 3, F=5.48, $p < 0.001$) of the variation in caught assemblage composition across trawls. Among the environmental variables, only depth ($p < 0.001$), latitude ($p < 0.05$), and fishing intensity ($p < 0.01$) were retained as significant, while no inertial variable was retained from the stepwise selection. The first two canonical axes from the RDA were considered statistically significant ($p < 0.001$ and $p < 0.05$).

From the ordination plot, it is evident that depth, SAR, and latitude are positively correlated with each other and with the canonical axis RDA1, driving the majority of the variation in species composition along this axis (Supplementary Figure S4). However, most species points were clustered at the center of the ordination plot, indicating similarity in assemblage composition across the samples. Depth was found to be the variable with the highest importance (correlation with RDA1 = 0.94).

As a result of the variation partition considering all the explanatory variables, non-inertial- related predictors explained 33% of the variance in the assemblage species composition across trawls. Inertial covariates explained 1% of the variation independently and an additional 4% in overlap with the other predictors. Nevertheless, 66% of the variation remained unexplained.

When examining benthic and demersal species separately, only one canonical axis remained significant ($p < 0.01$) for benthic species, directly correlated with depth as the sole selected variable, explaining 6% of the total variation in species biomass composition (Figure 4).

In contrast, the RDA model for demersal species yielded significant results, with both canonical axes effectively representing a portion of the dataset's variance ($p < 0.001$ and $p < 0.001$). Depth, latitude, longitude and fishing intensity were selected in the stepwise process, resulting in a model that explained

39% of the variance. Specifically, depth, latitude, and SAR were found to be significant and positively related to RDA1, with latitude also exhibiting a strong association with RDA2 (Figure 4). Similarly, in the variation partitioning analysis, 38% of the variation was attributed to non-inertial-related variables, while 3% was attributed to inertial ones, with an additional 4% explained by the combined influence of both groups.

3.3 Sensitivity assessment of the benthic assemblage

Overall, average functional richness was estimated to be 0.38 ±0.26 SD, average functional evenness 0.66 ±0.23 SD and average functional divergence 0.67 ±0.27 SD. When dissecting functional richness across depth strata, we observed higher scores between 100 and 200m (0.54 0.28 SD), with the lowest score recorded above 200m (0.25 ±0.25 SD) and an intermediate value below 100m (0.45 ±0.16 SD). Conversely, functional evenness displayed opposing trends, with higher values below 100m (0.71 ±0.18 SD) or above 200m (0.64 ±0.22 SD), while the lowest mean was observed in the intermediate bathymetric range (0.59 ±0.30 SD), although with values not significantly distant. Functional divergence followed a bathymetric gradient, with higher values at the shallowest depth range (0.83 ±0.13 SD) decreasing towards deeper areas (0.64 ±0.35 SD and 0.58 ±0.26 SD).

Despite these trends, linear models suggested that depth has a significantly negative effect only on functional richness (Table 3). Fishing intensity was not selected in the stepwise model selection process as it consistently proved to be nonsignificant. All models explained a portion of variance ranging from 10% for functional divergence to 17% for functional richness, indicating that the explanatory variables accounted for only a small portion of the variance expressed by the functional diversity indices. None of the investigated variables was selected during the stepwise selection for functional evenness.

Breaking down the benthic community into different trait modalities through the CWMs, we observed that the caught assemblages are characterized by species with longevity between 3-10 years (59%) or more (34%), with sizes mainly between 10-50 cm (50%), crawling (62%) on the sediment surface (90%). Feeding behavior is split among surface deposit feeders (36%), suspension feeders (25%), scavengers (20%), and predators (18%). Body protection spans from fragile species composing 40% on average, 32% of species with medium protection, and 28% of species with high body protection. Reproduction is mainly achieved through spawning of pelagic eggs (56%) followed by planktotrophic larval development (95%) (Supplementary Table S2).

RDA analysis did not find any significant predictors of the functional composition among the trawled assemblages. This is confirmed by the variation partitioning, where the predictors overall accounted for approximately 13%, with fishing intensity explaining only 1% in conjunction with the rest of the environmental predictors, excluding the spatial position of trawls, which itself explains 8% of the variation. Depth, slope, and latitude are positively related to the first canonical axes, while temperature and longitude are negatively correlated. SAR and depth are negatively related to the second canonical axis. Although not significant, the ordination plot of the RDA axes proved the homogeneity of the functional composition of the assemblage, with many traits concentrated at the center of the plot and few clusters branching slightly (Supplementary Figure S5).

The sensitivity of the assemblage is low, with an overall average of -6.29% 4.33 of expected change. Linear regression did not find any relevant predictors that significantly explained any change in variation of the indicator estimates (Table 3).

Table 3: Summary table of linear regression models with permutations applied to Functional richness (Fric), Functional evenness (Feve), Functional divergence (Fdiv) and Functional sensitivity (Sens) indices applied to the benthic portion of the assemblage with the three environmental variables accounted in the study: depth (m), seabed slope (°) and fishing intensity expressed as Swept Area Ratio (SAR; years −1). The significance of the linear coefficients is highlighted with asterisk symbols: < 0.001 '***' < 0.01 '**' < 0.05 '*'.

Predictors	**Fric**	**Feve**	**Fdiv**	**Sens**
Depth	-0.0007 *			
Seabed slope			-0.0207	
SAR				
Adj. R2	0.17		0.10	

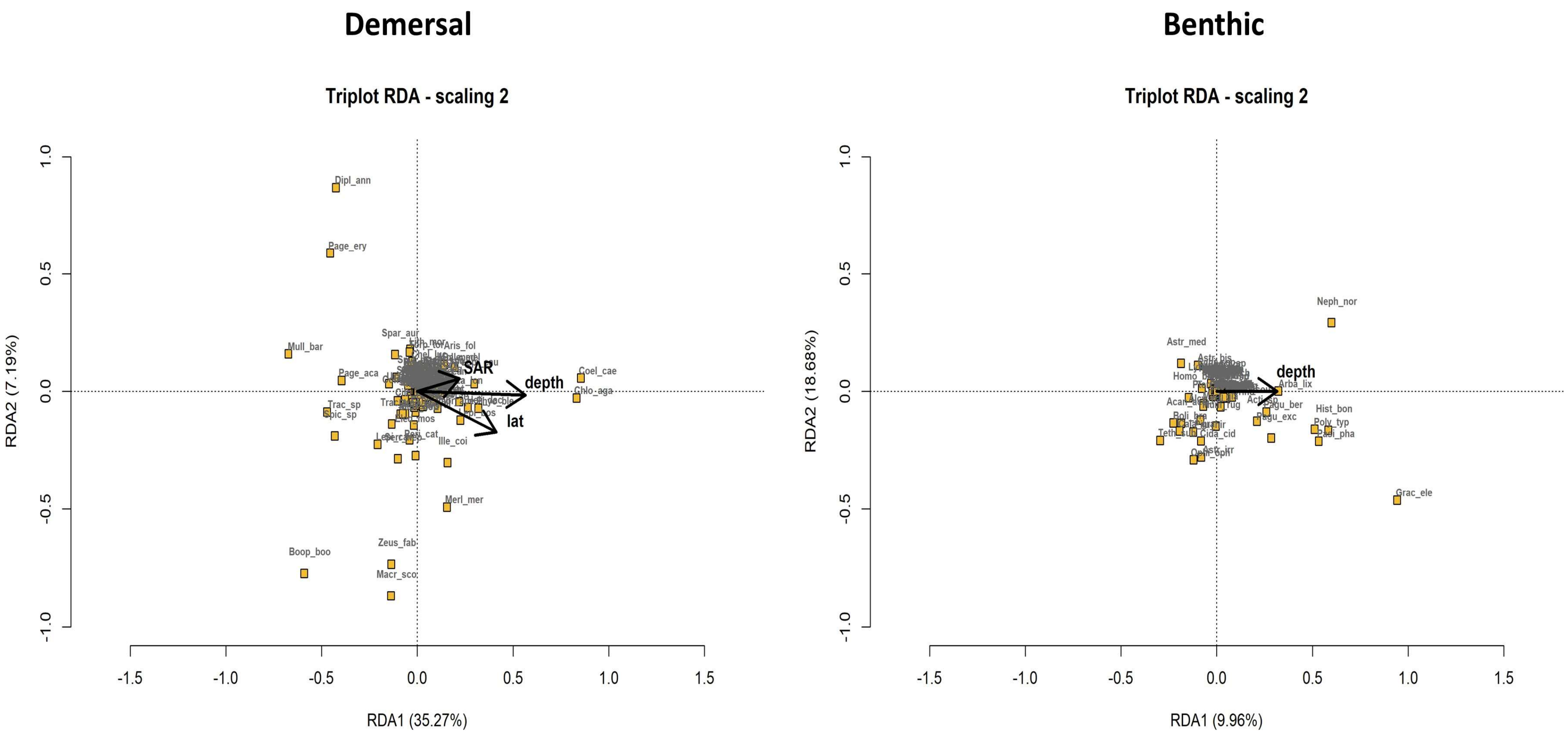


Figure 4: Redundancy analysis (RDA) ordination plot of the biomass composition of demersal (left) and benthic (right) species caught by the trawl samples. The significant variables selected after the stepwise selection are indicated in black.

4 Discussion

The application of a mixed approach, combining both trait analysis and the measurement of operational factors affecting net dynamics, has provided valuable insights into the structure of fishing assemblages in an area subjected to varying degrees of trawling pressure including no trawling. Additionally, it sheds light on how gear dynamics can influence species selection within these assemblages.

Our study's main findings indicate that motion variables related to otter door dynamics play a significant role in detecting changes in trawl performance for the total caught biomass of demersal-benthic assemblages. Specifically, species with higher mobility, such as demersal invertebrates and fish, are captured in smaller quantities when the otter door pitches down and heels more outward and their caught biomasses increase in the opposite direction until reaching a threshold point. Similarly, the roll angle also influences the capture of benthic epifaunal invertebrates, although in this case, the average towing velocity has a greater impact than the door's inclination.

Changes in vessel velocity and the related gradients of depth and fishing intensity undoubtedly influence the variations observed in otter board dynamics during towing. However, their influence is certainly less pronounced compared to other factors not investigated in our study.

Taxonomic composition is primarily influenced by variations in depth, while fishing intensity and spatial position within the study area contribute to shaping the structure of more mobile species. Upon closer examination of the functional composition of the benthic assemblage, we find that minimal variation can be explained, and the diversity and sensitivity of the community appear to be largely unaffected by the considered gradients.

In these considerations, otter board dynamics, described by their inclination, seem to play a secondary role compared to the major environmental constraints considered, explaining only a small portion of the variance in conjunction with other predictors.

4.1 Effects of otter doors dynamics in trawl performance

Speed serves as a primary factor in regulating the efficiency of the net by controlling the pulling forces exerted by the warps and the spreading force of the otter doors. Lower speeds (usually less than 2 knots) cause trawl doors to become unstable, potentially falling over sediment and failing to maintain the correct spread of the net. Conversely, speeds exceeding 2.5 knots (4.63 km/h) can lift the central part of the net, including the footrope and lateral bridles, reducing the entrapment of species living on the sediment surface [Engàs and Godø, 1989, Walsh, 1992, Somerton and Weinberg, 2001].

The significant influence of vessel speed we found on the total benthic biomass can be attributed to the fact that while variations in door inclination primarily affect the vertical and horizontal opening of the net, thus impacting the capture of more mobile species [Ona, 1999], speed variations not only affect these components but also affect the stability of all components that are in contact with the seabed. Loss of adherence of the footrope may increase the escapement of species living in direct contact with the sediment surface and can significantly affect trawl efficiency, especially for survey trawls with small mesh in the cod-end [Dickson, 1993].

This observation further aligns with our findings, where we identified speed as one of the main variables related to the various clusters of inertial responses. As towing speed increases, so does net drag and the flow across the face of the trawl doors. At some point, this increase in flow may overpower the ground sheer of the doors, imposing a lifting effect on the trawl that would be evident in bottom contact sensor data [Weinberg and Kotwicki, 2008]. This could result in an increasing the horizontal opening in many trawl designs followed by a decrease in the vertical opening increase in the distance of the footrope from the seabed [von Szalay and Somerton, 2005]. Other than the influence of speed, depth and fishing intensity describe the differences in trawl inertial clusterization. Depth produces changes in the horizontal spread of the trawl doors and net width, altering the catching performance of the gear [Weinberg and Kotwicki, 2015]. Fishing pattern history changes over time, affecting the physical properties of the surface seabed, as the furrows created by the door and all the ground components of the gear delve into the seabed surface. The persistence of the tracks could remain from months to years, especially in muddy seabed with low environmental heterogeneity [Oberle et al., 2018]. Therefore, grounds, where fishing intensity is high and continuous, would change their appearance and structure compared to unaffected sediments [Smith et al., 2007, Oberle et al., 2018, Bunke et al., 2019]. Even though trawl marks smooth with time, the tracks just below the sediment surface are still well-preserved and could be detected by an acoustic scan of the uppermost centimeters of the seafloor [Bradshaw et al., 2021]. Consequently, door behavior in seabeds more affected by trawling may exhibit differences compared to untrawled conditions, as the seafloor appears more homogeneous.

Nonetheless, many beds have been classified in the same cluster, and in general, we found low variation described by the three aforementioned variables, suggesting that inertial response of the door remained quite stable in our samples and with variations that could be related to other factors. It is important to note that otter trawling generally does not cause significant depletion over sediments, with an average penetration depth between 5 and 100 mm [Linnane et al., 2007], which is usually higher in mud but always lower than other towing gears such as dredging [Sciberras et al., 2018]. Therefore, the lower influence of door dynamics on the benthic portion of the assemblage could be attributed to a consistent low depletion of individuals caused by trawl passage, which remains approximately the same despite changes in door inclination, as depletion and penetration do not change significantly when removing the doors [Szostek et al., 2022]. Conversely, for the mobile portion of the assemblage, variations in otter board inclination, influencing horizontal and vertical net openings, have a greater impact on that portion of the assemblage that also moves in the water column. Unimodal responses of Ψ and Φ angles on the total biomass of mobile species showed the influence of the doors inclination on those species. As the door heels more inward, the caught biomass tends to increase until a limit where the upward force generated is too high to prevent the correct contact of the door to the sediment and to generate the right amount of spreading force to maintain the horizontal and vertical opening of the net. The same could be stated for the pitch angle; excessive pitch down (more negative values) or pitch up (more positive values) reduce the spreading force generated by the door, decreasing the catch efficiency of the net [SeaFish, 1993]. We generally observed a slight inward heel of the door (described by the positive values of Ψ) with a slight upward pitch (described by the negative values of Φ) in our samples that should indicate a normal condition of trawling activity.

We did not find any effect related to the change in the yaw of the otter door. In studies conducted by [O'Neill and Ivanovìc', 2016] and [Enerhaug et al., 2012], as the angle of attack increases (which can be detected by an increase in the Θ angle), both ground and lifting forces, crucial for ensuring the correct spread of the net, generally tend to increase, with an optimal threshold around 30-35°. However, this effect is less predominant than the effect related to towing velocity and the overall weight of the towed component. This could also explain why we did not observe significant alterations caused by the yaw angle on total catches, as on average, changes in yaw were confined to a range of 20°. It is important to note that theta, being the Z-axis longitudinal to the otter door, is related to the angle of attack, but it does not directly correspond to it, as one angle is between one component of the normal of gravity force and the other is between the shoe of the door and the direction of towing. Except for certain extreme cases, variations have little impact on the change in the angle of attack.

4.2 Influence of fishing intensity and environmental gradients on assemblage structure

Changes in the taxonomic composition of caught assemblages in the RDA are undoubtedly dictated and influenced by variations in fishing intensity and depth. However, this variation is not reflected in the functional composition, which remains more stable and unaffected by the gradient from the coast to offshore areas.

This condition is more apparent concerning epifauna, which demonstrates a certain homogeneity in its composition slightly influenced by the bathymetric gradient. As we move towards deeper zones, many variables such as temperature, nutrient concentration, dissolved oxygen, etc., change, affecting the distribution ranges of various species and ensuring their turnover [Garrabou et al., 2002]. However, in the study area, the range of samples seemingly does not suffice to highlight such changes.

The presence of a protected area near the coast, from which frequent inputs of terrestrial nutrients originate, along with high fishing intensity just outside this area, filters the community by selecting species adapted to such heterogeneity [Romano et al., 2016]. Since fishing intensity often influences the community similarly to areas with high environmental variability (a common condition in coastal environments) [Sciberras et al., 2013, Van Denderen et al., 2015], it is not unreasonable to consider that this condition in the area causes the community to be selected similarly, reducing the differences encountered from the coast to offshore. This is further emphasized by the fact that variations are only observed concerning taxonomic variation.

An explanation could arise from the fact that many benthic invertebrates we sampled are generalist species of muddy bottoms with relatively broad bathymetric ranges that fall within those considered in this study. An example is the seastars Tethyaster subinermis or Astropecten bispinosus, echinoderms widespread in Mediterranean continental shelves [Mangano et al. 2015, Terribile et al., 2016], whose presence in the samples along the gradient may have covered the biomass loss of the more sensitive components [Jennings et al., 2001, Hinz et al., 2009]. To confirm this, the assemblage's overall score from applying the functional sensitivity index reflects this low sensitivity to fishing impact. This finding is supported by the results of a meta-analysis conducted on experimental fishing impact studies [Kaiser et al., 2006] which concluded that otter trawling on muddy sediments, compared to other combinations of gear and substrata, had one of the least negative impacts on the benthic biota.

Species turnover may not be reflected in the functional composition of the community. Although many species display a different distribution range due to their niche adaptation, they may play a similar role in the community, increasing the functional redundancy of it [Tillin et al., 2006]. We have seen a high similarity in functional composition across the different samples, highlighted by the centrality of points in the RDA-constrained space, especially regarding benthic epifauna. Only functional richness showed a significant reduction proceeding offshore. Coastal shelf areas generally exhibit higher environmental heterogeneity compared to deeper slope areas thanks to the terrigenous inputs of nutrients and stress induced by waves and currents, increasing the number and patchiness of niches that species can exploit [Cosentino and Giacobbe, 2006, Fanelli et al., 2009]. In addition to this difference, the presence of higher fishing intensity offshore may act as a further process of narrowing the width of functional niches of the community, as the disturbance promotes the selection of more adapted species that increase in their abundance. However, despite these factors, the observed effect is not strongly marked in our community and is explained only in part by the bathymetric gradient, as no variations are observed in either the composition or the functional evenness. Nevertheless, although not significant, the functional divergence, describing the distance of the niche of the different species, appears to decrease as we proceed offshore, supporting what we observed for the functional richness.

The sample size could have influenced the lack of significance regarding the environmental predictors and fishing intensity, although such observations are not unique to our study case [Van Denderen et al., 2014, Van Denderen et al., 2015, Jac et al., 2020b, Bradshaw et al., 2024]. Small variations explained by the variables suggest that other mechanisms could influence the benthic community. For example, organic carbon concentration could play a role in creating differences between the trawled and untrawled areas that reflect differences in macrofauna functional traits. Specifically, a decline in community complexity and bioturbation capacity can lead to a decrease in sediment oxygenation and carbon cycling and result in higher sedimentary organic carbon concentrations [Tsikopoulou et al., 2022]. Recent studies in the same area have demonstrated that the biogeochemical composition of the sediment may differ due to trawling exposition, resulting in less organic matter available in trawled areas [Romano et al., 2016, Paradis et al., 2019].

Comparison in ecological response between unprotected and protected areas had varying results with some finding increases in sensitive taxa [Pipitone et al., 2000, Beukers-Stewart et al., 2005, Davies et al., 2021, Langlois et al., 2021], and others, like our study, finding no difference between protected area and control sites [Tillin et al., 2006, Sciberras et al., 2013, Bergman et al., 2015]. This variability in effects could be attributed to many factors, such as pre-designation fishing pressure, enforcement/adherence level, age of protection, size of the protected area, the level of protection, as well as the sensitivity/appropriateness of the monitoring effort to detect protection effects [Babcock et al., 2010, Greathead et al., 2020].

Despite the long period since the trawl ban, the mentioned processes may have prevented the recovery of the community to a state dominated by structurally complex taxa of colonial epifauna [Hinz et al., 2009]. In addition to this, the presence of illegal fishing activities within the Gulf, identified from VMS data and reported in previous study [Mangano et al., 2013], even a few prolonged passages over time are sufficient to create a chronic condition for the community such that new equilibrium conditions are created in which the species most resilient to such disturbance dominate [Hiddink et al., 2006]. Furthermore, the gulf is prohibited to trawling only, artisanal fishing within it is still permitted. Fixed gear such as gillnets, commonly used by local fishermen in the area, can affect bottom organisms and structure as their anchoring system could drag on sediment with waves and currents, and the loss of the net can cause ghost fishing or alter the community structure by offering niches previously absent [Grieve et al., 2014].

In our case where a small protection area is in proximity with high fishing intensity ground, recovery of the community usually proceeds by the slower process of larval settlement, a process where most larvae originate from either distant areas or from the small unaffected patches [Kaiser et al., 2018]. The majority of species we found, even those with more sensitive traits like soft corals (e.g., Alcyonium palmatum), produce pelagic eggs with a higher recovery potential compared to other longer-lived sessile emergent species [Budd, 2008]. This reproductive strategy could guarantee a discrete dispersal capacity and favor the resettlement of depleted populations even in a relatively short time, in comparison to other species where recovery has been seen to require decades [Lambert et al., 2014, Kaiser et al., 2018], maintaining the dominance of species that are better adapted to the combination of anthropogenic and environmental variation.

On the contrary, demersal fauna appeared to be more influenced by both the environmental gradient and fishing intensity, with significant effects reported in the RDA model for taxonomic composition. This aligns with previous findings observed in [Pipitone et al., 2000], where an increase in abundance of fish species was noted after the establishment of the ban period. Reduced fishing pressure likely boosted the survival and abundance of large females, leading to increased egg production and better recruitment conditions for recovery from overexploitation [Fiorentino et al., 2008].

Furthermore, a clearer distinction between deeper trawls characterized by species like Chlorophthalmus agassizi and Coelorinchus caelorhincus, and shallower ones dominated by Mullus barbatus, can be observed in the ordination plot. These differences in hydrological conditions between the shelf, characterized by high variability, and the slope, known for its stability, likely account for the pronounced differences in demersal fauna composition and structure across these regions [Colloca et al., 2003]. Deep-water species, adapted to oligotrophic conditions and specific environmental parameters like temperature, salinity, and light, may struggle to survive in the more heterogeneous environment of the shelf [Maynou and Cartes, 2000]. Conversely, species endemic to the shelf may find it challenging to compete and adapt to the stable conditions of the slope. This indicates that fishes may have a narrower bathymetric range of distribution compared to epifaunal invertebrates in adjunction to the benefit from the reduction in fishing pressure [Pipitone et al., 2023].

4.3 Uncertainty and limitations

The absence of a relationship found between door inclination and epifaunal composition may be due to reduced catch efficiency of the gear for this portion. It is crucial to consider from a technical standpoint that the design of the door can significantly influence the degree of contact. The V- door, traditionally used in many European fisheries and in our sample, is designed with a hinged bracket to which the warp is attached. This design ensures only light contact with the seabed, as it is primarily used on muddy grounds, where digging in must be avoided. Our results indicated that the pitch angle appeared quite stable across all samples, suggesting little to no perturbation that might have hindered the gear's contact. However, in such sediments, it has been observed that components of the gear generally in contact with the seabed, such as footropes, may detach more easily with changes in depth and wire length, and bottom contact sensors may struggle to track such changes [Weinberg and Kotwicki, 2008].

This detachment could influence the already low depletion rate caused by towing, especially for species that live in close contact with the seabed, such as epifauna, hindering the relationships investigated in the univariate and multivariate models, as well as the correspondence between the caught assemblage sensitivity and the actual one in the community. Comparisons between trawl and video sampling experiments in Mediterranean areas have shown that some sensitive species in benthic megafauna are undersampled with trawling surveys, and the gear's catch efficiency can mask the real composition of the community, especially in habitats with high heterogeneity [Jac et al., 2021]. As this effect is strongly dependent on habitat conditions, particularly sediment typology, conclusions regarding the efficacy of the two methods should be approached with caution. For example in [Jac et al., 2021], in muddy sediments like those in our study area, no method was conclusive in assessing the effect of trawling on benthic communities because, in most cases, although abrasion was generally high, it could not be reliably related to diversity indices. A comparison of measured angles with direct bottom contact observations during towing activities is necessary to validate such interpretations and to model more accurately the influence of doors inclination, seabed contact, and the amount of biomass captured.

The lack of a relationship between abrasion and the different indices for the two sampling methods could be explained by the small number of stations sampled and the unbalanced distribution of these stations along the abrasion gradient. Results from [Jac et al., 2020b] suggest that an increase in the number of stations sampled, particularly in areas of low abrasion, could enable the detection of a significant and negative effect of trawling. Furthermore, the strong zonation patterns in the epibenthic assemblage related to depth make it more challenging to address the effects of trawling activity, which is also strongly depth-stratified in the Mediterranean Sea [Dimech et al., 2008]. While a stratified approach with a comparison between untrawled and trawled areas could have provided significant effects, it is important to note that the use of continuous gradients allows for a more precise estimation of the effects of variable changes and helps clarify the relationships between species biomass and fishing impact.

4.4 Conclusion

The present study employed a mixed methodology, integrating functional trait analysis and inertial analysis of otter boards, to explore the composition of fishing assemblages in a region characterized by a gradient of trawling pressure. Key findings underscore the significant influence of otter door inclination and vessel speed on trawl performance, particularly affecting the total biomass of benthic-demersal species. While demersal fauna exhibited notable responses to depth gradients and fishing pressure, reactions among epifaunal species were less pronounced.

Results from the functional analysis may also provide a measure of which functional components are actually captured by the gear and their degree of vulnerability within these assemblages. Challenges in assessing trawling's impact on benthic communities underscore the need for further research and comparison with direct observation of the seafloor during trawling activity to validate the observed effect of door inclination and compare the sensitivity of the assemblage against the portion of the community not retrieved by the gear.

However, these preliminary findings offer initial guidance on the primary factors to investigate to evaluate trawl performance. For instance, pitch and heel angles proved to be more important than the yaw angle in determining the caught biomass, while gyroscope data exhibited greater stability than acceleration forces during towing. Therefore, future studies could focus on understanding how changes in these angles correlate with the penetration depth of the door and the forces governing net opening and dragging.

Furthermore, the importance of studying the inclination of the otter door during towing activities could also be related to understanding the actual footprint generated by the furrows during passage, as the otter door is the main component that delves into sediments, causing their displacement and resuspension [Bradshaw et al., 2021]. As the furrows generated change in function based on the angle of attack of the door, future studies relating changes in the yaw angle to alterations in the angle of attack could provide estimates of the actual surface trawled and the potential sediment resuspended.

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Chapter 6: General Discussions

The present research widely examined the ecological impacts of trawling on benthic communities along the continental shelves of Sicily, leveraging extensive data analysis and focusing on a trait-based approach. This research enhanced the understanding of how trawling modifies community structures and functions, particularly influencing species trait compositions in regions subject to intense fishing activities. Additionally, the research facilitated the development and application of a novel and salient impact assessment framework, specifically designed to evaluate the effectiveness of detecting potential effects induced by trawling in the benthic community.

Ecological Effects of Trawling Inferred from Trait Analysis

The benthic-demersal community we analyzed revealed that its current state results from both chronic bottom trawling and variations in bathymetry. Similar patterns have been observed across various fishing grounds along the continental shelf of the Strait of Sicily, areas subjected to decades of trawling activities [Mangano et al., 2013; Consoli et al., 2016; Terribile et al., 2016; Milisenda et al., 2017]. In these contexts, bathymetry significantly influences the turnover and composition of the community.

Depth correlates directly with gradients in temperature, primary production, nutrient concentration, sediment characteristics, and current patterns, all of which can restrict species distribution. As a result, depth often emerges as the primary driver of community distribution [Farrè et al. 2016, Terribile et al., 2016, Peristeraki et al. 2017]. Most variations in the demersal domain are attributed to bathymetry, followed by bottom temperature and fishing intensity, with seabed shear stress and slope also playing roles, particularly in taxonomic composition. When considering functional composition, fishing intensity and slope demonstrate stronger effects. For the benthic domain, fishing intensity, bottom temperature, and bathymetry primarily drive the constrained variation explained by the multivariate model using taxonomic data, with temperature excluded in models using functional data.

Overall, the variables investigated accounted for more variance in the demersal domain than in the benthic one. Models applied to species count data generally showed a slightly better fit than those applied to functional composition. Despite the varied distribution ranges of many species due to niche adaptation, they often play similar roles within the community, increasing functional redundancy [Tillin et al. 2006]. This similarity in functional composition across different samples was particularly evident in the centrality of points in the multivariate space, especially regarding benthic epifauna both in the results obtained in chapter 2 and 5.

The communities observed and described for the first time under the functional lens were characterized by demersal organisms measuring 10-20 cm, with lifespans of 3-10 years, pelagic eggs, and predominantly predatory behavior. The benthic domain primarily included organisms measuring 2-10 cm, with similar lifespans, releasing eggs into the water column or brooding, crawling on the seabed or remaining attached to it, and feeding on suspended organic matter or dead animals.

The notable similarity in functional space across these communities at regional scale – on a central area of the Mediterranean basin – can be attributed to the combination of higher environmental heterogeneity found in shallower areas and the selective adaptation induced by trawling gradients in deeper communities. Coastal shelf areas generally exhibit more environmental heterogeneity than deeper slope areas, due to terrigenous nutrient inputs and stress induced by waves and currents, which increase the number and diversity of niches exploitable by species [Cosentino and Giacobbe, 2006, Fanelli et al., 2009].

As we move toward shallower areas, primary production increases due to continental nutrient runoff and rising temperatures. These combined effects potentially shape the niches of species in the community, favoring those with higher thermal tolerance and benefiting from increased productivity. The positive effects of seabed chlorophyll concentration on benthic biomass and diversity were also observed, mirroring increases in infaunal biomass in the North Sea as sediment chlorophyll content rose, as reported by Hiddink et al. [Hiddink et al. 2006].

On the deeper portion of the shelf areas, since fishing intensity often produces selective forces similar to gradients of natural environmental variability [Sciberras et al., 2013, Van Denderen et al., 2015] —a common condition in coastal environments—it is reasonable to consider that this condition causes the community to be selected in a similar manner, thus reducing the differences from the coast to offshore. This factor further emphasizes that variations in our results are more pronounced in taxonomic variation, while functional composition remains stable and often unexplained by the investigated gradients.

The novel approach of coupling taxonomic analysis with functional ones through Biological Trait Analysis and diversity indices has proven to be an effective approach for enhancing the understanding and interpretation of community responses in chronically disturbed areas. In fact, relying solely on standard diversity indices applied to the taxonomic composition of assemblages may not accurately reflect the influence of fishing disturbances compared to functional changes that persist longer over time, allowing for better interpretation of variations even in communities already adapted to such conditions [de Juan et al. 2007, Farriols et al. 2017, Sciberras et al. 2018].

Some observed changes and gradients of response were also mirrored by the application of the trait-based approaches we applied in chapter 3 and 4. Applications of the longevity models on a Mediterranean context showed that the sensitivity of benthic communities to trawling varies significantly with depth. In outer shelf areas, where the depth exceeds 100 meters, an increase in trawling intensity is linked to a community shift towards species with shorter lifespans, suggesting that these deeper communities, while less influenced by terrestrial inputs and surface productivity, are particularly sensitive to the physical disturbances caused by trawling.

Interestingly, in shallower areas (less than 100 meters), an increase in trawling intensity correlates unexpectedly with an increase in the average lifespan of the community. This paradoxical finding could provide insights into how local contexts may exhibit rates of depletion and recovery for certain species that differ from those assumed in the models, indicating that while broad regional assessments hold significance, these observations may relate to specific species responses, like those observed for some soft corals on the Sicilian continental shelf [Ambroso et al. 2013]. Therefore, our results could guide further understanding of the components of the benthic community that need deeper investigation into the effects induced by trawling on their recovery and distribution.

The use of trait distribution models within the trait-based framework allowed for a flexible description and identification of where certain traits are expressed and the main variables driving their distribution. This methodological approach provided a suitable tool for mapping the spatial distribution of traits and understanding their responses to environmental gradients and trawling disturbances, supported by the evaluation of trait contributions within the framework of trait-based vulnerability assessment, highlighting the critical importance of traits such as longevity and mobility. The provided outcomes, spatially explicit and functional based maps, represent a user-friendly interface of easy reading for stakeholders, representing a crucial tool to start informing the debate on local action and management plans on co-management context.

Species with longer lifespans are often more susceptible to disturbances because their slower reproductive rates and longer juvenile phases mean that recovery from population declines can be prolonged [Hiddink et al., 2019]. In the context of trawling, which can cause significant mortality and habitat disruption, species with shorter lifespans may be able to repopulate more quickly, thus showing greater resilience. Mobility significantly affects the ability of species to evade trawling gear, impacting their risk of capture and mortality [Thrush et al. 2002]. In the trait-based assessment framework, species mobility is categorized into various levels, from sessile to highly mobile. Sessile or low-mobility species are at a higher risk of being impacted by trawling as they cannot escape the path of the trawl. In contrast, highly mobile species may avoid trawling nets more effectively, leading to different survival rates and potential biases in the species composition of trawled areas.

The sensitivity assessment, therefore, assigned higher scores to communities with a significant presence of long-lived species and less mobile species, signaling higher vulnerability and potentially greater ecological impacts. This aspect of the assessment is particularly important for conservation efforts, as it highlights the need to protect sessile long-lived species that are crucial for the stability and diversity of marine ecosystems.

Implications for Management and Conservation

The integration of trait-based analysis into the assessment of trawling impacts provides a robust framework for understanding and managing the ecological effects of trawling. The methodologies developed in the study, both trait-based and quantitative, enable more refined monitoring of benthic communities. By identifying key traits that influence vulnerability, such as longevity and mobility, managers can monitor these indicators to assess ecosystem health and resilience. From a management perspective, the framework we developed in chapter 4 could be relevant for Marine Strategy Framework Directive (MSFD) purposes. It facilitates the identification of potential threats to benthic communities caused by trawling at the habitat scale and enables the study of different management scenarios, particularly those related to changes in trawling effort and its spatial distribution. This allows for the estimation of fluctuations in community vulnerability in targeted MSFD areas and provides an early warning tool for community changes in response to potential future fishing scenarios.

The comparison with the PD approach assessed in chapter 3 also demonstrates that both methodologies identify similar risk areas. This correlation serves as evidence that different approaches can complement each other, and our results could guide the selection of optimal indicators for assessment at local or regional levels. Particularly, the importance of longevity proves that the application of the PD approach is a good estimator of impact in our study region, especially in the deeper zones of the continental shelf in the Strait of Sicily, where high levels of disturbance are reached.

These methodologies facilitate the development of more informed regulations regarding trawling practices and the implementation of spatial management strategies. By utilizing the detailed maps of community vulnerability and trawling intensity provided by our study, managers, decision makers and policy makers can identify critical habitats that require protection from trawling activities, fostering the dialogues and the creation of a solid science-policy nexus. Although a specific threshold was not set in this study, it is possible to adopt a fixed percentage change to estimate a determined footprint that could help in highlighting high-risk areas, similar to the method used in [Eigaard et al. 2017].

The establishment of the MSFD by the European Union in 2008 advocated the development of indicators for assessing and monitoring the impact of human pressures on the marine environment [Borja et al. 2016]. Recognizing trawling as one of the most significant pressures on the seabed, it became imperative to develop indices to study its impact. Our framework adopts a step-by-step approach that allows for the representation and spatial description of community vulnerability to fishing impacts. This process aimed to evaluate the inclusion of selected traits derived from literature information and provide feedback on the relevance of those traits in the final score. The obtained results can be used to further improve the overall index and guide the selection of traits for other methodologies assessing the community’s status [Jac et al. 2020a, 2020b].

Influence of gear dynamics in assemblage composition

Our study highlighted the complex interactions between trawl gear dynamics, environmental factors, and species characteristics that shape the catch composition of benthic-demersal assemblages.

The primary findings demonstrated that motion variables related to otter door dynamics significantly influence trawl performance for the total caught biomass of demersal-benthic assemblages. Specifically, species with higher mobility, such as demersal invertebrates and fish, were captured in smaller quantities when the otter door pitches downward and heels outward, with their captured biomass increasing as the door's movement reverses, reaching a threshold point. Likewise, the roll angle influences the capture of benthic epifaunal invertebrates, although in this instance, the average towing velocity had a more significant impact than the door’s inclination.

We observed a notable influence of vessel speed on the total benthic biomass, which can be attributed to how variations in door inclination affect the net's vertical and horizontal openings, impacting the capture of more mobile species [Ona, 1999]. Variations in speed not only influence these components but also affect the stability of all components in contact with the seabed. A loss of adherence of the footrope may increase the escapement of species in direct contact with the sediment surface [Grieve et al. 2014], significantly affecting trawl efficiency, especially for survey trawls with small mesh at the cod-end [Dickson, 1993].

This detachment could influence the already low depletion rate caused by towing, particularly for species closely associated with the seabed, such as epifauna [Hiddink et al. 2017]. This complicates the relationships explored in univariate and multivariate models, as well as the correspondence between the sensitivity of the caught assemblage and the actual community composition. Comparisons between trawl and video sampling experiments in Mediterranean areas have shown that some sensitive species in benthic megafauna are undersampled by trawling surveys, and the gear’s catch efficiency can mask the real community composition, especially in habitats with high heterogeneity [Jac et al., 2021]. Given the strong dependency on habitat conditions, particularly sediment typology, caution is necessary when drawing conclusions about the efficacy of these methods. For instance, in Jac [Jac et al., 2021], no method in muddy sediments conclusively assessed the impact of trawling on benthic communities because, although abrasion was generally high, it could not be reliably linked to diversity indices. A comparison of measured angles with direct bottom contact observations during towing activities is necessary to validate such interpretations and more accurately model the influence of door inclination, seabed contact, and biomass capture.

Our mixed-method approach, integrating functional trait analysis and inertial analysis of otter boards, was used to explore the composition of fishing assemblages in a region characterized by a gradient of trawling pressure. Key findings underscore the significant impact of otter door inclination and vessel speed on trawl performance, particularly affecting the total biomass of benthic-demersal species. While demersal fauna showed notable responses to depth gradients and fishing pressure, the reactions among epifaunal species were less pronounced. The results from the functional analysis also provide insights into which functional components are actually captured by the gear and their degree of vulnerability within these assemblages.

General considerations and future perspectives

In conclusion, the thesis effort allowed to measure a negative impact of trawling on benthic and demersal communities in continental shelf environments on a central area of the Mediterranean Sea. Although these responses are often obscured due to the temporal layering of impacts, which leads to the selection of less sensitive species, forming a community that appears functionally similar across gradients. Investigating different approaches and trait-based methodologies has allowed us to identify areas most affected by this impact and highlighted which areas and relationships need further exploration to understand how such factors affect community response to trawling. Future comparisons of functional diversity indices, calculated by integrating different sampling techniques, could better verify how trawl samples may be suitable for detecting impacts in chronic fishing grounds and provide solid validation of our interpretation of the relationship between door dynamics and catch assemblage composition.

Currently, the application of our framework is limited to assessing the response of benthic infauna-epifauna to trawling, which is expressed and linked to a linear response of the community to trawling distribution. In the future, employing meta-analysis and regression techniques on variations in faunal trait abundance across quantified gradients in trawling intensity could help estimate non-linear effects in the response of different trait modalities. Using regression techniques on effect sizes of trait modalities according to fishing intensity also offers a method to determine coefficients that more effectively integrate the exposure component with the intrinsic sensitivity of the community. This expansion could broaden the framework’s applicability to a wider range of species. For instance, incorporating studies that consider more mobile species like fishes and cephalopods (often targeted by commercial activities) and analyzing responses at different habitat levels could extend the framework’s applicability to better describe the vulnerability not only of the benthic portion of the community but also of other potentially impacted components.

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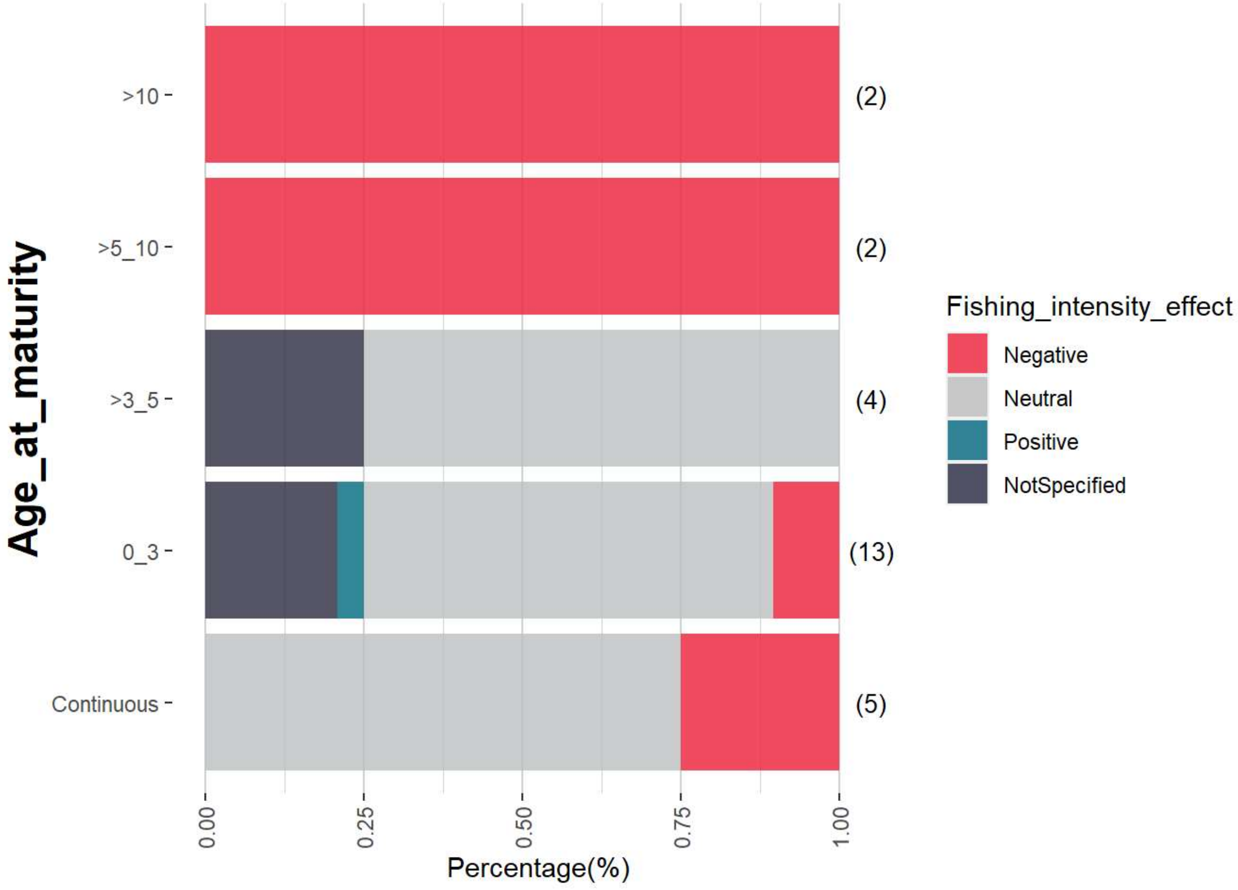
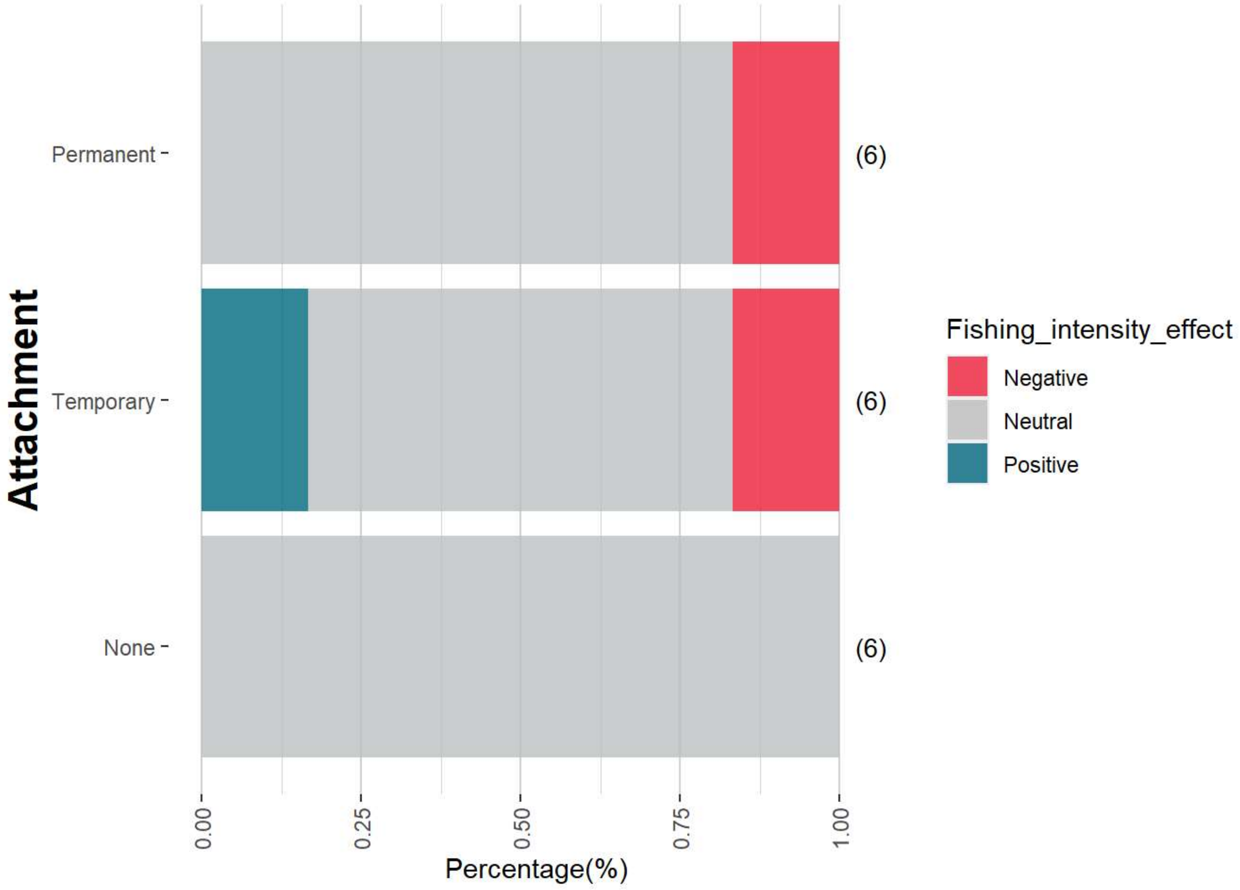
Section 1.1 - Supplementary Material M1

G. Di Bona

2023-08-08

Proportion of observations across the investigated papers linking the trait modalities positively, negatively or without significance or not specified in the study to trawling disturbance

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(6)
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Percentage(%)
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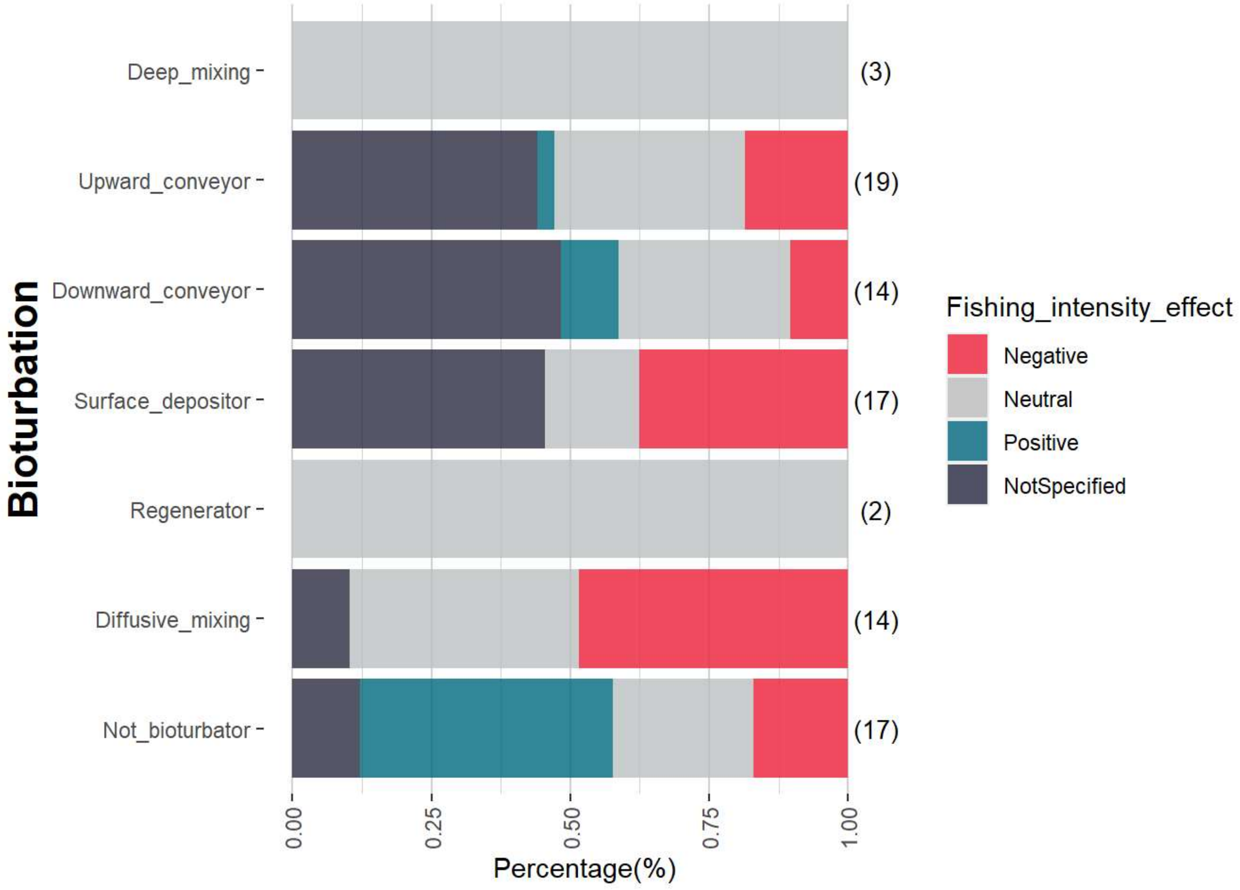
Neutral
Positive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Upward_conveyor
Downward_conveyor
Surface_depositor
Regenerator
Diffusive_mixing
Not_bioturbator
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(19)
(14)
(17)
(2)
(14)
(17)
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0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
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Positive
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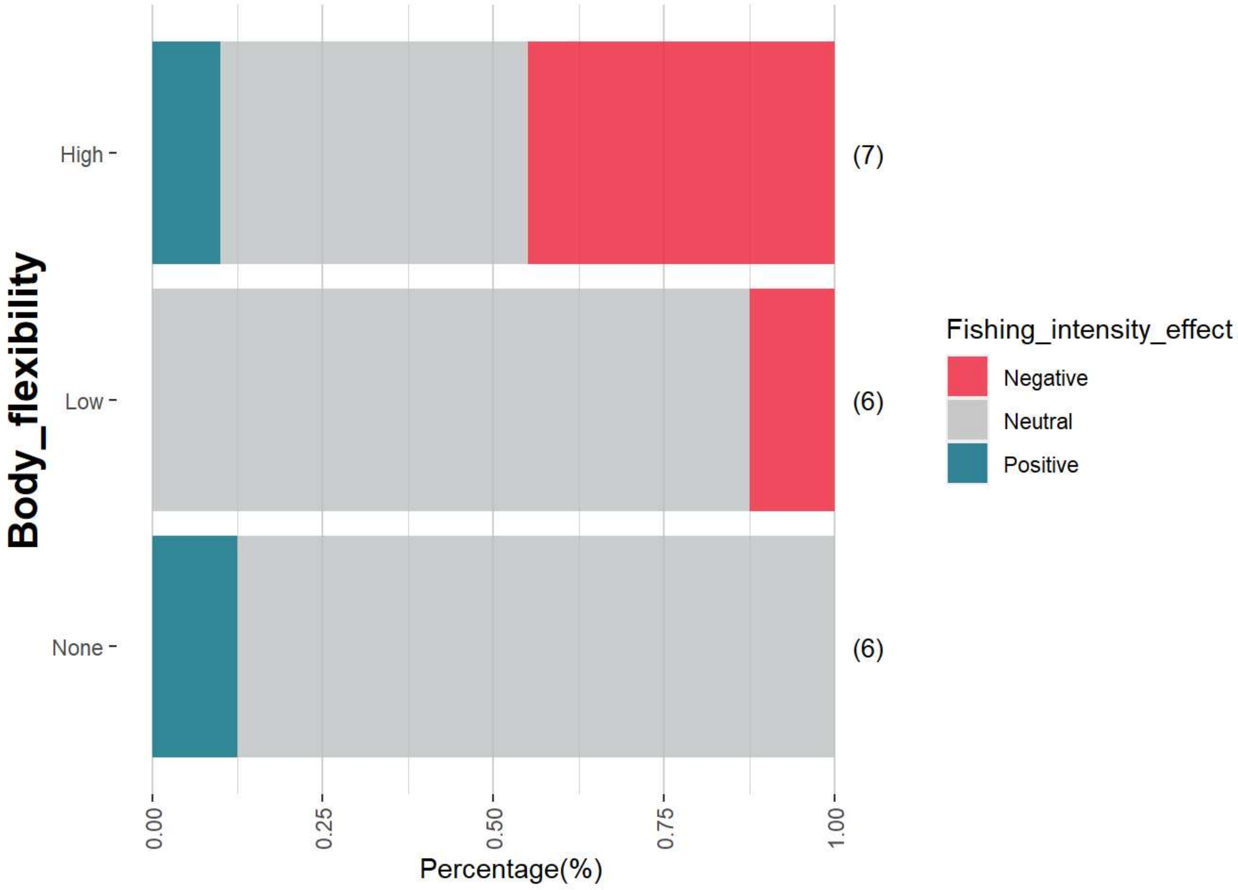
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(6)
(6)
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1.00
Percentage(%)
Fishing_intensity_effect
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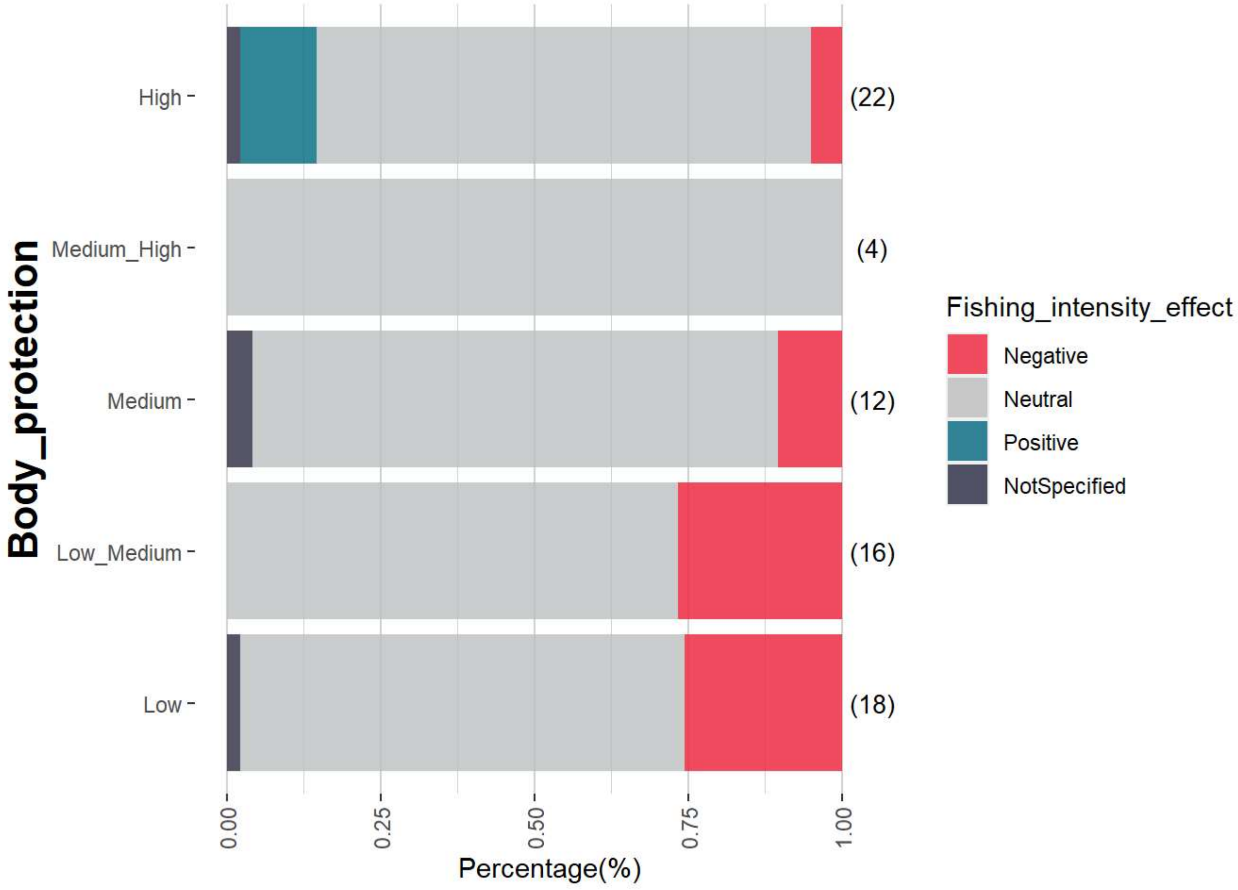
Neutral
Positive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Medium_High
Medium
Low_Medium
Low
(22)
(4)
(12)
(16)
(18)
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1.00
Percentage(%)
Fishing_intensity_effect
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Positive
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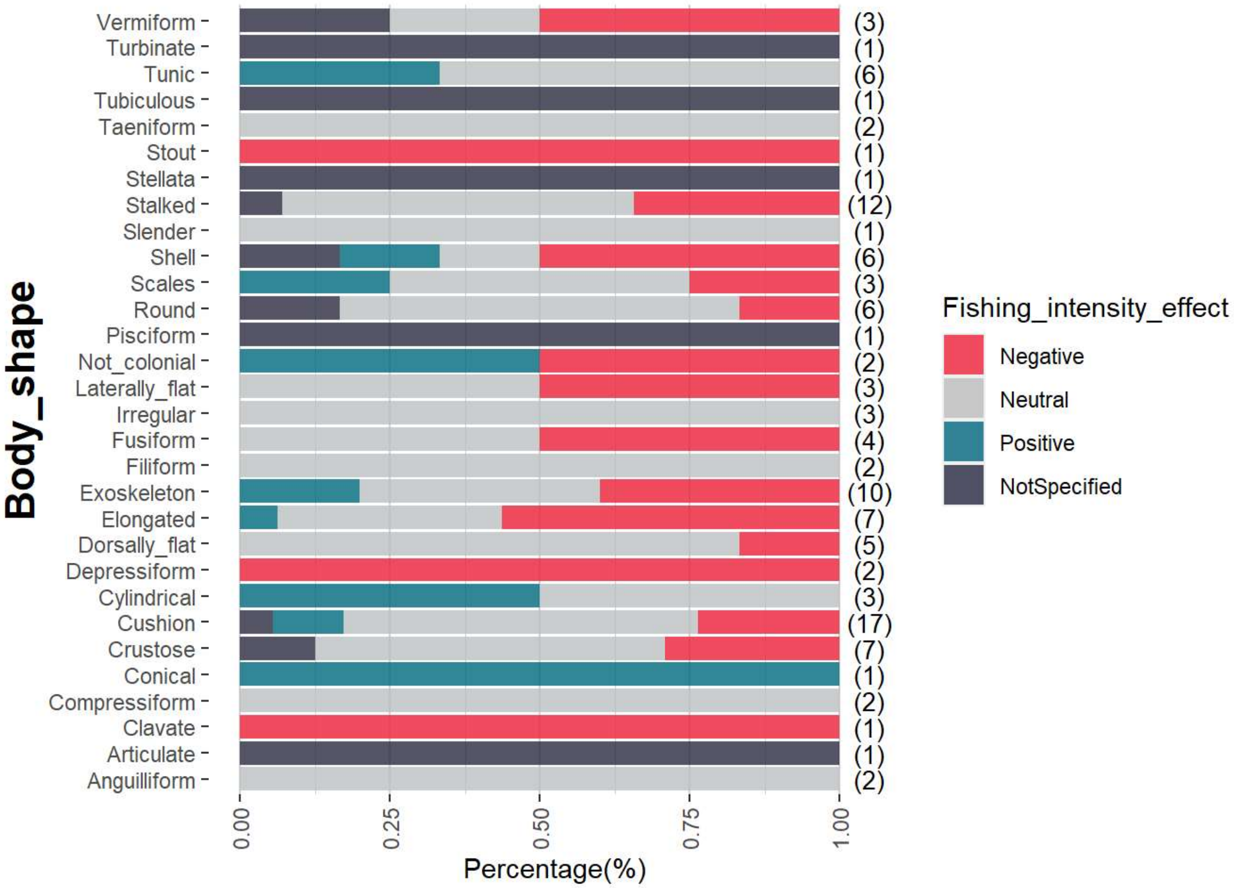
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Turbinate (1)
Tunic (6)
Tubiculous (1)
Taeniform (2)
Stout (1)
Stellata (1)
Stalked (12)
Slender (1)
Shell (6)
Scales (3)
Round (6)
Pisciform (1)
Not_colonial (2)
Laterally_flat (3)
Irregular (3)
Fusiform (4)
Filiform (2)
Exoskeleton (10)
Elongated (7)
Dorsally_flat (5)
Depressiform (2)
Cylindrical (3)
Cushion (17)
Crustose (7)
Conical (1)
Compressiform (2)
Clavate (1)
Articulate (1)
Anguilliform (2)
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0.25
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Percentage(%)
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Positive
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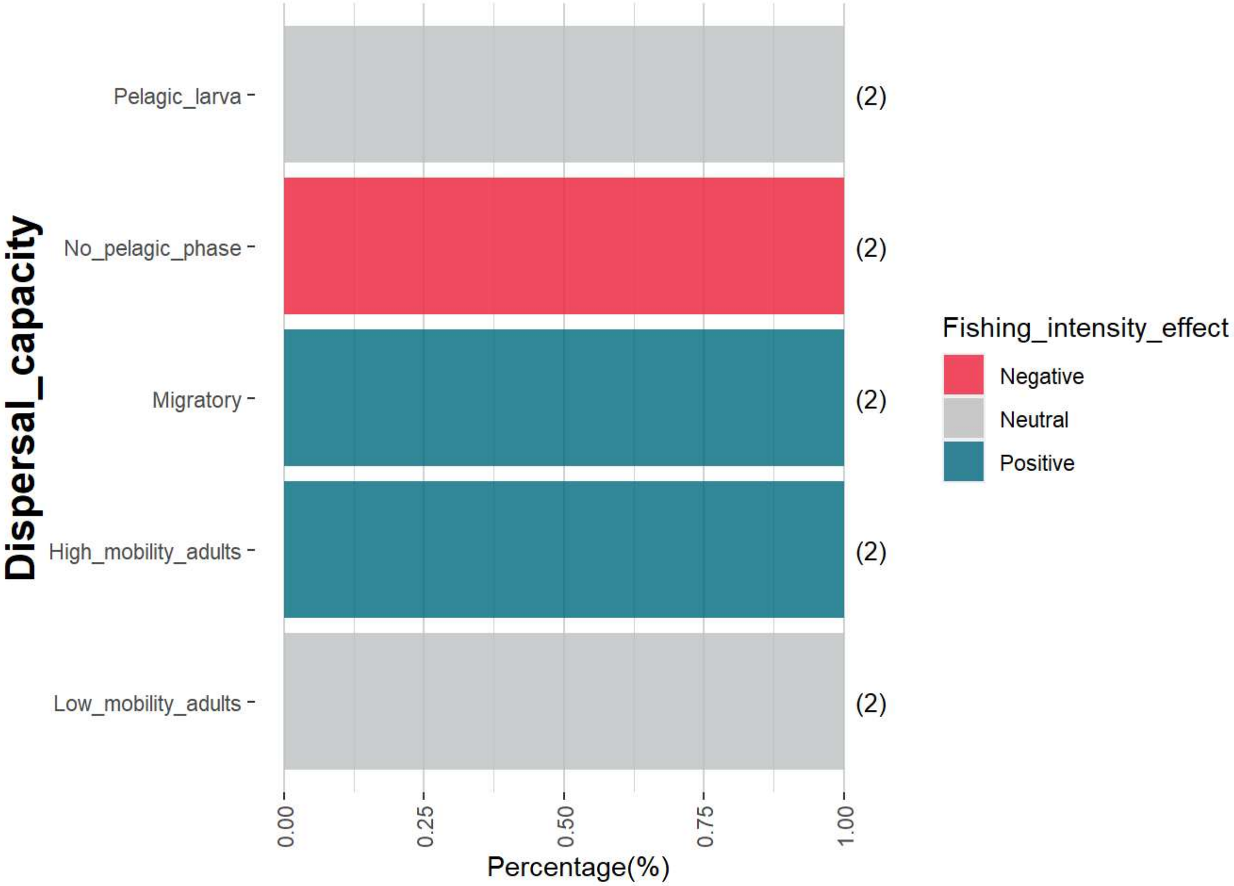
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No_pelagic_phase (2)
Migratory (2)
High_mobility_adults (2)
Low_mobility_adults (2)
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0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
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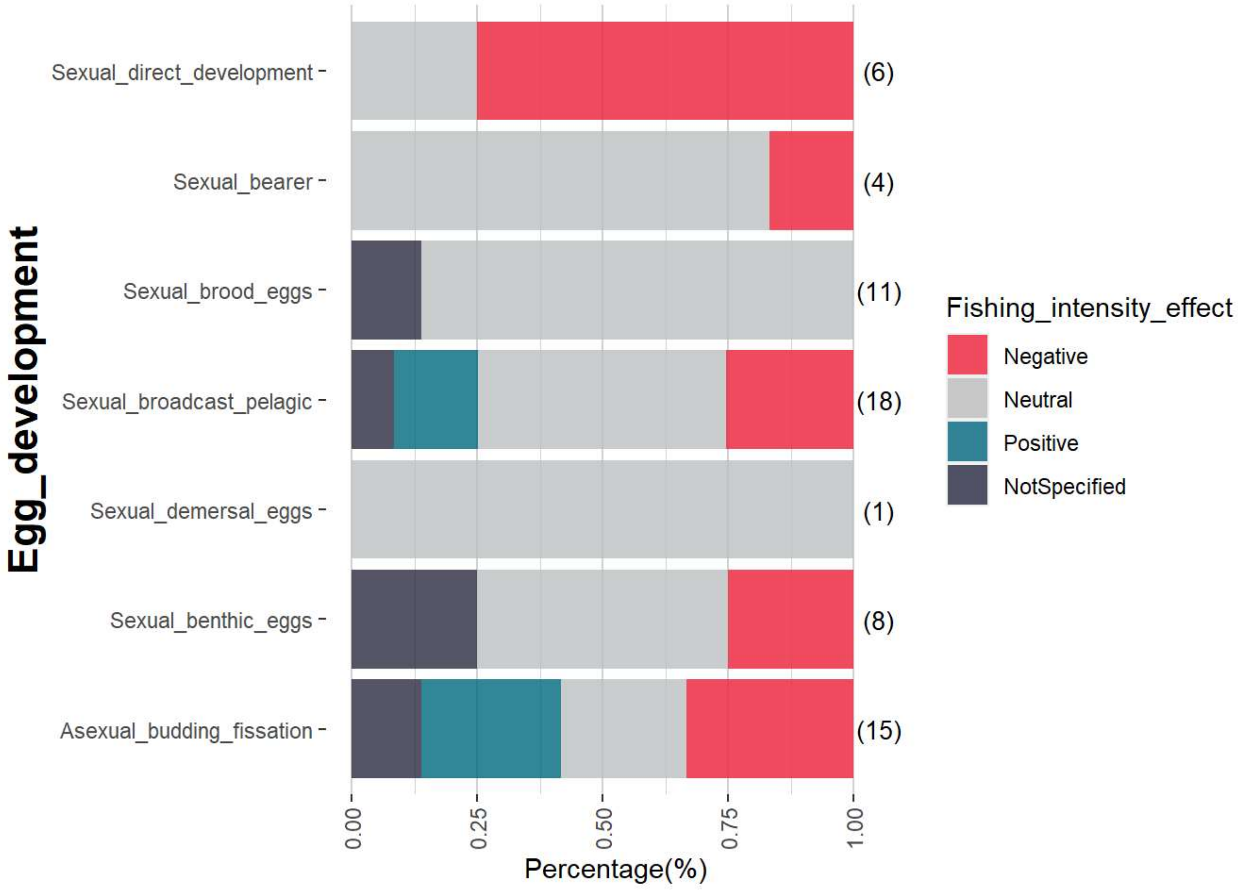
Neutral
Positive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Sexual_direct_development
Sexual_bearer
Sexual_brood_eggs
Sexual_broadcast_pelagic
Sexual_demersal_eggs
Sexual_benthic_eggs
Asexual_budding_fissation
(6)
(4)
(11)
(18)
(1)
(8)
(15)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
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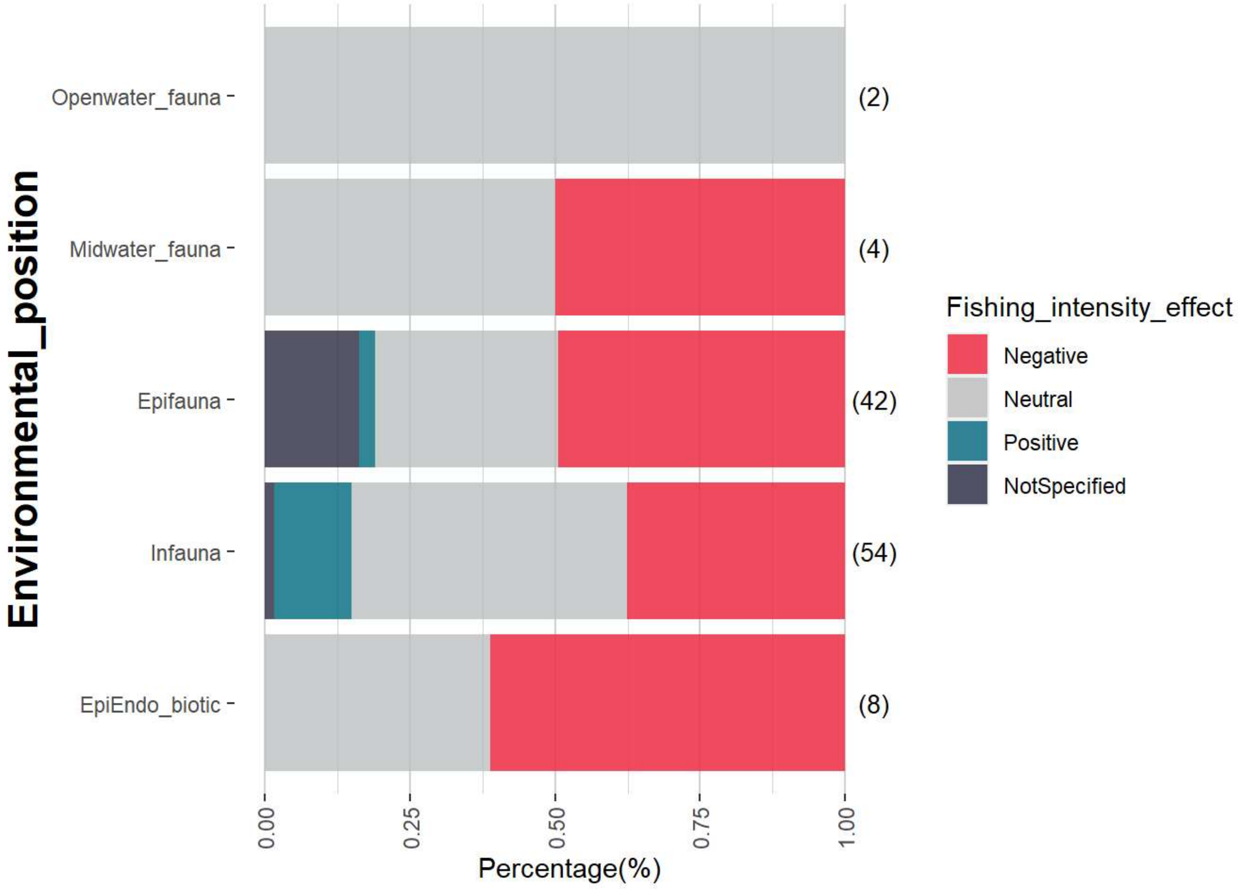
Neutral
Positive
NotSpecified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Midwater_fauna
Epifauna
Infauna
EpiEndo_biotic
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(4)
(42)
(54)
(8)
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0.25
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Percentage(%)
Fishing_intensity_effect
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Positive
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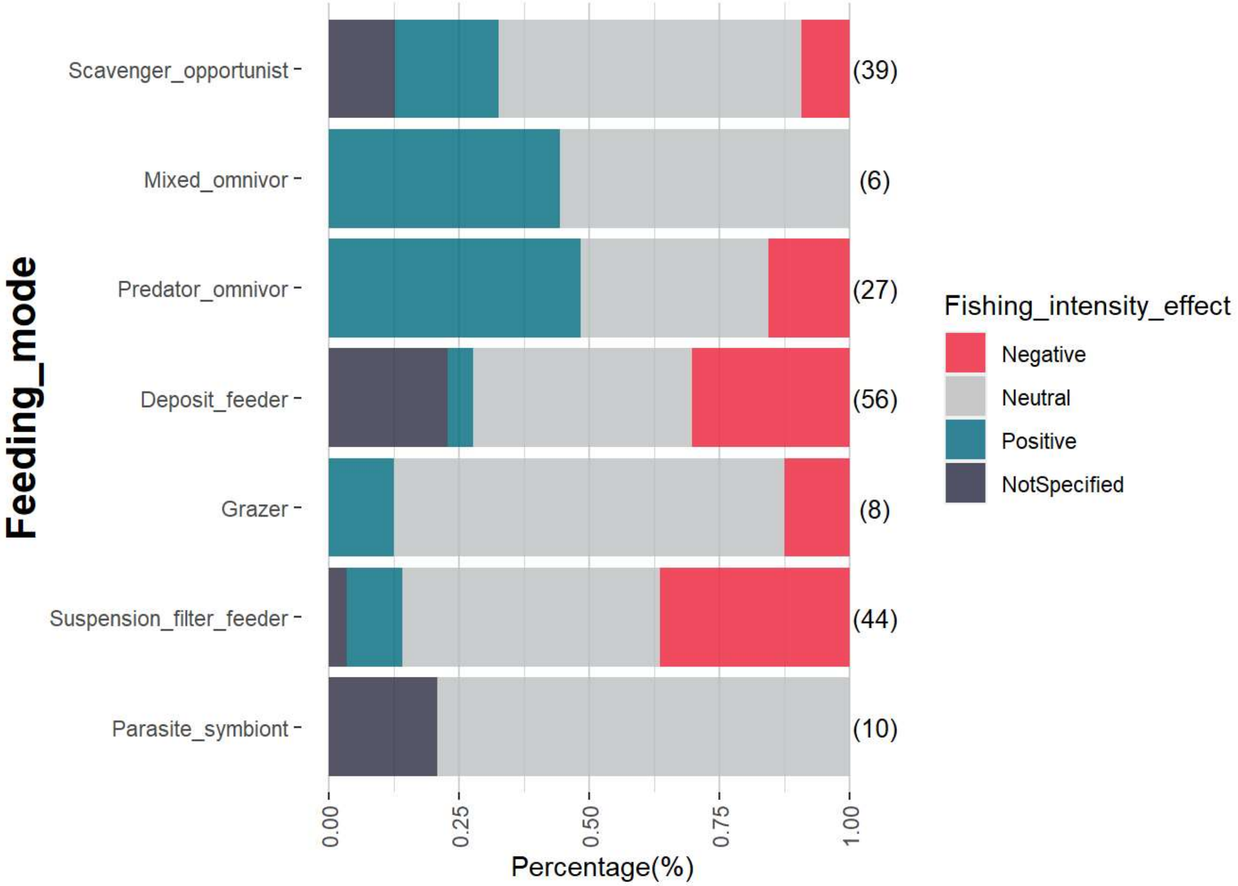
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Mixed_omnivor
Predator_omnivor
Deposit_feeder
Grazer
Suspension_filter_feeder
Parasite_symbiont
(39)
(6)
(27)
(56)
(8)
(44)
(10)
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1.00
Percentage(%)
Fishing_intensity_effect
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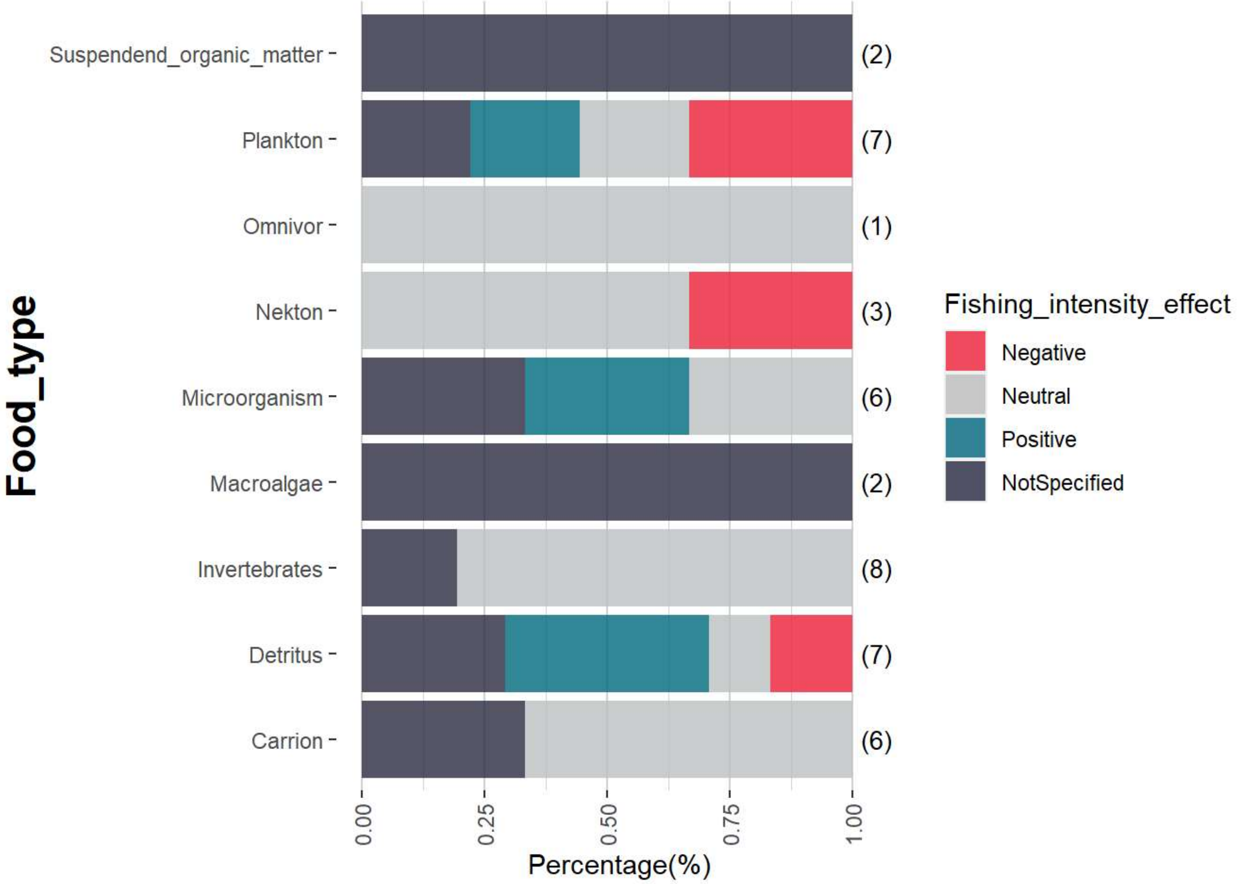
Neutral
Positive
NotSpecified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Nekton
Microorganism
Macroalgae
Invertebrates
Detritus
Carrion
(2)
(7)
(1)
(3)
(6)
(2)
(8)
(7)
(6)
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0.75
1.00
Percentage(%)
Fishing_intensity_effect
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Positive
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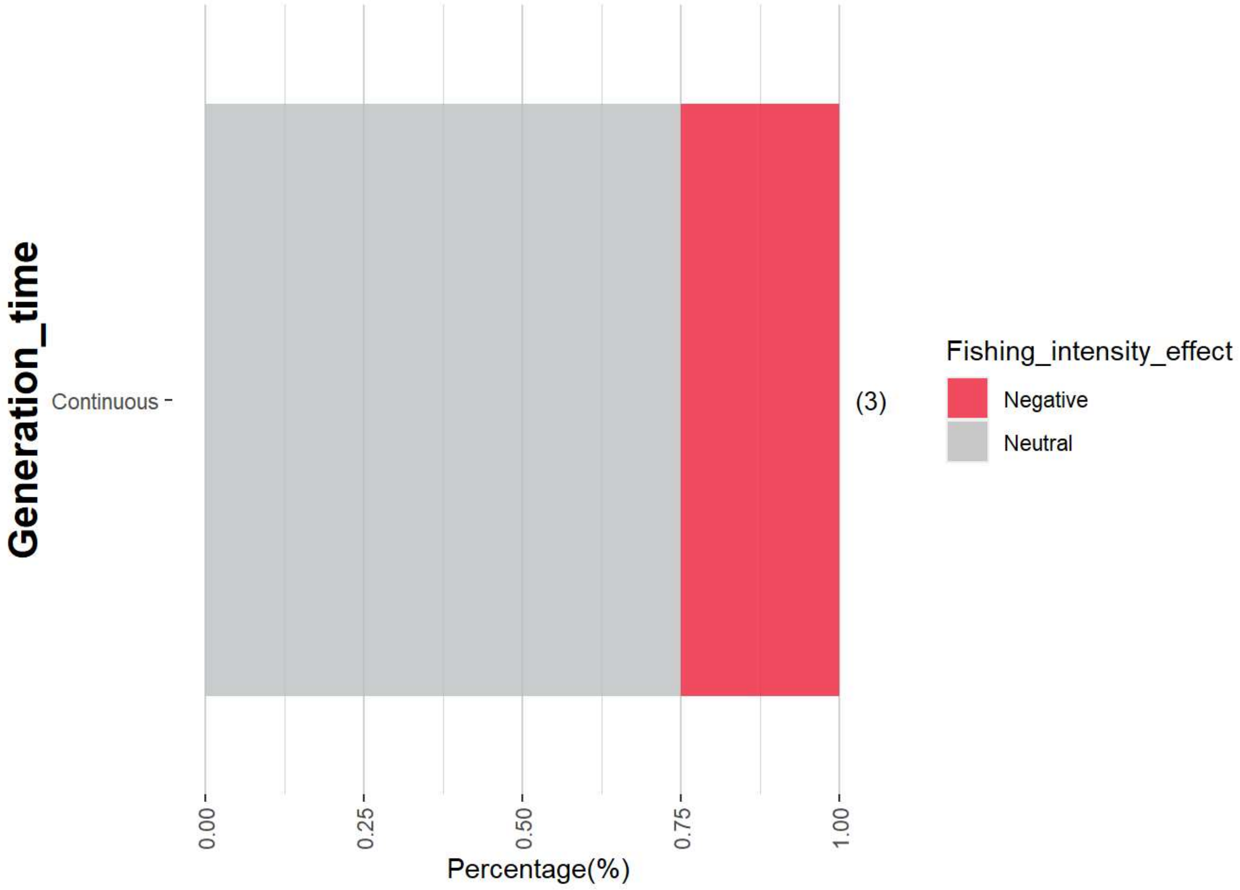
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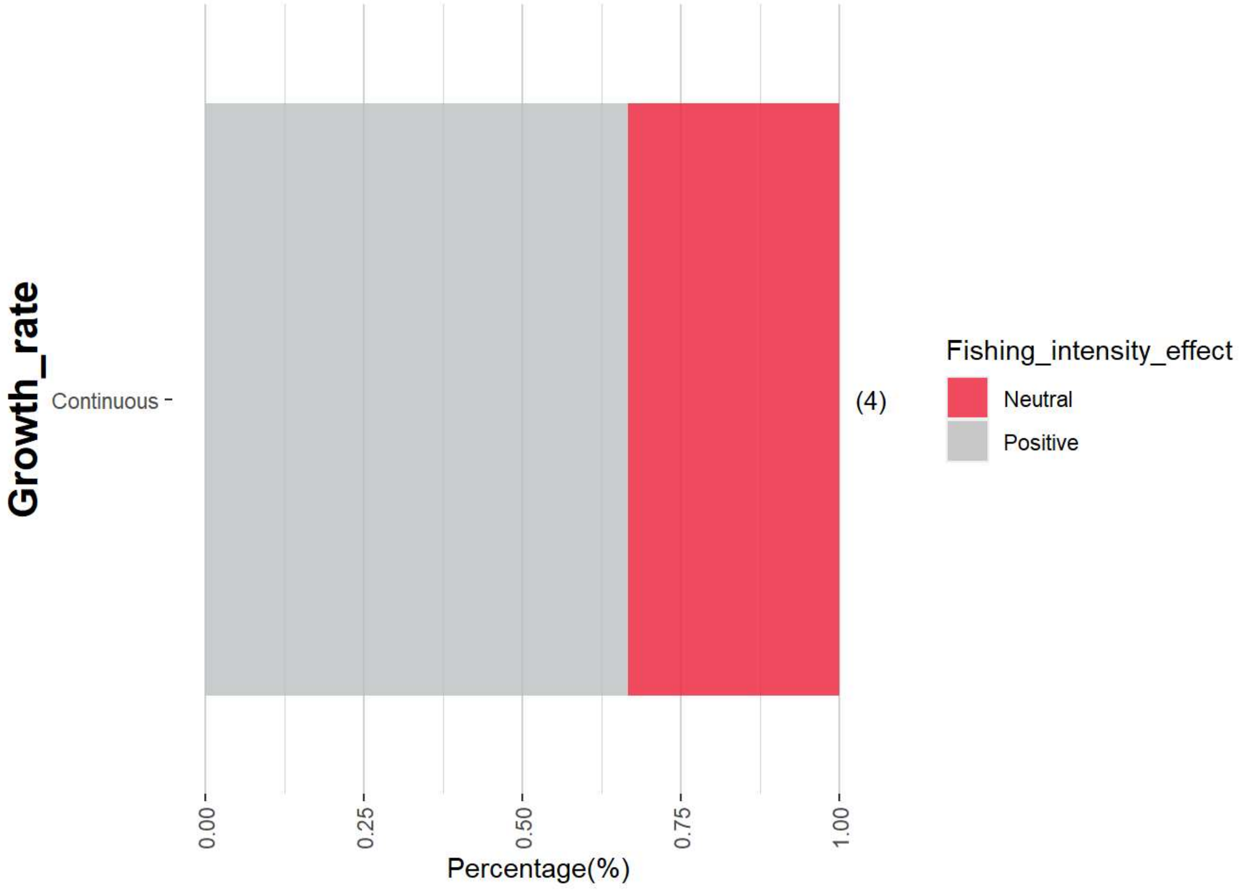
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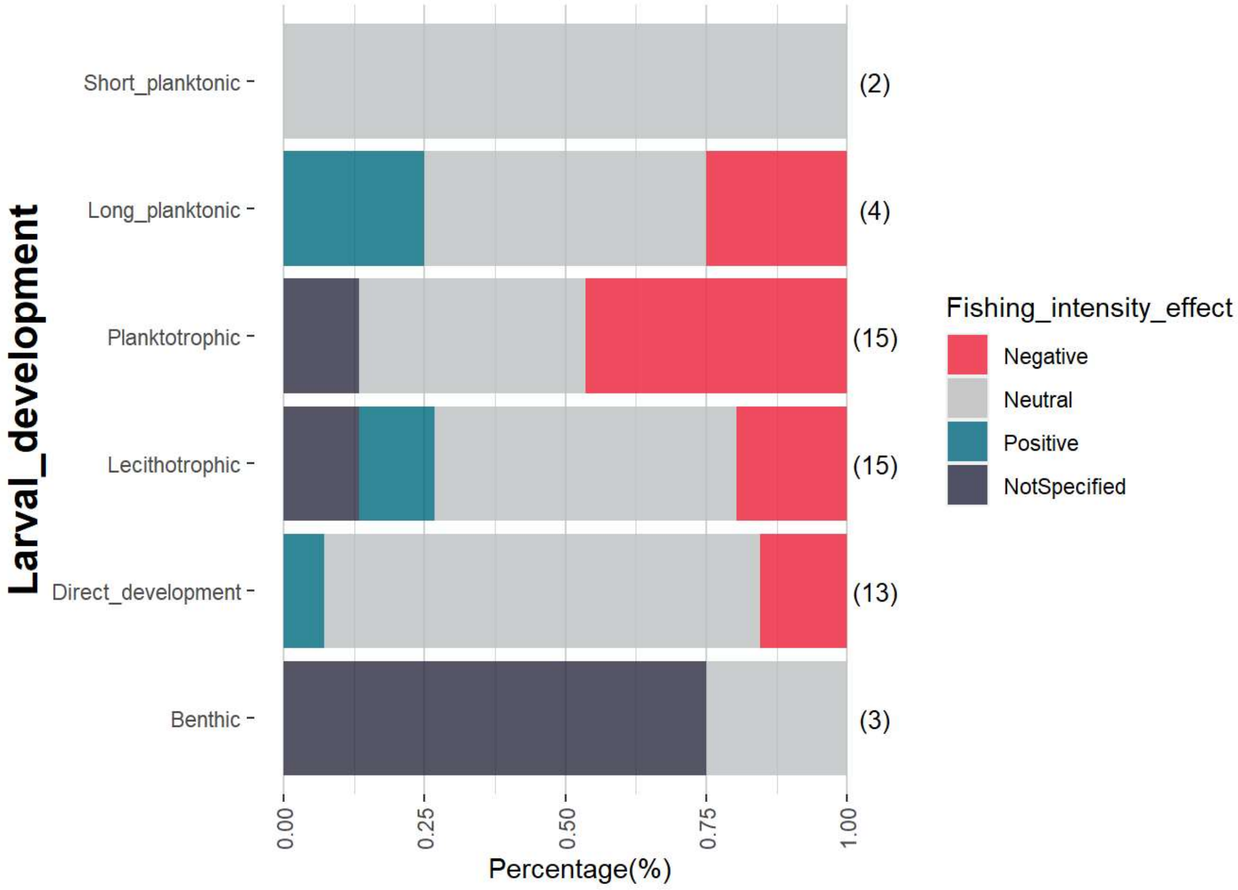
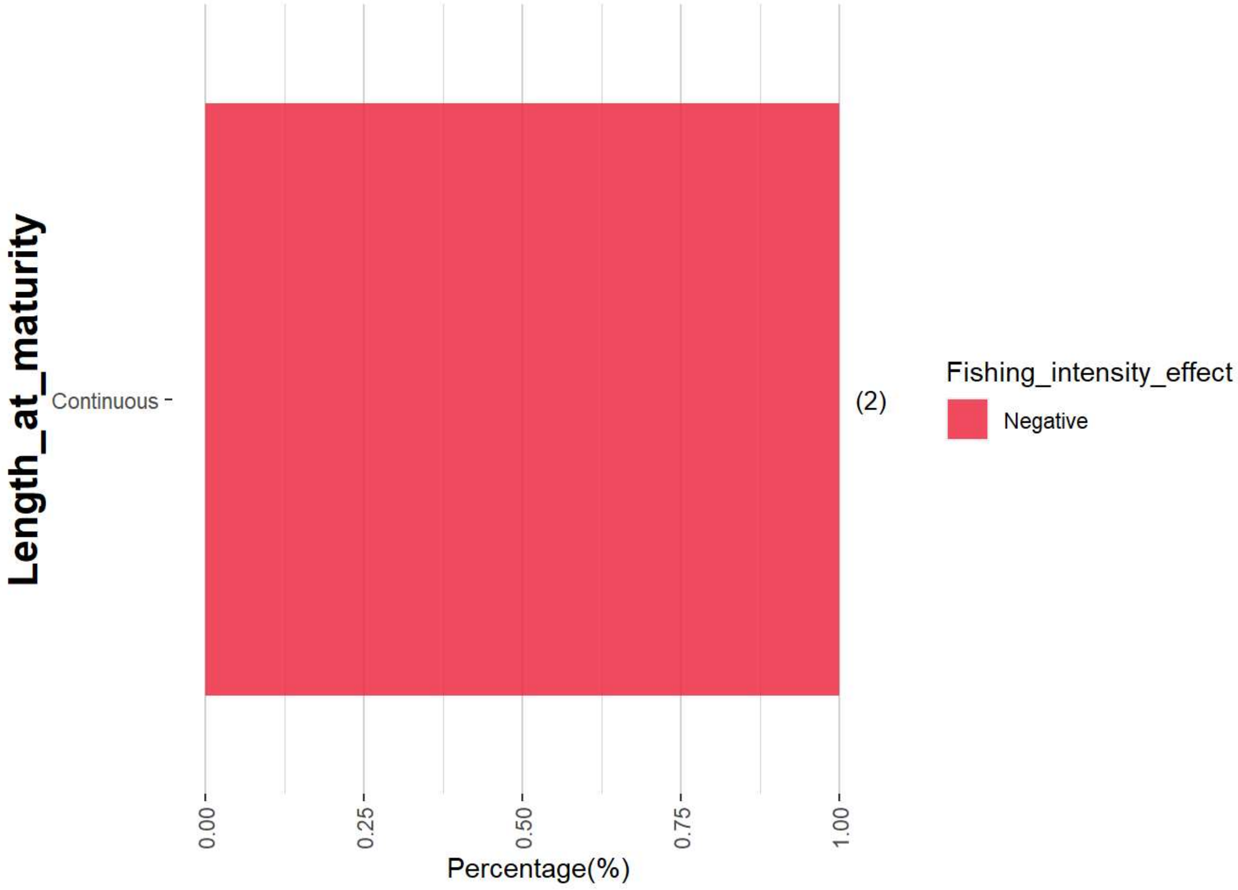


Larval_development
Short_planktonic
Long_planktonic
Planktotrophic
Lecithotrophic
Direct_development
Benthic
(2)
(4)
(15)
(15)
(13)
(3)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified



Length_at_maturity
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1.00
Percentage(%)
Fishing_intensity_effect
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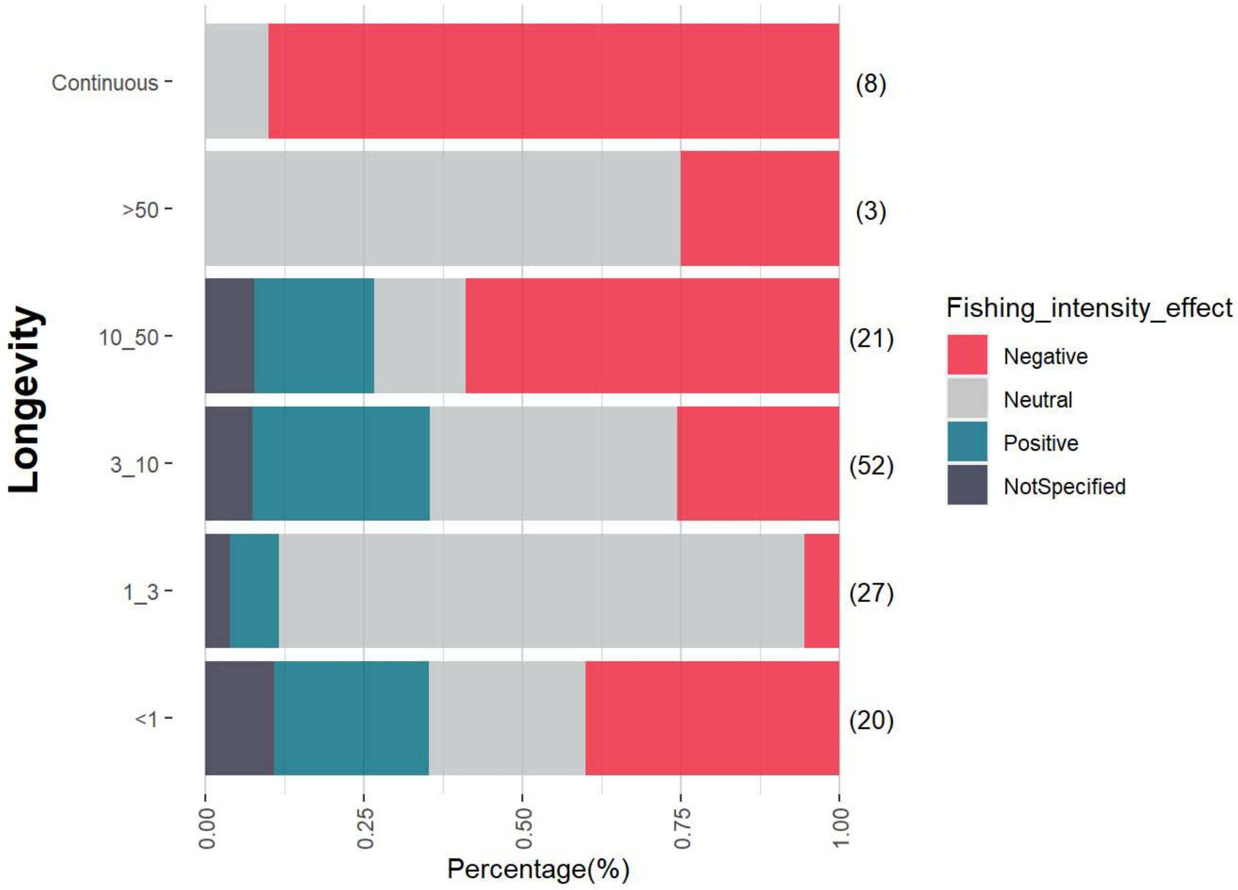
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10_50
3_10
1_3
<1
(8)
(3)
(21)
(52)
(27)
(20)
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0.25
0.50
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Percentage(%)
Fishing_intensity_effect
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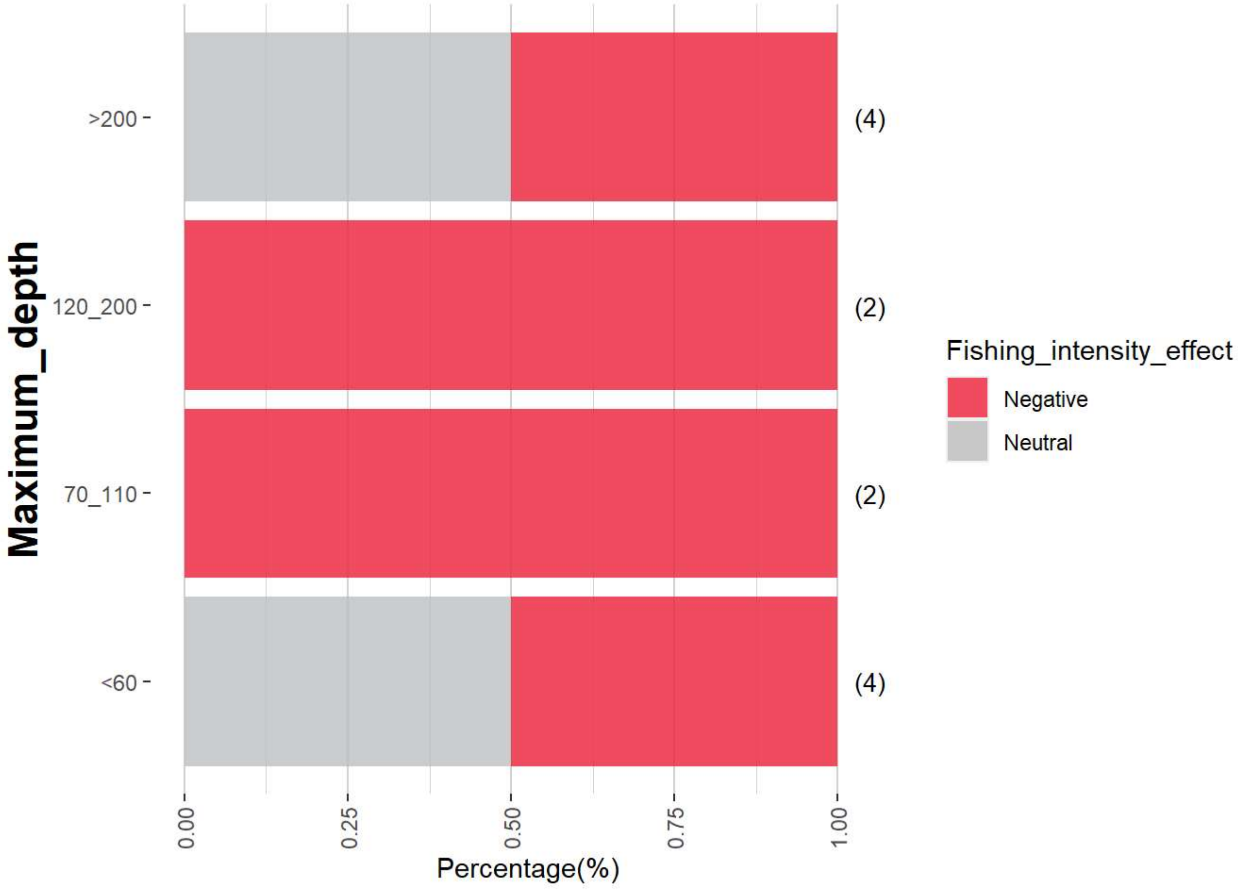
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Fishing_intensity_effect
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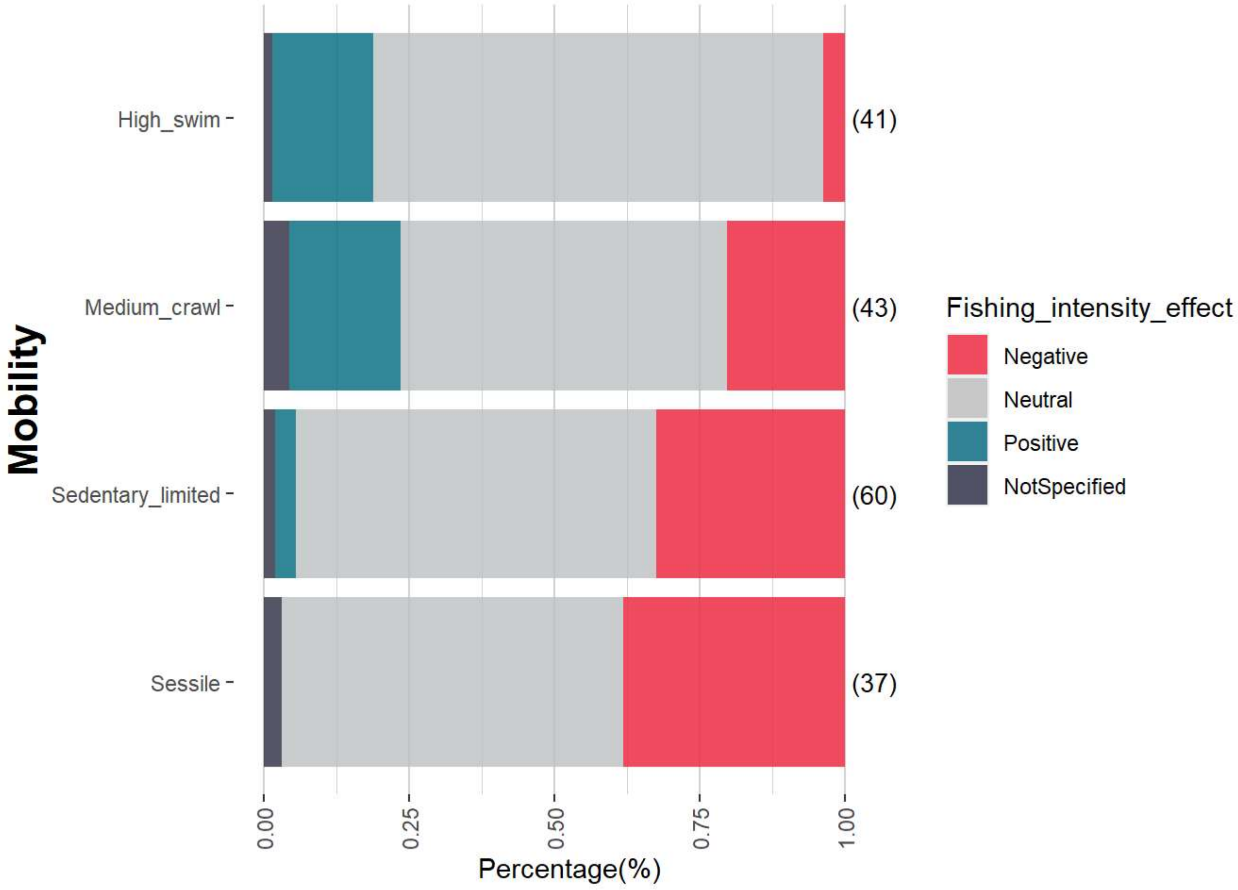
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Medium_crawl
Sedentary_limited
Sessile
(41)
(43)
(60)
(37)
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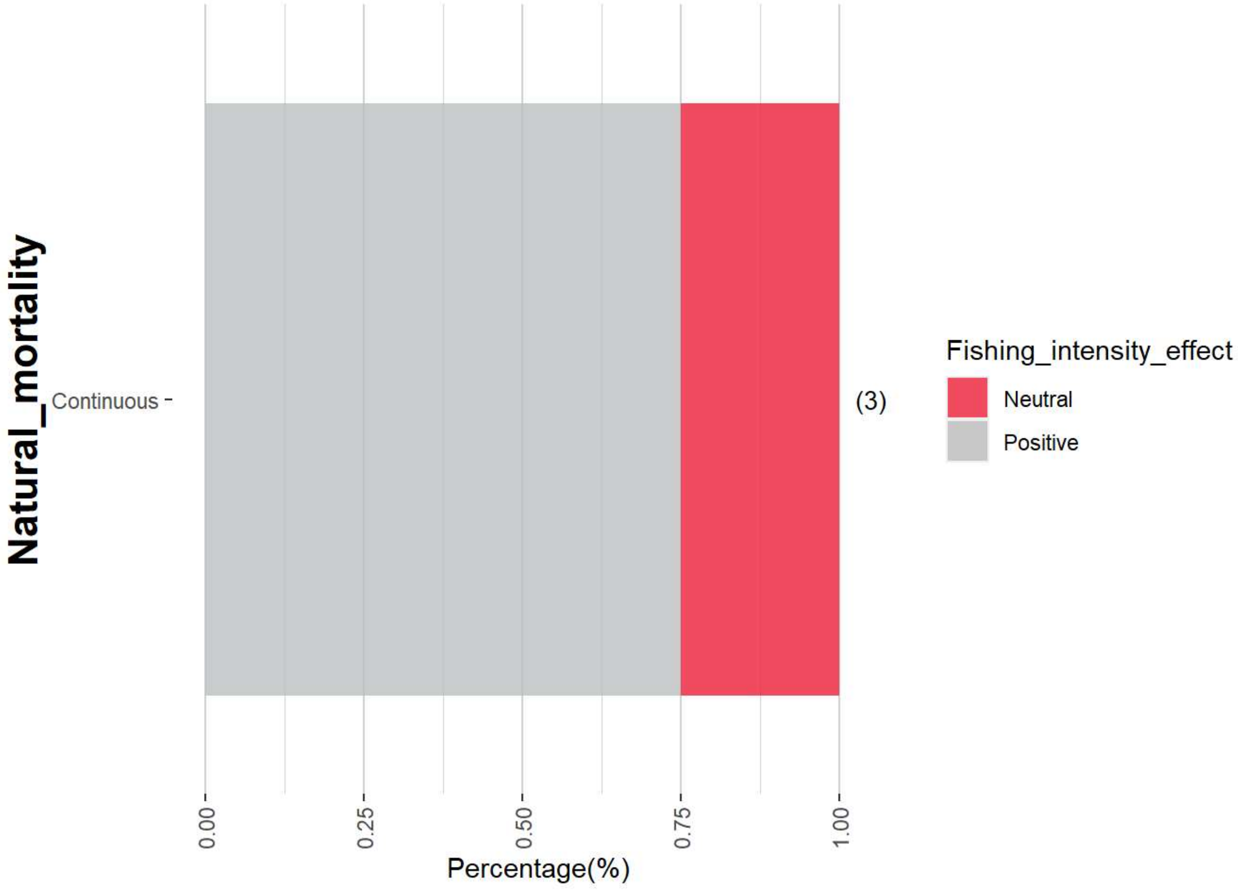
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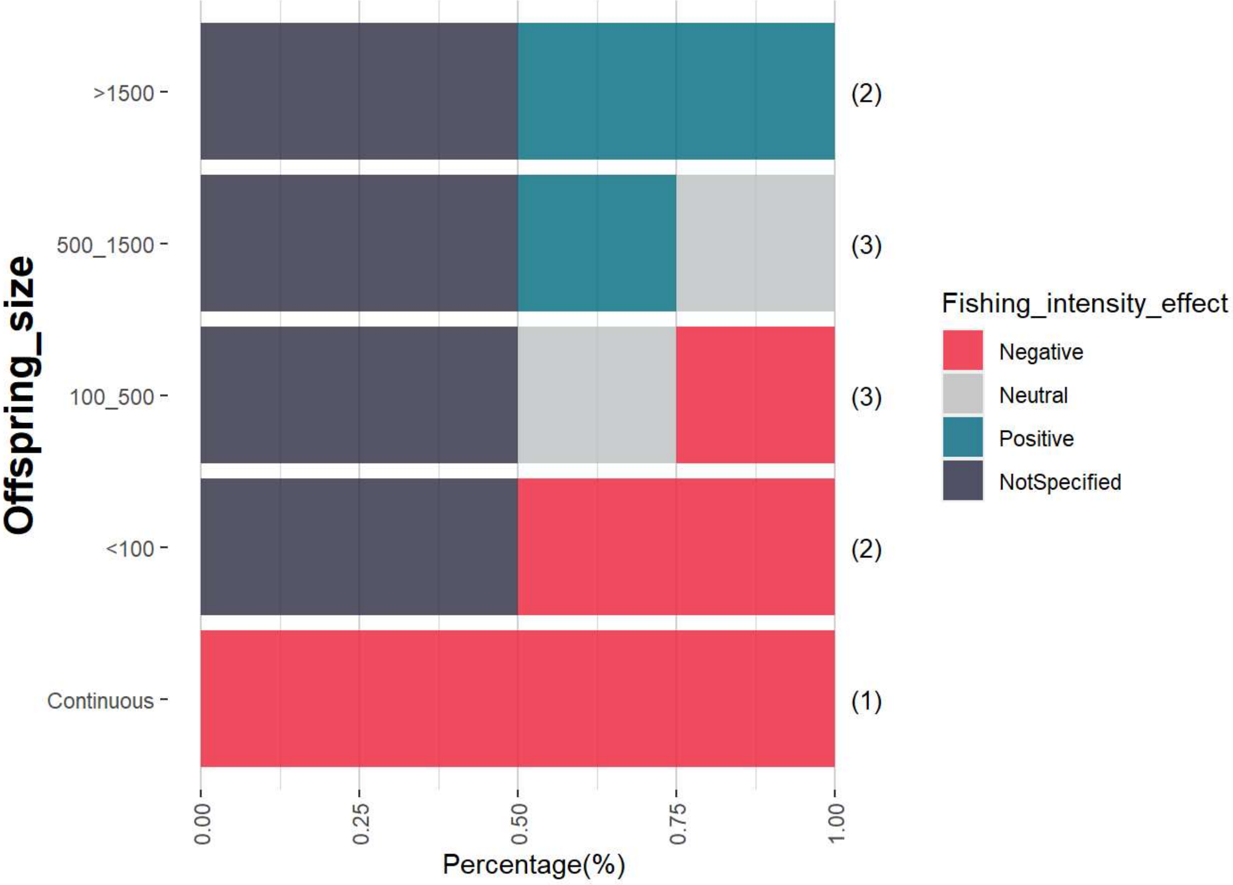
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(3)
(3)
(2)
(1)
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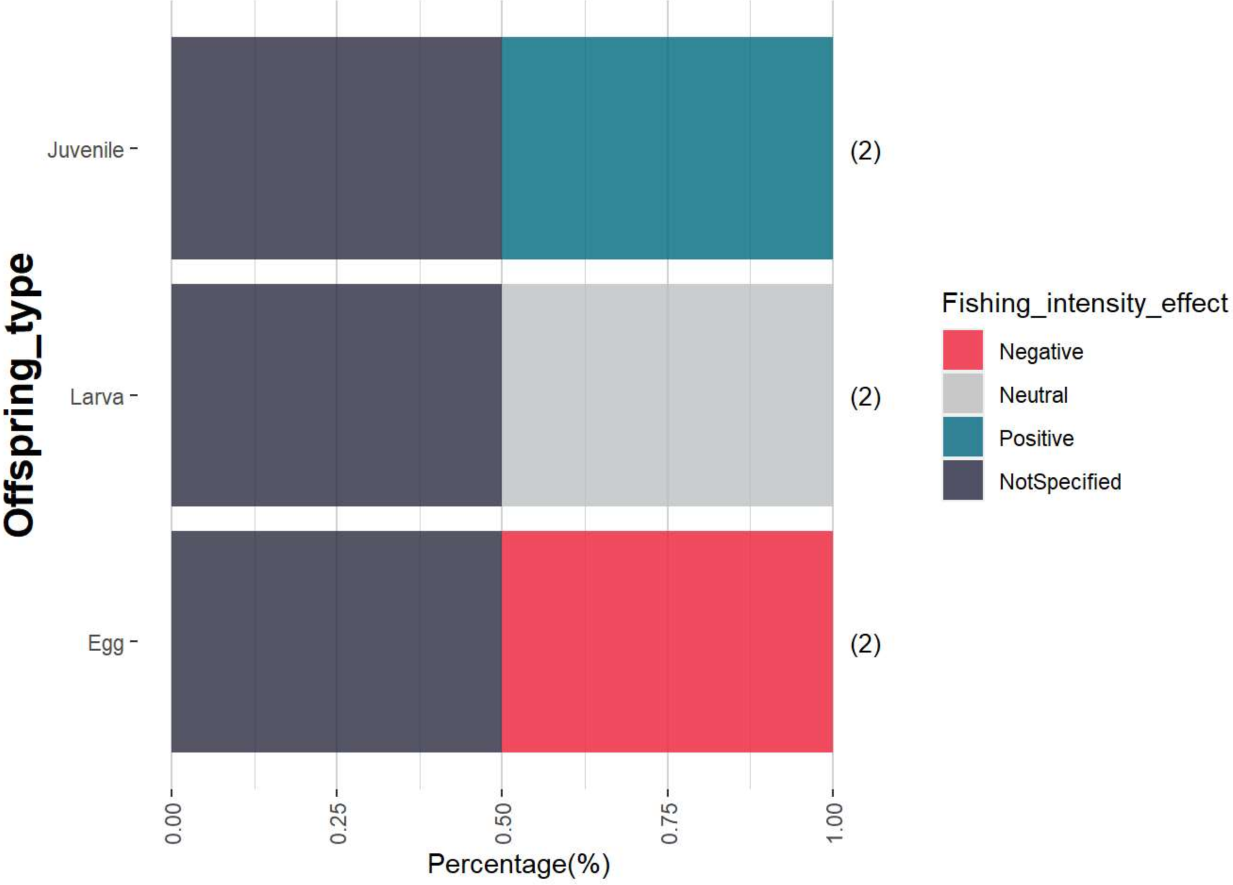
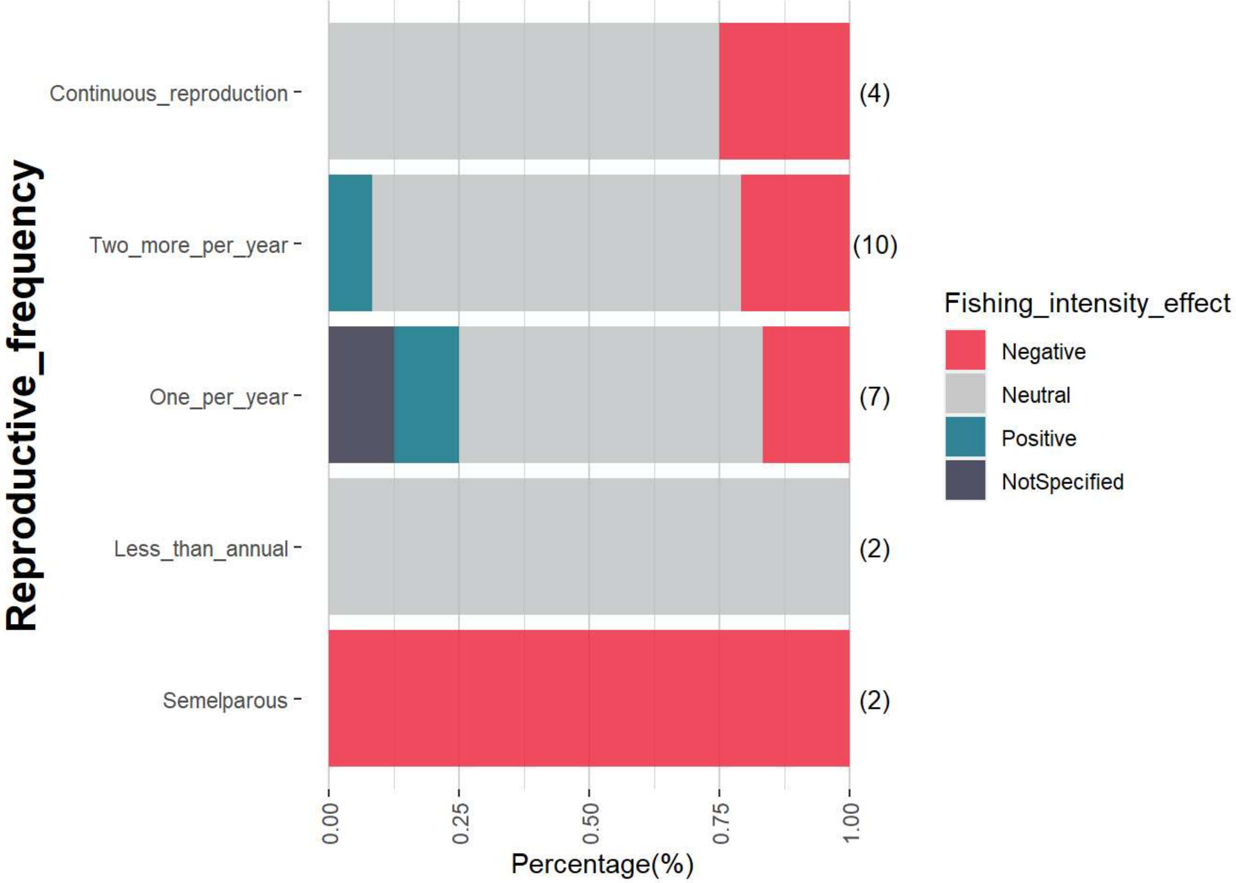
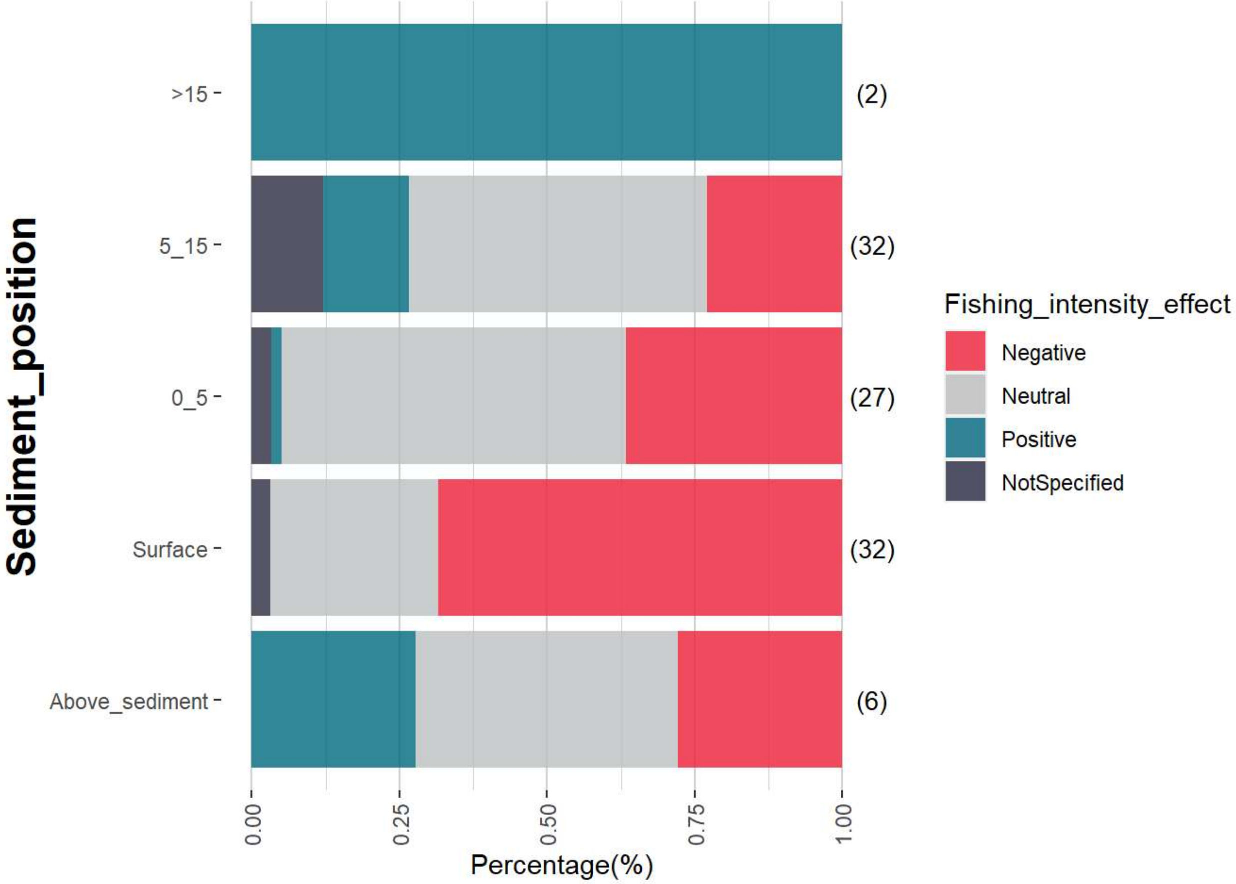
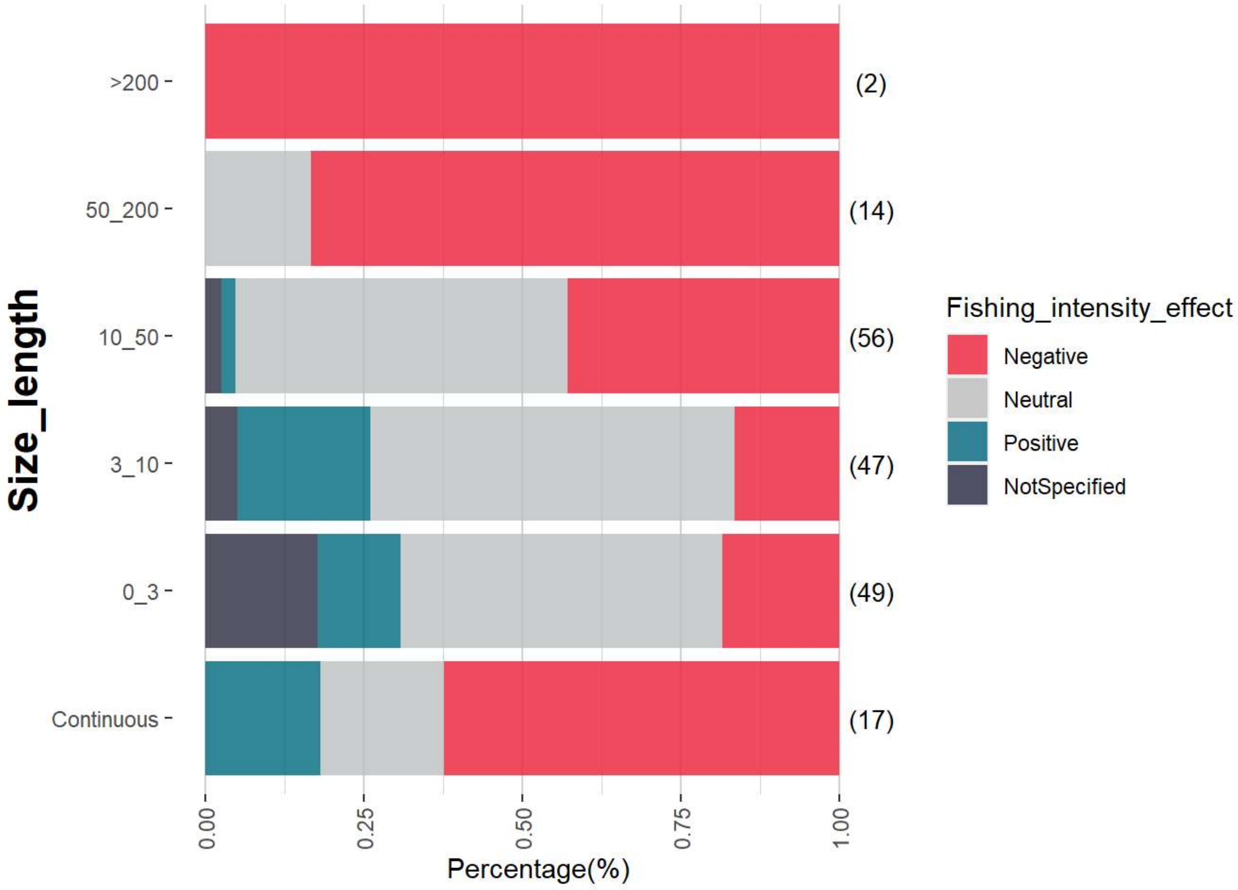
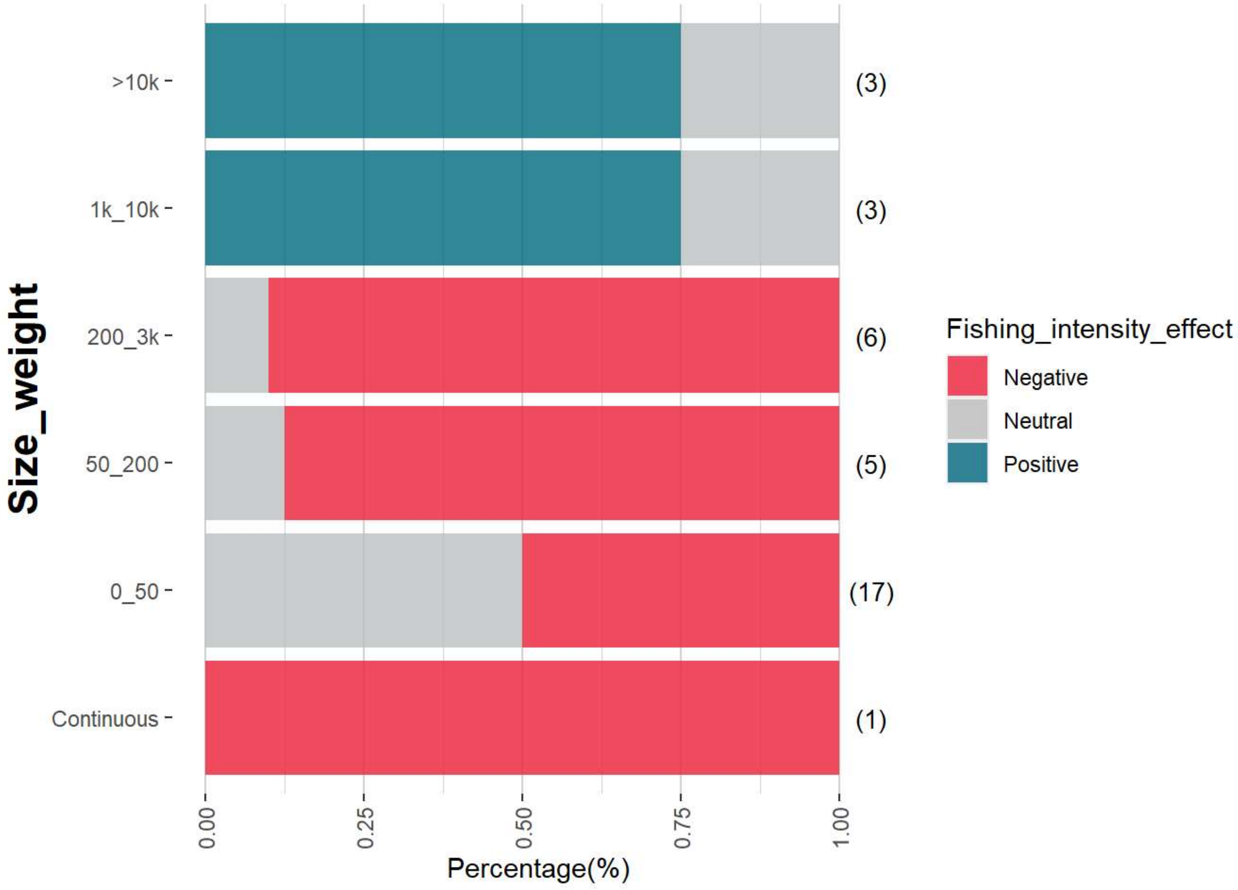
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

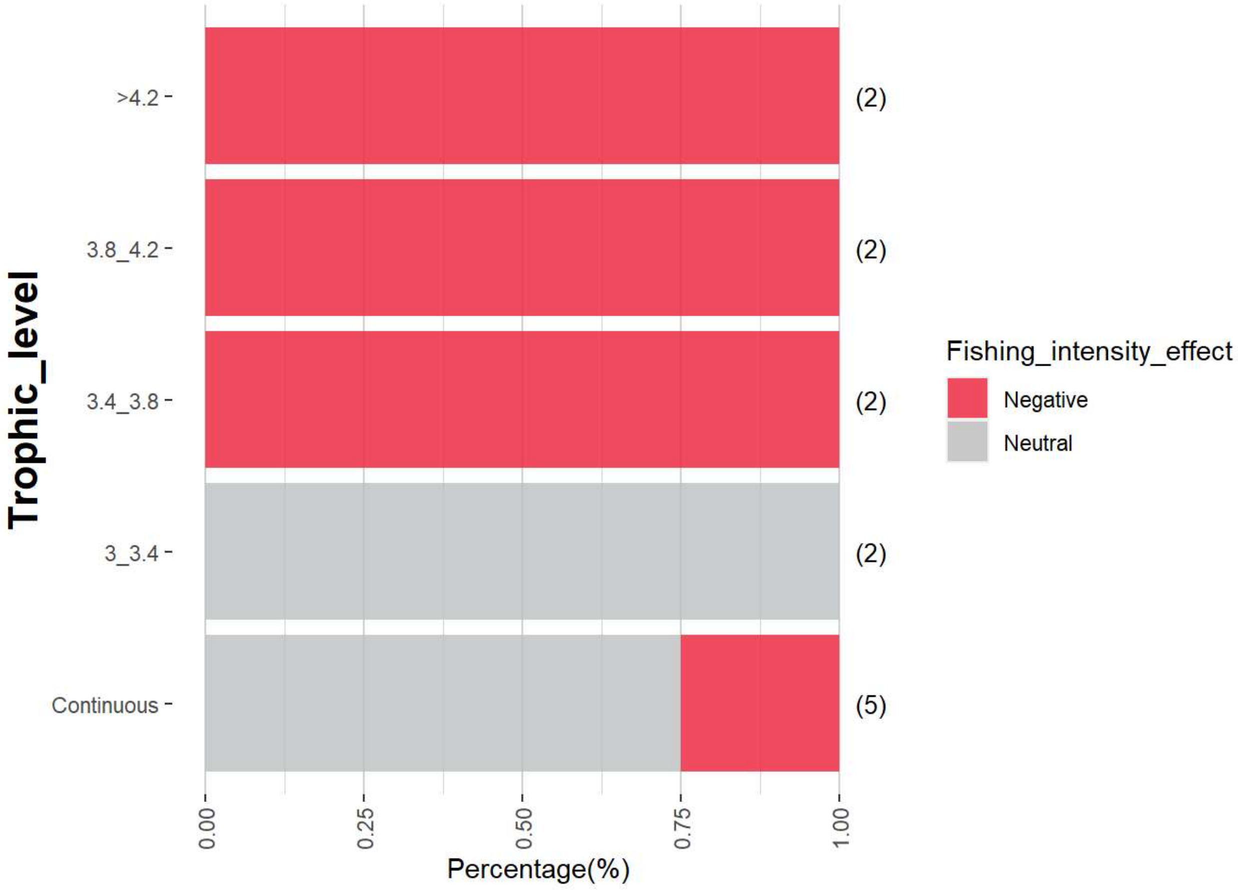

Offspring_type
Juvenile
Larva
Egg
(2)
(2)
(2)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Reproductive_frequency
Continuous_reproduction
Two_more_per_year
One_per_year
Less_than_annual
Semelparous
(4)
(10)
(7)
(2)
(2)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Sediment_position
>15
5_15
0_5
Surface
Above_sediment
(2)
(32)
(27)
(32)
(6)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Size_length
>200
50_200
10_50
3_10
0_3
Continuous
(2)
(14)
(56)
(47)
(49)
(17)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Size_weight
>10k
1k_10k
200_3k
50_200
0_50
Continuous
(3)
(3)
(6)
(5)
(17)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive

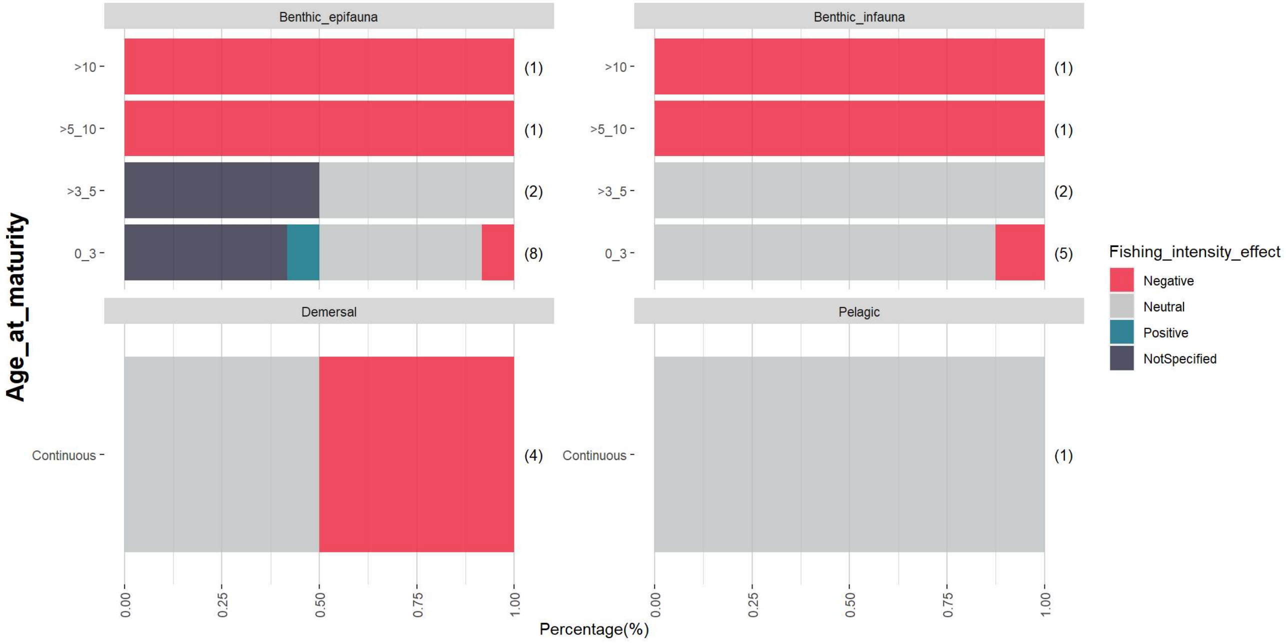

Trophic_level
>4.2
3.8_4.2
3.4_3.8
3_3.4
Continuous
(2)
(2)
(2)
(2)
(5)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral

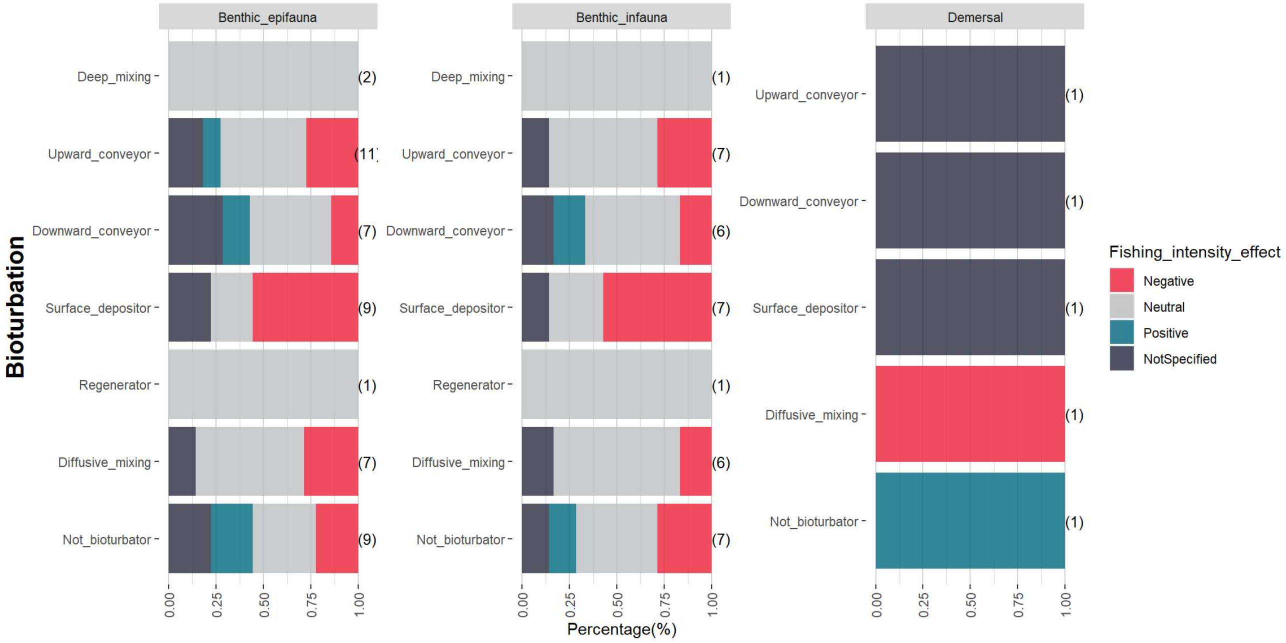
Section 1.1 - Supplementary Material M2

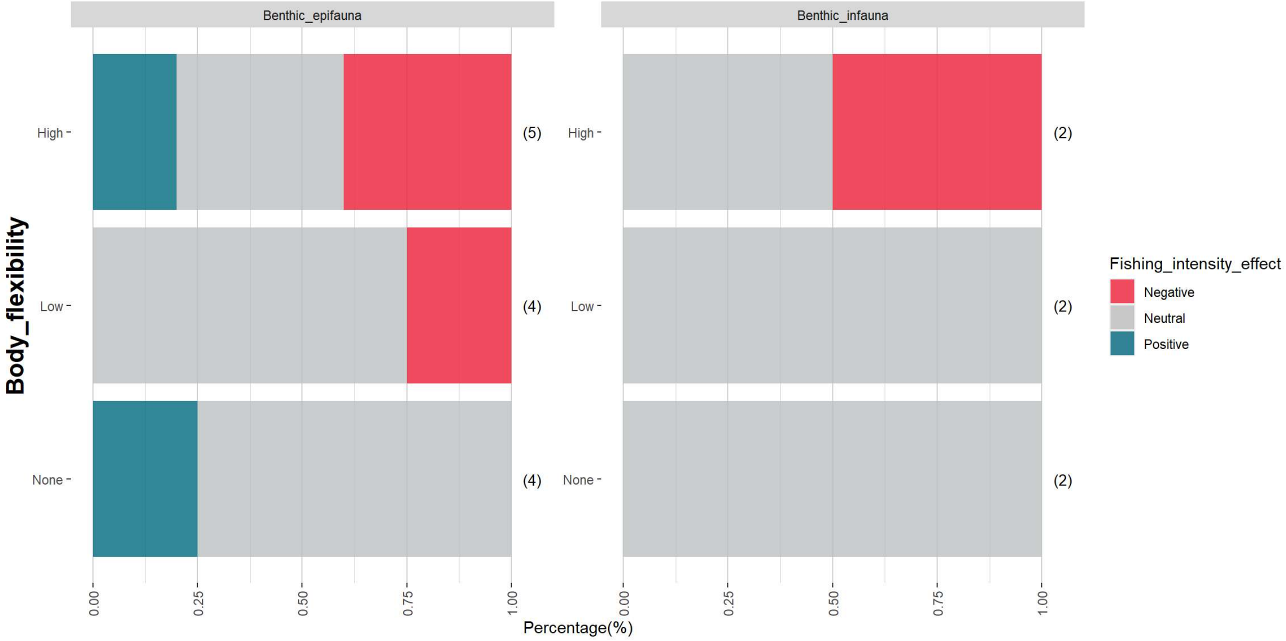
G. Di Bona

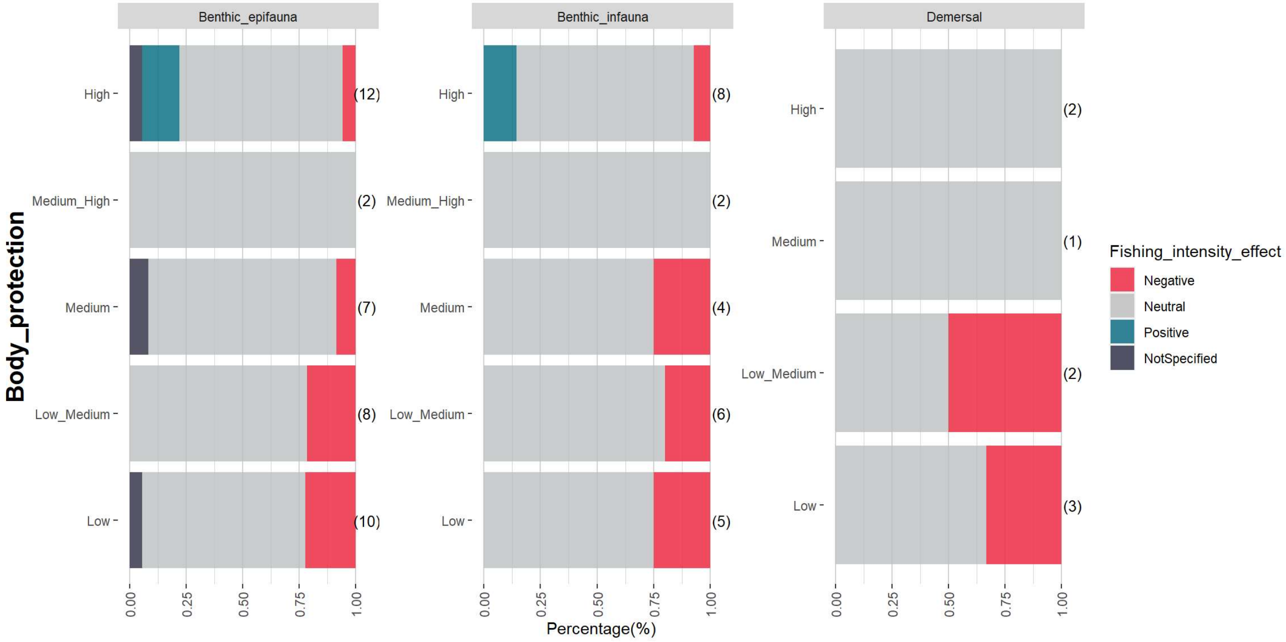
2023-08-08

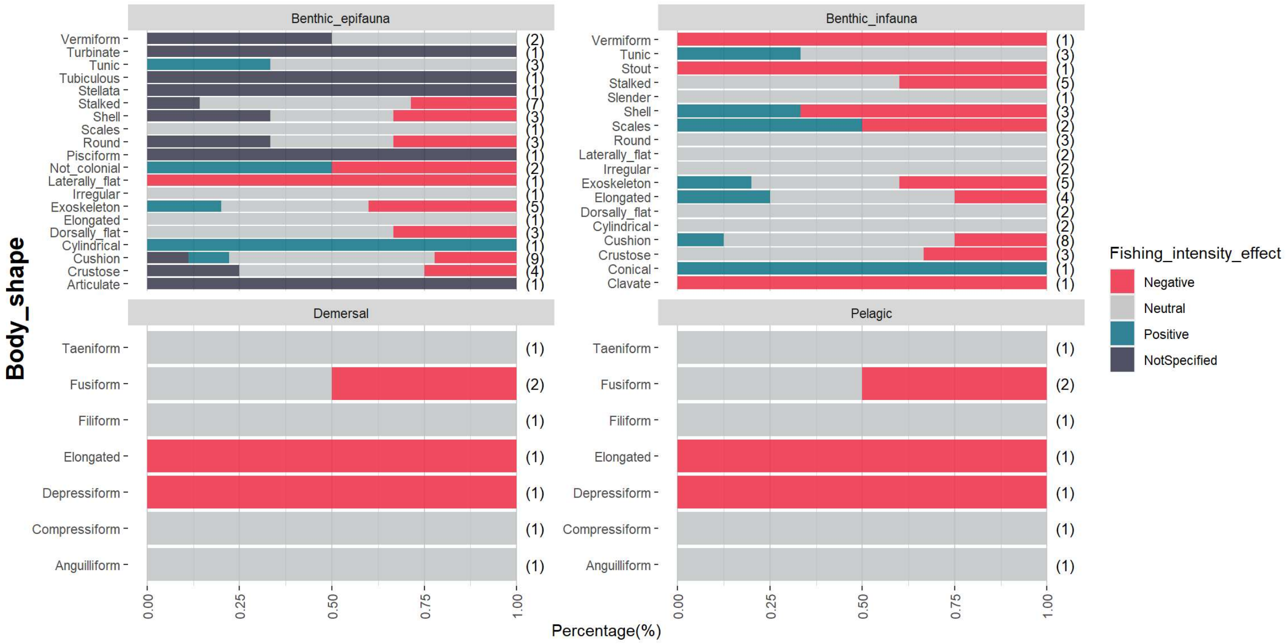
Proportion of observations across the investigated papers linking the trait modalities positively, negatively or without significance or not specified in the study to trawling disturbance according different communities.

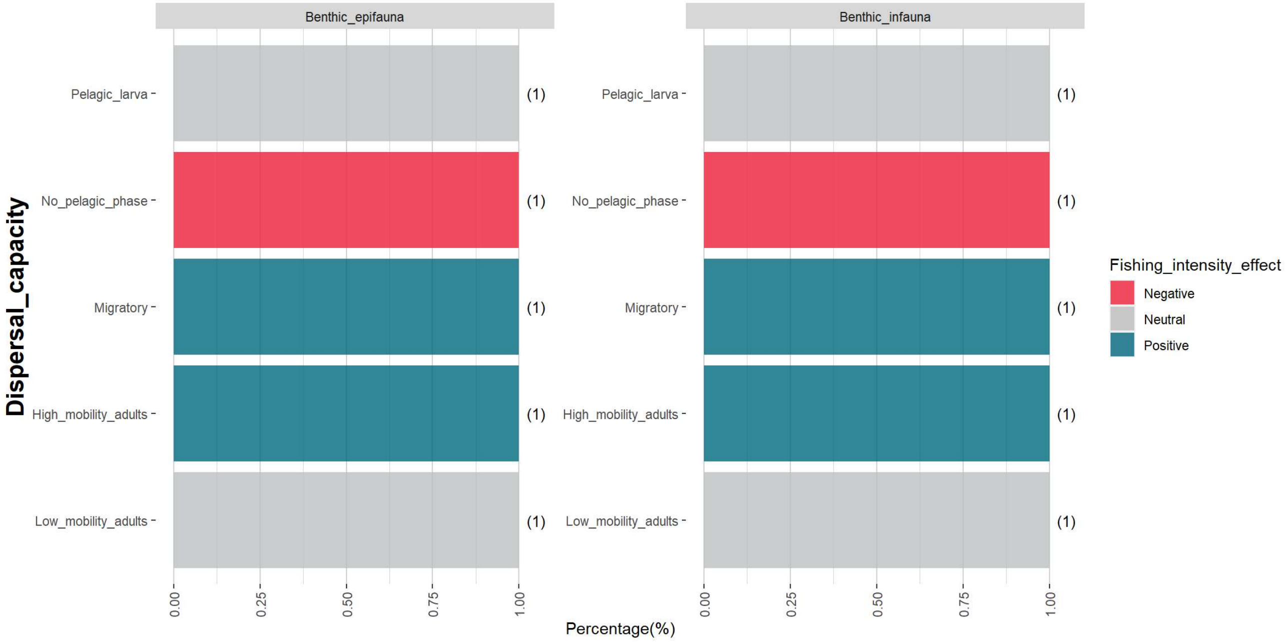


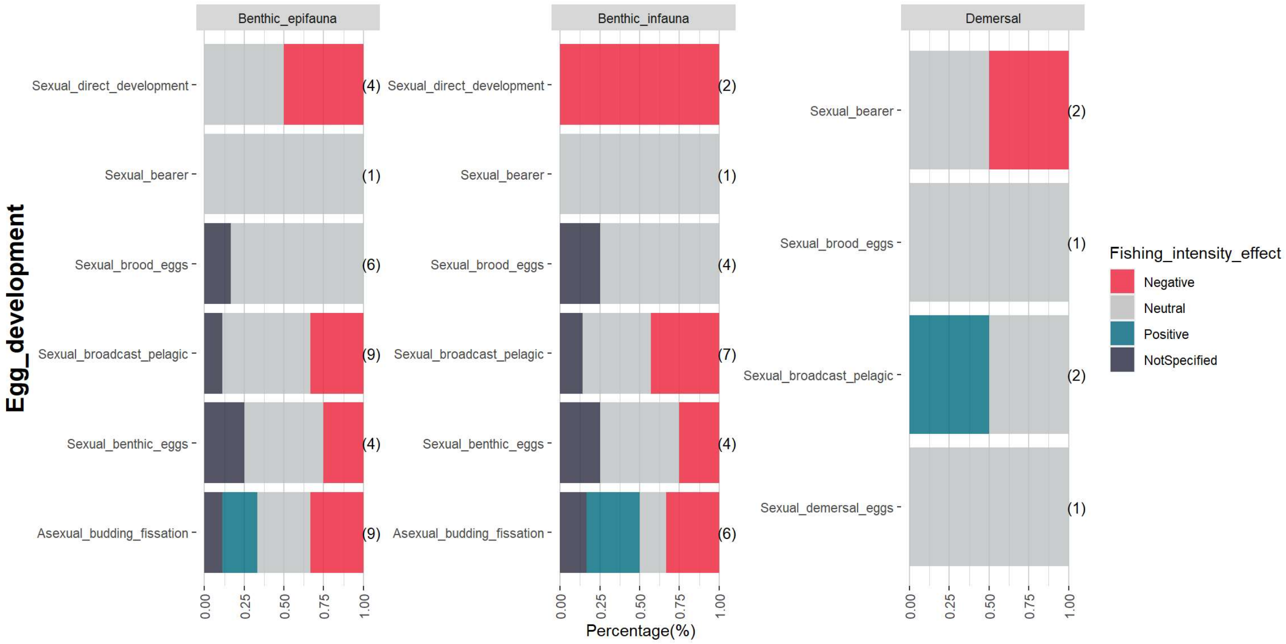


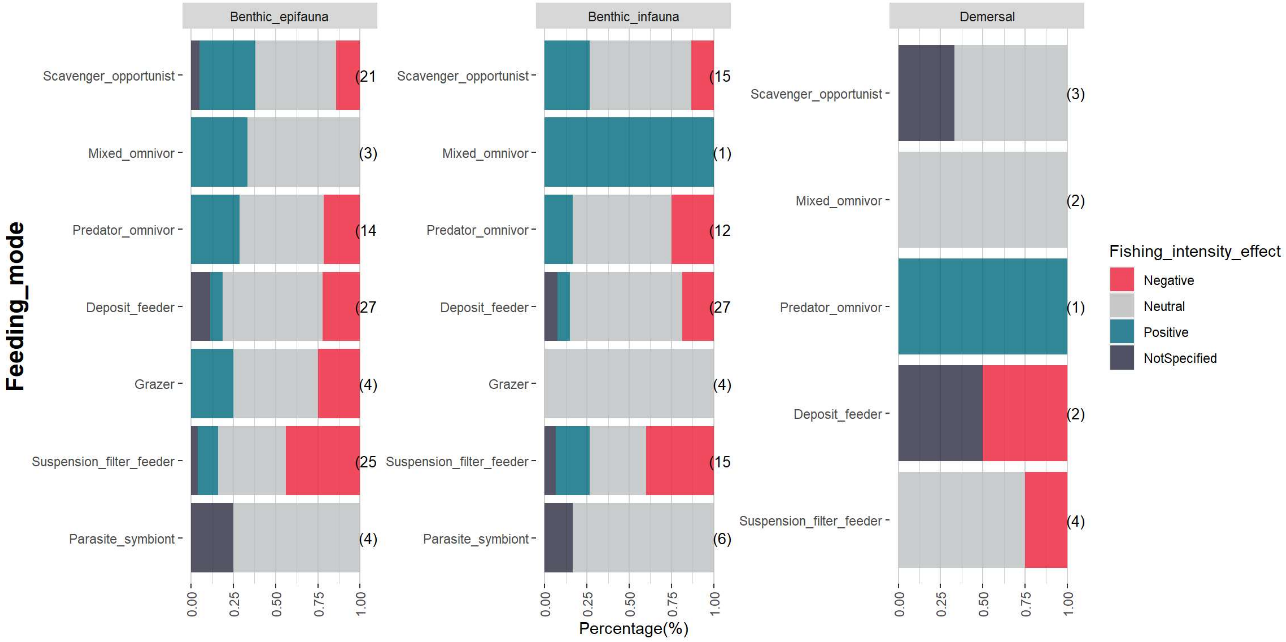

Benthic_epifauna
Benthic_infauna
Body_flexibility
High
Low
None
(5)
(4)
(4)
(2)
(2)
(2)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive

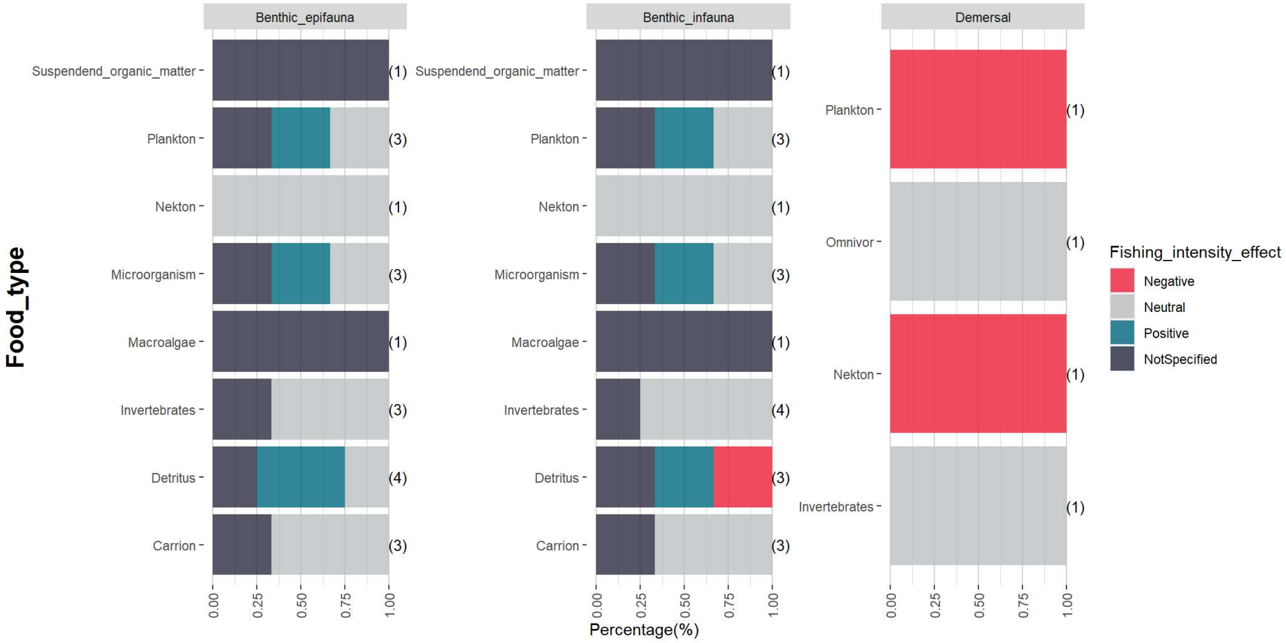

Benthic_epifauna
Benthic_infauna
Demersal
Body_protection
High
Medium_High
Medium
Low_Medium
Low
(12)
(2)
(7)
(8)
(10)
(8)
(2)
(4)
(6)
(5)
(2)
(1)
(2)
(3)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Body_shape
Benthic_epifauna
Vermiform (2)
Turbinate (1)
Tunic (3)
Tubiculous (1)
Stellata (1)
Stalked (7)
Shell (3)
Scales (1)
Round (3)
Pisciform (1)
Not_colonial (2)
Laterally_flat (1)
Irregular (1)
Exoskeleton (5)
Elongated (1)
Dorsally_flat (3)
Cylindrical (1)
Cushion (9)
Crustose (4)
Articulate (1)
Benthic_infauna
Vermiform (1)
Tunic (3)
Stout (1)
Stalked (5)
Slender (1)
Shell (3)
Scales (2)
Round (3)
Laterally_flat (2)
Irregular (2)
Exoskeleton (5)
Elongated (4)
Dorsally_flat (2)
Cylindrical (2)
Cushion (8)
Crustose (3)
Conical (1)
Clavate (1)
Demersal
Taeniform (1)
Fusiform (2)
Filiform (1)
Elongated (1)
Depressiform (1)
Compressiform (1)
Anguilliform (1)
Pelagic
Taeniform (1)
Fusiform (2)
Filiform (1)
Elongated (1)
Depressiform (1)
Compressiform (1)
Anguilliform (1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

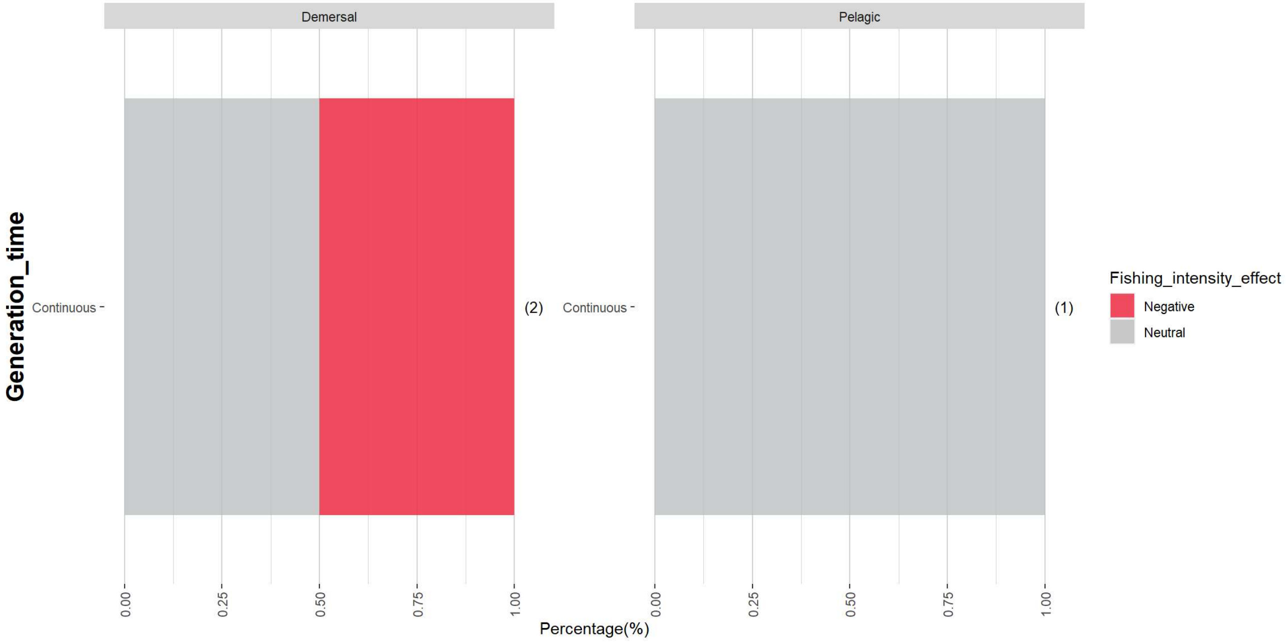

Dispersal_capacity
Benthic_epifauna
Pelagic_larva (1)
No_pelagic_phase (1)
Migratory (1)
High_mobility_adults (1)
Low_mobility_adults (1)
Benthic_infauna
Pelagic_larva (1)
No_pelagic_phase (1)
Migratory (1)
High_mobility_adults (1)
Low_mobility_adults (1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive


Egg_development
Benthic_epifauna
Benthic_infauna
Demersal
Sexual_direct_development
Sexual_bearer
Sexual_brood_eggs
Sexual_broadcast_pelagic
Sexual_benthic_eggs
Asexual_budding_fissation
Sexual_demersal_eggs
(4)
(1)
(6)
(9)
(4)
(9)
(2)
(1)
(4)
(7)
(4)
(6)
(2)
(1)
(2)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

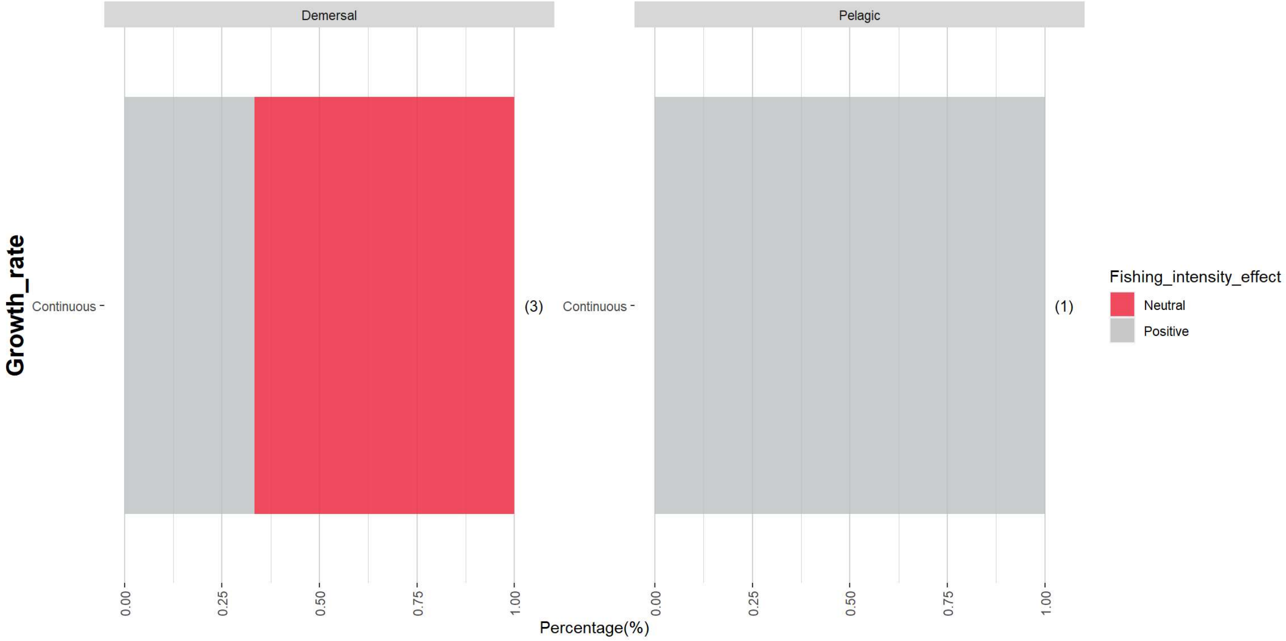

Feeding_mode
Benthic_epifauna
Benthic_infauna
Demersal
Scavenger_opportunist
Mixed_omnivor
Predator_omnivor
Deposit_feeder
Grazer
Suspension_filter_feeder
Parasite_symbiont
(21
(3)
(14
(27
(4)
(25
(4)
(15
(1)
(12
(27
(4)
(15
(6)
(3)
(2)
(1)
(2)
(4)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

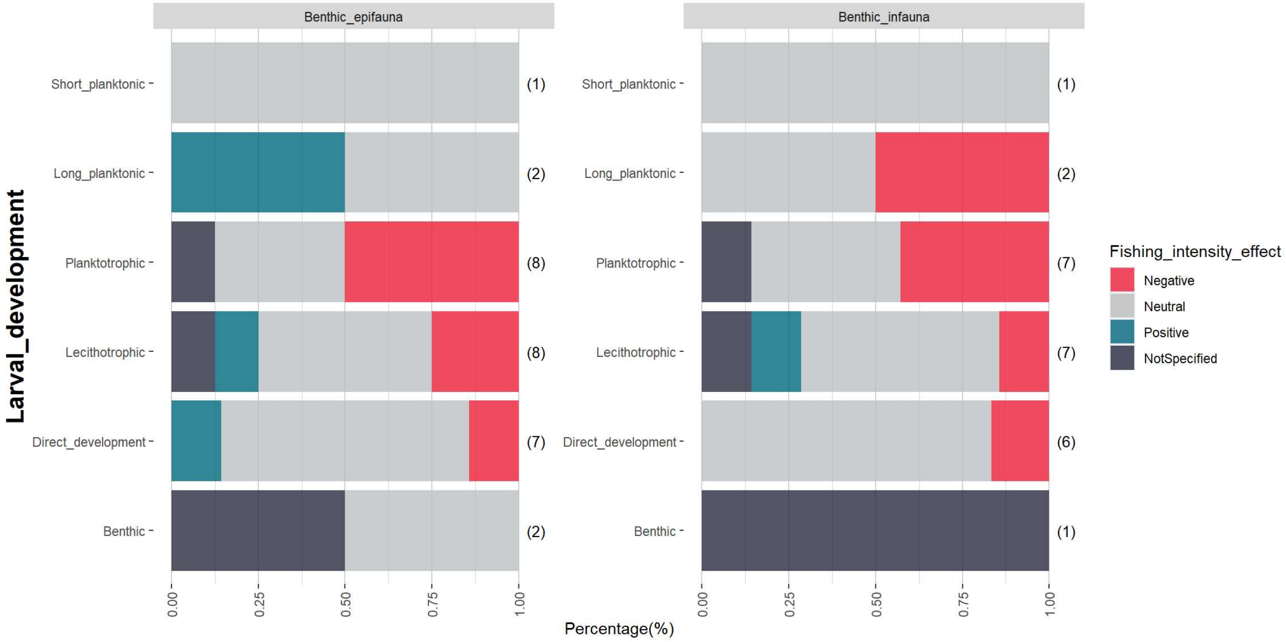


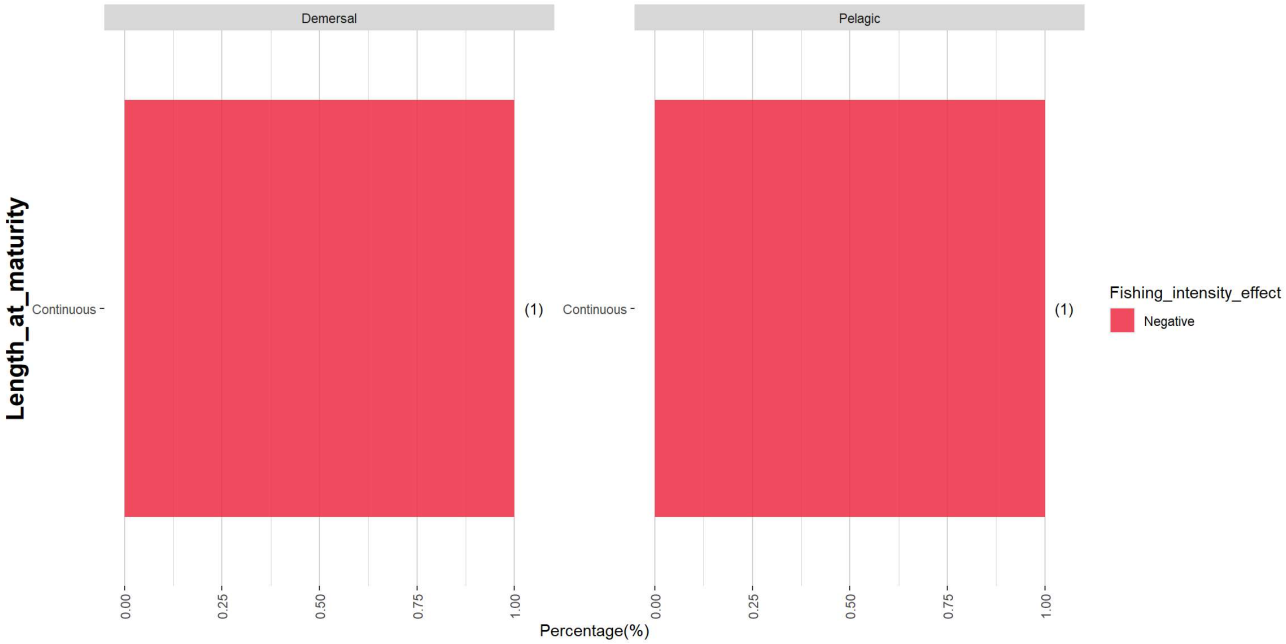
Benthic_epifauna
Benthic_infauna
Demersal
Food_type
Suspendend_organic_matter
Plankton
Nekton
Microorganism
Macroalgae
Invertebrates
Detritus
Carrion
Omnivor
(1)
(3)
(1)
(3)
(1)
(3)
(4)
(3)
(1)
(3)
(1)
(3)
(1)
(4)
(3)
(3)
(1)
(1)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

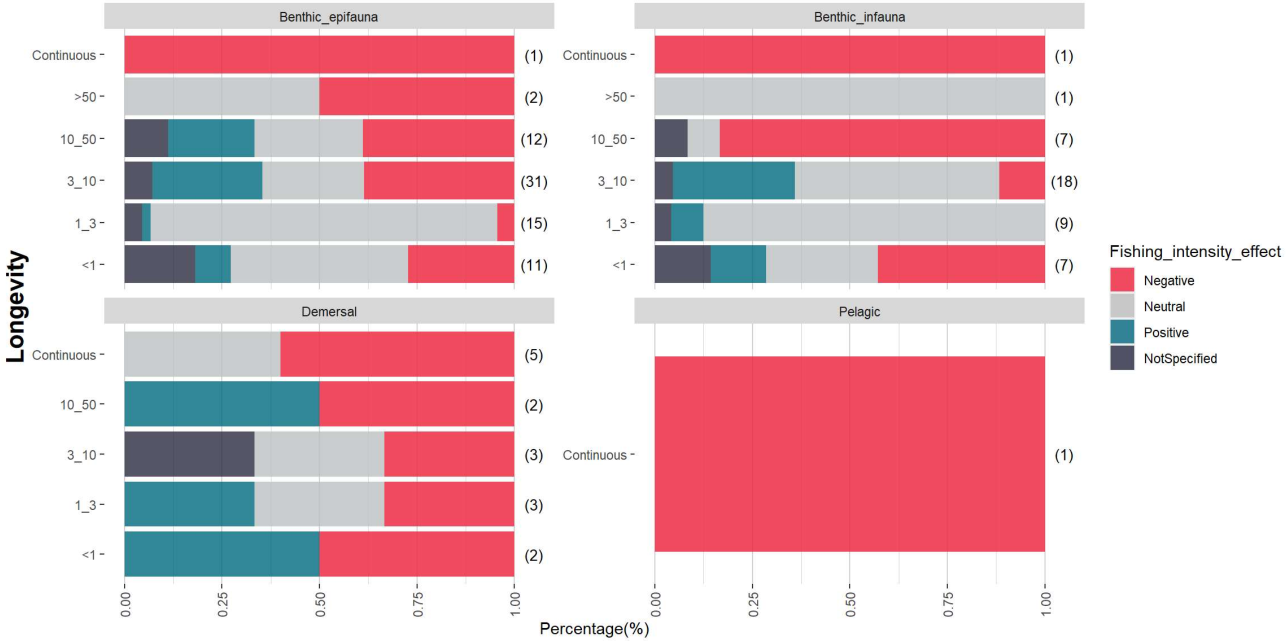


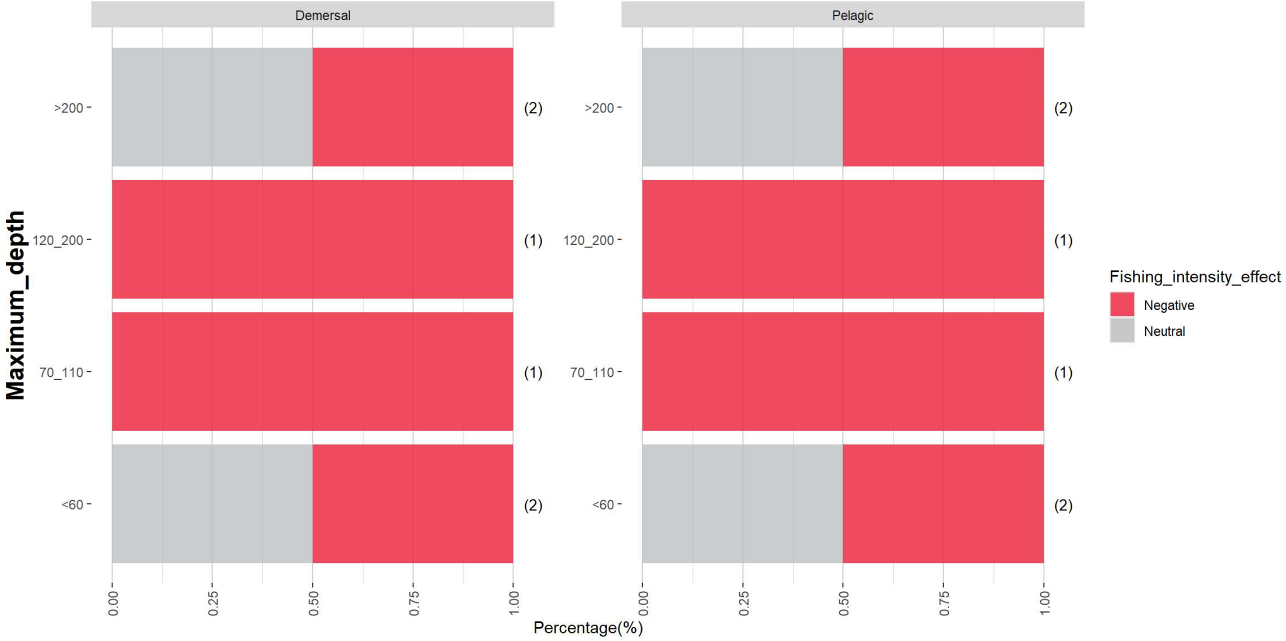
Demersal
Pelagic
Generation_time
Continuous
(2)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral

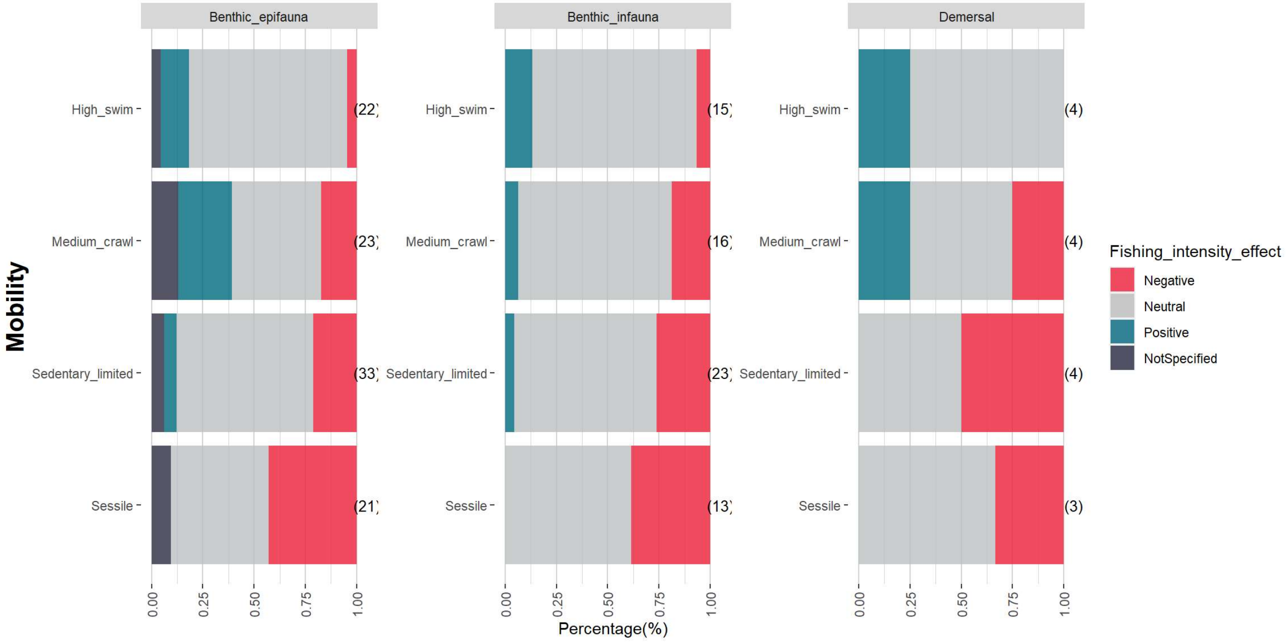

Demersal
Pelagic
Growth_rate
Continuous
(3)
Continuous
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Neutral
Positive

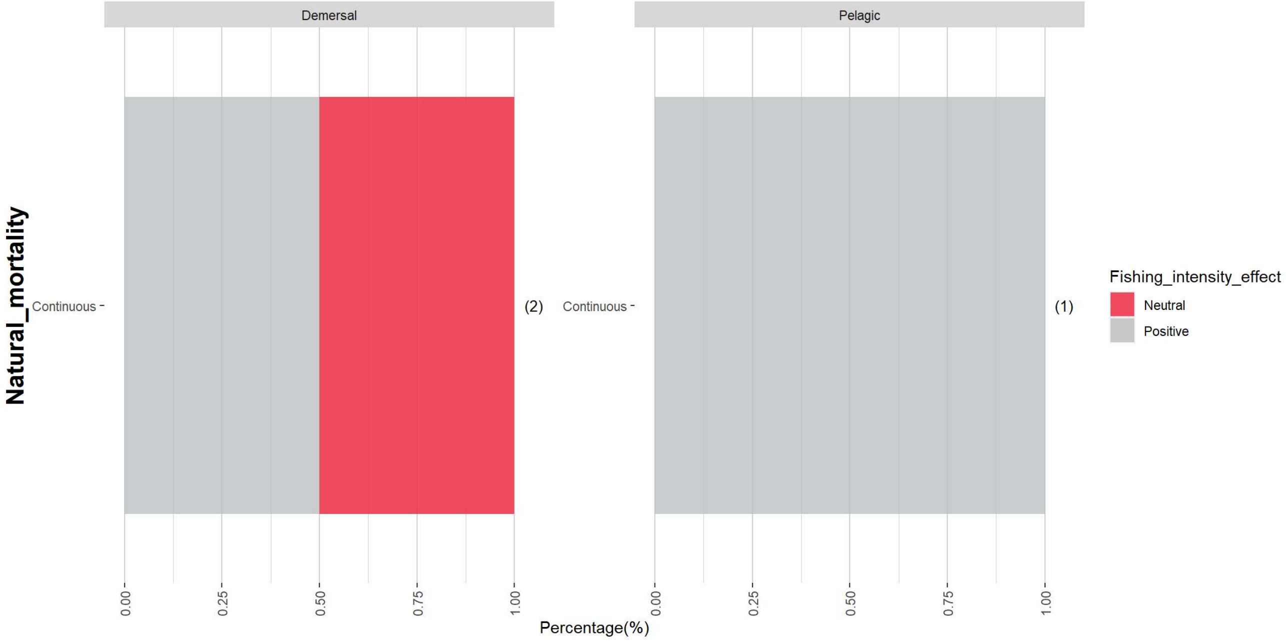

Benthic_epifauna
Benthic_infauna
Larval_development
Short_planktonic
(1)
Long_planktonic
(2)
Planktotrophic
(8)
Lecithotrophic
(8)
Direct_development
(7)
Benthic
(2)
Short_planktonic
(1)
Long_planktonic
(2)
Planktotrophic
(7)
Lecithotrophic
(7)
Direct_development
(6)
Benthic
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

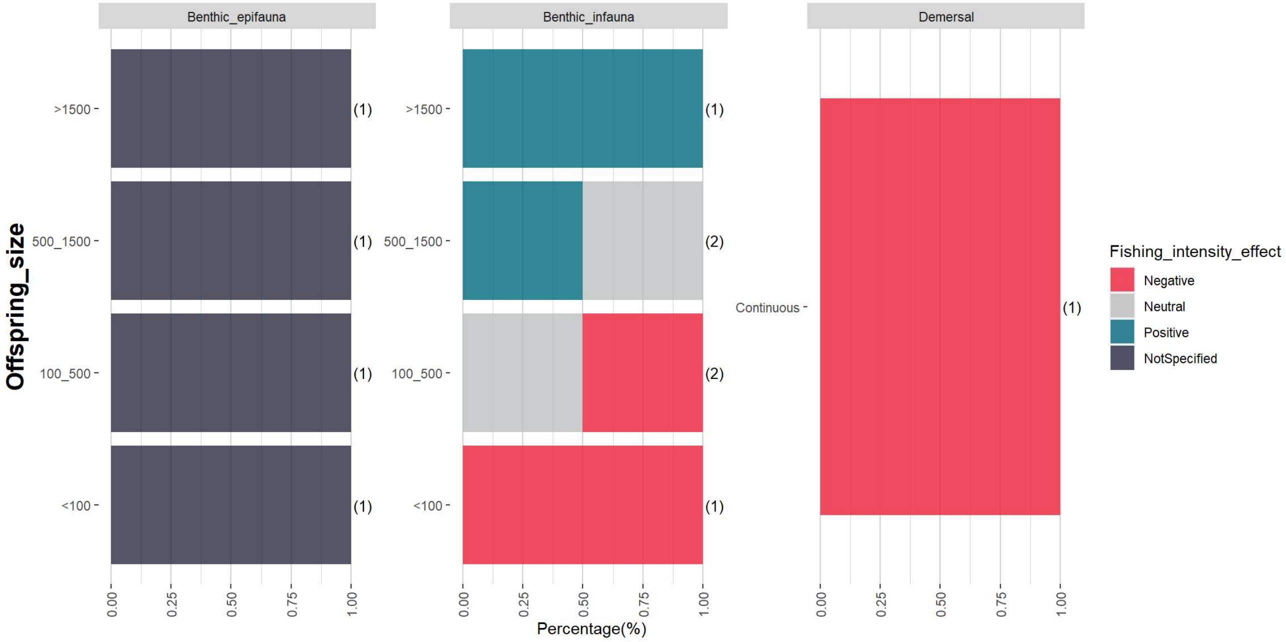

Length_at_maturity
Demersal
Pelagic
Continuous
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative

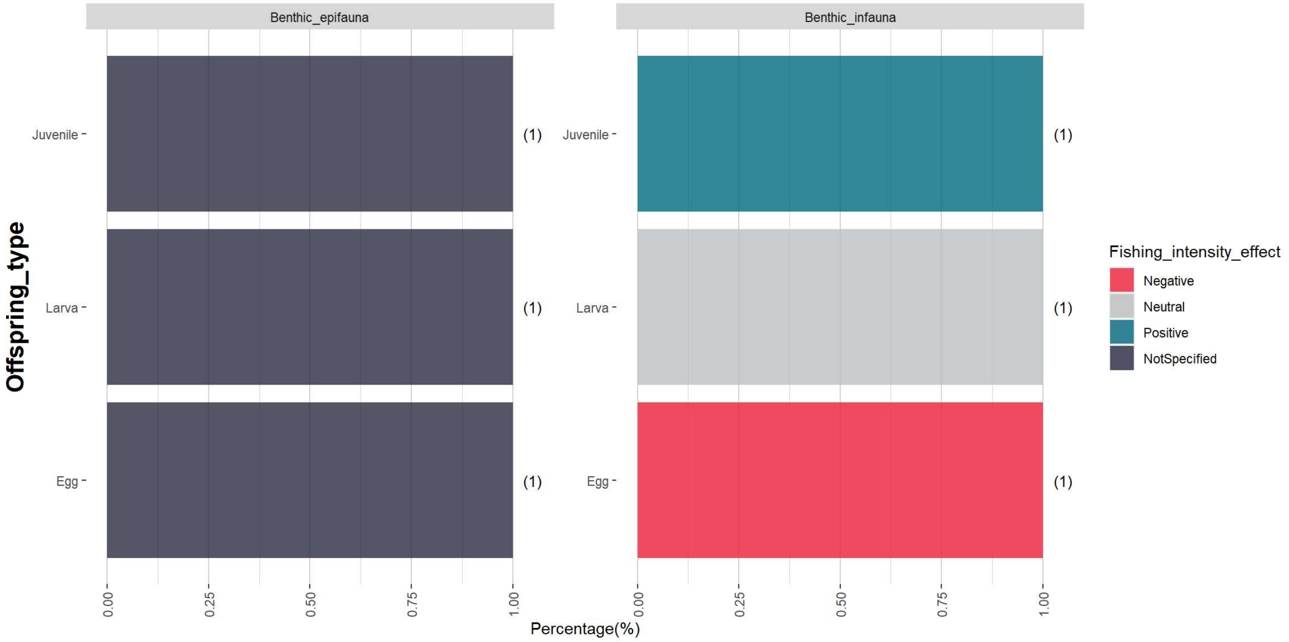

Longevity
Benthic_epifauna
Benthic_infauna
Demersal
Pelagic
Continuous
>50
10_50
3_10
1_3
<1
(1)
(2)
(12)
(31)
(15)
(11)
(1)
(1)
(7)
(18)
(9)
(7)
(5)
(2)
(3)
(3)
(2)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

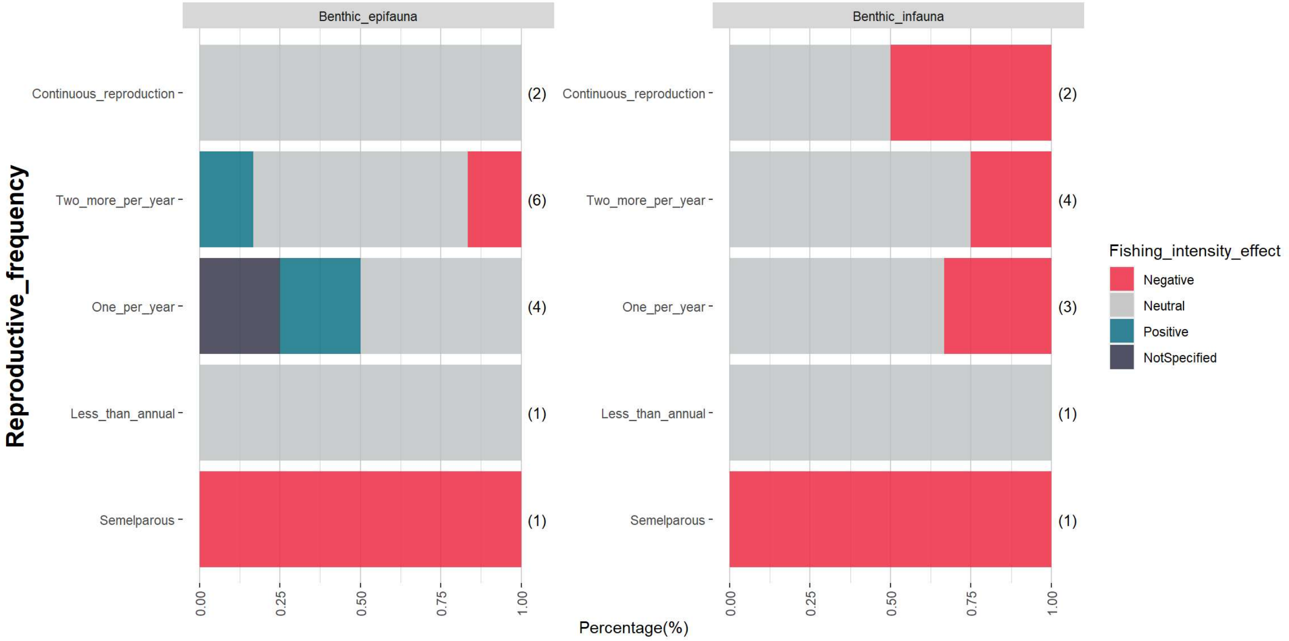

Demersal
Pelagic
Maximum_depth
>200
120_200
70_110
<60
(2)
(1)
(1)
(2)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral

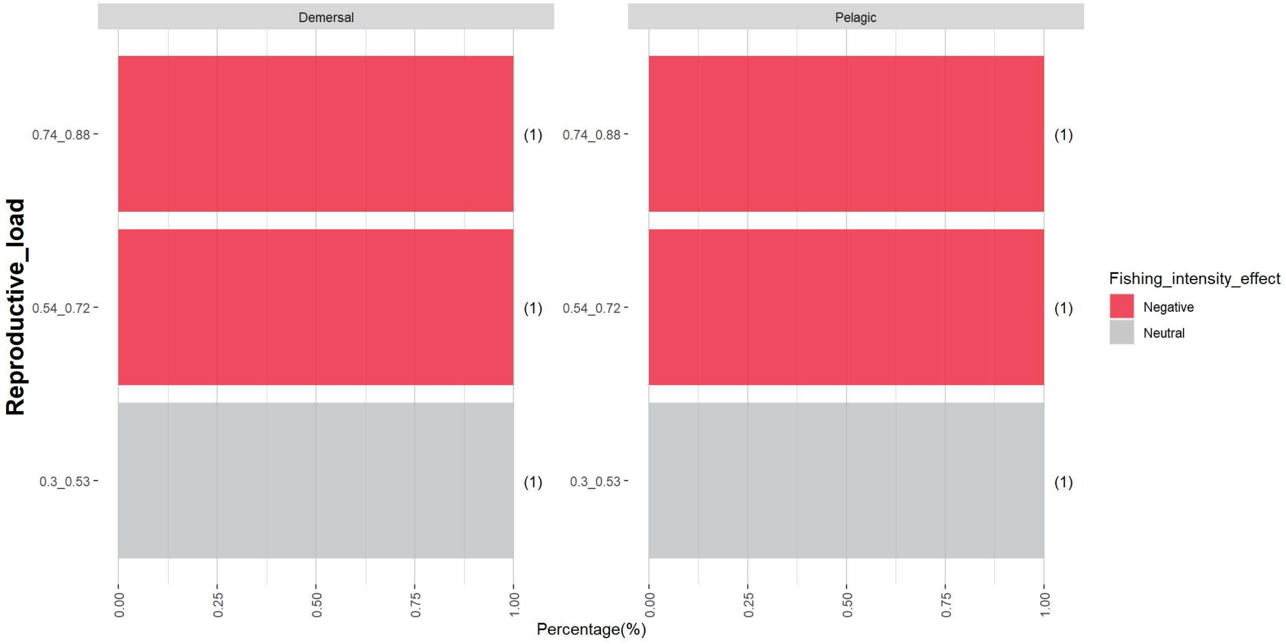

Benthic_epifauna
Benthic_infauna
Demersal
Mobility
High_swim
Medium_crawl
Sedentary_limited
Sessile
(22)
(23)
(33)
(21)
(15)
(16)
(23)
(13)
(4)
(4)
(4)
(3)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

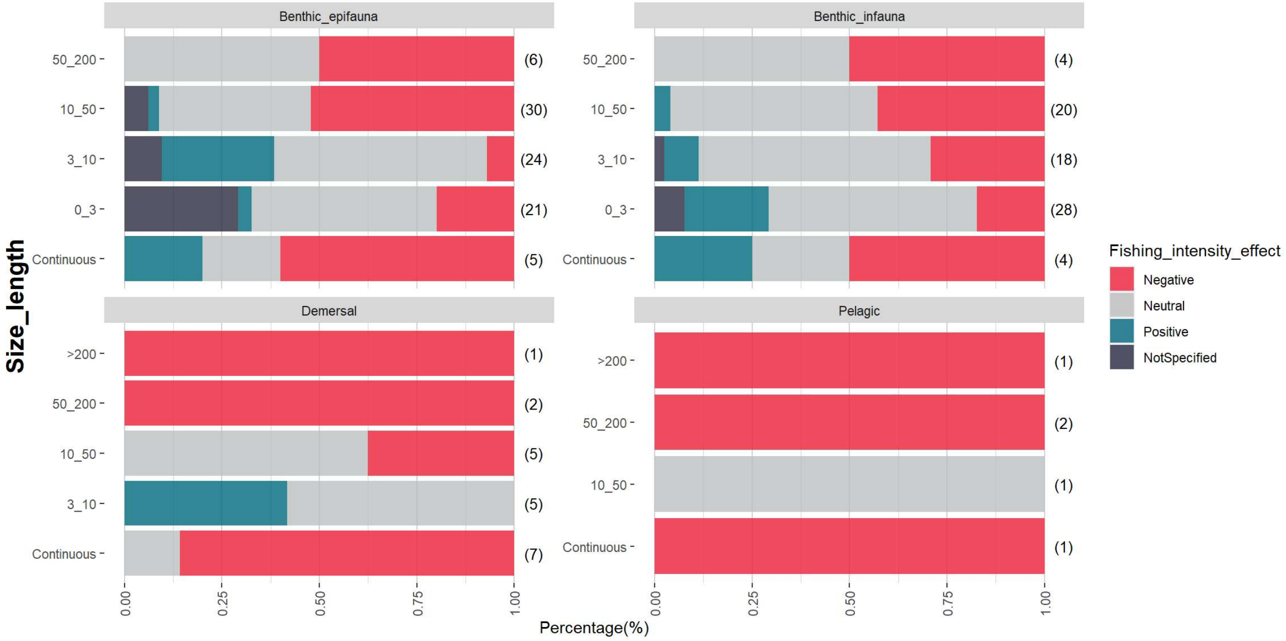

Demersal
Pelagic
Natural_mortality
Continuous
(2)
Continuous
(1)
0.00
0.25
0.50
0.75
1.00
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Neutral
Positive

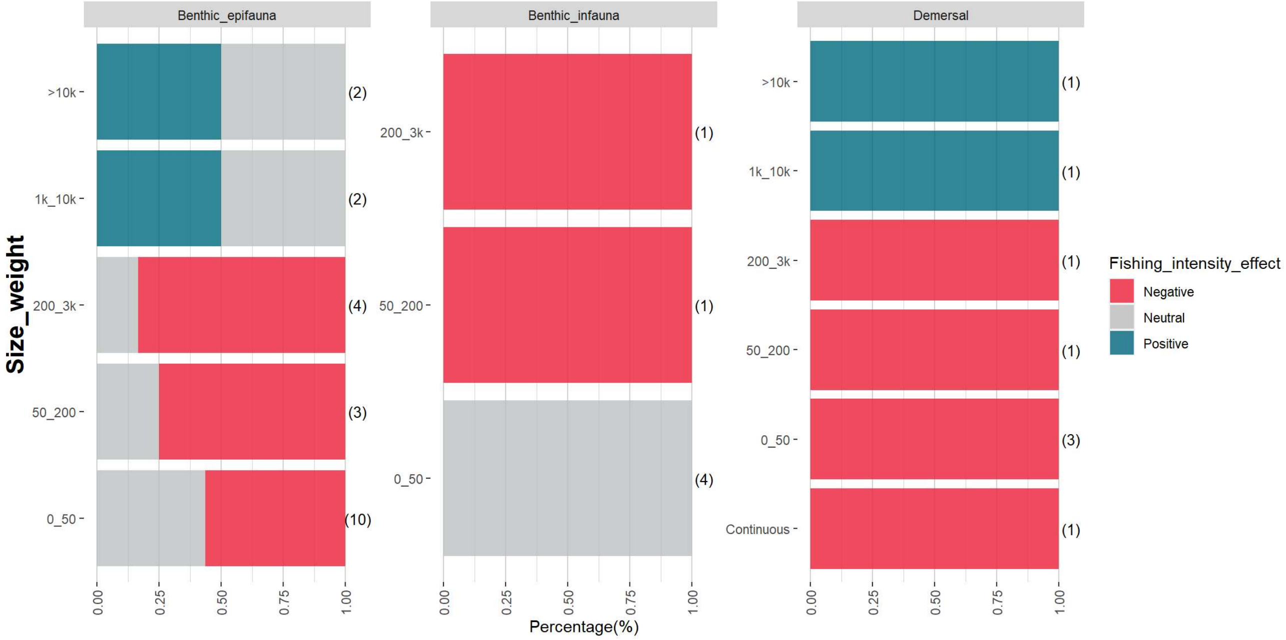

Benthic_epifauna
Benthic_infauna
Demersal
Offspring_size
>1500
500_1500
100_500
<100
(1)
(1)
(1)
(1)
>1500
500_1500
100_500
<100
(1)
(2)
(2)
(1)
Continuous
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified

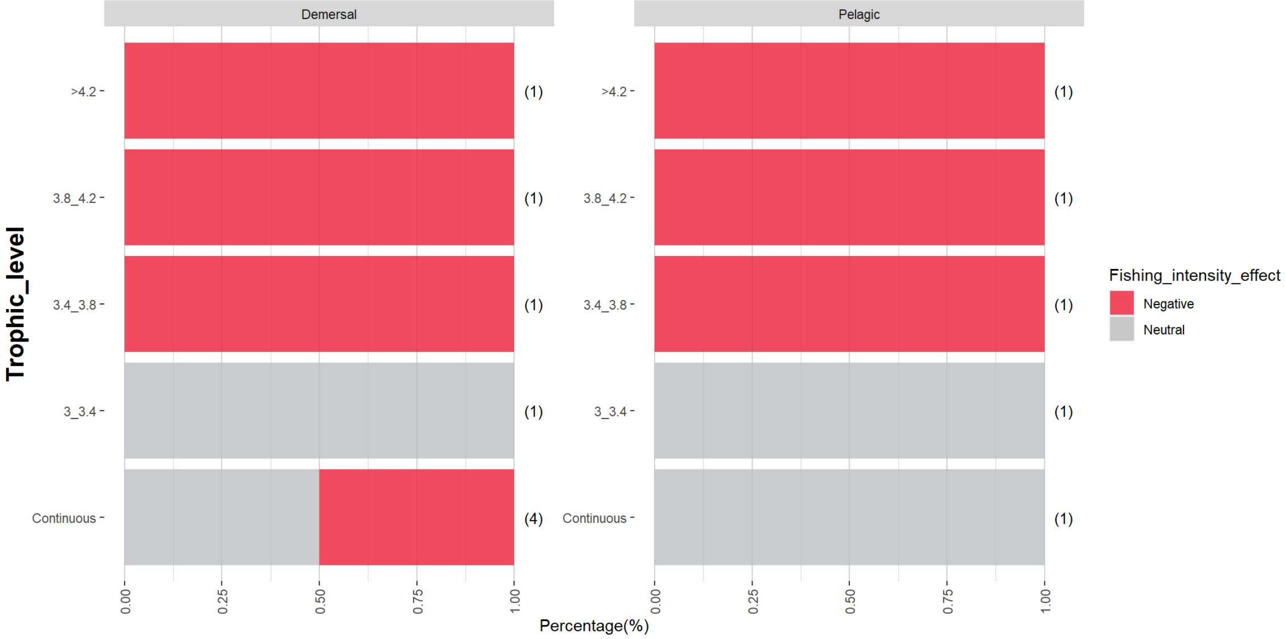

Benthic_epifauna
Benthic_infauna
Offspring_type
Juvenile
Larva
Egg
(1)
(1)
(1)
(1)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Benthic_epifauna
Benthic_infauna
Reproductive_frequency
Continuous_reproduction
Two_more_per_year
One_per_year
Less_than_annual
Semelparous
(2)
(6)
(4)
(1)
(1)
(2)
(4)
(3)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Demersal
Pelagic
Reproductive_load
0.74_0.88
0.54_0.72
0.3_0.53
(1)
(1)
(1)
(1)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral


Benthic_epifauna
Benthic_infauna
Demersal
Pelagic
Size_length
50_200
10_50
3_10
0_3
Continuous
(6)
(30)
(24)
(21)
(5)
(4)
(20)
(18)
(28)
(4)
>200
50_200
10_50
3_10
Continuous
(1)
(2)
(5)
(5)
(7)
>200
50_200
10_50
Continuous
(1)
(2)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive
NotSpecified


Benthic_epifauna
Benthic_infauna
Demersal
Size_weight
>10k
1k_10k
200_3k
50_200
0_50
Continuous
(2)
(2)
(4)
(3)
(10)
(1)
(1)
(4)
(1)
(1)
(1)
(1)
(3)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral
Positive


Demersal
Pelagic
Trophic_level
>4.2
3.8_4.2
3.4_3.8
3_3.4
Continuous
(1)
(1)
(1)
(1)
(4)
(1)
(1)
(1)
(1)
(1)
0.00
0.25
0.50
0.75
1.00
Percentage(%)
Fishing_intensity_effect
Negative
Neutral

Chapter 2: A functional trait-based approach to disentangle trawling disturbance onto bentho-demersal assemblage composition: evidence from a heavily exploited fishing ground (South-central Mediterranean Sea)

Supplementary material

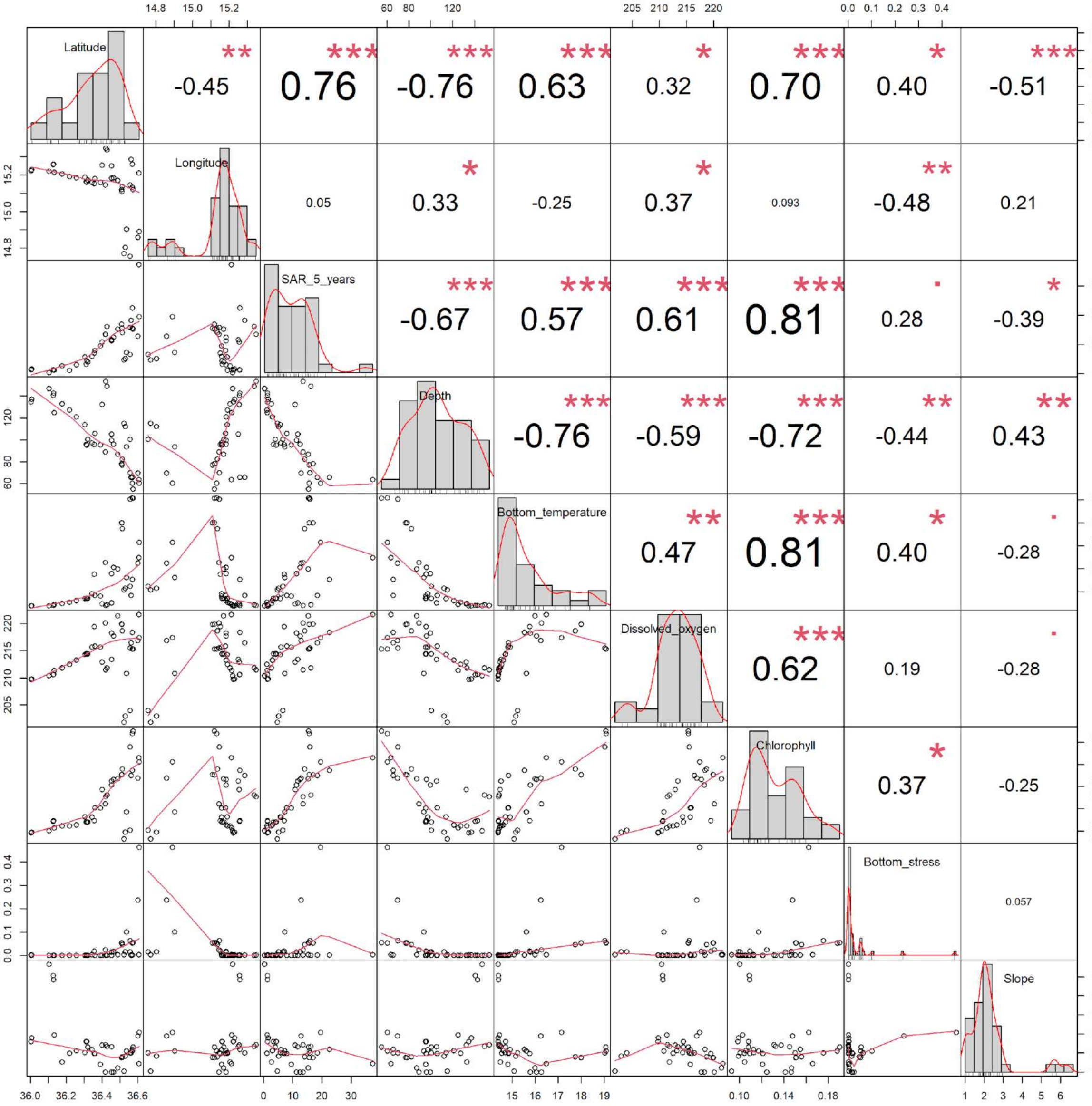
S1 – Variables associated with the sampled hauls and summary of the two clusters obtained from the k-mean classification.

SAR: Average annual swept area ratio from 2016 to 2020, Depth: bathymetry value, Btemp: modelled average temperature at the seabottom, DO: modelled average dissolved oxygen at the seabottom, Chl: modelled average chlorophyll concentration at the seabottom, Stress: shear bottom stress due to the currents, Slope: seabed slope, k-mean clusters: k-mean classification results using variables associated to the hauls.

Haul ID	**SAR**	**Depth (m)**	**Btemp (°C)**	**DO (mmol/L)**	**Chl (mg/L)**	**Stress (N/m^2)**	**Slope (°)**	**k-mean cluster**
HCP1_1	15.35	54.91	19.08	215.34	0.190	0.0554	2.31	2
HCP1_2	15.67	76.97	18.01	219.88	0.151	0.0535	1.76	2
HCP1_3	16.94	78.34	18.00	219.91	0.151	0.0534	1.74	2
HCP1_4	15.66	60.29	19.09	215.31	0.188	0.0537	2.10	2
HCP1_5	13.49	89.09	16.27	220.12	0.125	0.0250	1.00	2
HCP1_6	5.89	97.41	14.92	215.66	0.112	0.0041	2.18	1
HCP1_7	1.37	134.7	14.40	209.76	0.098	0.0024	2.60	1
HCP1_8	1.58	137.21	14.40	209.78	0.099	0.0024	2.79	1
HCP1_9	0.36	146.91	14.39	210.37	0.100	0.0015	6.66	1
HCP1_10	1.22	124.97	14.45	211.37	0.103	0.0015	2.94	1
HCP1_11	2.72	133	14.49	211.82	0.105	0.0016	1.52	1
HCP1_12	1.12	127.3	14.55	212.51	0.104	0.0014	1.98	1
HCP1_13	3.02	121.09	14.62	213.24	0.106	0.0013	2.12	1
HCP1_14	5.66	113.92	14.71	214.29	0.113	0.0010	2.025	1
HCP1_15	7.98	105.98	14.84	215.83	0.121	0.0013	1.98	1
HCP1_18	14.02	82.47	17.74	218.67	0.156	0.0471	1.80	2
HCP1_21	7.25	93.62	15.63	210.80	0.117	0.1016	2.10	1
HCP1_22	4.72	115.13	15.09	201.78	0.093	0.0035	1.06	1
HCP1_23	5.17	112.20	15.16	202.93	0.099	0.0161	1.83	1
HCP1_24	6.60	100.52	15.24	203.99	0.101	0.0172	2.01	1
HCP1_M1	37.37	63.78	16.49	221.70	0.166	0.0041	1.43	2
HCP1_M2	22.53	65.84	15.54	218.39	0.155	0.0032	2.19	2
HCP1_M3	18.36	65.84	14.84	216.48	0.150	0.0027	2.00	2
HCP2_1	9.46	95.59	14.81	215.69	0.121	0.0010	1.41	1
HCP2_2	15.26	87.02	15.99	221.42	0.147	0.0042	1.22	2
HCP2_3	15.89	70.01	19.03	215.49	0.176	0.0636	2.00	2
HCP2_4	11.68	105.36	14.52	213.38	0.145	0.0011	2.33	1
HCP2_7	10.83	132.46	14.48	212.90	0.137	0.0009	2.41	1
HCP2_8	3.31	95.75	14.72	214.42	0.108	0.0010	2.59	1
HCP2_9	4.34	95.25	14.72	214.42	0.108	0.0010	2.60	1
HCP2_10	7.06	95.87	15.77	219.46	0.109	0.0110	1.96	1
HCP2_11	4.05	100.59	14.72	214.42	0.108	0.0010	2.31	1
HCP3_1	12.81	69.49	16.25	216.85	0.148	0.2378	2.89	2

HCP3_2	19.49	60.35	17.15	217.44	0.162	0.4617	3.07	2
HCP3_3	16.17	149.05	14.44	211.84	0.132	0.0020	2.35	1
HCP3_4	13.53	153.62	14.40	211.46	0.131	0.0022	2.43	1
HCP3_5	1.31	142.65	14.40	210.63	0.109	0.0018	5.85	1
HCP3_6	1.32	140.82	14.40	210.60	0.109	0.0018	6.07	1
HCP3_7	12.49	96.01	16.06	217.70	0.147	0.0179	1.00	2
HCP3_8	11.25	99.67	15.79	218.28	0.141	0.0150	1.00	2
Cluster 1	5.51	118.84	14.73	211.73	0.111	0.0072	2.64	
Cluster 2	17.10	74.67	17.02	218.20	0.157	0.0732	1.83	

S2 – Correlation charts of the variables considered in the study (values are expressed as Pearson's correlation coefficient while the symbols represent the significance level of the p-value: ' for p<0.1, * for p<0.05, ** for p<0.01, *** for p<0.001)

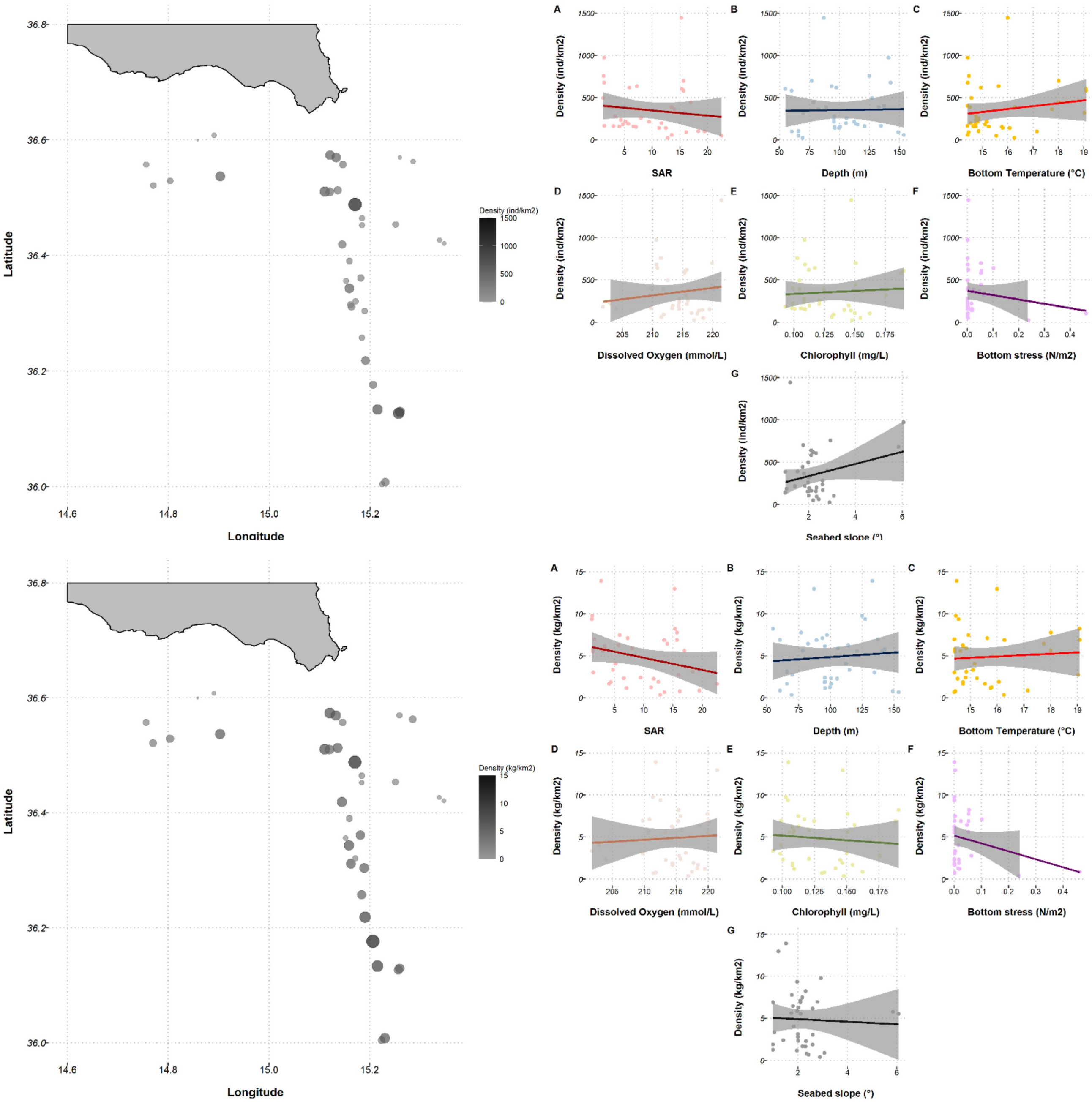


S3 - List of species collected and identified during the fishing surveys in the study area.

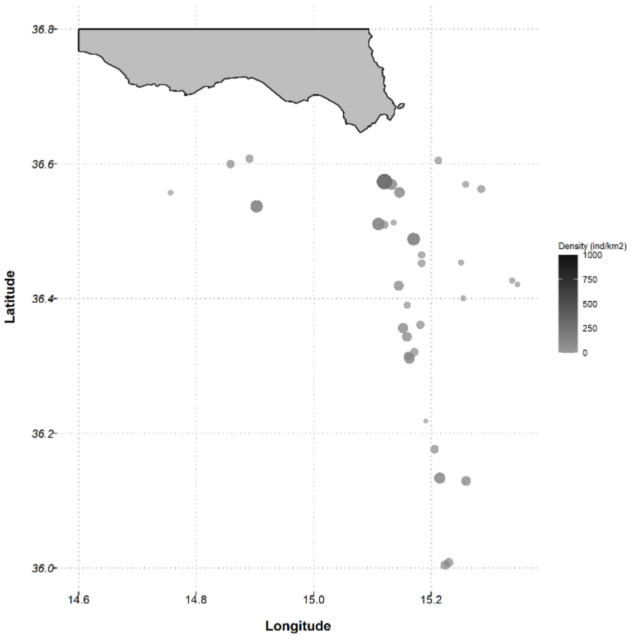
Species
Demersal
Fish
Argentina sphyraena (Linnaeus, 1758)
Arnoglossus laterna (Walbaum, 1792)
Blennius ocellaris (Linnaeus, 1758)
Boops boops (Linnaeus, 1758)
Capros aper (Linnaeus, 1758)
Centracanthus cirrus (Rafinesque, 1810)
Cepola macrophthalma (Linnaeus, 1758)
Chelidonichthys lucerna (Linnaeus, 1758)
Conger conger (Linnaeus, 1758)
Cubiceps gracilis (Lowe, 1843)
Deltentosteus quadrimaculatus (Valenciennes, 1837)
Diplodus annularis (Linnaeus, 1758)
Echelus myrus (Linnaeus, 1758)
Engraulis encrasicolus (Linnaeus, 1758)
Gobius niger (Linnaeus, 1758)
Hippocampus guttulatus (Cuvier, 1829)
Lepidopus caudatus (Euphrasen, 1788)
Lepidotrigla cavillone (Lacepède, 1801)
Lophius piscatorius (Linnaeus, 1758)
Macroramphosus scolopax (Linnaeus, 1758)
Merluccius merluccius (Linnaeus, 1758)
Mullus barbatus (Linnaeus, 1758)
Muraena helena (Linnaeus, 1758)
Ophidion barbatum (Linnaeus, 1758)
Pagellus erythrinus (Linnaeus, 1758)
Pagrus pagrus (Linnaeus, 1758)
Peristedion cataphractum (Linnaeus, 1758)
Phycis phycis (Linnaeus, 1766)
Sciaena umbra (Linnaeus, 1758)
Scorpaena notata (Rafinesque, 1810)
Scorpaena scrofa (Linnaeus, 1758)
Serranus cabrilla (Linnaeus, 1758)
Serranus hepatus (Linnaeus, 1758)
Spicara maena (Linnaeus, 1758)
Spicara smaris (Linnaeus, 1758)
Synodus saurus (Linnaeus, 1758)
Tetronarce nobiliana (Bonaparte, 1835)
Torpedo marmorata (Risso, 1810)
Torpedo torpedo (Linnaeus, 1758)
Trachurus trachurus (Linnaeus, 1758)
Trigla lyra (Linnaeus, 1758)
Umbrina cirrosa (Linnaeus, 1758)
Uranoscopus scaber (Linnaeus, 1758)
Zeus faber (Linnaeus, 1758)
Mollusca
Illex coindetii (Vérany, 1839)
Loligo vulgaris (Lamarck, 1798)
Octopus vulgaris (Cuvier, 1797)
Sepia officinalis (Linnaeus, 1758)
Sepiola rondeletii (Leach, 1817)
Crustacea
Parapenaeus longirostris (Lucas, 1846)
Squilla mantis (Linnaeus, 1758)
Benthic
Crustacea

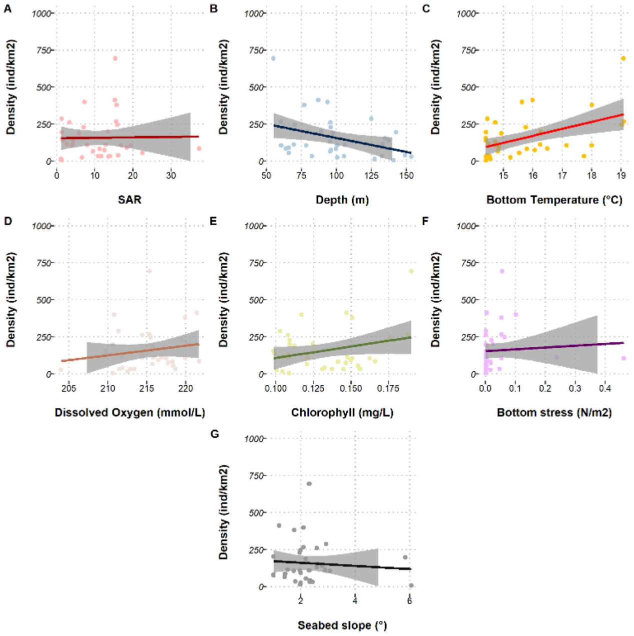
Aegaeon lacazei (Gourret, 1887) *Calappa granulata* (Linnaeus, 1758) *Dardanus arrosor* (Herbst, 1796) *Dardanus calidus* (Risso, 1827) *Ethusa mascarone* (Herbst, 1785) *Goneplax rhomboides* (Linnaeus, 1758) *Lepas sp.* (Linnaeus, 1758) *Liocarcinus depurator* (Linnaeus, 1758) *Medorippe lanata* (Linnaeus, 1767) *Munida rugosa* (Fabricius, 1775) *Nephrops norvegicus* (Linnaeus, 1758) *Pagurus alatus* (Fabricius, 1775) *Pagurus bernhardus* (Linnaeus, 1758) *Pagurus excavatus* (Herbst, 1791) *Spinolambrus macrochelos* (Herbst, 1790)
Mollusca *Aequipecten opercularis* (Linnaeus, 1758) *Aplysia sp.* (Linnaeus, 1767) *Bolinus brandaris* (Linnaeus, 1758) *Bursatella leachii* (Blainville, 1817) *Calliostoma sp* (Swainson, 1840) *Galeodea echinophora* (Linnaeus, 1758) *Galeodea rugosa* (Linnaeus, 1771) *Philinopsis depicta* (Renier, 1807) *Pteria hirundo* (Linnaeus, 1758) *Tonna galea* (Linnaeus, 1758) *Turritellinella tricarinata* (Brocchi, 1814) *Venus verrucosa* (Linnaeus, 1758) *Euopisthobranchia*
Echinodermata *Antedon mediterranea* (Lamarck, 1816) *Astropecten aranciacus* (Linnaeus, 1758) *Astropecten bispinosus* (Otto, 1823) *Astropecten irregularis* (Pennant, 1777) *Astrospartus mediterraneus* (Risso, 1826) *Ceramaster granularis* (Retzius, 1783) *Diadema setosum* (Leske, 1778) *Echinus melo* (Lamarck, 1816) *Echinaster sepositus* (Retzius, 1783) *Leptometra phalangium* (Müller, 1841) *Marthasterias glacialis* (Linnaeus, 1758) *Parastichopus regalis* (Cuvier, 1817) *Peltaster placenta* (Müller & Troschel, 1842) *Pisaster brevispinus* (Stimpson, 1857) *Psammechinus microtuberculatus* (Blainville, 1825) *Spatangus purpureus* (Müller, 1776) *Sphaerechinus granularis* (Lamarck, 1816) *Stylocidaris affinis* (Philippi, 1845)
Other *Alcyonium sp.* (Linnaeus, 1758) *Calliactis parasitica* (Couch, 1842) *Pennatula phosphorea* (Linnaeus, 1758) *Phallusia mammillata* (Cuvier, 1815) *Pteroeides griseum* (Bohadsch, 1761) *Porifera*

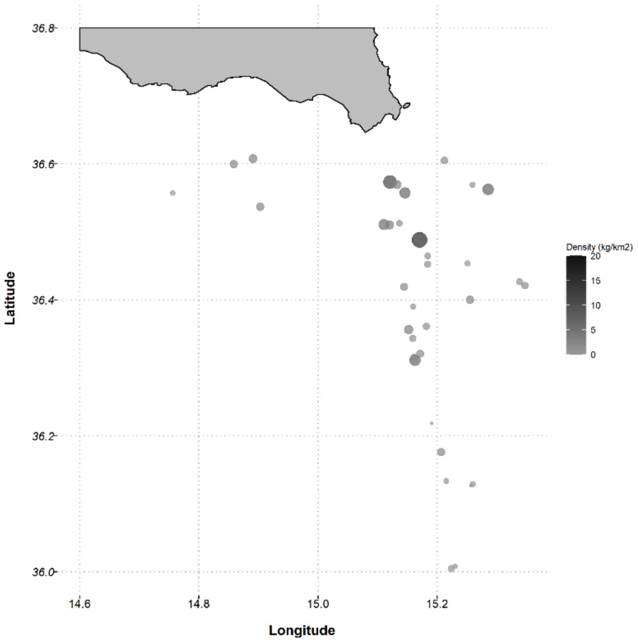
S4 – Distribution of demersal densities (total number of individual and biomasses/km^2) along the study area (as can be seen in the bubble plot where bigger points represent higher density values) and along the selected variables (as can be seen in the scatter plots with linear trends). For each haul, densities were obtained by dividing total individuals/biomasses by the corresponding swept area.

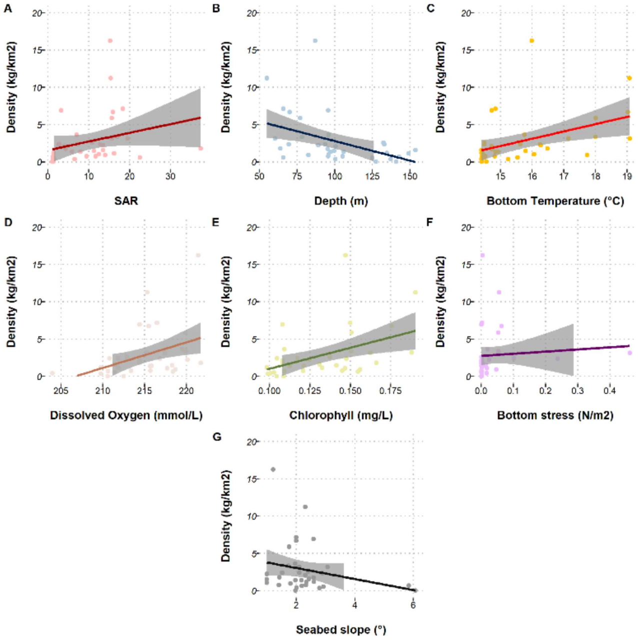


S5 – Distribution of benthic densities (total number of individual and biomasses/km^2) along the study area (as can be seen in the bubble plots where bigger points represent higher density values) and along the selected variables (as can be seen in the scatter plots with linear trends). For each haul, densities were obtained by dividing total individuals/biomasses by the corresponding swept area.

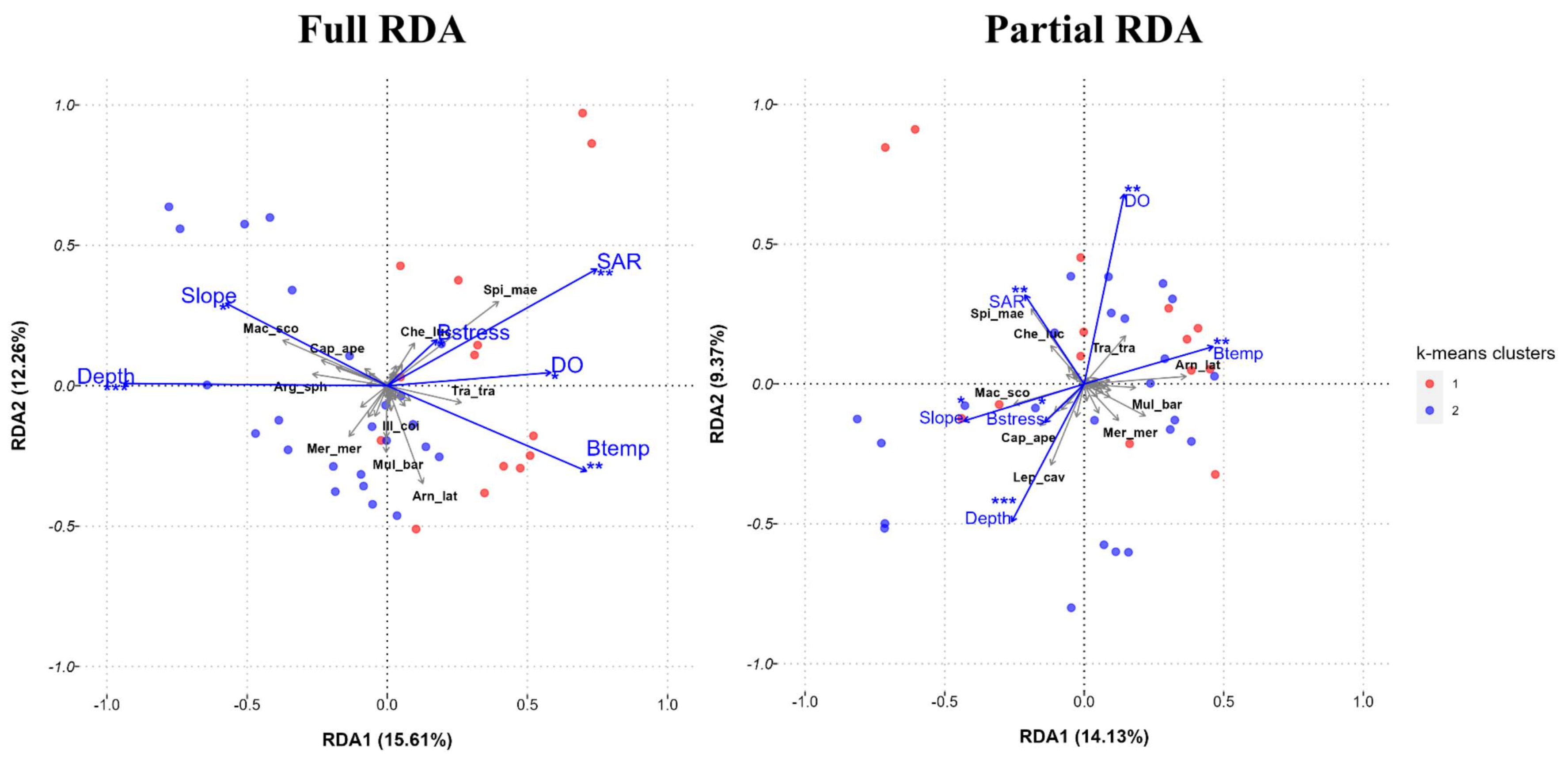

36.8
36.6
36.4
36.2
36.0
Latitude
14.6
14.8
15.0
15.2
Longitude
Density (ind/km2)
1000
750
500
250
0


A
B
C
D
E
F
G
Density (ind/km2)
1000
750
500
250
0
SAR
0
10
20
30
Depth (m)
50
75
100
125
150
Bottom Temperature (°C)
15
16
17
18
19
Dissolved Oxygen (mmol/L)
205
210
215
220
Chlorophyll (mg/L)
0.100
0.125
0.150
0.175
Bottom stress (N/m2)
0.0
0.1
0.2
0.3
0.4
Seabed slope (°)
2
4
6


36.8
36.6
36.4
36.2
36.0
Latitude
14.6
14.8
15.0
15.2
Longitude
Density (kg/km2)
20
15
10
5
0

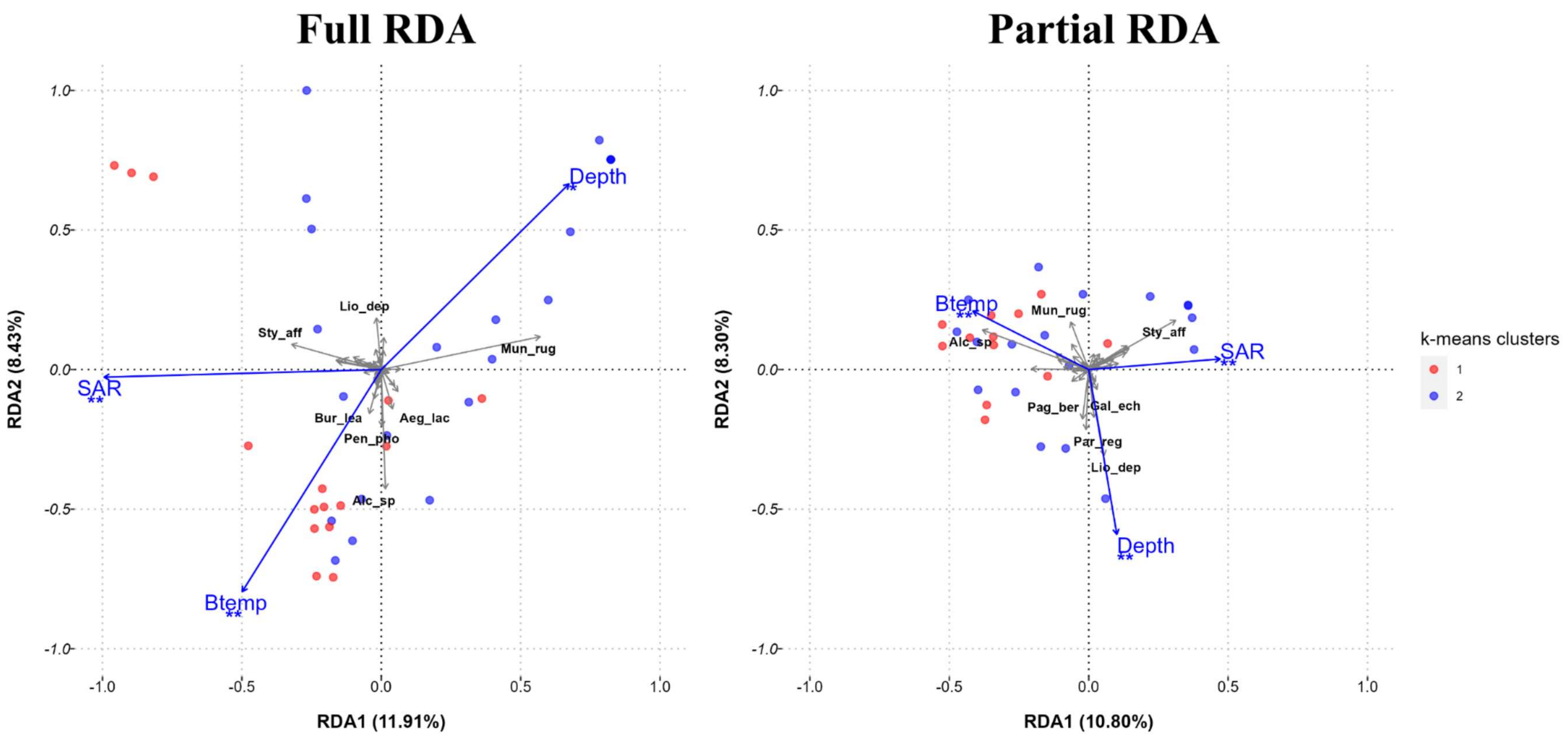

A
B
C
D
E
F
G
Density (kg/km2)
20
15
10
5
0
SAR
0
10
20
30
Depth (m)
50
75
100
125
150
Bottom Temperature (°C)
15
16
17
18
19
Dissolved Oxygen (mmol/L)
205
210
215
220
Chlorophyll (mg/L)
0.100
0.125
0.150
0.175
Bottom stress (N/m2)
0.0
0.1
0.2
0.3
0.4
Seabed slope (°)
2
4
6

S6 - Ordination of the all demersal species along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, * for p<0.001.**


Full RDA

Partial RDA

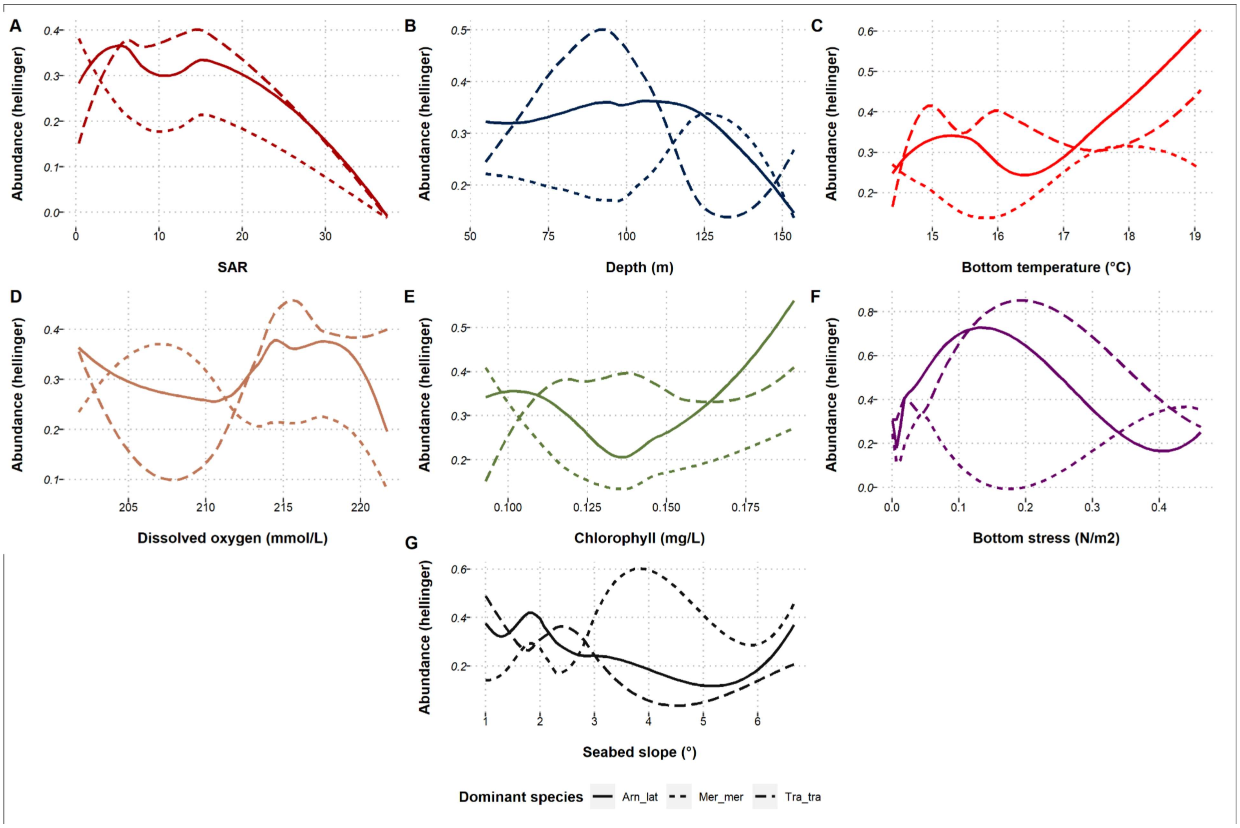
S7 - Ordination of the all benthic species along the two main axes of Redundancy Analysis (RDA) triplot for all the sampled hauls. On the left the RDA triplot of the model accounting stewpwise selected variables while on the right is displayed the partial RDA accounting spatial coordinates (Latitude and Longitude) as conditioning factor. Colors of the points represent the clusters obtained from a k-means classification according to the variables associated to the hauls (SM1-S1). Stars represent the significance level of the p-value for each term: * for p<0.05, ** for p<0.01, * for p<0.001.**



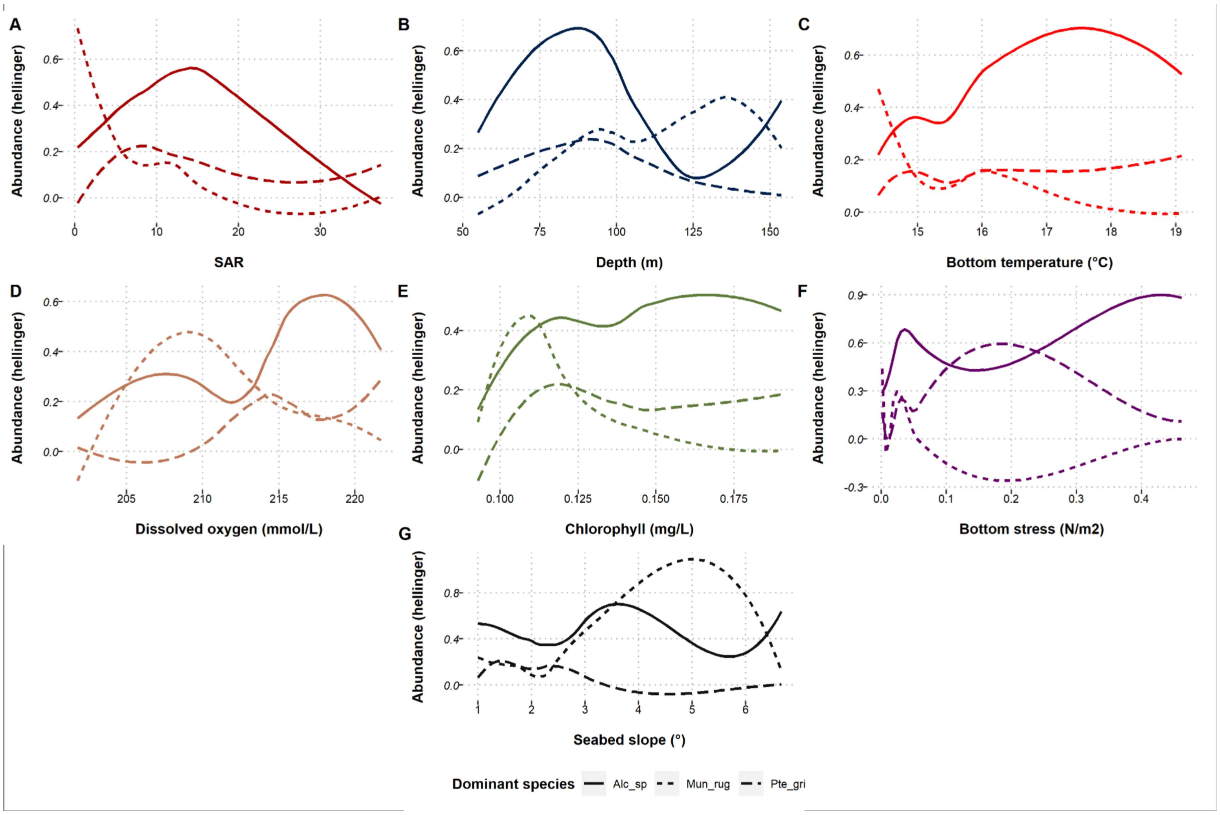
S8 – Variation partitioning between environmental (Env), anthropogenic (Ant) and spatial variables (Spat) accounted in RDA models for demersal and benthic domains. Combinations (Env+Ant, Env+Spat, Ant+Spat, All) constitute the proportion of variation explained by the coo occurence of both the variables in the model while Tot and Res represent the total variation explained by the model and by the residuals, respectively. See Table 5 for the environmental variables considered in each RDA model.

Variation explained by	Demersal		Benthic	
	Taxonomic	Functional	Taxonomic	Functional
Env	17%	17%	7%	
Ant	3%	7%	2%	
Spat	4%	3%	6%	12%
Env+Ant				
Env+Spat	2%		1%	13%
Ant+Spat	6%	3%	6%	2%
All	2%		1%	
Tot	34%	30%	23%	27%
Res	66%	70%	77%	73%

S9 - Distribution along the selected variables of the main dominant demersal species abundances. Arn_lat: *Arnoglossus laterna*, Mer_mer: *Merluccius merluccius*, Tra_tra = *Trachurus trachurus*



S10 - Distribution along the selected variables of the main dominant benthic species abundances. Alc_sp: *Alcyonium sp*., Mun_rug: *Munida rugosa*, Pter_gri = *Pteroides griseum*.


A
B
C
D
E
F
G
Abundance (hellinger)
0.0
0.2
0.4
0.6
0.8
0.9
0.3
-0.3
0
10
20
30
SAR
50
75
100
125
150
Depth (m)
15
16
17
18
19
Bottom temperature (°C)
205
210
215
220
Dissolved oxygen (mmol/L)
0.100
0.125
0.150
0.175
Chlorophyll (mg/L)
0.0
0.1
0.2
0.3
0.4
Bottom stress (N/m2)
1
2
3
4
5
6
Seabed slope (°)
Dominant species
Alc_sp
Mun_rug
Pte_gri

Supplementary Materials for

Chapter 3: Estimating trawling impact effects on benthic community: application of a quantitative and mechanistic framework along the Sicilian continental shelf (Central Mediterranean Sea)

Table S1: Comparison between observed and predicted cumulative biomass proportion among the models selected for each of the sixteen conditions investigated for estimating the longevity composition of the community.

Condition	Model	Mean difference between predicted and observed data	Spearmann correlation coefficient between predicted and observed data
Incl-1km-3yrs-NoD	Cumb ll + SAR_3 + Depth + Depth*SAR_3 + (1 — ID)	0.00235264	0.916035
Incl-1km-5yrs-NoD	Cumb ll + SAR_5 + Depth + Depth*SAR_5 + (1 — ID)	0.007082939	0.916187
Incl-3km-3yrs-NoD	Cumb ll + SAR_3 + Depth + (1 — ID)	-0.071207918	0.8955299
Incl-3km-5yrs-NoD	Cumb ll + SAR_5 + Depth + (1 — ID)	-0.071484209	0.895257
Incl-1km-3yrs-D	Cumb ll + SAR_3 + Depth + Depth*SAR_3 + (1 — ID)	-0.011716657	0.91559
Incl-1km-5yrs-D	Cumb ll + SAR_5 + Depth + Depth*SAR_5 + (1 — ID)	-0.001298026	0.9158675
Incl-3km-3yrs-D	Cumb ll + SAR_3 + Depth + (1 — ID)	-0.087100547	0.8952519
Incl-3km-5yrs-D	Cumb ll + SAR_5 + Depth + (1 — ID)	-0.087349586	0.8950461
Excl-1km-3yrs-NoD	Cumb ll + Depth + (1 — ID)	0.000005261	0.9049562
Excl-1km-5yrs-NoD	Cumb ll + Depth + (1 — ID)	0.003036191	0.9049562
Excl-3km-3yrs-NoD	Cumb ll + Depth + (1 — ID)	-0.070131386	0.9049562
Excl-3km-5yrs-NoD	Cumb ll + Depth + (1 — ID)	-0.070131386	0.9049562
Excl-1km-3yrs-D	Cumb ll + Depth + (1 — ID)	-0.008288128	0.9048411
Excl-1km-5yrs-D	Cumb ll + Depth + (1 — ID)	-0.001825939	0.9049562
Excl-3km-3yrs-D	Cumb ll + Depth + (1 — ID)	-0.079034926	0.9049562
Excl-3km-5yrs-D	Cumb ll + Depth + (1 — ID)	-0.079034926	0.9049562

Table S2: Parameters of the fixed effects of the final selected model for estimating the longevity composition of the benthic community with the following condition: SAR Inclusion - 1 x 1 km SAR resolution - 3 years average - no depth filtering.

Predictor	Parameter	Estimate	Std.Error	p-value
	Intercept	-6.5391	1.11271	<0.001
Longevity	ln (L)	2.58245	0.21391	<0.001
Fishing intensity	ln (SAR+0.01)	-0.9071	0.30571	0.00301
Depth	ln (D)	0.21942	0.20485	0.28411
Depth x Fishing intensity	ln(D) x ln (SAR+0.01)	0.20372	0.07197	0.00464

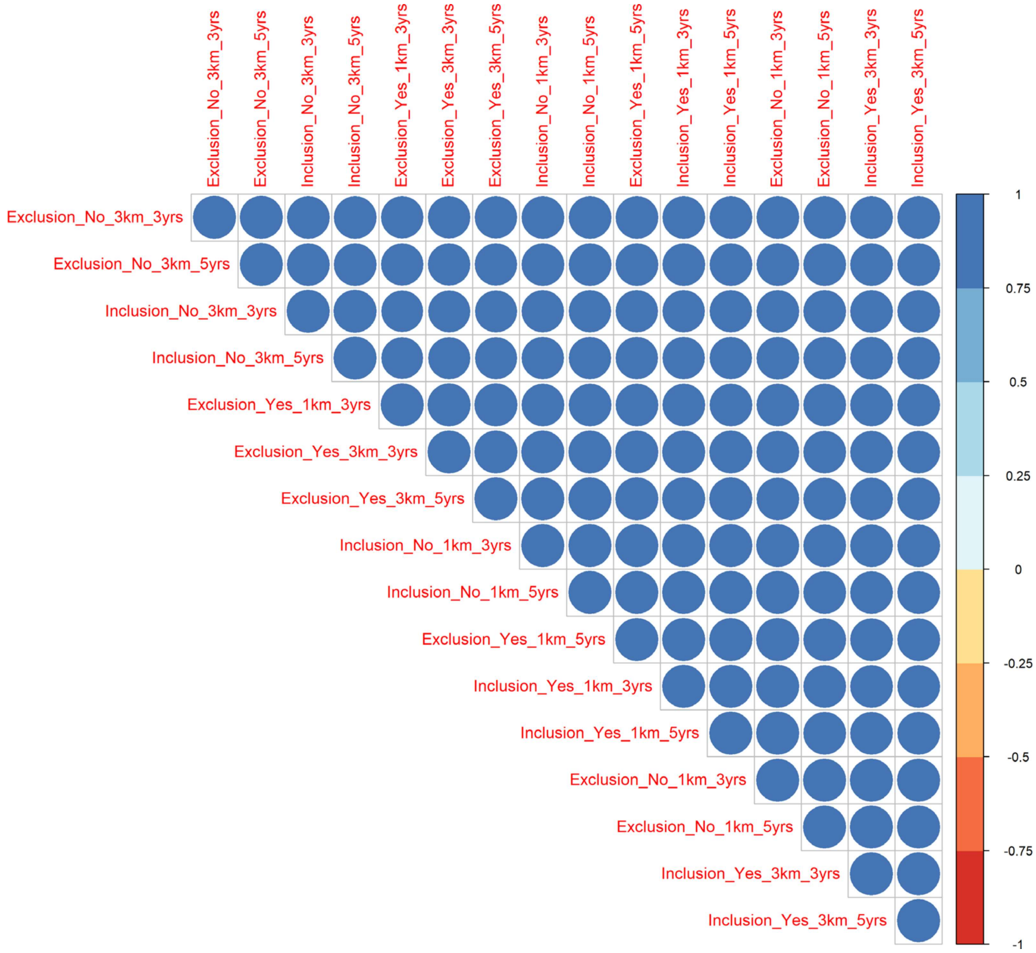


Figure S1: Correlation between median longevities obtained through the different combinations of data selection for modeling: SAR Inclusion or Exclusion criteria with a threshold value of 0.5, Depth limited data (<= 200 meters), spatial resolution of the fishing intensity layer (1x1 km or 3x3 km) and time period average of the fishing intensity values (3 years or 5 years prior to the sampling period) .

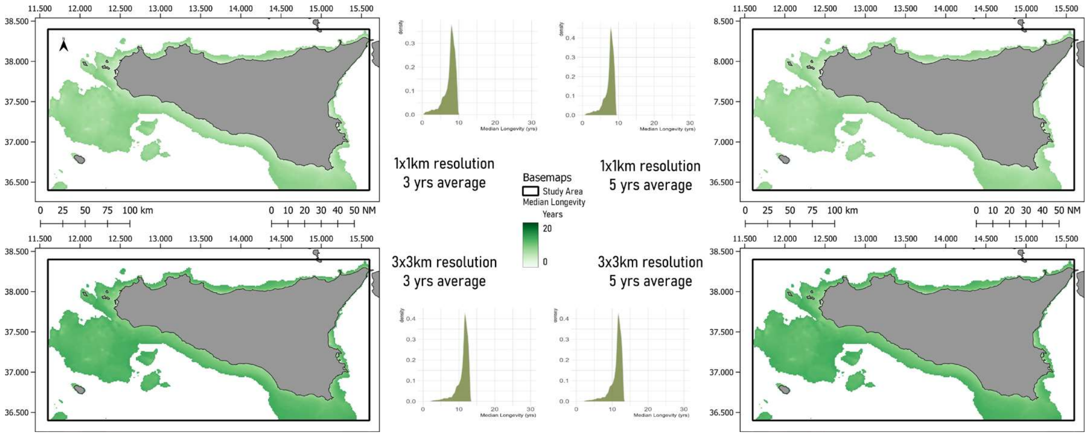


Figure S2: Median longevity estimation and distribution around the study area based on exclusion conditions.

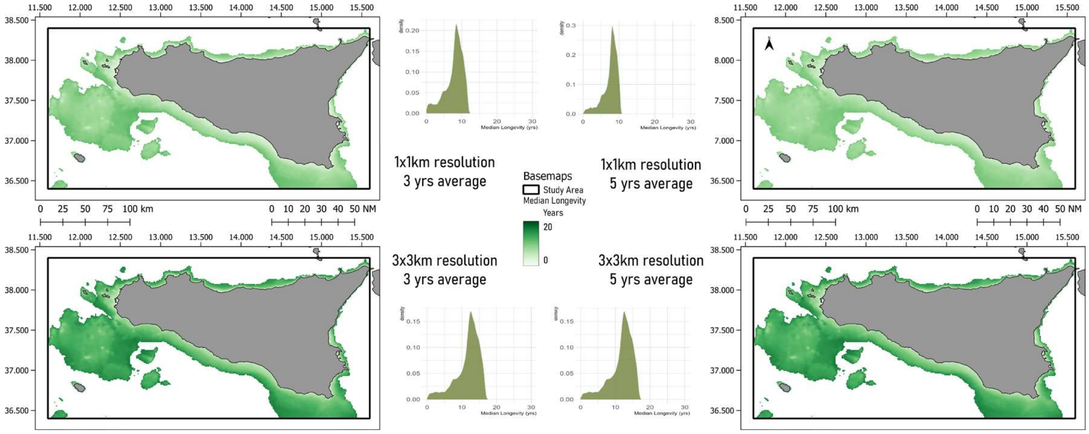


Figure S3: Median longevity estimation and distribution around the study area based on exclusion conditions with depth limited data.

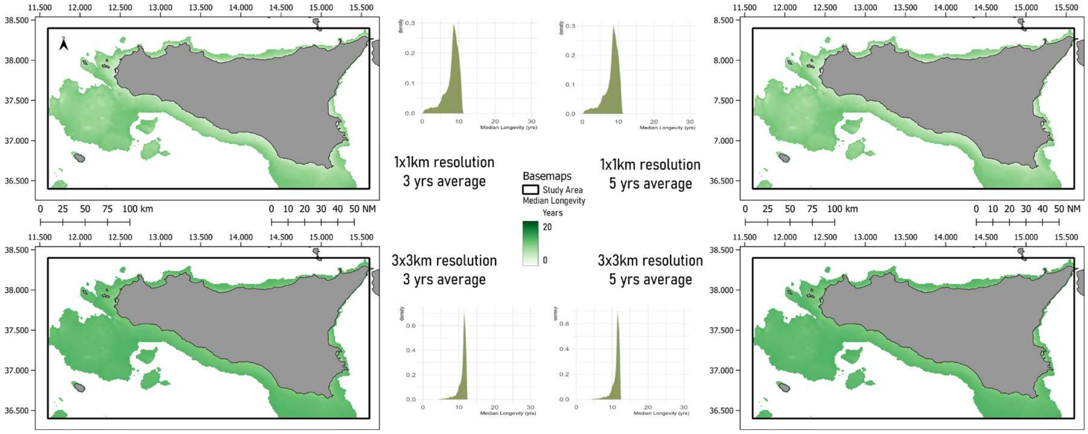


Figure S4: Median longevity estimation and distribution around the study area based on inclusion conditions.

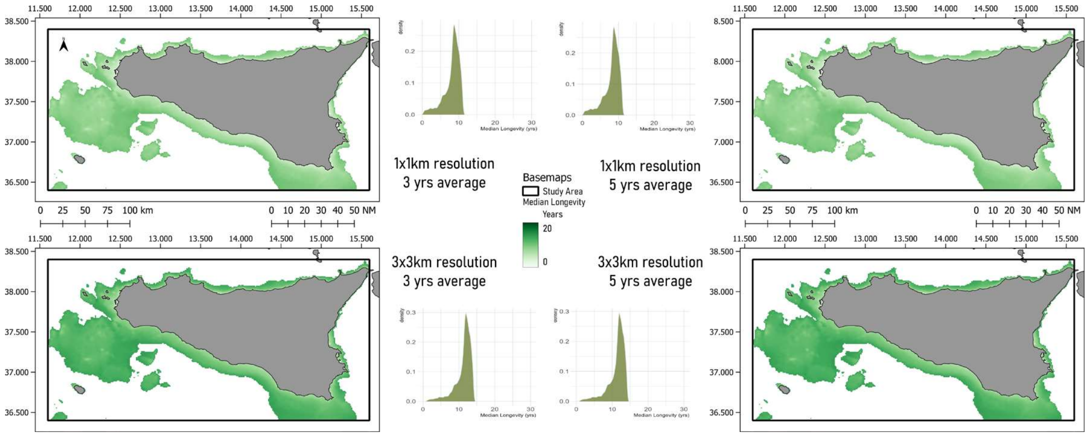


Figure S5: Median longevity estimation and distribution around the study area based on inclusion conditions with depth-limited data.

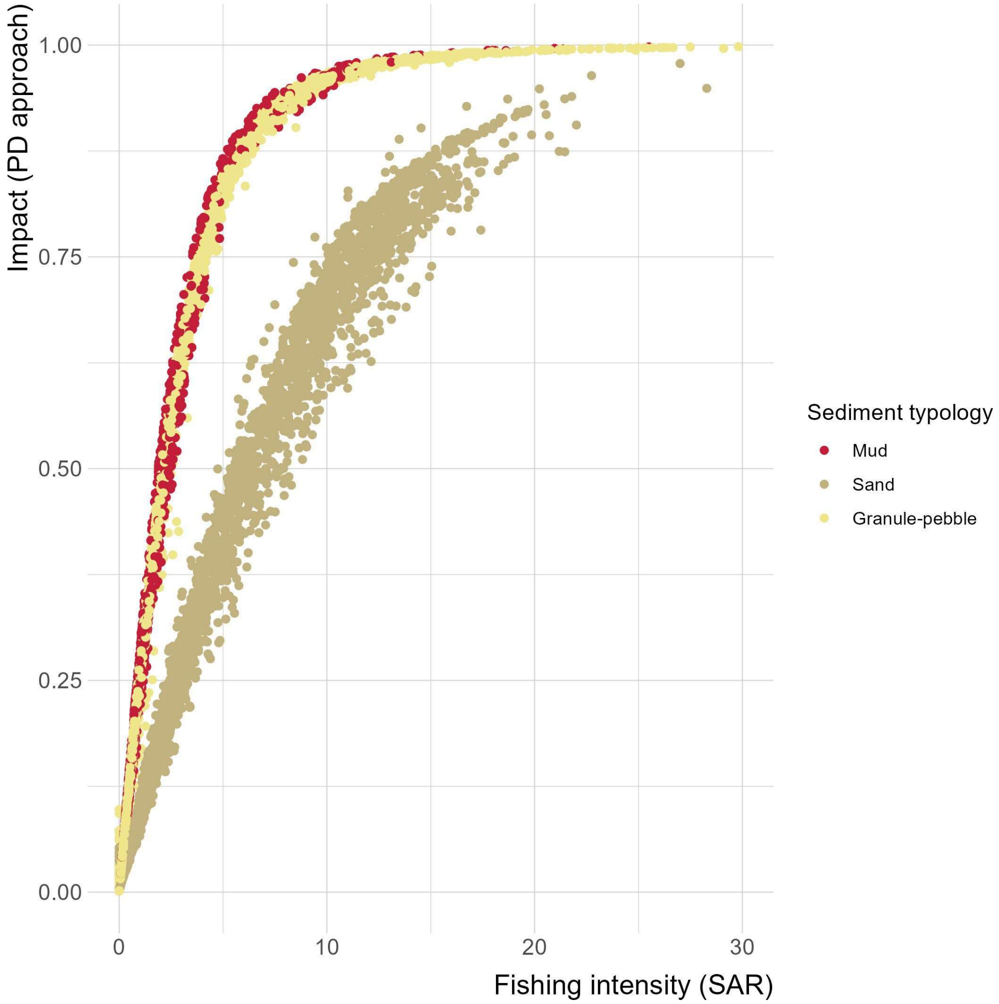


Figure S6: Relation between fishing intensity and PD approach impact estimates according to the different sediment typologies occurring in the continental shelf of the study area. As can be seen, muddy and granule sediments reach higher impacts at the same level of fishing intensity than sandy habitats due to the different depletion rates that bottom otter trawling could generate.

Table S3: Parameters of the fixed effects of the final selected model for estimating the longevity composition of the benthic community with the following condition: SAR Exclusion - 1 x 1 km SAR resolution - 3 years average - no depth filtering.

Predictor	Parameter	Estimate	Std.Error	p-value
	Intercept	-2.6148	1.521	0.0856
Longevity	ln (L)	2.5583	0.2946	<0.001
Depth	ln (D)	-0.6059	0.3409	0.0755

Supplementary Materials for

Chapter 4: Trait-based framework to assess the vulnerability of marine communities to bottom trawling activities

Table S1: Studies used for extracting the effect sizes of the eight selected response traits related to trawling pressure.

Study ID	Study Reference	Site	Geographical location	Habitat (EU-NIS code)	Depth	Fishing gear	Fishing intensity effect	Target	Traits considered	Response variable
1	Bolam, S. (2014). Predicting the effect of trawling based on biological traits of organisms and functional correlates of these traits to predict which functions may be disproportionally affected. BENTHIS Deliverable, 4	Metanalysis of 59 different experimental manipulations or observations of the effects of fishing disturbance on benthic fauna and communities, extracted from 30 separate publications	Europe, America, Australia/New Zealand	A5.1/A5.4; A5.2; A5.3; A5.6	0-133	Beam trawl, otter trawl, dredge	Comparison between an area that was experimentally fished to a non fished area or protected area where no bottom fishing was allowed or an area that was only very lightly fished. Fishing intensity must be explicitly established through local knowledge of study authors or estimated using fishing effort from VMS data	Infauna and Epifauna	Bioturbation; Body protection; Body shape; Egg development; Feeding mode; Larval development; Living habitat; Longevity; Mobility; Sediment position; Size (length).	Individual species abundances, Total abundance, Diver sity
2	Gonzalez-Irusta, J. M., De la Torriente, A., Punzon, A., Blanco, M., and Serrano, A. (2018). Determining and mapping species sensitivity to trawling impacts: the benthos sensitivity index to trawling operations (besito). ICES Journal of Marine Science, 75(5):1710–1721	Galician and Cantabrian shelf	Southern Europe	A5.1/A5.4; A5.2; A5.3; A6.2; A6.3; A6.4; A6.5	70-500	otter trawl; twin trawl	SAR from VMS data. Five levels of trawling effort: very low effort (SAR¡0.2), low effort (0.2 SAR 0.96), medium effort (0.96 SAR 1.62), high effort (1.62 SAR 3.83) and very high effort (SAR¿3.83). Comparison made between very low and medium observations.	Epifauna	Attachment; Body flexibility; Body rotection; Feed-ing mode; Longevity; Mobility; Size (length); Sediment position	Relative trait modality biomasses
3	Hiddink, J. G., Jennings, S., Sciber ras, M., Bolam, S. G., Cambi'e, G., Mc-Connaughey, R. A., Mazor, T.,Hilborn, R., Collie, J. S., Pitcher, C. R., et al. (2019). Assessing bottom trawling impacts based on the longevity of benthic invertebrates. Journal of Applied Ecology, 56(5):1075–1084	Metanalysis of 31 articles providing data on 30 comparative trawl vs untrawled studies	Europe, North America	A5.1/A5.4; A5.2; A5.3; A5.6	0-420	Beam trawl, otter trawl, dredge	Comparative trawled vs untrawled contrast studies where a commercially trawled area was compared with a reference that was not trawled or only lightly trawled. Fishing intensity must be explicitly established through local knowledge of study authors or estimated using fishing effort from VMS data	Infauna And Epifauna	Bioturbation; Body shape; Egg development; Feeding mode; Larval development; Living habitat; Longevity; Mobility; Sediment position; Size (length);	Individual species abundances

4	Lambert, G. I., Jennings, S., Kaiser, M. J., Davies, T. W., and Hiddink, J. G. (2014). Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. Journal of Applied Ecology, 51(5):1326–1336	Isle of Man	Northern Europe	A5.1 / A5.4;	0-100	otter trawl, dredge	Fishing categories 'low' and 'high' are defined as lower and higher than the median fishing intensity (SAR) extrapolated from VMS data	Epifauna	Attachment; Body flexibility; Feeding mode; Longevity; Size (length);	Individual species abundances
5	McLaverty, C., Dinesen, G. E., Gislason, H., Brooks, M. E., and Eigaard, O. R. (2021). Biological traits of benthic macrofauna show size-based differences in response to bottom trawling intensity. Marine Ecology Progress Series, 671:1–19	Kattegat sea	Northern Europe	A5.2; A5.3;	0-100	Bottom trawl	Generalized linear mixed model of trait modality CWM with fishing intensity, expressed as SAR, as one of the predictors	Infauna	Bioturbation; Body shape; Egg development; Feeding mode; Larval Development; Living habitat; Longevity; Mobility; Sediment position; Size (length);	Relative trait Modality biomasses (CWM)
6	Tillin, H., Hiddink, J. G., Jennings, S., and Kaiser, M. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series, 318:31–45	North Sea	Northern Europe	A5.1/A5.4; A5.2; A5.3;	25-150	Beam trawl, otter trawl	Linear model of trait modality biomasses with fishing intensity, expressed as SAR, as predictor	Epifauna	Attachment; Feeding mode; Longevity; Mobility; Size (weight)	Individual species abundances
7	Van Denderen, P. D., Bolam, S. G., Hiddink, J. G., Jennings, S., Kenny, A., Rijnsdorp, A. D., and Van Kooten, T. (2015). Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Marine Ecology Progress Series, 541:31–43	North Sea and Irish Sea	Northern Europe	A5.1/A5.4; A5.2; A5.3;	25-150	Beam trawl, otter trawl	SAR from VMS data for classifying sampling sites. Low trawl disturbance sites as SAR 0.2 yr1, intermediate trawl disturbance 0.2- SAR 0.5 yr1. All other sampling sites were grouped into the high trawl disturbance group. Comparisons made between low and high	Infauna and Epifauna	Bioturbation; Body shape; Egg development; Feeding mode; Larval Development; Living habitat; Longevity; Mobility; Sediment position; Size (length);	Relative trait modality biomasses

Table S2: Habitat weighting factor derived from geological susceptibility and recovery scores in [Grabwoski et al. 2014], indicating the percent reduction in structure and time for restoration due to fishing gear contact. Susceptibility (S) measures the percent reduction in a habitat feature's structure due to fishing gear contact, while Recovery (R) indicates the time needed for its functional value to be restored. Scores were assigned based on scientific literature and expert judgment. Geological scores for various sediment types and shear stress levels (L ≤ 0.194 N/m^2 and H >0.194 N/m^2) were considered. The sum of S and R for each habitat combination was normalized between 0 and 1 to determine the final weighting factor.

Energy	Substrate	Susceptibility	Recovery	Wf
L	Mud	3.4	1.6	0.416667
L	Sand	3.4	2.2	0.466667
L	Granule	2.7	3.7	0.533333
L	Cobble	3.7	3.2	0.575
L	Boulder	2.8	3.2	0.5
H	Mud	3.3	1.5	0.4
H	Sand	3.3	1.8	0.425
H	Granule	2.7	2	0.391667
H	Cobble	3.3	2.6	0.491667
H	Boulder	2.7	3.1	0.483333

Table S3: Number of samples and summary of each predictor (mean ± standard deviation) for the three surveys used for applying the vulnerability framework in the study area. Unit of measure: Depth (m), Seabed slope (°), Shear stress (N/m^2), Dissolved oxygen (µmol/l), Chlorophyll (mg/l), SAR (1/year). Sediments were classified according to the Wentworth classification.

Survey -	Year	Sample size	N mud	N sand	N granule-pebble	Depth	Slope	Shear Stress	Dissolved oxygen	Chlorophyll a	SAR
UNIPA MCM	2010-2013	105	62	33	10	185.13 ±156.06	3.68 ±3.38	0.001 ±0.001	203.23 ±9.15	0.128 ±0.048	1.26 ±2.36
ISPRA	2016-2020	57	14	40	3	56.18 ±9.88	0.84 ±0.58	0.026 ±0.037	213.96 ±6.06	0.168 ±0.036	3.38 ±4.63
UNIPA HARMONY	2019-2020	11		10	1	81.69 ±15.76	0.18 ±0.14	0.041 ±0.025	215.80 ±6.05	0.150 ±0.028	12.13 ±4.16

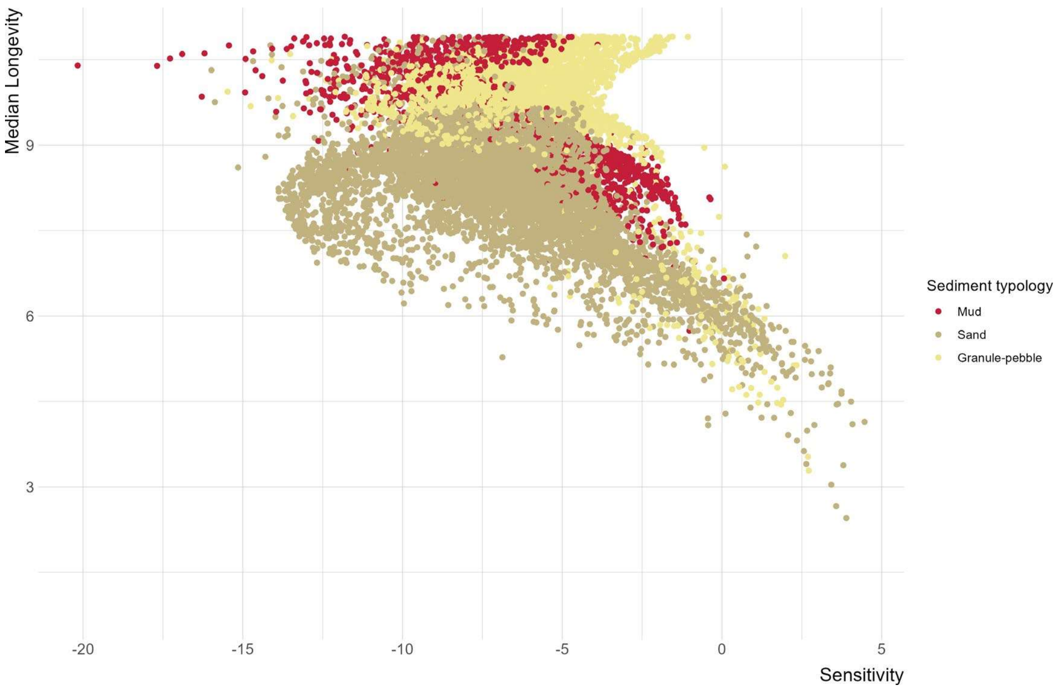


Figure S1: Scatterplot comparing sensitivity estimates obtained from the framework with median longevities derived from the PD approach, with points distinguished by different sediment typologies.

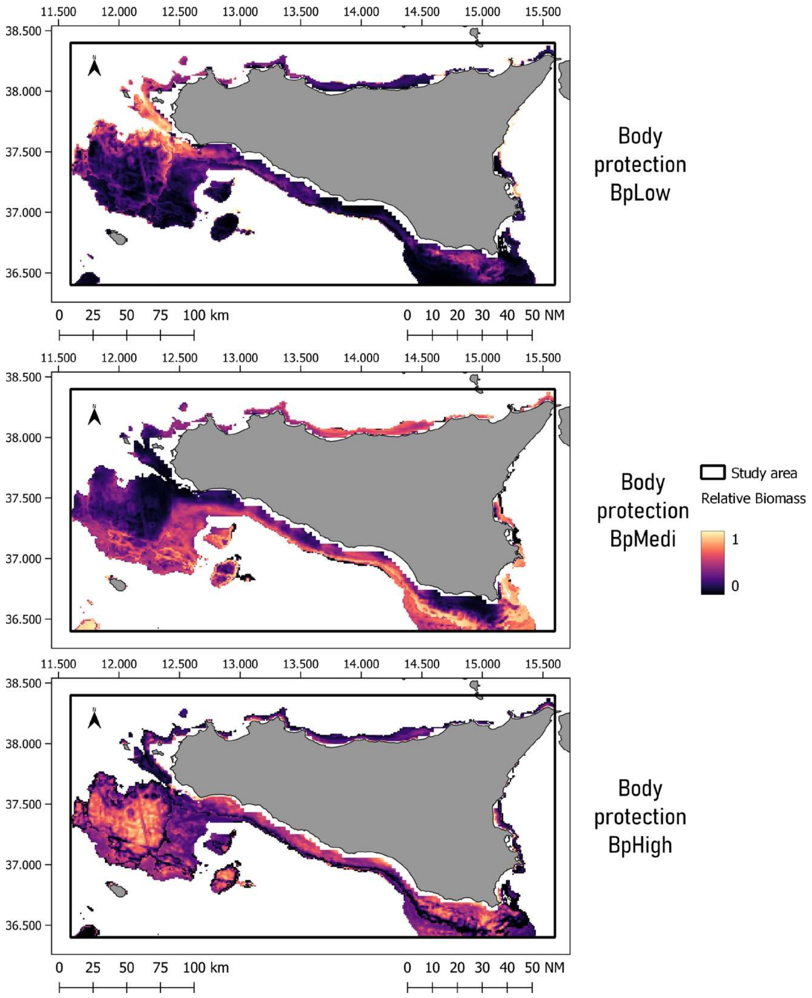


Figure S2: Maps of the untrawled distribution of the body protection modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

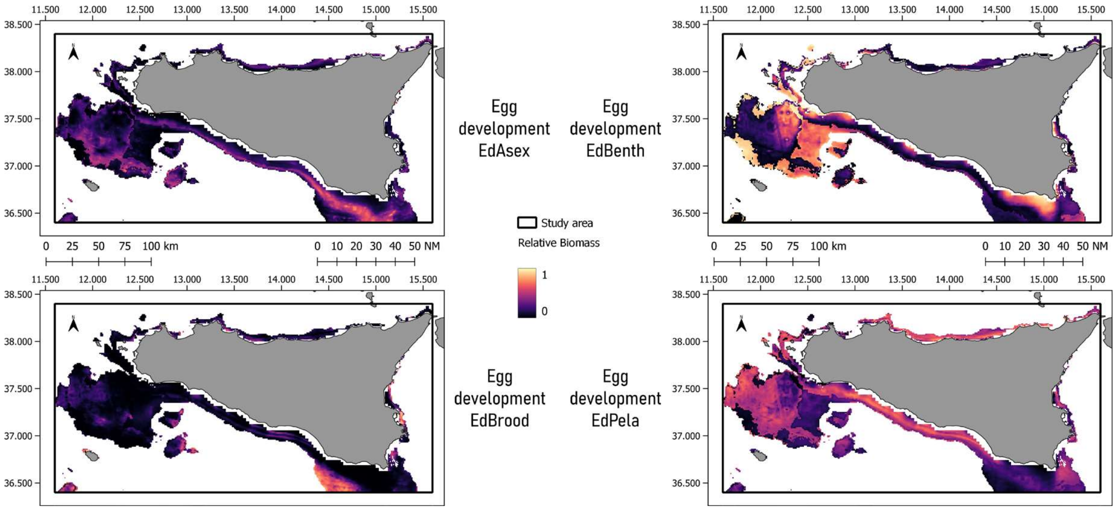


Figure S3: Maps of the untrawled distribution of the egg development modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

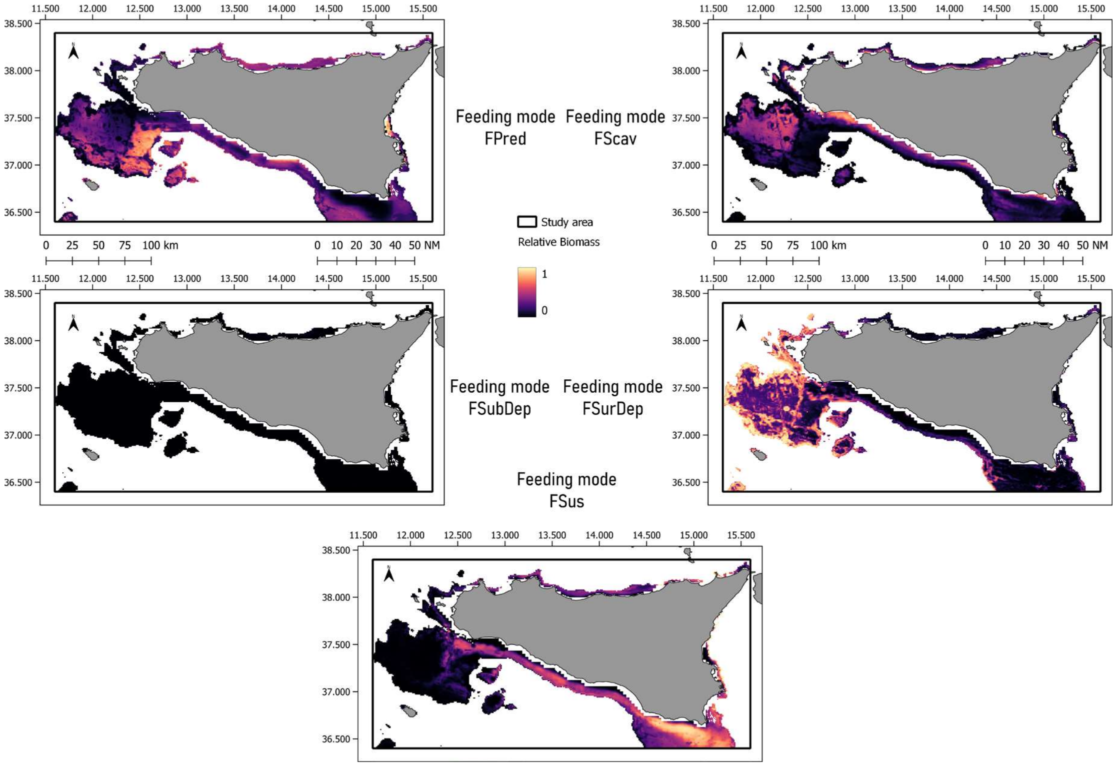


Figure S4: Maps of the untrawled distribution of the feeding mode modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

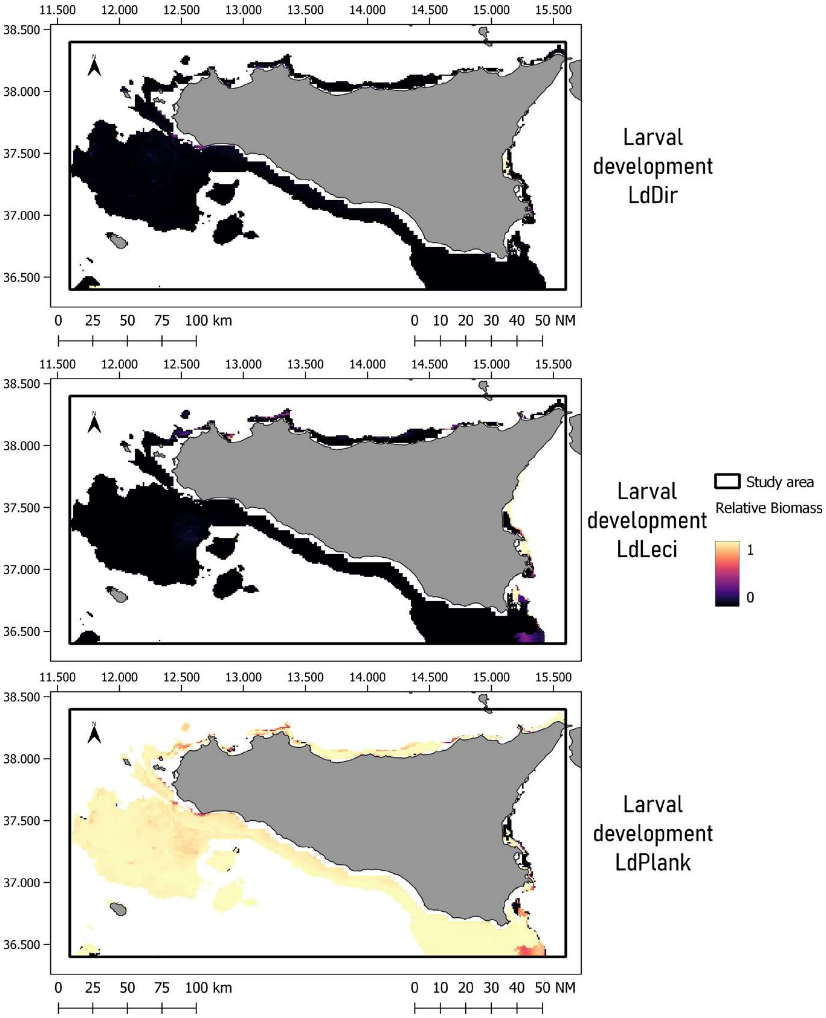


Figure S5: Maps of the untrawled distribution of the larval development modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

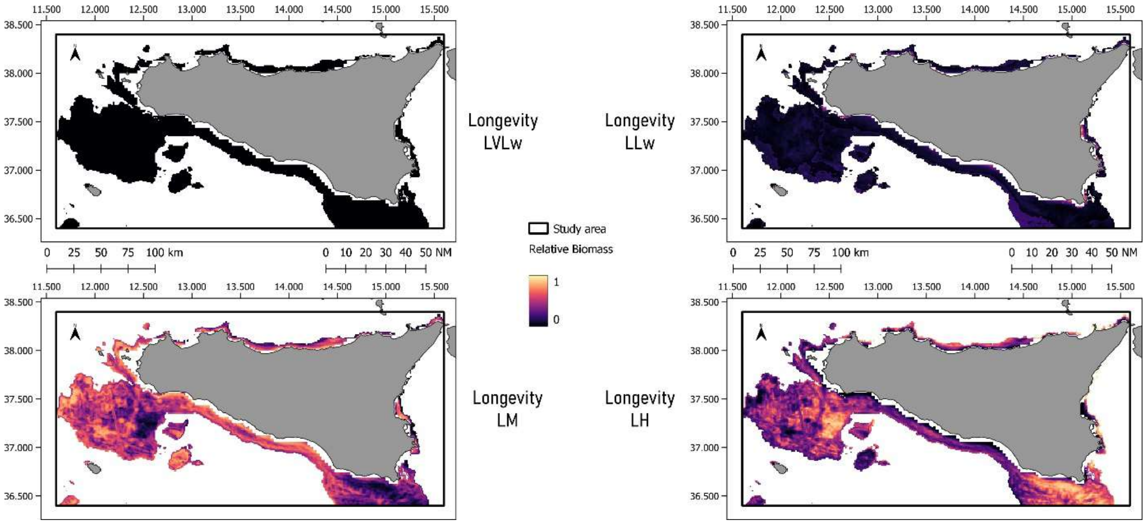


Figure S6: Maps of the untrawled distribution of the feeding mode modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

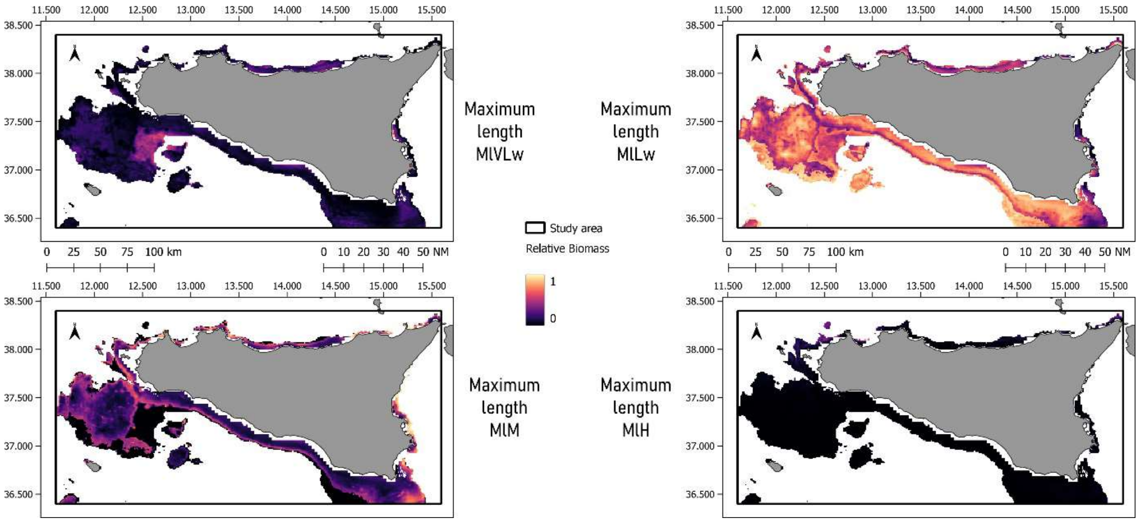


Figure S7: Maps of the untrawled distribution of the maximum length modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

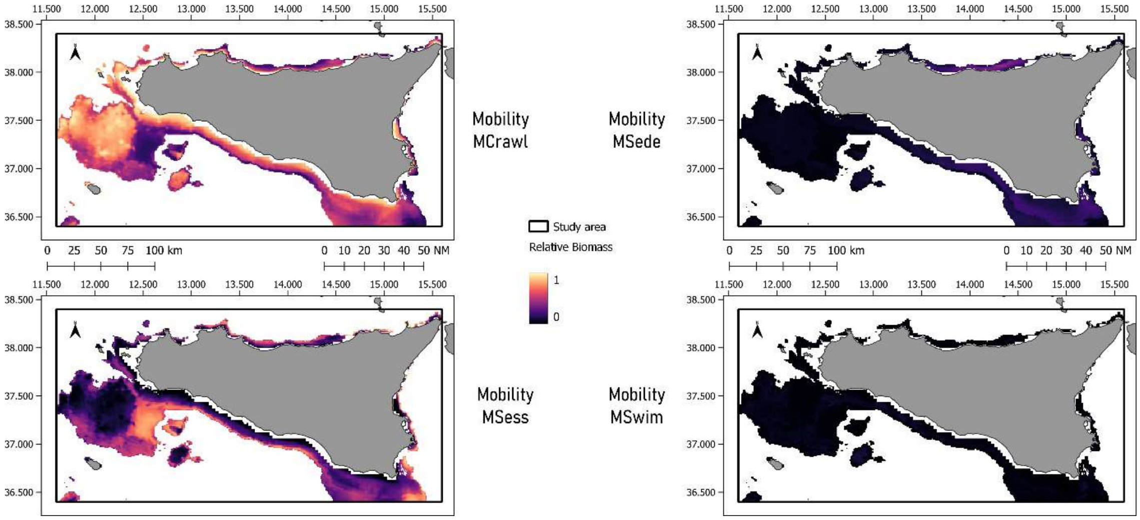


Figure S8: Maps of the untrawled distribution of the mobility modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

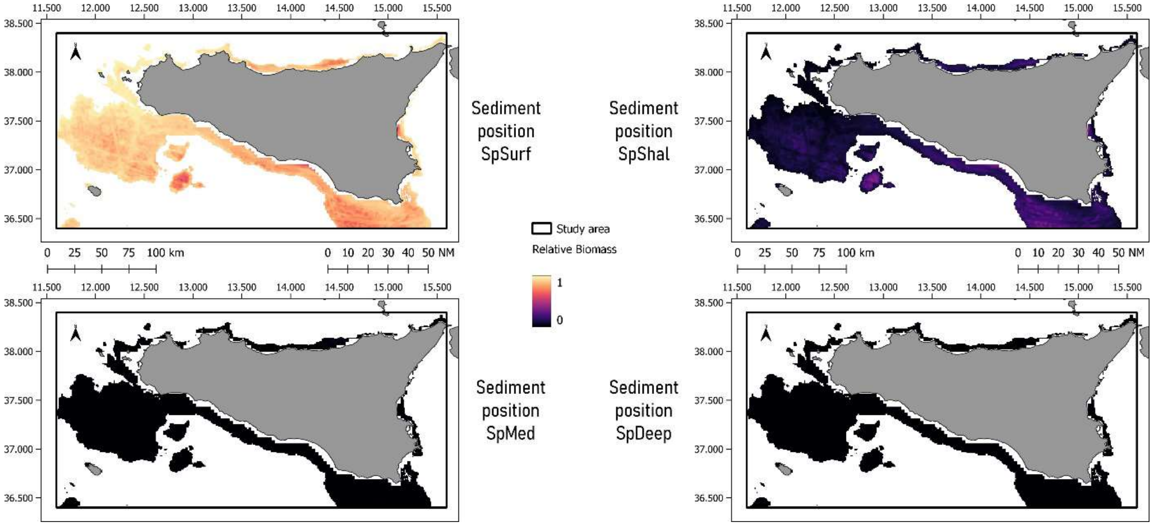


Figure S9: Maps of the untrawled distribution of the sediment position modalities' relative biomasses obtained from the delta GAM models setting SAR = 0.

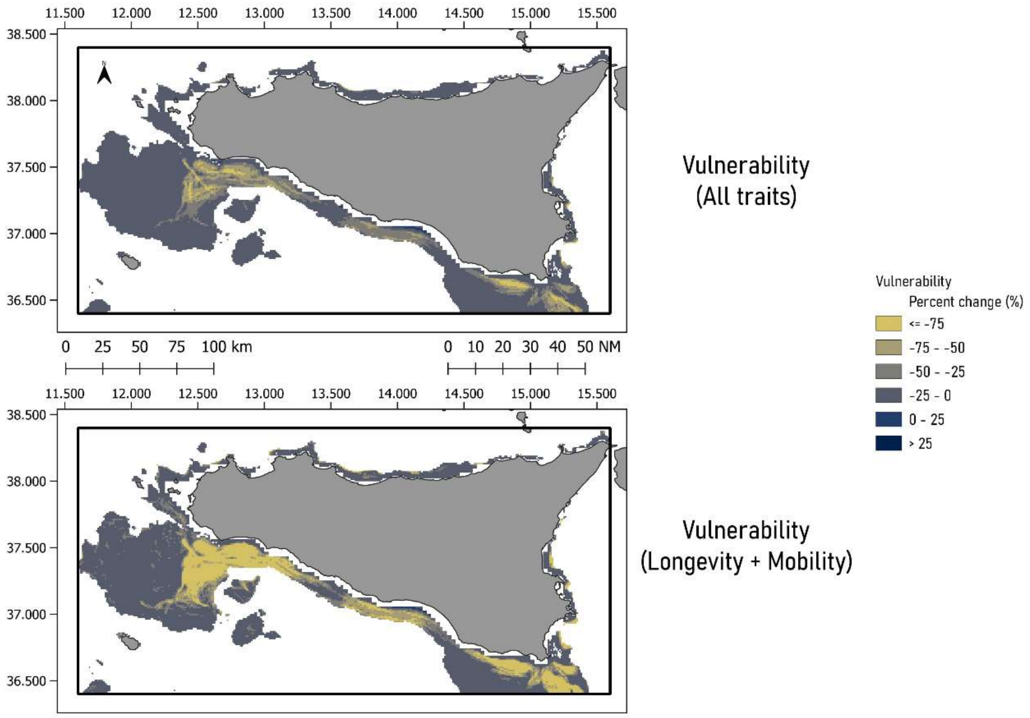


Figure S10: Comparison of the maps of vulnerability score distribution across the study area using all eight selected traits and only those traits exhibiting the highest deviation in sensitivity analysis regarding their contribution to vulnerability scores.

Supplementary Materials for

Chapter 5: Integration of assemblage indicators and measurement of otter door inclination to identify pattern of impact associated with trawling gear

Table S1: Performance statistics per number of clusters obtained after the application of DTW-PAM algorithm on the inertial time series of the otter doors (Gyroscope and Inclination across the three axes). Sil = Silhouette Index (to be maximized), SF = Score Function (to be maximized), CH = Calinski-Harabasz index (to be maximized), DB = Davies-Bouldin index (to be minimized) ,DBstar = Modified Davies-Bouldin index (to be minimized) ,D = Dunn index (to be maximized), COP = COP index (to be minimized)

Performance index	K = 2	K = 3	K = 4	K = 5	K = 6	K = 7
Sil	0.0675	-0.1321	-0.0929	-0.1224	-0.1537	-0.1309
SF	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
CH	2.4650	1.6227	1.4045	1.3623	1.0733	1.2177
DB	1.2904	1.2655	1.5544	1.4765	1.2588	1.0968
DBstar	1.2904	1.4982	1.5544	1.5222	1.2795	1.2167
D	0.4423	0.2914	0.2928	0.2717	0.2914	0.2717
COP	0.7087	0.6911	0.9068	0.6280	0.8118	0.5978

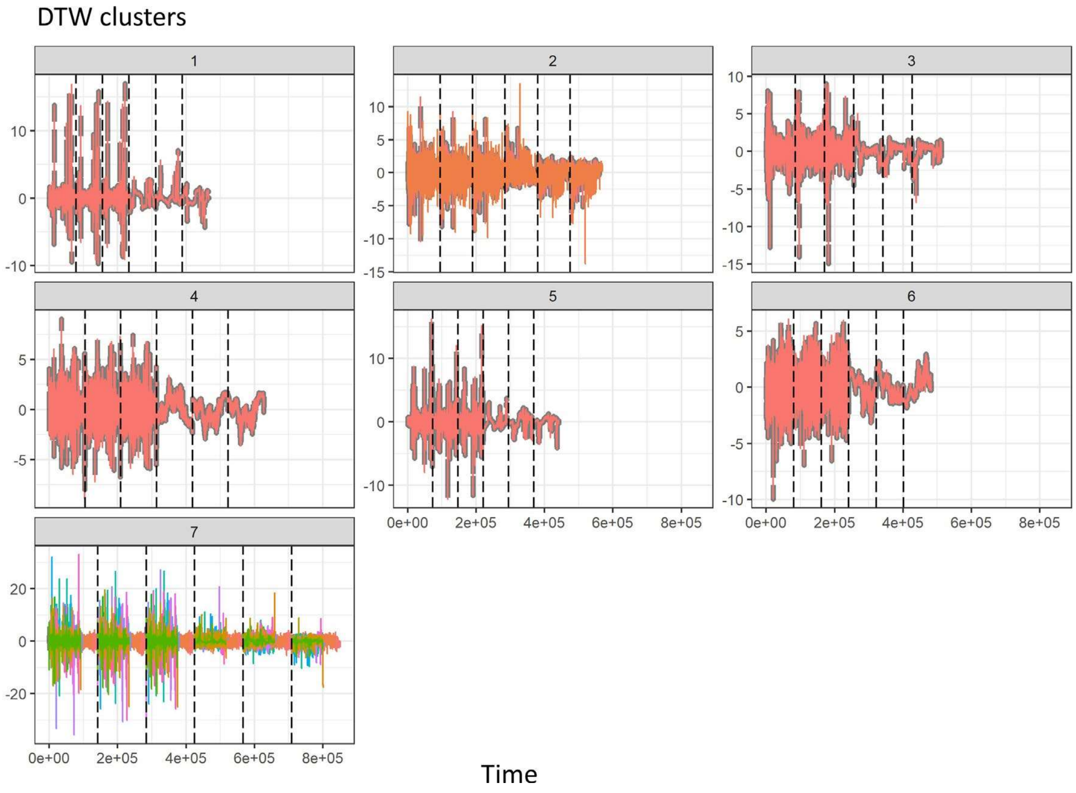


Figure S1: Results of the Dynamic Time Warping (DTW) cluster algorithm application. For each obtained cluster, the graph shows the multivariate time series of the trawls across the timestamps.

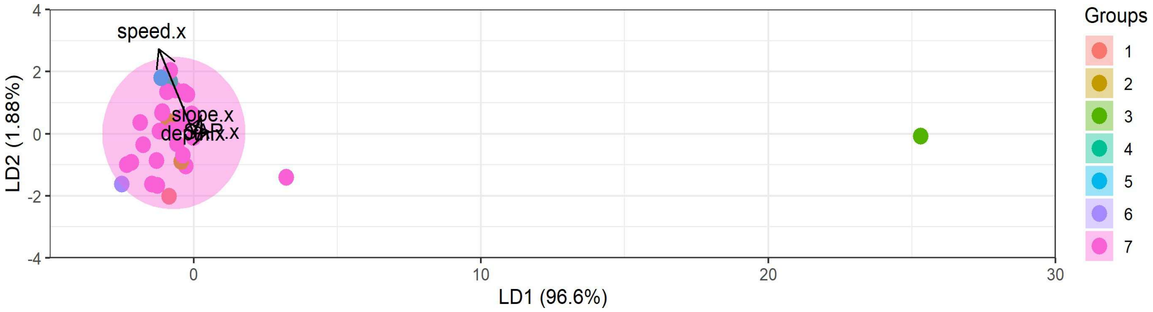


Figure S2: Linear Discriminant Analysis ordination plot with DTW clusters of the inertial response of the otter door during the samples. Colors represent the different clusters while arrows are the variables that explains the groups. The length of the arrow highlights the importance of the variable. In this case it can be noticed how all the different clusters are similar in investigated variable scores and it is vessel speed to drive a light separation of the clusters.

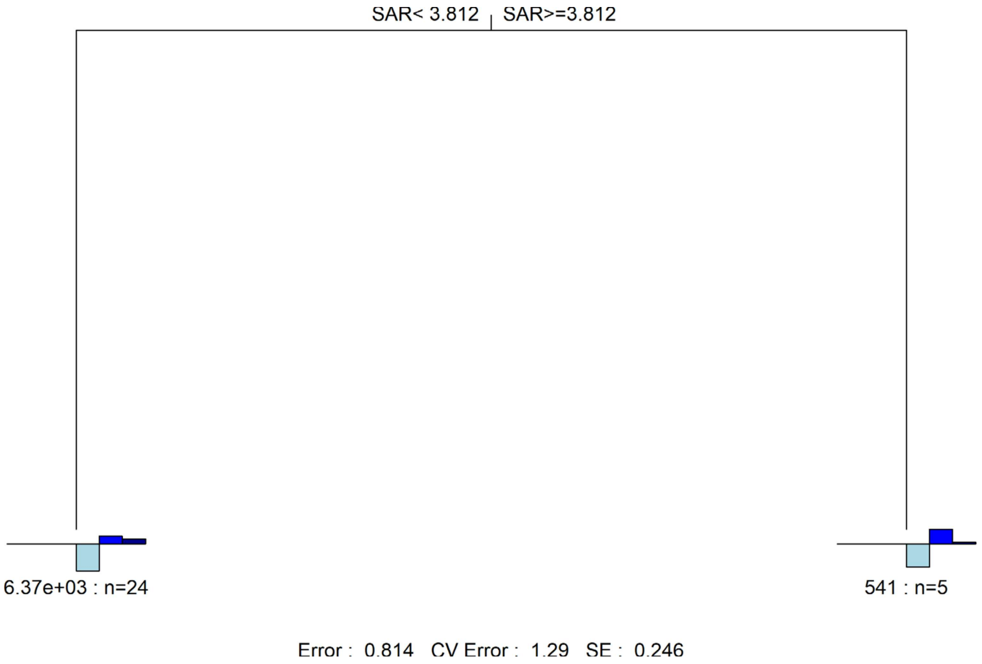


Figure S3: Multivariate Regression Tree (MRT) results defining inertial response of the doors, expressed by inclination angles and gyroscope data, of the sampled trawls constrained by the four investigated variables (sediment typology, depth, seabed slope, Swept Area Ratio (SAR) and vessel speed). RE = Residual error, CVRE = Cross-validated relative error, SE = standard error.

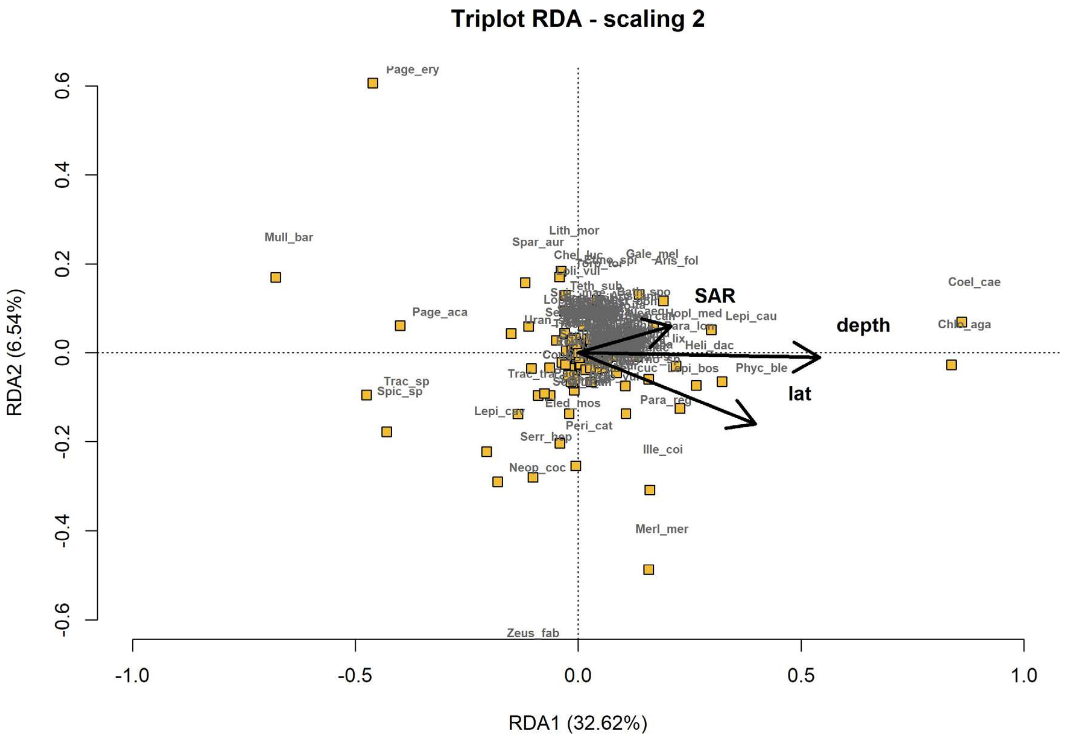


Figure S4: Redundancy analysis (RDA) ordination plot of the biomass composition of the assemblages caught by the trawl samples. The significant variables selected after the stepwise selection are indicated in black. Species names codes could be found in Supplementary table.

Table S2: Average Community Weighted Means (CWM) scores for each modality of the eight biological traits used for assess the functional diversity and sensitivity of the benthic assemblage in the samples.

Trait	Modality	Average %
Longevity	<1 years	0.00
Longevity	1-3 years	6.25
Longevity	3-10 years	59.49
Longevity	>10 years	34.17
Maximum length	0-3 cm	7.91
Maximum length	3-10 cm	26.28
Maximum length	10-50 cm	50.09
Maximum length	>50 cm	15.62
Sediment position	Surface	90.60
Sediment position	0-5 cm	7.95
Sediment position	5-15 cm	0.89
Sediment position	>15 cm	0.47
Mobility	Sessile	24.83
Mobility	Sedentary	6.68
Mobility	Crawler	62.72
Mobility	Swimmer	5.78
Feeding behavior	Surface deposit feeder	36.40
Feeding behavior	Subsurface deposit feeder	0.00
Feeding behavior	Predator	18.58
Feeding behavior	Scavenger	20.13
Feeding behavior	Suspension feeder	24.89
Body protection	Low	39.90
Body protection	Medium	32.52
Body protection	High	27.57
Egg development	Asexual	3.30
Egg development	Benthic eggs	30.24
Egg development	Pelagic eggs	55.90
Egg development	Brooded eggs	10.46
Larval development	Direct	0.37
Larval development	Lecithotrophic	1.74
Larval development	Planktotrophic	95.40

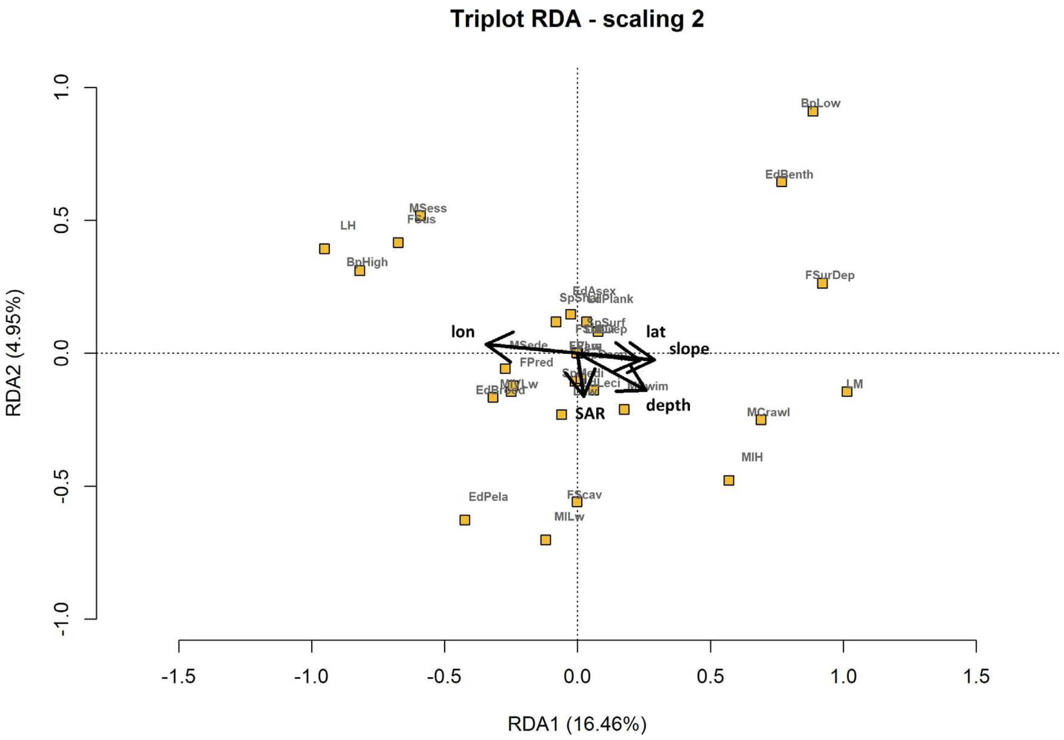


Figure S5: Redundancy analysis (RDA) ordination plot of the Community Weighted Mean (CWM) composition of the benthic assemblages caught by the trawl samples. Trait modalities code can be found in Supplementary Table.