Ecological impacts of offshore structures on North Sea biodiversity and food webs

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This thesis is dedicated to
my dear parents Guozhu and Lifang
and beloved wife Shiyu.

"I seem to have been only like a boy playing on the seashore,
and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary,
whilst the great ocean of truth lay all undiscovered before me."

Isaac Newton

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Contribution statement

I hereby declare that this PhD thesis, the chapters and associated publications is my own work and has not been submitted for another degree, either at University of Essex or elsewhere. My supervisory team (Drs Eoin J O'Gorman, Thomas C. Cameron, Murray S.A. Thompson and Elena Couce) provided guidance on conceptualisation, methodology and editing thesis and manuscript drafts. My research collaborators (Drs Natalie Hicks, Corinne Whitby, Clement Garcia, Christopher P. Lynam, Gareth E. Thomas) also provided mentorship and contributions with this thesis, including data compilation, data analysis, organising fieldwork and valuable feedback on drafts.

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Abstract

Offshore structures including oil and gas (O&G) platforms and offshore wind turbines induce spatially and temporally extensive anthropogenic changes that profoundly influence the North Sea ecosystem. However, there are currently inadequate understandings of the biodiversity and food webs associated with offshore structures and their likely responses to future changes. This limits the development of ecologically sound management policies to address emerging issues such as decommissioning and the expansion of offshore renewables. This thesis utilises a series of approaches to assess ecological impacts of offshore structures on the North Sea biodiversity and food web structure. First, the links between O&G-associated sediment contamination and benthic invertebrate biodiversity and food web structures are assessed in a before-after control-impact (BACI) design, highlighting loss of larger individuals, shorter food chains and simpler food webs with more dietary generalists in the high contamination areas. Second, three O&G decommissioning scenarios are analysed to assess benthic ecological recovery, showing a non-linear trajectory from reduced diversity and food web complexity in the short term to a greater density of trophic interaction and more intermediate species in the long term. Third, the effects of both O&G platforms and wind turbines on marine fish biodiversity and food web responses are examined at the North Sea scale using Bayesian INLA models, revealing that wind turbines benefit total fish biomass. The study shows the biggest piscivores are negatively affected whilst small planktivores benefit. Cumulative effects of both structures in the past three decades were estimated to inform cumulative changes at each fish response. This thesis synthesises the major contributions of new insights in the context of wider application and informing future decision-making process and provides future research directions for biodiversity and food web studies in the context of offshore structures.

CHAPTER ONE

Integrating biodiversity and food web perspective to inform offshore structure management

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This chapter is a general review of the literature on the global and regional development of offshore O&G exploitation and wind farms as well as marine biodiversity and food web patterns associated with the context of offshore energy structures.

1.1. *Overview of offshore structures*

1.1.1 *Expansion of offshore structures in the global oceans*

Anthropogenic activities have profoundly reshaped global seascapes through marine infrastructure construction (Bugnot et al., 2021). The increasing needs of obtaining energy drive the rapid sprawl of offshore energy structures, including oil and gas (O&G) platforms and renewable wind turbines (Figure 1). Industrial exploitation of offshore O&G resources has been developed since the 1960s,

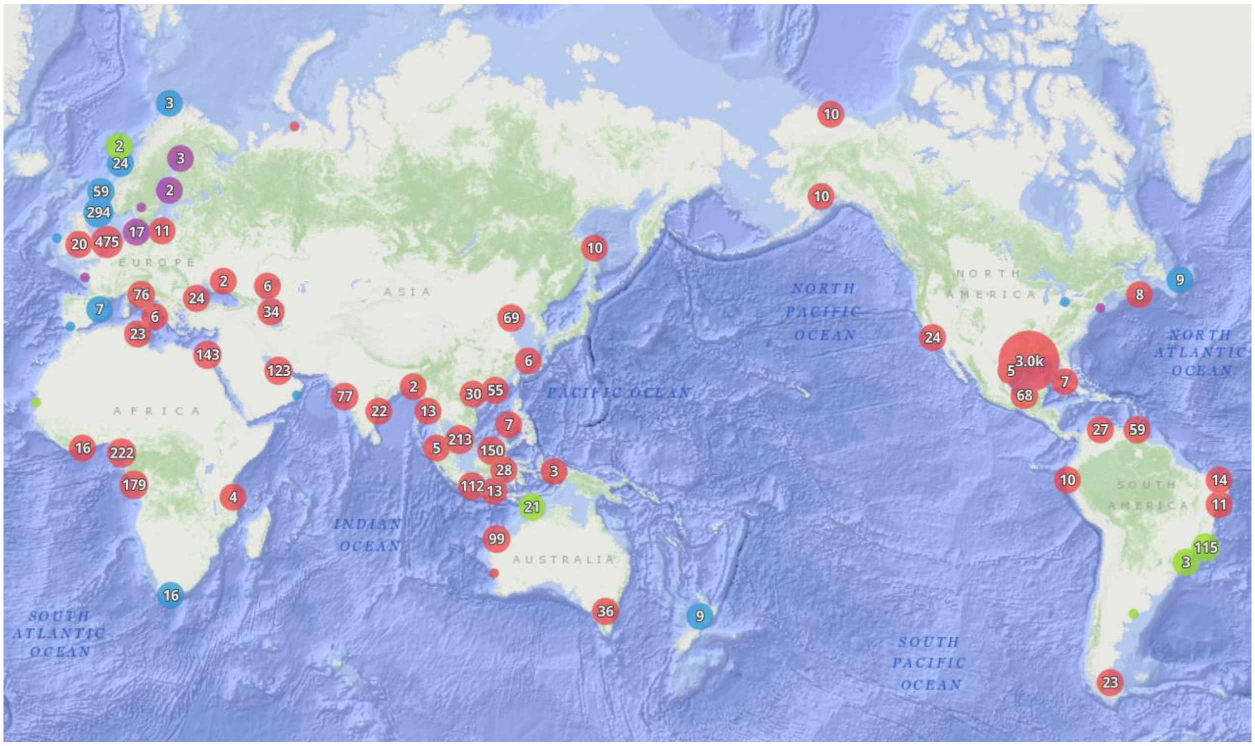

Figure 1: Map of offshore energy structure from 1940 to 2020. Red circles indicate fixed platforms; Blue circles indicate subsea structures; Green circles indicate floaters; Purple circles indicate wind turbines. (Source: https://arcg.is/15K9ez0).

leading to over 12,000 offshore platforms and a 180,000 km^2 network of subsea pipelines and associated infrastructure (McLean et al., 2022). Continued O&G offshore expansion is predicted in the coming years given the relatively stable oil production and increased natural gas output

(Gourvenec, Sturt, Reid, & Trigos, 2022). On the other hand, the emerging establishment of offshore wind turbines follows the rising awareness of reducing carbon emission, mitigating impacts of climate change and limiting global warming to below 2°C above pre-industrial levels to meet the target set in the Paris agreement. It highlights a paradigm shift from fossil fuels to sustainable clean energy and incentivises an massive global deployment of offshore renewable infrastructure (Ouro et al., 2024). As of 2019, over 6,900 offshore wind turbines were constructed globally (Zhang, Tian, Sengupta, Zhang, & Si, 2021). To satisfy a global target of 2,000 GW by 2050, it is estimated that more than 5,000 new offshore wind turbines are required to be installed each year to meet an annual increase of 70 – 90 GW, which will cover over 500,000 km^2 of the global oceans (Putuhena, White, Gourvenec, & Sturt, 2023).

1.1.2 The development of offshore energy structures in the North Sea

The North Sea has pioneered the industrialisation of offshore energy structures. O&G exploitation has become one of the most enduring and spatially extensive anthropogenic stressors over decades since the first O&G commissioning in the 1960s (Manson, 2006). As of 2023, there was a total of 590 O&G fixed and floating platforms constructed, most of which were located in the jurisdictions of the United Kingdom, the Netherlands, Norway, Denmark and Germany (Martins, Carter, Rouse, & Russell, 2023). With the maturation of hydrocarbon reserves in the late 1990s, O&G production started to decline, resulting in a saturation of O&G installations. The decadal presence of these O&G installations will also require decommission in the coming decades when approaching the end of their operational life cycle or becoming economically unviable (Fowler et al., 2020). In contrast with relatively stable trends of O&G development, the first commercial offshore wind farm emerged in Denmark in 1999 and witnessed an exponential growth to over 4,000 turbines in 2023 (Barthelmie, Courtney, Højstrup, & Sanderhoff, 1994). The spatial distribution of offshore wind turbines is mostly in the southern coastal waters of the North Sea, including the United Kingdom, Belgium, the Netherlands, Germany and Denmark (Wright et al., 2020). With the vision of over 350 GW by 2050 in the EU energy and climate goals of EU countries, it is foreseeable that offshore renewable wind will become a main pillar of offshore construction in the North Sea (Putuhena et al., 2023).

1.2. Management challenges for offshore structures

The proliferation of offshore structures has become a major issue in the global oceans, yet the inadequate knowledge of their ecological impacts in the marine environment hinders the best ecological practices in their robust evidence-based management. The main challenges can be summarised in the following aspects: 1) limited data availability covering the structure and adjacent environment before, during and after the commencement of production; 2) increasing needs of decommissioning with limited understanding of best practices and associated short- and long-term environmental and ecological consequences; and 3) lack of adequate quantitative assessments accounting for future development of offshore structures to understand how the large magnitude of expansion or decommissioning might affect marine ecosystems.

1.2.1 Data limitations

To establish the causation between observed environmental and ecological patterns and introduced offshore structures, a “reference” is needed for experimental design to set as the baseline of relative changes. However, it is difficult to identify such ecological baselines, especially for O&G platforms present over decades, given that the baseline in the surrounding marine ecosystem is shifting with respect to other anthropogenic stressors (e.g., trawling; shipping) and climate change (C. C. Murray, Agbayani, & Ban, 2015). To address it, the current studies either adopted a Before-

After-Control-Impact (BACI) design (Wilber, Brown, Griffin, DeCelles, & Carey, 2022) or canonical analysis (Henry, Harries, Kingston, & Roberts, 2017). BACI design used two sets of data representing the status quo of background and impact conditions, respectively. With background variability accounted in the background group, differences between impact data and background data capture the true effects of offshore structures. Canonical analysis, including variance partitioning, provides a useful tool to quantify individual contributions of predictors on the response variable (Lai, Zou, Zhang, & Peres-Neto, 2022). It helps disentangle the effects of different explanatory variables and account for background environmental variability (Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004).

However, there are many factors that restrict the data acquisition for offshore structure appraisals. First, research cruises or fisheries surveys near offshore structures generally need permission to have access, considering the safety and security concerns (Fortune & Paterson, 2018). The owners of the structure often need to conduct the environmental impact assessment (EIA) and submit it to the relevant authority (e.g., North Sea Transition Authority) to obtain consent for future development programmes (OPRED, 2018). However, the raw data used for making these assessment reports are often inaccessible to other users because of expensive access costs, data being archived in an inappropriate format, lack of standardisation and quality control, or missing metadata (F. Murray et al., 2018). In addition, data collection takes time and requires large amounts of human and financial resources. There are also no economic incentives for industries to publish acquired data to the public without regulatory and mandatory requirements. This potentially causes duplicated efforts when policy-makers or research studies require a certain amount of data to arrive at the best management decisions (i.e., decommissioning scenarios) (Cordes et al., 2016).

1.2.2 Decommissioning dilemma

A substantial number of existing O&G platforms and many offshore wind turbines will have to be decommissioned in the coming decades. However, it remains controversial which decommissioning approaches can achieve minimal negative impacts on marine ecosystem as there are limited studies and available data examining short- and long-term trajectories post-decommissioning across a variety of alternative scenarios. The current policy preference is complete removal of aging infrastructure, which was adopted in the European nations under the Oslo and Paris Commission's Decision 98/3 in the OSPAR maritime areas (Fowler et al., 2020). The OSPAR Decision (Ministerial Meeting of the OSPAR Commission, 1998) implements a precautionary principle on the disposal of disused offshore structures, prefers the reuse, recycling or final disposal on land for decommissioning, and prohibits the dumping and leaving disused offshore structures wholly or partially in place within the OSPAR maritime area. Most offshore structures are required to be completely removed with few derogations. This policy was guided by a "clean seabed" ideology with the intention of protecting the marine environment by removing redundant resources to minimise negative impacts. However, there were limited considerations in terms of the ecology of decommissioning offshore structures, which include the assessment of ecosystem functioning and service the structures are providing or could provide by repurposing into artificial reefs, the spatial extent and persistence of disturbances associated with decommissioning processes, and environmental and ecological consequences after decommissioning.

It is estimated that over £24bn will be invested on decommissioning costs over the next 10 years (2023 to 2032) (North Sea Transition Authority, 2024b), which constitutes a large expenditure for industries with manpower and materials. Recent studies suggest that decommissioning options may have wider impacts on marine ecosystems, calling for comprehensive assessments on the benefits, risks and trade-offs between decommissioning options and an ecosystem-based approach to account for ecosystem services and functions (Sommer et al., 2019; S. M. Watson et al., 2023). These alternative decommissioning options include 1) partial removal, where the foundation is left in situ and the top sections are removed; 2) topping, where the top section is removed and left in situ next to the foundation; 3) toppling, where the whole structure is toppled in situ; and 4) partial removal and relocating the top section in another designated reefing area (Fowler et al., 2020). More studies are required to comparatively analyse the ecological and environmental outcomes across different options. For example, Spielmann, Dannheim, Brey, and Coolen (2023) evaluated complete and partial decommissioning of three offshore wind turbines and found that partial removal via leaving scour protection layers in situ could preserve a substantial percentage of macrofauna. As complete removal might not always be the best option, more post-decommissioning monitoring surveys are required to determine the chosen decommissioning options on a case-by-case basis.

1.2.3 Assessments of cumulative impacts and future projections

Cumulative effects are defined as the additive, interactive, and synergistic effects of anthropogenic activities that accumulate over time and space to cause environmental changes (Judd, Backhaus, & Goodsir, 2015). However, inadequate assessments of cumulative effects of offshore energy structure development result in uncertainties of associated environmental and ecological consequences, creating obstacles for the upscaling of offshore energy development and improving current regulatory and consenting procedures (Willsteed, Jude, Gill, & Birchenough, 2018). Assessing cumulative effects is vital for conservation policy as it drives pressing environmental challenges including 1) ecosystem resilience and tipping points; to understand whether localised effects observed in individual offshore structures are upscaled to a wider ecosystem context, resulting in biodiversity loss and degraded marine food webs (Chen et al., 2024); 2) habitat modifications and species redistribution due to behaviour changes of species interacting with novel abiotic and biotic conditions, habitat removal and destruction and introduced disturbances and risks (Maxwell et al., 2022; Van Elden, Meeuwig, Hobbs, & Hemmi, 2019); and 3) spatial and temporal heterogeneity in the development of offshore structures; the characteristics of spatial aggregations (i.e., high density of O&G installations within O&G reserves and intense construction of offshore wind turbines in coastal waters), historical magnitude and persistence of discharged pollutants and estimated rates of biodegradation, and temporal shifts from O&G platforms to offshore wind turbines in recent years require comprehensive assessments.

It is also important to integrate future scenarios of offshore structures (i.e., exponential increase of offshore wind turbines; decommissioning of aging O&G installations) into considerations in terms of predicting trends of ecosystem impacts. This is an interdisciplinary challenge because the available space open for offshore energy expansion is limited compared to the policy goals (Devine-Wright, 2011) and such marine spatial use is often fragmented and sectorial (Gusatu, Yamu, Zuidema, & Faaij, 2020). The need to understand whether the deployment of offshore structures is compatible with biodiversity hotpot areas (e.g., marine protected areas) (Lloret et al., 2022), how the integrated planning can be realised to balance trade-offs and achieve multi-uses with other marine users (i.e., fisheries) (Trifonova et al., 2025), and where suitable locations are to promote ecological benefits for wildlife and fisheries (Dorrell et al., 2022) relies on advanced understandings of ecological mechanisms associated with offshore energy structures.

1.3 Offshore structures as an emerging anthropogenic stressor

Depending on the current life cycle phase and associated ecological assemblages, offshore structure could have both negative and positive effects on marine ecosystems (Figure 2). On the negative side, offshore marine artificial structures (MAS) have “stepping stone” effects that facilitate the dispersal and establishment of non-indigenous species, which potentially have adverse impacts on native species and ecosystem functions (McLean et al., 2022; Schaefer et al., 2024). In addition, the construction and decommissioning of offshore structures introduce physical disturbance to nearby seabed habitats, modifying habitats for benthos and demersal fishes (Causon & Gill, 2018; Wilber et al., 2022). Besides that, stressors associated with certain offshore energy structures further result in changes in species behaviours, distribution and community structure. For example, underwater noises and electromagnetic fields generated from the operation of offshore wind turbines can cause physical injury and communication impediment on fish (Gill, Bartlett, & Thomsen, 2012). The discharges of O&G drilling muds and produced waters contain contamination such as hydrocarbons and heavy metals, negatively affecting biodiversity and the abundance of benthic invertebrates (Ellis, Fraser, & Russell, 2012; Olsgard & Gray, 1995).

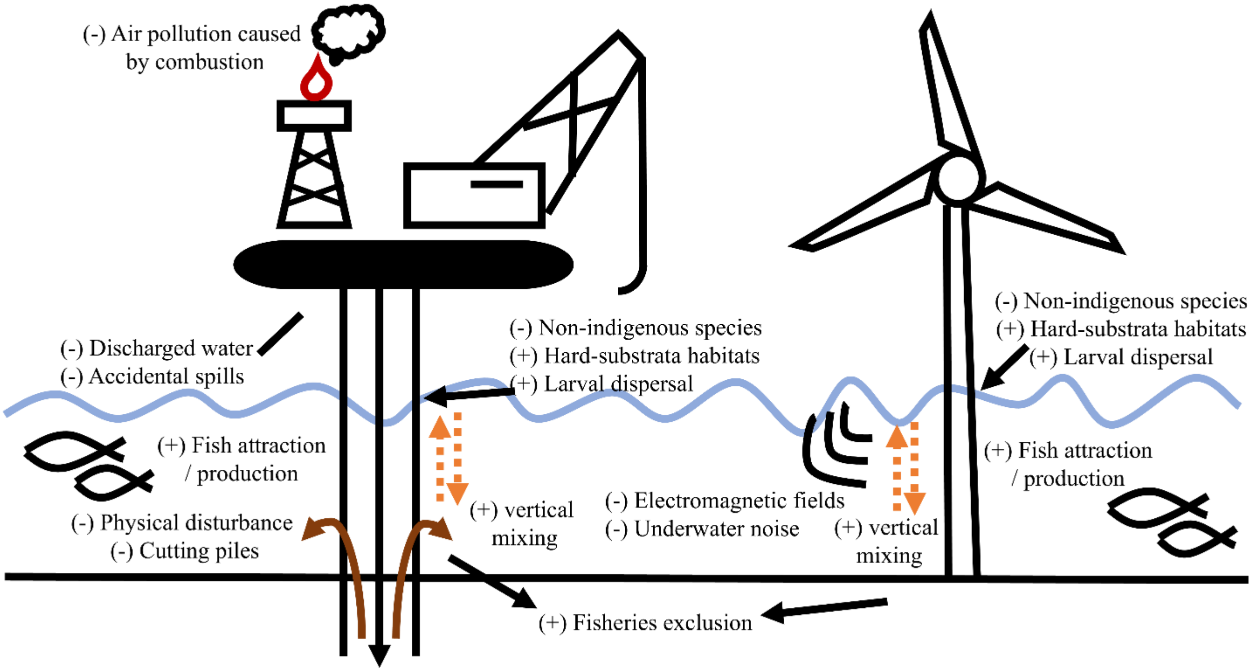

Figure 2: The positive (+) and negative (-) effects of O&G platforms and offshore wind turbines on the marine ecosystem.

On the positive side, the introduction of MAS establishes novel habitats to marine ecosystems, especially in environments with limited hard substrata and natural reefs (i.e., the North Sea) (Van Elden et al., 2019). The new hard substrata in the offshore environment enable the colonisation, recruitment and succession of sessile invertebrates, which becomes a biodiversity hotspot in a localised context (J. W. Coolen, Van Der Weide, et al., 2020). There are knock-on effects on higher trophic levels, as colonised invertebrates improve food availability of mobile marine fish and provide faeces to nourish sediment with organic materials (Buyse et al., 2023; D. A. Coates, Deschutter, Vincx, & Vanaverbeke, 2014), reshaping local ecosystems with higher secondary production and biodiversity (Claisse et al., 2014). These benefits provide an important scientific basis for “rig-to-reef” policies to maintain MAS ecosystem functions and services after repurposing them into permanent reefs (Macreadie, Fowler, & Booth, 2011).

1.3.1 Artificial reef effects

Artificial reefs refer to man-made structures being intentionally placed in the marine environment to enhance aquatic resources and biodiversity through mimicking natural reef habitats (Bohnsack & Sutherland, 1985). The artificial reef effect is commonly associated with biological changes at the submerged areas in the context of offshore energy structures, involving benthic invertebrates, demersal and benthopelagic fishes and marine mammals (J. Dannheim et al., 2018). The artificial reef effect interacts with both larval and adult life stages of marine individuals. When it comes to larval stages, the effect is also known as "stepping stone" or ocean sprawl effects, which indicates offshore proliferations of MAS facilitates the geographic dispersal of invertebrate and fish larvae (Henry et al., 2018).

The artificial reef effect is an important impact pathway explaining the ecosystem functioning and services associated with offshore energy structures. The most prominent feature is that introduced MAS provide novel habitats to allow for initial colonisation of hard substrata communities, which lays a basis for subsequent habitat-reforming and ecological interaction processes (Schroeter, Reed, & Raimondi, 2015). The three-dimensional complex structure creates more space for marine organisms to settle in and utilise as refuges. In environments lacking natural reefs, offshore energy structures could potentially fill up the missing niche by acting as a form of intertidal zone considering the vertical structure extending from the seabed throughout the full water column above the water surface. The epifaunal communities often exhibit distinct vertical zonation, characterised different species assemblages colonising in the splash zone, high and low intertidal zones, and shallow and deep subtidal zones (De Mesel, Kerckhof, Norro, Rumes, & Degraer, 2015). For example, barnacles and mussels tend to dominate near the water surface, while anemones and filter feeding amphipods usually occupy the deeper subtidal zone (Degraer et al., 2020). The vertical zonation pattern could be driven by the resilience and sensitivity of different species to extreme environmental changes (i.e., temperature and desiccation) (Foster, 1971) and resource differentiation among co-existing epifaunal communities in reflection of partitioned trophic niches (N. Mavraki, Degraer, Moens, & Vanaverbeke, 2020). In addition to spatial patterns, the succession of sessile benthos experiences an initial colonisation stage with a few species, shifting into a more diverse and abundant intermediate phase and then reaching a stable phase with advantaged species dominating the areas of hard substrata (J. W. Coolen, Van Der Weide, et al., 2020)

The increasing number of MAS across a wider spatial extent indicates an increased likelihood for marine larvae interacting with and settling on these infrastructures. For pelagic dispersal, particle tracking is a commonly used method in biophysical models to simulate larval dispersal processes using ocean hydrodynamic conditions (Swearer, Treml, & Shima, 2019). The presence of offshore energy structures affects seascape connectivity via dynamic flow regimes (i.e., wave and current) (Li, Xiao, Wang, Peyrard, & Gonçalves, 2023) and larval behaviour modifications (Leis, 2020; Simpson, Radford, Tickle, Meekan, & Jeffs, 2011). The underlying mechanisms of MAS-induced larval behaviours remain unclear, leading to the challenge of parameterising behavioural inputs into dispersal modelling to accurately quantify the impacts of offshore energy structures on ecological connectivity (James, Polton, Mayorga-Adame, Howell, & Knights, 2023). More in-depth research is required to study distinct biological assemblages in terms of their dispersal ability, migration patterns, ocean hydrodynamics, and time to metamorphosis (Treml, Ford, Black, & Swearer, 2015). For physical connectivity, the proliferation of MAS unintentionally establishes ecological corridors for the dispersal of indigenous and non-indigenous species extending beyond their natural range across large spatial scales. For example, coral species that do not have a pelagic dispersal ability can spread across the North Sea by taking advantages of the highly inter-connected

O&G pipeline network (Henry et al., 2018). Non-indigenous species including the Pacific oyster (*Crassostrea gigas*) and marine splash midge (*Telmatogeton japonicus*) were found to colonise the offshore structures in the southern North Sea (De Mesel et al., 2015). The settlement of these species on offshore energy structures will further contribute to population range extensions as they become new source populations in these patchy offshore habitats.

Offshore structures are often known as non-designated (de facto) marine protected areas (MPAs), given the exclusion of fishing activities around the structure. The legal statutes including the Offshore Installations (Safety Zones) Order issued under the Petroleum Act 1987 in the UK establishes a radius of 500 m safety zone around each offshore installation. The redistribution of fishing efforts around the structure reduces the anthropogenic disturbance on reef habitats, allowing for both epifaunal and fish species to thrive (Ashley, Mangi, & Rodwell, 2014; J. W. P. Coolen et al., 2022; Love et al., 2006).

1.3.2 Attraction-production hypothesis

The presence of artificial reefs usually attracts high density of fish, supporting high catchability and prolonged residence period (Bohnsack, Ecklund, & Szmant, 1997; Bohnsack & Sutherland, 1985). However, the underlying ecological mechanism shaping the fish aggregation near the MAS remains unclear. The attraction-production hypothesis was therefore established to posit a broad continuum balancing two alternative ecological mechanisms: attraction and production (Layman & Allgeier, 2020). The attraction hypothesis considers that fish in the surrounding environment are drawn towards the artificial reefs as a consequence of behavioural changes or habitat preferences, but without any overall increase in regional production (Bohnsack, 1989; Brickhill, Lee, & Connolly, 2005). In contrast, the production hypothesis proposes that fish populations benefit by settling in artificial reefs with additional habitats and more feeding opportunities, which ultimately lead to net gains in fish secondary production and biomass across the wider region (J. T. Reubens, Degraer, & Vincx, 2011). Whilst either extreme of this hypothesis oversimplifies the ecological processes in a real world context, both hypotheses potentially coexist along the intervening continuum. For example, fish species with thigmotactic tendencies prefer MAS over natural habitats and benefit from consuming colonised epifaunal communities and sheltering from exploitation and predators, which increases survival rate and individual growth (Brickhill et al., 2005).

Understanding where artificial reefs fall within the continuum of the attraction-production hypothesis is vital because it concerns the performance of using artificial reefs as a conservation approach to mitigate habitat degradation and fish stock rebuilding (Komyakova, Chamberlain, Jones, & Swearer, 2019; Love et al., 2006). For the attraction hypothesis, the introduction of artificial reefs results in fish population redistribution while their total abundance in the area remains unchanged. The aggregation of fish assemblages to a limited space could potentially create suboptimal habitat quality, increase risks of local extinction, reduce ecosystem resilience, and other adverse effects on vulnerable species with limited adaptive potential (i.e., low learning capacity, little behavioural adaptations, low dispersal potential, small populations and low fecundity) (Swearer et al., 2021). For the production hypothesis, net benefits from artificial reefs increase carrying capacity of local ecosystems with additional habitats for spawning, feeding, and sheltering, resulting in a greater number of juveniles developing into spawning adults (Brickhill et al., 2005). However, the performances of artificial reefs in relation to natural reefs can vary depending on their design (i.e., size; structural complexity), age of installation, local habitat characteristics (i.e., proportion of natural reefs; distance between artificial and natural reef), the development of reefing organisms, and other factors (Abelson & Shlesinger, 2002; Perkol-Finkel, Shashar, & Benayahu, 2006; Simon, Joyeux, & Pinheiro, 2013).

As MAS, O&G platforms and wind turbines share similar characteristics to attract the colonisation of sessile invertebrates and the aggregation of fish populations. The reproductive potential of fishes and invertebrates on O&G platforms and wind turbines is associated with the extent of fish utilising colonised sessile invertebrates, life history stages and the level of residency (McLean et al., 2022). The beneficial effects are evidence if certain fish species commonly use offshore energy structures as feeding ground to consume benthos and amphipods. For example, Atlantic cod (*Gadus morhua*), pouting (*Trisopterus luscus*), and Arctin sculpin (*Myoxocephalus scorpioides*) were found to have affinity on these structures as predators to biofouling communities (J. Reubens, Degraer, & Vincx, 2014; Wilber et al., 2022). Trophic needs are often associated with life stages, especially fish feeding and growing seasons. For example, pouting feeds on fouling invertebrates on offshore wind turbines during the summer and autumn, while migrating to their spawning grounds (J. Reubens et al., 2014). This raised the question to what extent does the deployment of offshore energy structures overlap with the fish spawning grounds (Lacroix et al., 2020). The extent of residency is driven by fish habitat preference, fish biological traits, and their feeding strategies. For highly migratory fish, the cosmopolitan spans indicates low spatial overlap with offshore energy structures (Snodgrass, Orbesen, Walter, Hoolihan, & Brown, 2020). In California, rockfish species tend to use O&G platforms as sheltering habitats with their preference on structure complex reefs (Love et al., 2006). The settlement of marine sessile invertebrates endows offshore structures with artificial reef effects to attract high abundance and diversity of fishes (Claisse et al., 2014). With enhanced food sources, offshore structures appeal to benthopelagic and benthic fishes which consume fouling organisms and resident for an extended time (Ninon Mavraki, Degraer, & Vanaverbeke, 2021). High heterotrophic production rates in reef fishes were found in California O&G platforms, showing high recruitment and growth rates (Claisse et al., 2014). Fish affinity on structures could be driven by multiple incentives, despite some of them violating their common choice. For example, flatfish in the southern North Sea were found to be more abundant and larger near offshore wind turbines even though they normally tend to occupy sandy habitats (Buyse et al., 2023). This can be attributed to the fishing effort redistribution due to safety zone regulations in the areas surrounding offshore structures.

1.3.3 Food web effects

The majority of organismal biomass colonising MAS consists of various suspension feeding taxa (J. W. Coolen, Bittner, et al., 2020). The dominance of biofiltering organisms on offshore structures has strong effects on absorbing food particles from the surrounding water column, clearing seawaters via biofiltering effects, and enriching adjacent sediment with fecal pellet production (N. Mavraki et al., 2022). For example, blue mussels (*Mytilus edulis*) were found to be predominantly colonising hard substrata of offshore wind turbines, having locally active hotspots of biological activities interacting with local environment through grazing phytoplankton and copepods (Maar, Bolding, Petersen, Hansen, & Timmermann, 2009). Compared to natural habitats in deeper waters where mussel beds are limited by food supply, offshore energy structures provide advantageous environments with faster food supply via advection (Frechette, Butman, & Geyer, 1989), leading to significantly higher biomass. In addition, colonised suspension feeders can produce faeces and pseudo-faeces to provide organic materials for benthic detritivores (D. A. Coates et al., 2014). This leads to oxygen depletion and the increase of total mineralisation rate with increased deposition of reactive organic carbon in the surface sediment, which potentially contributes to carbon storage as carbon sinks (Emil De Borger et al., 2021). For macrofaunal communities close to offshore structures, studies found higher species richness and density compared to samples farther away (D. A. Coates et al., 2014). This will induce trophic cascading effects on benthic ecosystem functioning.

The colonisation of sessile invertebrates on offshore structures attracts species at the higher trophic level, developing a hard-substrate dependent marine food web composed of predatory, symbiotic, and commensal species (E. De Borger et al., 2025). Many marine fishes are attracted to the structures due to enhanced food availability. For example, dietary and isotopic analysis found that biofouling organisms *Jassa herdmani* was a primary diet composition in benthopelagic fishes such as pouting and juvenile cod, while the decapod porcelain crab *Pisidia longicornis* was mainly fed by benthic fish like sculpin (Ninon Mavraki et al., 2021). Both *J. jerdmani* and *P. longicornis* are exclusively found in the subtidal habitats of artificial reefs in high densities, while they are much less abundant in natural habitats (J. T. Reubens et al., 2011). The shifts in diet composition support that MAS-associated prey provide nutrient-rich (i.e., fatty acid, lipid) ingredients for certain fish species. The benefit of improved food availability is also found in the flatfish like plaice *Pleuronectes platessa*, with a diet shift towards hard-substrata associated prey species (Buyse et al., 2023). The presence of offshore structures could also alter local primary productivity via the increase of phytoplankton and detritus (J. Wang, Zou, Yu, Zhang, & Wang, 2019). The elevated food supply for zooplankton indirectly supports the biomass and production of planktivorous species such as anchovies.

1.3.4 Bio-physical effects of offshore structures

MAS alter marine ecosystems through restructuring a variety of hydrodynamic processes at a local and regional scale, which indirectly influences the development and distribution of marine species. One main consequence associated with the presence of MAS is changes in vertical mixing near the structure. Studies found that in seasonal stratified shelf seas (i.e., the North Sea), mixing is enhanced beside offshore wind turbines, resulting in significant temperature difference in a depth profile (the doming of thermocline) and an increase of nutrient vertical transport toward the surface water (Floeter et al., 2017). Over the scale of 0.1 – 10 km, dynamical instabilities induced by MAS have strong influence on biogeochemistry, supporting phytoplankton blooms and enhancing primary productivity (Mahadevan, 2016). The increase of plankton production with enhanced mixing leads to bottom-up effects across trophic levels, triggering more biological activities including the attraction of economically important fish species and wildlife as the feeding ground (Dorrell et al., 2022).

Due to structure-induced friction and blocking, MAS could change the remobilisation of sediments through enhanced turbulence downstream of the foundation at the local scale (van Berkel et al., 2020). For macrofaunal communities, altered current regimes influence food and oxygen supply, leading to localised sedimentary hypoxia and the concentrations of organic matters (Wilding, 2014). This becomes a stressor for benthic community structure and biodiversity as few species are capable of adapting to anoxic sediment or organic enrichment (M. C. Nordström & Bonsdorff, 2017; Pearson & Rosenberg, 1978). For fish communities, elevated turbidity attributed to the increase of sediment resuspension in the water column reduces the efficiency of predators in capturing prey (Abrahams & Kattenfeld, 1997; Ortega, Figueiredo, da Graca, Agostinho, & Bini, 2020). This could potentially alter trophic dynamics and the relative predator-prey body mass ratio.

1.3.5 Biological effects of contamination from O&G exploitation

The North Sea has the largest extent of O&G exploitation among OSPAR maritime regions due to the long history of development and the greatest number of O&G installations (Saravanan, Stokke, Malinovsky, & Taylor, 2023). What accompanies O&G exploitation are multiple types of contamination byproducts derived from O&G life stages. The contamination byproducts contain organic and inorganic naturally occurring chemicals, such as trace metals, petroleum hydrocarbons, naturally occurring radioactive materials (NORM), and so on (J. M. Neff, 2002). Bioavailable chemicals over certain concentrations are associated with toxic effects on marine organisms, accumulating in body tissues and transferring to organisms at upper trophic levels through food chains (Mai et al., 2024).

The primary source of crude oil contamination to sea from O&G activities is produced water, which is a mixture of formation water, condensation water, re-injection water and other substances derived during O&G extraction (Utvik, 1999). The volume of produced water typically increases when the O&G reservoir becomes mature and the volume of hydrocarbons decreases (Saravanan et al., 2023). Though environmental regulations limit the total amount of oil before discharge, it still contains hazardous compounds and elements including trace metals, polycyclic aromatic hydrocarbons (PAHs), phenol, and alkylphenol, and NORM (Beyer, Goksøyr, Hjermann, & Klungsøyr, 2020). Metals that come from artificial addition to separate O&G during the production process and anti-fouling layers to prevent erosion include barium, iron, manganese, mercury, and zinc (J. Neff, Lee, & DeBlois, 2011). The exposure of metals could cause negative impacts on individual development, growth, behaviours, fecundity at gene and cell to individual and population levels (Spangenberg & Cherr, 1996; Zheng et al., 2019). PAHs that come from incomplete combustion of fossil fuels, O&G spills, and discharge of O&G contaminated wastes can be split into high and low molecular weight (HMW or LMW) PAHs depending on the number of benzene rings (2-3 benzene rings for LMW PAHs; 4 and more benzene rings for HMW PAHs). HMW PAHs with low water solubility usually combine with particle organic matter and accumulate on the surface sediment, where they persist due to high recalcitrance against microbial degradation (Folwell, McGenity, Price, Johnson, & Whitby, 2016; Silva, Marques, & Gonçalves, 2024). LMW PAHs with high water solubility tend to be bioavailable to marine organisms (Vaezzadeh et al., 2019). The alkylphenol substances are commonly observed with higher concentrations in filter feeding organisms and associated with endocrine disrupting effects (David, Fenet, & Gomez, 2009). NORM is missing the associated environmental quality guidelines in the existing environmental monitoring regulations (MacIntosh, Dafforn, Penrose, Chariton, & Cresswell, 2021). However, radioactive materials that naturally occur in the rock layer accumulate in O&G infrastructure during drilling and production, leading to the exposure of radiation to marine organisms and biological risks on physiological functions, reproduction, and gene expression (Koppel et al., 2023).

Drill cuttings are generated from the O&G drilling process, consisting of fragments of reservoir rocks, drilling muds used for lubricating drill string and petroleum residuals (Ellis et al., 2012). The decadal expansion of O&G exploration and production in the North Sea has produced large quantities of drill cuttings. It is estimated that there are over 12 million m^3 of drill cuttings accumulated on the seabed of the Northern and Central North Sea (Breuer, Shimmield, & Peppe, 2008). The industrial discharge of drill cuttings is a major source of contamination and physical disturbance to marine organisms nearby because it not only contains hydrocarbons, heavy metals, alkylphenols, NORM, and other hazardous substances, but also negatively affects benthic organisms through physical smothering (Henry et al., 2017). The historical cuttings were often left in situ while anthropogenic activities including decommissioning and trawling activities might resuspend hazardous substances into the water column and become bioavailable.

There has been a shift in the ecological footprint of O&G drill cuttings due to stringent legislation of environmental regulations in the North Sea. Since 1984, the discharge of oil-based drilling muds was prohibited in the OSPAR maritime region (OSPAR Commission, 2000). The conventional use of oil-based drilling muds used to be diesel and kerosene, which includes a variety of hydrocarbons such as PAHs, alkanes and alkylphenols (McLaren & Rawlins, 2022). The oil-based drilling muds were then replaced by water-based or synthetic fluids, which contain lower concentrations of trace metals such as mercury, lead, and cadmium and use low-aromatic hydrocarbons that are generally considered to be less toxic to the environment (Bakke, Klungsoyr, & Sanni, 2013). However, physical disturbances such as burial and contaminated sediment redistribution due to decommissioning activities can still have negative effects on marine benthos (Trannum, Setvik, Norling, & Nilsson, 2011). The comparison of contamination concentration with sediment quality threshold showed that most adverse effects occurred within 0 – 500 m from O&G structures (Chen et al., 2024; McLaren & Rawlins, 2022).

1.4 Food webs

1.4.1 Concepts

Food webs are theoretical representations characterising the networks of predator-prey interactions across biological organisms in communities (S. L. Pimm, 1979; S. L. Pimm, Lawton, & Cohen, 1991). Biological organisms in food webs are broadly differentiated into consumers and resources to distinguish their relative roles in trophic interactions. Trophic interactions exhibit a variety of forms to transfer energy and materials across biological organisms and trophic levels, including predator-prey, herbivore-plant, and host-parasite interactions. Trophic ecologists often partition biological organisms into trophic groups. For example, marine invertebrates are classified into predators, detritivores, filter feeders, grazers, scavengers, and parasitic fluid feeders based on common feeding traits within the feeding group (Jennifer A Dunne, 2009).

1.4.2 Linking food webs to ecosystem functions

Efforts of food web studies unveil perspectives of ecosystem status. First, food webs characterise vertical and horizontal diversity as well as the distribution of biological organisms within communities (Shaopeng Wang, 2020). Food web theories provide a schematic approach to depict multitrophic interactions and trophic structure (Figure 3). The integration of diversity and food web structure offers a comprehensive understanding of the relationship between ecosystem

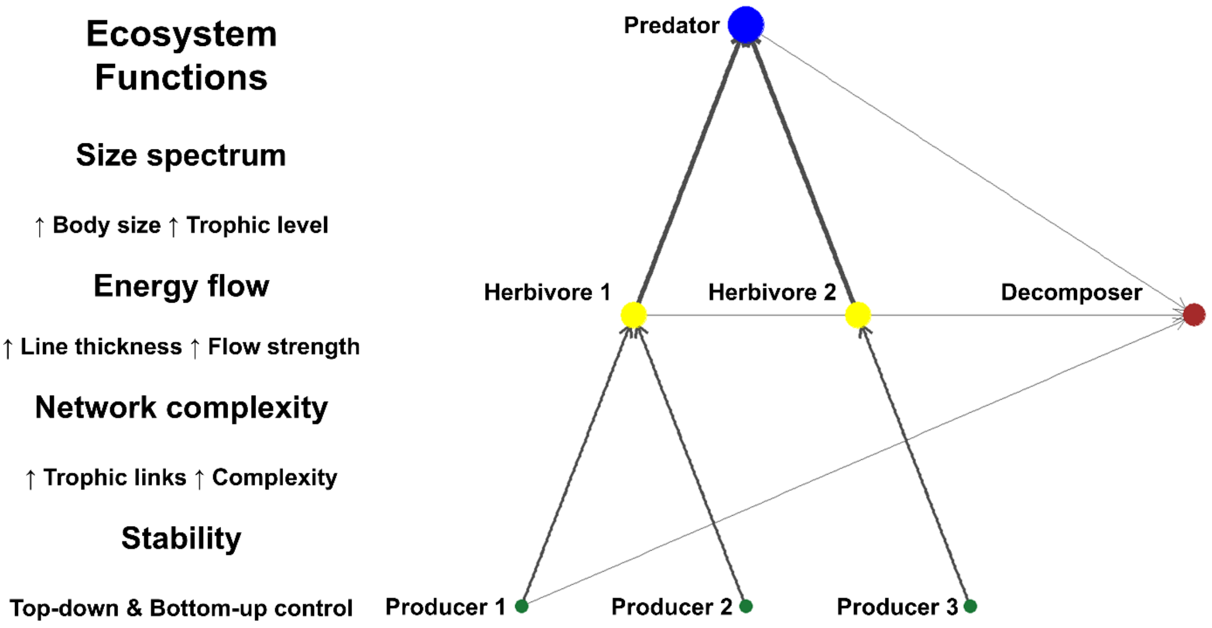

Figure 3: A simple food web diagram showing different trophic roles of biological organisms. The thickness of interactions represents the strength of energy transfer. The food web structure links to ecosystem functions shown on the left.

functioning and multifaceted diversity. For example, the distinct number of species within one trophic level reflects horizontal diversity while the maximum number of trophic levels reflects vertical diversity, which closely links to ecosystem stability and functioning (J. E. Duffy et al., 2007; Loreau et al., 2001; Rooney & McCann, 2012; Tilman, Isbell, & Cowles, 2014).

Theoretical and empirical studies have shown not only the effects of species diversity in multiple ecosystems (e.g., terrestrial and aquatic ecosystems) on consumer-resource interactions (J.E. Duffy, Paul Richardson, & Canuel, 2003; Mulder, Koricheva, Huss-Danell, Högberg, & Joshi, 1999), altering resource use rates in some biological compartments (Cardinale, Palmer, & Collins, 2002), and organic matter biogeochemical cycle (Danovaro et al., 2008), but also the effects of top-down trophic control on resource uptake, primary production and total abundance at lower trophic levels (C. P. Lynam et al., 2017; S. Wang & Brose, 2018). Exploitations of trophic network complexity in food web studies helps to capture realistic trophodynamics across different ecosystems (Pace, Cole, Carpenter, & Kitchell, 1999). Food web complexity is commonly used as a measure of ecosystem stability in theoretical studies because it promotes resistance to external disturbances such as climate change by providing multiple redundant pathways for energy to flow through the food web (Vallina & Le Quere, 2011). Trophic cascades are one of the most prominent features in ecosystem studies. Given intensified environmental impacts (e.g., ocean warming) and anthropogenic stressors (e.g., fishing), species at higher trophic levels are often susceptible to disproportionate effects, leading to richness loss, simplified food web structure and inducing direct interactions with species at adjacent trophic levels and indirect interactions with species at lower trophic levels (Österblom et al., 2007; Owen L Petchey et al., 2004). The trophic pathways amplify disturbances across multiple trophic levels in ecosystem food webs, which may modify interspecific interaction strengths, lead to changes in body mass and energy transfer between consumers and resources, and even cause a regime shift (Kirby & Beaugrand, 2009; Luhring & DeLong, 2020; Möllmann, Müller-Karulis, Kornilovs, & St John, 2008). Finally, studies investigating spatial and temporal heterogeneity of food webs could reveal environmental variables and varying degrees of impacts on ecological communities over space and time. Environmental gradients and consequently spatial variations of food webs mainly attribute to species turnover, trophic skewness in extinction, and changes in ecological networks in response to environmental impacts (Susanne Kortsch et al., 2018; Pellissier et al., 2018; Tylianakis & Morris, 2017). Temporal dynamics of food webs may function as a descriptor to assess changes in ecosystem functioning at different phases (S. Kortsch et al., 2021). Therefore, food web studies have become increasingly important as a critical tool for ecological conservation and ecosystem management (Kytinou, Sini, Issaris, & Katsanevakis, 2020).

1.4.3 Characteristics of marine food webs

Food webs in marine ecosystems demonstrate unique qualities that distinguish them from their counterparts in other ecosystems. In the marine environment, there are many species with a broad diet spectrum, which means they tend to be omnivorous and generalist consumers feeding on other species across multiple trophic levels (Jennifer A Dunne, Williams, & Martinez, 2004). High omnivory in marine food webs is strongly linked with food web stability and shaping relationships between biodiversity and ecosystem functioning (Bruno & O'Connor, 2005; Owen L Petchey et al., 2004). Besides that, food webs in marine ecosystem are often characterised by high connectance (Jennifer A Dunne et al., 2004). Empirical evidence examining structural properties of food web topologies show that there are a greater number of trophic links per species in marine food webs than those in other ecosystems (Joel E Cohen, 1994; Link, 2002). High connectance in marine food webs plays a vital role in mediating trophic cascades and reducing secondary species extinctions following a perturbation (Estrada, 2007). In addition, marine food webs share common characteristics with food webs in aquatic systems in general. A typical example is size structure, with bigger organisms typically eating smaller organisms due to gape size limitations (Guy Woodward, Speirs, Hildrew, & Hal, 2005). This size structure has important implications for food web structure (O. L. Petchey, Beckerman, Riede, & Warren, 2008) and also the strength of interactions given the predictable relationship between body size and metabolic demand (Brown, Gillooly, Allen, Savage, & West, 2004). Body size describes trophic network structure and interaction strengths between consumers and resources (Jennings, 2005). It also positively correlates with trophic levels regarding consumers in marine food webs, which implies that species with larger body size tend to occupy higher trophic levels (Potapov, Brose, Scheu, & Tiunov, 2019). Another example is top-down regulation of marine plankton, with studies showing that trophic cascading effects are stronger in the marine than terrestrial food webs due to higher-level predation (Shurin et al., 2002).

1.4.4 Food web assessments in conservation management

Since they capture ecological processes, complex ecosystem dynamics, and ecosystem functions, ecologists are interested in food webs to understand the consequences of ecosystem shifts in response to external disturbances. For the past decades, the increasing awareness of ecosystem management and the urgency of developing policies has integrated ecological understandings to untangle effects of climatic and anthropogenic stressors on ecosystems. Food webs have been widely used to study how different ecosystems respond to the individual and combined effects of these stressors. Using marine ecosystem as an example, temperature is one of the most enduring and spatially extensive stressors. Temperature can determine food web structure, trophic dynamics and life-history processes through metabolism and species redistribution patterns (Albouy et al., 2014; du Pontavice, Gascuel, Reygondeau, Maureaud, & Cheung, 2020; O'Connor, Piehler, Leech, Anton, & Bruno, 2009). Anthropogenic stressors vary in forms but could be broadly categorised into biological resource exploitation and environmental alternations. An example for biological resource exploitation is commercial fishing, which harvests the economically important species at high trophic levels, leading to shifts in species dominance, biomass and biodiversity loss and compromises entire food web persistence (Essington, Beaudreau, & Wiedenmann, 2006; Gilarranz, Mora, & Bascompte, 2016; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998). Anthropogenic nutrient inputs is another example of environmental alternations, which may benefit primary production of marine phytoplankton but hinder benthic trophic pathways (Tewfik, Rasmussen, & McCann, 2005). Progress in modelling methods has facilitated scenario projections of marine ecosystems under coupled effects from multiple stressors (Niiranen et al., 2013). Species coexisting under the constraint of environmental control are likely to share similar ecological traits as a result of environmental filtering effects (Sommer, Harrison, Beger, & Pandolfi, 2014). Changes in community structure may also occur, with species turnover influencing the properties of the trophic network of feeding interactions (S. Kortsch et al., 2021). With trait composition varying along environmental gradients, the topological metrics of food web structure will also change along stressor gradients (Pecuchet et al., 2022). It is crucial to jointly study the interconnections between biodiversity and food web structure as the community composition and food web structure are associated with ecosystem function, stability, and resilience against external disturbances.

1.5 Study area

The North Sea is a shallow marginal sea of the Atlantic Ocean connecting the British Channel and the Norwegian Sea. Its seafloor mainly consists of sand, mud and gravel (Eisma, 1987). Such a sand-dominated soft bottom environment is accompanied with outstanding physical and biological gradients, transitioning from shallow, seasonal, and productive at the continental south to the oceanic and stable north (Pecuchet et al., 2018). Climatic variability amplifies complex physical oceanographic conditions of the North Sea, linking hydrodynamic processes (i.e., ocean circulation and organic matter transport) to climatic variables (i.e., temperature and wind) (Otto et al., 1990).

Biological communities inhabiting the North Sea demonstrates biotic responses to the fluctuations of North Sea physical oceanographic environment. As a main primary producer, phytoplankton is bound to the North Sea productivity. Patterns of phytoplankton biomass are distinctive across the latitudinal gradient of the North Sea, with diatoms dominating in the south while dinoflagellates are the main taxa in the north (P. Reid, Lancelot, Gieskes, Hagmeier, & Weichart, 1990). Phytoplankton-derived primary production also differs across the North Sea, with primary production usually peaking from May to August and reaching low levels from November to February in the south (Joint & Pomroy, 1993). In terms of zooplankton, the North Sea is dominated by small copepods that feed on diatoms, which are also a main food source for juvenile fish. The zooplankton communities also exhibit a north-south pattern: the northern zooplankton communities are dominated by (e.g., *Calanus finarchicus*) and are very similar to zooplankton from the Atlantic Ocean, while *Calanus helgolandicus* dominates in the southern North Sea (Fransz, Colebrook, Gamble, & Krause, 1991). However, historical records of thermal abnormal events caused pervasive dominance of warm resilient zooplankton species, which benefited fish species such as horse mackerel (P. C. Reid, Edwards, Beaugrand, Skogen, & Stevens, 2003). As for macrofauna, the spatial distribution is highly associated with sediment type, while phytoplankton availability and temperature play an important role (Heip et al., 1992).

The North Sea is heavily susceptible to anthropogenic activities and climate-driven environmental variability (Capuzzo et al., 2018; Clark & Frid, 2001). Anthropogenic activities, including fishing and offshore energy industrialisation, have been one of the most spatially extensive and temporally enduring industries modifying marine ecosystems. Climatic variability on hydrodynamic features has also profoundly modified ecosystem structure and baseline. Understanding the impacts of these anthropogenic stressors accounting for climatic variability is of vital importance to provide robust evidence for North Sea ecosystem-based management.

Commercial fishing has been exploiting fish resources for centuries, with the North Sea one of the world's most productive fishing grounds for economic fish species including cods and lings (Poulsen, 2007). Concerns over intensive fishing activities and the impacts on marine ecosystems gained increasing attentions in the 1990s. A typical and destructive fishing practice is bottom trawling, which can cause massive disturbance on the seafloor, leading to changes in benthic communities and loss of vulnerable species (De Groot, 1984; Frid, Harwood, Hall, & Hall, 2000). Loss of apex fish predators could shift the species dominance in the communities, e.g., in the Gulf of Maine, long-term fishing caused a shift from a cod-dominant to crustacean-dominant ecosystem. The removal of economically important fish allows their prey species to have higher survival rates between larval to juvenile stages, increasing the biomass of juvenile individuals.

The North Sea ecosystem has been profoundly affected by MAS. O&G exploitation, as pioneering offshore industrialisation activities in the past decades, has introduced hundreds of O&G platforms and associated installations. The sprawl of these O&G structures, together with the rapid expansion of offshore renewable structures in the recent decades, induces changes to the marine environment. The distribution of these two types of MAS is shown in the Figure 4. Ecological impacts of MAS in the North Sea ecosystem include structurally complex hard substrata, which is contrary to the soft sediments that dominate the benthos of the North Sea. This additional habitat structure enables colonization by fouling organisms that can increase the trophic complexity of the local ecosystem, and the connectedness could in turn strengthen ecological stability (De Mesel et al., 2015; Larcom, McKean, Brooks, & Fisher, 2014; van der Molen et al., 2018).

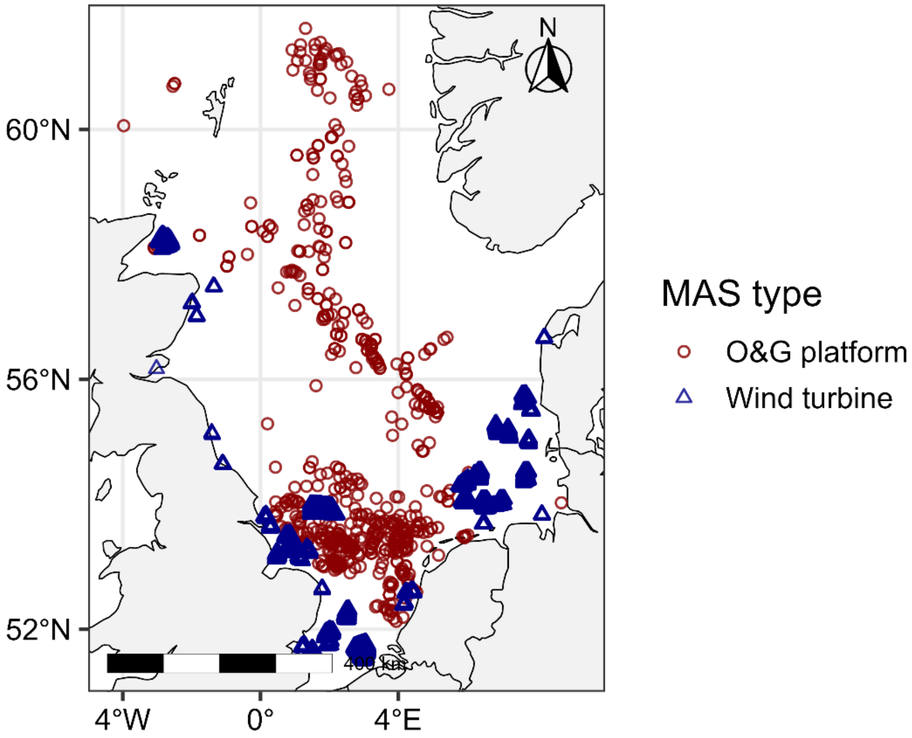

Figure 4: The geographic distribution of O&G platforms (grey circles) and wind turbines (grey triangles) in the North Sea (MAS structure data extracted from Martins et al., 2023).

1.6 Thesis outlines and main goals

This PhD thesis focuses on the ecological impacts of MAS in the North Sea to better understand how the development of offshore energy affects marine biodiversity and food web structure and ultimately have consequences for ecosystem functioning. The thesis utilises a number of methods from multiple before-after-control-impact (BACI) framework to meta-analytic approach and food web modelling at a variety of spatial scales to investigate the local and regional effects of MAS to the North Sea biodiversity and food webs and provide links between anthropogenic-driven changes in the environmental conditions and ecological responses. The three data chapters can be split into two main components, highlighting diversity metrics and trophic structure of benthic invertebrates and fish communities respectively. While both first and second data chapters focus on benthos, the MAS phases of interest look into active operating versus post-decommissioning.

Chapter 2 examines the abundance, biomass, species richness and Pielou's evenness of the entire benthic invertebrate communities and six distinct individual feeding guilds using stomach content analysis and taxon-specific body size estimates. Food web structure at each sample is constructed using predator-prey interactions based on the presence of predators and preys in the sample. It is a more holistic approach not only assessing changes in community structural aspects but also trophic topological dimension, which provides insights of ecosystem resilience and food web complexity. Benthic biodiversity and food web responses are compared across three distance-based treatments characterising the extent of O&G associated contamination from high to the background condition. This shows the spatial limits of the impacts of O&G platforms and highlights the focus of benthic monitoring and management areas.

Chapter 3 expands benthic biodiversity and food web metrics and compares them before and after MAS decommissioning in the multiple BACI design to examine the patterns of benthic recovery at three different timescales and removal options. In the meta-analytical framework, differences in difference of metrics across surveys at multiple eligible O&G platforms were standardised using Hedge's g effect sizes, with significant metrics showing substantial changes in benthic biodiversity and food web structures attributed to MAS decommissioning and post-decommissioning recovery.

This aims to provide scientific evidence to support better MAS decommissioning practices to call for long-term systematic sampling across MAS life phases and assess short- and long-term effects.

Chapter 4 utilises a novel approach to integrate spatially and temporally extensive otter trawl fish data into large-scale assessments of MAS effects. It assesses the general effects of O&G platforms and offshore wind turbines across the North Sea for the past three decades on fish biodiversity and biomass metrics at the community dimensions (α, β, γ diversity, total abundance and biomass) and on fish functional groups, such as planktivores, benthivores, bentho-piscivores and piscivores The interpolation from observed fish data generates spatial estimates of fish abundance, total biomass, typical length, α-, β- and γ diversity at each prediction grid cell. Fish taxa are linked with modelled and observed feeding information to classify them into planktivore, benthivore, bentho-piscivore and piscivore, following an ascending order of body size and trophic level that respectively links to primary production, secondary production and fish production. A Bayesian INLA framework is used to model MAS effects and large-scale environmental variables on fish responses. It detects striking patterns of guild-specific effects on fish biodiversity and food web metrics with O&G platforms and wind turbines, showing biased negative effects on large fish pisicivores whilst small fish gains.

Chapter 5 synthesises the contributions of three data chapters and presents key future directions that can be implemented to obtain a more comprehensive dataset and supplement existing research efforts with alternative methods to gain the wider state of knowledge of MAS impacts.

Each chapter addresses specific research questions, data compilation, and detailed analysis results, which were formatted as individual research articles that are either published, under revision or in preparation for submission. The thesis is structured under the united theme of assessing the impacts of offshore structures on marine biodiversity and food web properties.

CHAPTER TWO

Oil and gas platforms degrade benthic invertebrate diversity and food web structure

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Abstract

Oil and gas exploitation introduces toxic contaminants such as hydrocarbons and heavy metals to the surrounding sediment, resulting in deleterious impacts on marine benthic communities. This study combines benthic monitoring data over a 30-year period in the North Sea with dietary information on > 1,400 taxa to quantify the effects of active oil and gas platforms on benthic food webs using a multiple before-after control-impact experiment. Contamination from oil and gas platforms caused declines in benthic food web complexity, community abundance, and biodiversity. Fewer trophic interactions and increased connectance indicated that the community became dominated by generalists adapting to alternative resources, leading to simpler but more connected food webs in contaminated environments. Decreased mean body mass, shorter food chain lengths, and the dominance of small detritivores such as *Capitella capitata* near to structures suggested a disproportionate loss of larger organisms from higher trophic levels. These patterns were associated with concentrations of hydrocarbons and heavy metals that exceed OSPAR's guideline thresholds of sediment toxicity. This study provides new evidence to better quantify and manage the environmental consequences of oil and gas exploitation at sea.

Keywords: benthic communities, marine food web, trophic structure, contamination, man-made structure, marine ecosystem, North Sea

2.1 Introduction

Food webs represent the network of trophic interactions among biological organisms in a community (S. L. Pimm, 1979; S. L. Pimm et al., 1991). Human activities profoundly affect food web architecture and the associated composition of functional traits (U. Brose et al., 2019; Morin & Lawler, 1995) by altering global patterns of biodiversity and predator-prey interactions (Storch et al., 2022). For example, discharge of organic pollutants can cause declines of sensitive species, inducing community turnover and altering the diet and trophic position of consumer species (Pearson & Rosenberg, 1978; Xu, Shin, & Sun, 2022). The targeted loss of top predators in highly size-structured marine food webs, due to commercial fishing for example, can shorten mean food chain length and cause cascading effects on other trophic levels (Essington et al., 2006; C. P. Lynam et al., 2017; Pauly et al., 1998; Owen L Petchey et al., 2004). There is growing interest in integrating the perspectives of community and food web properties to understand anthropogenic impacts on natural communities (Susanne Kortsch et al., 2018).

The North Sea is a continental shelf ecosystem with a plethora of human uses, including the extraction of hydrocarbons. The associated proliferation of oil and gas platforms may have some benefits, by providing a complex hard structure in a region dominated by soft sediments. This may support the settlement of sessile invertebrates and algal biofilms, which could fuel a more complex food web (Brandt, Hansen, Diederichs, & Nehls, 2014; De Mesel et al., 2015; Fujii, 2015; Ronconi, Allard, & Taylor, 2015). The presence of platforms establishes exclusion zones that benefit fish communities in a heavily trawled sea (Sheahan et al., 2001). However, hydrocarbon exploitation activities around oil and gas platforms release contaminants into the environment via drill cuttings and accidental spills (Stokke, Marappan, & Taylor, 2022). These discharged wastes contain hazardous substances such as hydrocarbons and heavy metals which pose a risk to the environment

(Breuer et al., 2008; Kingston, 1992). Whether overall effects of oil and gas platforms on the adjacent marine biota are deleterious and consistent across different stages of hydrocarbon exploitation activities from production to decommissioning remains under debate (Melbourne-Thomas et al., 2021; Sommer et al., 2019; van der Stap, Coolen, & Lindeboom, 2016). Despite efforts to quantify effects on community composition (Delefosse et al., 2020; Larcom et al., 2014; Wright et al., 2020), no study to date has unravelled how oil and gas platforms alter food web properties (Fortune & Paterson, 2018). Changes in trophic structure could have far-reaching consequences by destabilizing ecosystem functionality and reshaping resilience to external disturbance (Hautier et al., 2015; Mestre, Rozenfeld, & Araujo, 2022; E. J. O'Gorman, Fitch, & Crowe, 2012). Thus, assessment of food webs has important implications for ecologically-sound management of oil and gas platforms.

Marine invertebrates play fundamental roles in ecosystem functioning and are susceptible to oil contamination, making them well suited to monitoring the zone of influence and ecological impacts of platforms (Suchanek, 1993). The exposure of hydrocarbons and heavy metals can have ecotoxicological effects on invertebrate organisms throughout their life cycle from embryos to adults (Bellas, Saco-Alvarez, Nieto, & Beiras, 2008; W. X. Wang & Rainbow, 2005). Hydrocarbons persist in the marine environment (especially aromatic compounds) and can chronically impair physiological functions, such as respiration, feeding, and reproduction (Adzigbli & Yuewen, 2018). Heavy metals exert toxicity via bioaccumulation, resulting in disrupted enzymatic activities and changes in cellular processes (Chiarelli & Roccheri, 2014). Benthic invertebrate communities close to oil and gas platforms generally exhibit lower biodiversity and altered community composition compared to pristine sites (R. Daan, Booij, Mulder, & Van Weerlee, 1996; Ferrando et al., 2015; Olsgard & Gray, 1995). Even after the cessation of hydrocarbon exploitation, legacy effects on benthic invertebrate communities may persist over years (Gates & Jones, 2012; Jones, Gates, & Lausen, 2012).

However, due to the absence of a coordinated monitoring and assessment strategy, no study to our knowledge has undertaken a multiple before-after control-impact (MBACI) study across oil and gas platforms on benthic communities. MBACI studies can establish causal links between an intervention (hydrocarbon exploitation from oil and gas platforms in this case) and ecological responses such as change in species richness and food web properties, whilst accounting for potentially confounding spatial and temporal variation. If this design is applied across multiple comparable sites, then generalisations about the treatment can be made (Cordes et al., 2016; M. S. Thompson et al., 2018). This study aimed to compare benthic biodiversity and food web metrics in a MBACI design across multiple platforms to test the following hypotheses: (1) concentrations of hydrocarbons and heavy metals are higher in the sediment close to platforms after production commences; (2) sensitive species are lost in the contamination sites, decreasing species richness and community biomass; and (3) food webs become simpler.

2.2 Materials and methods

2.2.1 Data compilation

Biotic and environmental data were collated from the UK Benthos Database v5.17, an online inventory of UK offshore benthic monitoring surveys from 1975 to 2015 (Offshore Energies UK, 2015). Infrastructure information at each sampled platforms was extracted from the online interactive mapping data repository for the UK Continental Shelf (North Sea Transition Authority, 2024a). 553 benthic grab samples were collected from a total of nine platforms with associated (i) coordinates, sampling year, and distance to sampled platforms (Table S1), (ii) concentrations of hydrocarbons and heavy metals in the sediment, and (iii) abundance and taxonomic data of benthic invertebrates. The invertebrates were identified to the lowest possible taxonomic level (typically species); thus, all taxa henceforth are referred to as species.

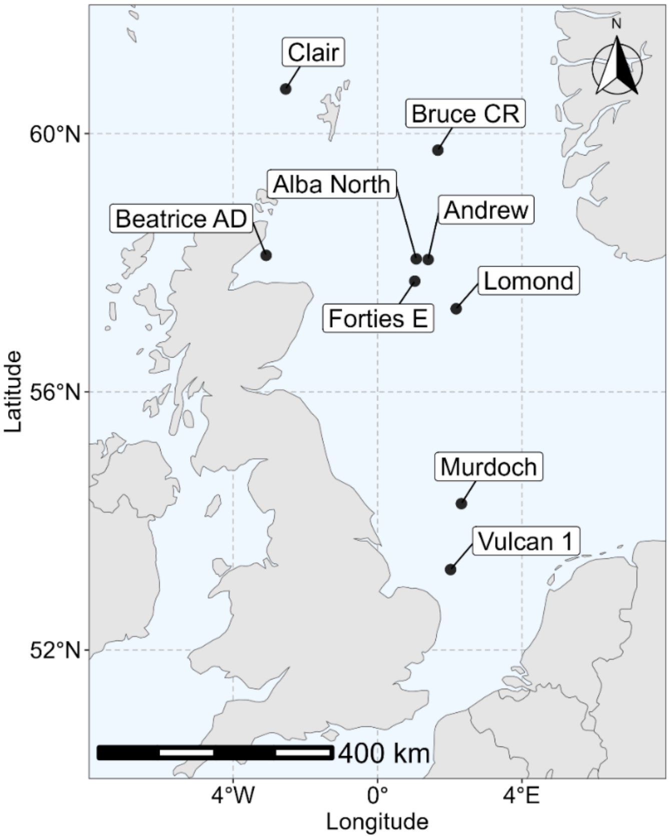

Figure 1: Locations of nine platforms in the North Sea with sampling before and after the commencement of oil and gas production at a range of distances from the structure.

The distribution of platforms covers the southern and northern North Sea and Atlantic margin (Figure 1). All samples spanned from pre-commissioning to post-commissioning periods of oil and gas production to capture both baseline conditions and those when active operations were underway. The average body mass of each species was estimated from trait information of benthic invertebrates in the North Atlantic region, which was compiled based on published reports of *in* *situ* observations, laboratory experiments, and online datasets (Clare et al., 2022). Trophic interactions were compiled for every species based on peer-reviewed sources in the supplementary data.

2.2.2 Response variables

Hydrocarbon and heavy metal concentrations in the sediment were measured at the same sampling site as the benthic invertebrate samples. Hydrocarbons were sub-divided into *n*-alkanes, and polycyclic aromatic hydrocarbons (PAHs) which were further delineated into high-molecular-weight PAHs (HMW-PAHs) with more than three aromatic rings, and low-molecular-weight PAHs (LMW-PAHs) with three or fewer rings. The ecological impacts of HMW- and LMW-PAHs on benthic invertebrates were considered separately, as HMW-PAHs are highly toxic to a diverse range of organisms, and their hydrophobicity and tendency to be absorbed to organic matter results in low bioavailability and a high recalcitrance to biodegradation (Folwell et al., 2016) A total of five heavy metals were analysed, including Cadmium (Cd), Chromium (Cr), Copper (Cu), Nickel (Ni), and Lead (Pb). Any values of hydrocarbon and heavy metal concentrations that were below the threshold for detection of 0.01 μg g-1 were assigned a value of 0.

A total of 1,422 species were compiled from the data, with taxonomic information verified using the World Register of Marine Species (Ahyong et al., 2023). The mean abundance of benthic invertebrate species across all the replicate surveys conducted at each site was enumerated. The sampling gear (i.e., Van Veen, Day, or Hammo grabs) and sieve mesh size (0.5 or 1 mm) were merged as a composite variable for use in statistical models. Every species was assigned to one of six trophic groups based on their distinct feeding behaviours. For predators and parasites, a literature review was conducted to ascertain their prey or host species based on published articles and databases (Table S2). For any predator or parasite species with no available diet information, prey or host species were inferred from other taxa within the same taxonomic level. Species in the detritivore, scavenger, filter feeder, and grazer groups were assumed to feed on a certain set of basal resources.

2.2.3 Experimental design

The patterns of total hydrocarbon concentration in the sediment along distance to sampled platforms were described using generalized additive models (Figure 2). This helped identify three separate 'treatments' for use in subsequent analyses: (1) the 'impact', which was up to 500 m until predicted concentrations of total hydrocarbon before and after commissioning of hydrocarbon production converged, (2) the 'buffer' (500 – 1,500 m), which typically continued to exhibit declining concentrations of total hydrocarbon with increasing distance from the structure, and (3) the 'control' (1,500 – 5,000 m), which exhibited very little change in the concentrations.

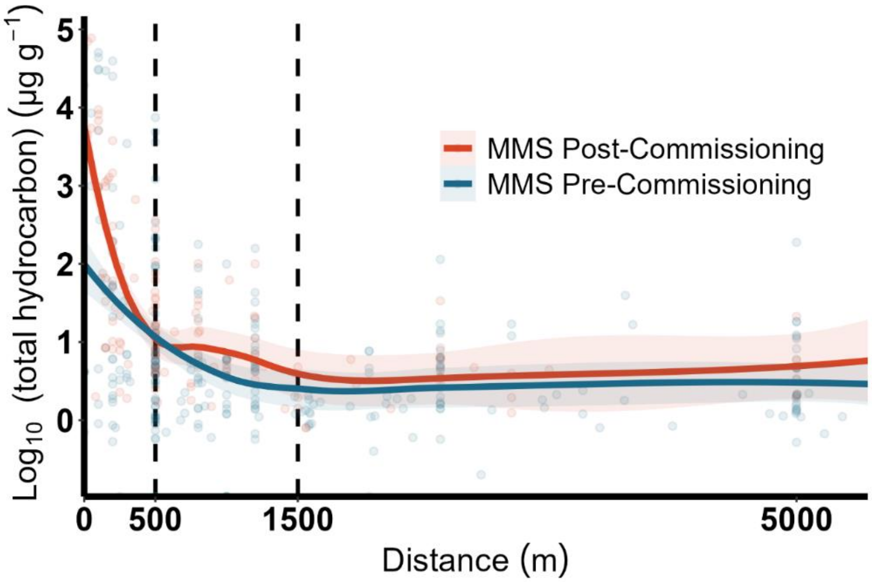

Figure 2: Log$_{10}$-transformed concentrations of total hydrocarbon in the sediment along a distance gradient before (blue) and after (red) the commencement of oil and gas production. The "intersect" of the two smoothing curves at approximately 500 m away from the platforms was used to

distinguish the ‘impact’ sites with high levels of total hydrocarbon concentrations. The second cutoff point around 1,500 m was used to distinguish the ‘control sites where hydrocarbon concentrations approached the background level.

2.2.4 Statistical analysis

All statistical analyses were conducted in R v4.2.1 (R Core Team, 2025). The effects of platforms on diversity and food web metrics were examined using a multiple-before-after control-impact (MBACI) experiment. Here, the true impact and buffer treatments were only considered as samples taken after the start of oil and gas production in the ‘impact’ and ‘buffer’ sites, respectively. All other samples were considered as control treatments, including the samples taken from baseline surveys in the ‘impact’ and ‘buffer’ sites prior to the commencement of oil and gas exploitation, which acted as temporal controls for the post-commissioning samples (M. S. Thompson et al., 2018). This design helps to simplify the statistical model from the interactions between distance categories (<500 m, 500-1,500 m, >1,500 m) and time period (before, after) into one grouping variable (impact, buffer, control). Using pooled data from multiple oil and gas platforms, the increased statistical power enables the identification of general patterns of changes in benthic communities and variations on the total effects of response variables *(Gurevitch, Morrow, Wallace, & Walsh, 1992)*. The study selected 13 complementary and widely-used metrics to describe the vertical (e.g., number of trophic levels) and horizontal (e.g., number of species within a trophic level) dimensions of food web architecture, including: abundance, individual mean body mass, species richness, Pielou’s evenness, proportions of basal, intermediate, and top species, mean trophic level, generality, standard deviation of normalised generality (generalitySD), vulnerability, standard deviation of normalised vulnerability (vulnerabilitySD), link richness, linkage density, and connectance. The definitions and ecological implications of all metrics are described in the

Table S3. Each metric was enumerated in R using the '*cheddar'* package, with mean trophic level calculated using the '*PreyAveragedTrophicLevel'* function (Hudson et al., 2013; Levine, 1980).

Models of each response were fit using linear mixed effect models (LMEs) in the *lme4* (Bates, Mächler, Bolker, & Walker, 2015). The BACI treatment was the explanatory variable in all LMEs (three levels: Impact, Buffer, Control). Differences between means of response metrics across the BACI treatments were examined using Tukey's pairwise comparisons using *multcomp* (Bretz, Hothorn, & Westfall, 2008). Results of Tukey's Honest Significant Difference (HSD) were shown using compact display letters in *multcompView* (Graves & Piepho, 2006; Wickham, 2016). Platform identify, sampling gear and sampling year was fitted as a random variable across all initial models to account for inherent differences across platforms and non-independence of observations. The significance of each random variables as well as the fixed variable was tested using Alkaike Information Criteria (AIC). Only significant variables were retained in the final models. The model with the most parsimonious random effect structures were identified for each ecological metric in the lowest AIC values.

The importance of each benthic species in response of BACI treatment was analysed using *Randomforest* package (Liaw & Wiener, 2002). Here, 70% of the data for each treatment was randomly sampled to train the random forest model, with the remaining 30% used for validation. Species with the highest contributions to the BACI treatment were selected as indicator species. Pairwise correlations of individual hydrocarbon compound and heavy metal concentrations were tested using the Spearman rank coefficient. Pairwise correlations between the abundance of each trophic group and individual hydrocarbon compound and heavy metal concentrations were analysed using the Mantel test, with results visualized using the '*LinkET'* package (Huang, 2021)

2.3 Results

2.3.1 Chemicals

All contaminants assessed were higher at impact sites relative to buffer and control sites (Figure 3). There was a significant effect of the BACI treatment with concentrations of *n*-alkanes 50,576% higher ($F_{2,550} = 109.1$, $p < 0.001$; Figure 3a), HMW-PAHs 1,110% higher ($F_{2,550} = 9.8$, $p < 0.001$; Figure 3b), LMW-PAHs 434% higher ($F_{2,550} = 24.0$, $p < 0.001$; Figure 3c), and heavy metals 336% higher ($F_{2,550} = 29.3$, $p < 0.001$; Figure 3d) on average in the impact sites relative to the control sites. Similar results were observed for individual hydrocarbon and heavy metal compounds (Figures. S6-S7). Buffer site contaminant levels were not statistically different from control sites. Pairwise comparisons of BACI treatments are shown in the Table S6.

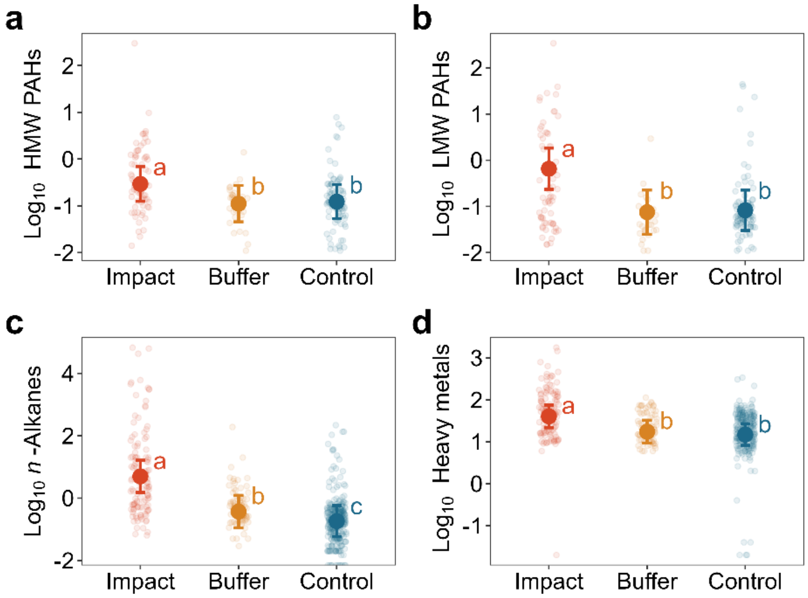

Figure 3: Log_{10}-transformed concentrations of (a)HMW-PAHs, (b) LMW-PAHs, (c) *n*-alkanes, and (d) heavy metals within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from

platforms. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

2.3.2 Biomass and diversity

For biomass and diversity metrics, there were significant reductions within impacted sites compared to control sites (Figure 4). There was a significant effect of the BACI treatment with total abundance 17% lower ($F_{2,550} = 25.9$, $p < 0.001$; Figure 4a), mean body mass 28% lower ($F_{2,550} = 10.8$, $p < 0.001$; Figure 4b), species richness 28% lower ($F_{2,550} = 40.2$, $p < 0.001$; Figure 4c), and Pielou's evenness 12% lower ($F_{2,550} = 40.6$, $p < 0.001$; Figure 4d) on average in the impact sites relative to the control sites.

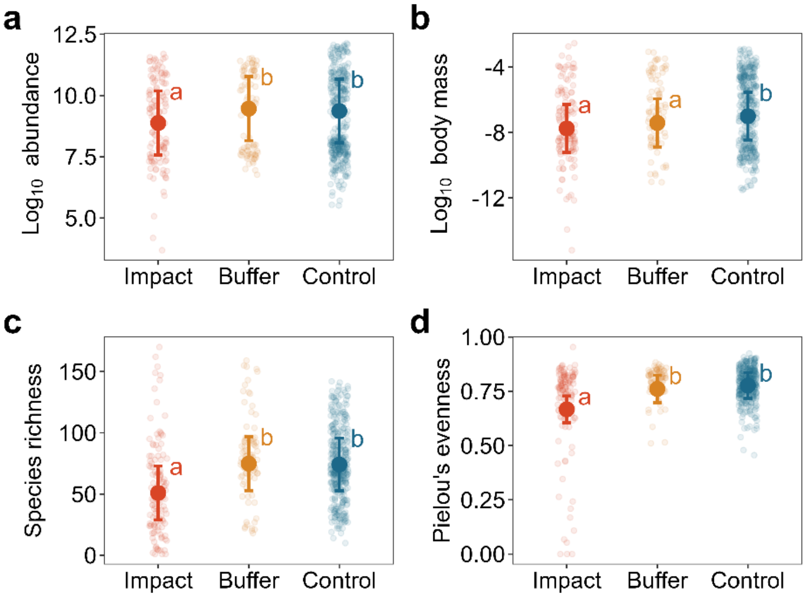

Figure 4: Log_{10} transformed (a) abundance and (b) individual mean body mass, (c) species richness, and (d) Pielou's evenness of benthic samples within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from platforms. Compact display letters show significant differences between BACI treatments (Tukey's HSD test, $p < 0.05$).

Responses in the buffer sites largely replicated control conditions but for mean body mass, where control and impact sites were statistically different from one another while the buffer sites were not different from the other treatments (Figure 2.4b). Pairwise comparisons of BACI treatments for biomass and diversity metrics are shown in Table S7.

2.3.3 Food web structure

There was a significant effect of the BACI treatment on community composition and food web structure (Figure 5). The proportion of basal species was 46% higher ($F_{2,550} = 59.8$, $p < 0.001$; Figure 5a), proportion of intermediate species 16% lower ($F_{2,550} = 51.8$, $p < 0.001$; Figure 5b), and proportion of top species 34% higher ($F_{2,550} = 12.2$, $p < 0.001$; Figure 5c) on average in the impact sites relative to the control sites. Mean trophic level was 5% lower ($F_{2,550} = 30.7$, $p < 0.001$; Figure 5d), link richness 19% lower ($F_{2,550} = 22.1$, $p < 0.001$; Figure 5g), and linkage density 10% lower ($F_{2,550} = 33.5$, $p < 0.001$; Figure 5h) on average in the impact sites relative to the control sites. No significant effect of the BACI treatment was observed on generality and vulnerability (Tukey's HSD, $p > 0.05$; Figure S8). GeneralitySD was 6% lower ($F_{2,550} = 5.5$, $p = 0.004$; Figure 5e), vulnerabilitySD 20% lower ($F_{2,550} = 12.0$, $p < 0.001$; Figure 5f), and connectance 16% higher ($F_{2,550} = 11.5$, $p < 0.001$; Figure 5i) on average in the impact sites relative to the control sites. Pairwise comparisons of BACI treatments for food web metrics are shown in Table S8.

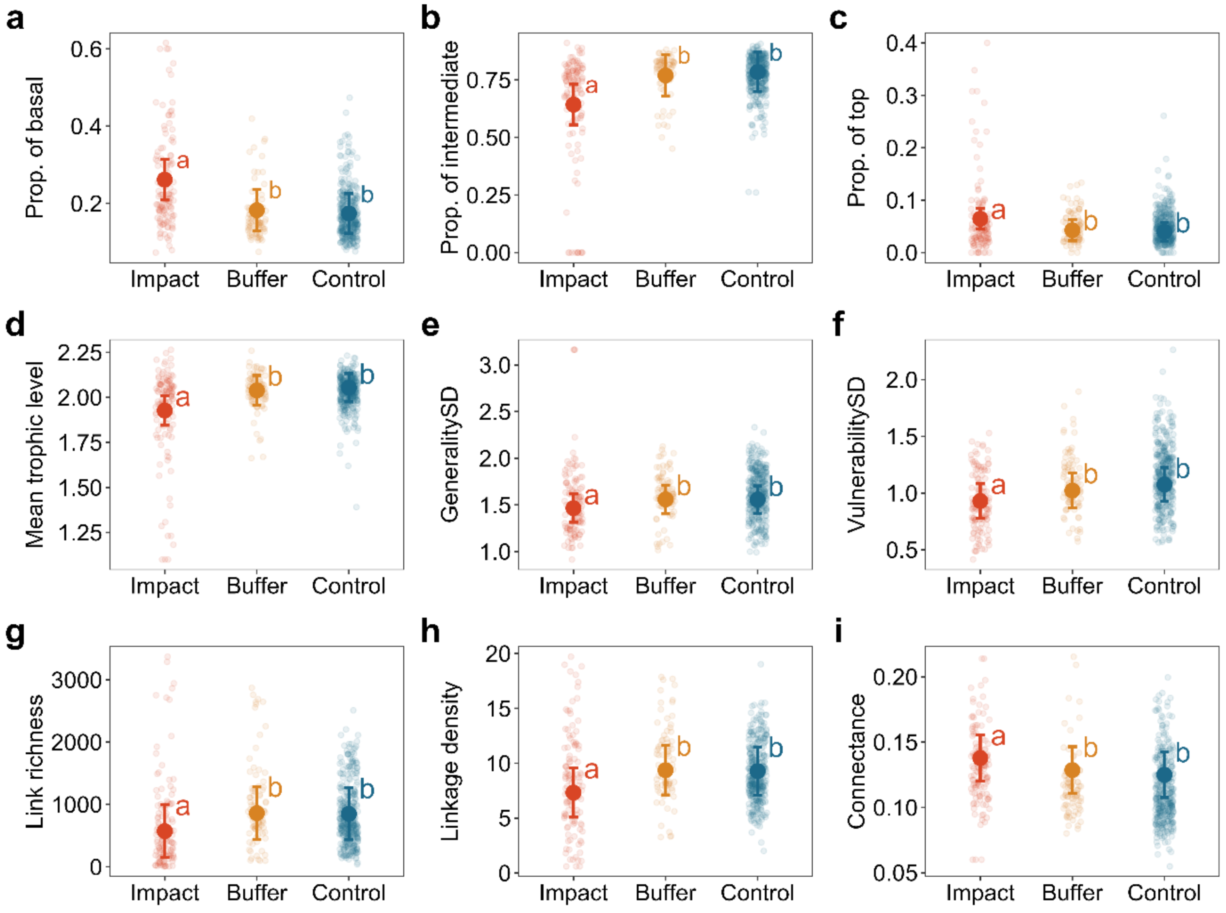

Figure 5: (a) Proportion of basal species, (b) proportion of intermediate species, (c) proportion of top species, (d) mean trophic level, (e) generalitySD, (f) vulnerabilitySD, (g) link richness, (h) linkage density, and (i) connectance of benthic food webs within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from platforms. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

2.4 Community composition

There were contrasting effects of contamination on the abundance and richness of different trophic groups, indicating that hydrocarbons and heavy metals disproportionately affect different parts of the food web (Figures. S2-S3). A significant decrease in abundance was observed in the impact sites compared to the buffer and the control for detritivores, filter feeders, and predators, with no significant effect on the other three trophic groups (Figure S2). There was also a significant reduction in species richness in the impact sites compared to the buffer and control for detritivores, grazers, filter feeders, and predators, with no significant difference for the remaining two trophic groups (Figure S3). The Spearman rank coefficient tests showed that concentrations of hydrocarbons and heavy metals were positively correlated with each other. The Mantel test results showed that significant correlations between environmental variables and trophic groups were mainly negative. Strong negative correlations were observed for filter feeders and detritivores when they interact with Cr, Cu, Ni, and Pb (Mantel's $r < -0.2$; Figure 6). The n-alkanes, however, were positively correlated with filter feeders and detritivores, which contained the top ten indicator species of the BACI treatment (Figure S5).

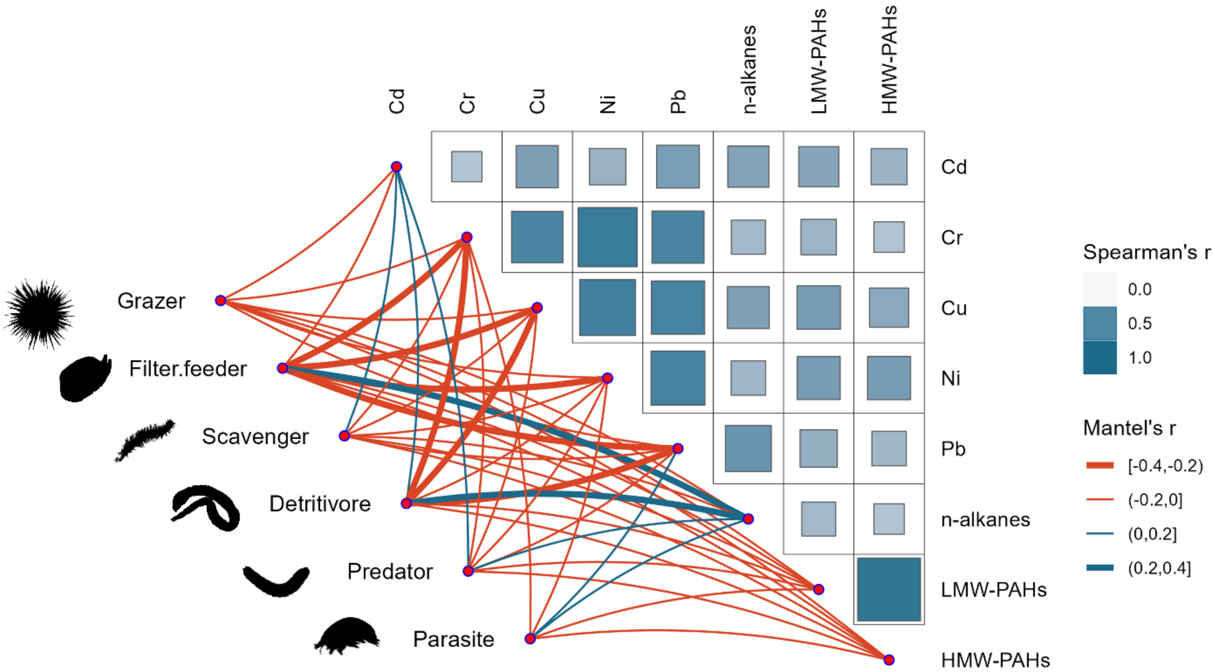

Figure 6: Correlations among the abundance of six trophic groups, heavy metals, and hydrocarbons. Square size and colour gradient represent correlation strength (Spearman rank correlation: larger

square with deeper blue indicate stronger correlation). Only lines with p-values less than 0.01 are shown. The colour and thickness of lines represent correlation direction and strength (Mantel test: red – negative correlation; blue – positive correlation; thicker lines are stronger correlation). An indicator species is attached to each trophic group as identified by the random forest model (Figure S4).

2.5 Discussion

Anthropogenic activities in the marine environment have profound impacts on biodiversity and ecosystem functioning (Carrier-Belleau, Drolet, McKindsey, & Archambault, 2021). Understanding ecological responses of benthic communities to oil and gas platforms is essential for assessing industrial impacts on marine ecosystems (Birchenough & Degraer, 2020). For the first time, this study demonstrated negative causal relationships between oil and gas exploitation activities and benthic food web complexity. The underlying changes in benthic community composition are driven by loss of sensitive species, loss of larger organisms, declining abundance, and dominance of opportunistic species. These are typical indications of ecosystems under disturbance, which in general align with earlier non-BACI studies examining the effects of drilling wastes from oil and gas platforms (Ellis et al., 2012; Henry et al., 2017). By linking platform exploitative activities with changes in the food web, this study also demonstrates a more holistic perspective that informs the interdependence of community turnover and food web patterns along environmental gradients (Frelat et al., 2022).

2.5.1 Contamination concentrations

Elevated concentrations of total hydrocarbons and heavy metals were identified up to 500 m from platforms, but not beyond this range, which supports our first hypothesis (see Fig. 3). Sources of these contaminants are associated with exploratory drilling, hydrocarbon exploitation, historical accumulation of drilling piles, and natural seeps from the oil fields (Razaz, Di Iorio, Wang, Daneshgar Asl, & Thurnherr, 2020; Stokke et al., 2022). Elevated hydrocarbon concentrations prior to the commencement might be attributed to exploratory-drilling contamination or naturally high background concentrations near natural seeps (Steichen Jr, Holbrook, & Osenberg, 1996). For hydrocarbon concentrations after the commencement, the use of oil-based muds as drilling fluids may have been a key source of oil release into the benthic environment (Breuer et al., 2008; Davies et al., 1984), until they were prohibited with the adoption of OSPAR Decision 2000/3 (OSPAR Commission, 2000). Produced water from oil and gas reservoirs after drilling also contains heavy metals used in the drilling processes and naturally occurring PAHs from crude oil (Jacobs, Grant, Kwant, Marquenie, & Mentzer, 1992), and its dissipation may cause continuous exposure of hazardous substances on benthic habitats near the structure. Discharged PAHs and heavy metals may accumulate in the benthos through sedimentation, owing to their hydrophobic nature or being absorbed by particles (M. Liu, Zhang, Liao, Chen, & Fan, 2015; Shih, Binh, Chen, Chen, & Dong, 2016), where their effects on ecological communities may persist long after drilling activities cease.

This study provides an objective approach for determining the zone of influence based on total hydrocarbon concentrations measured at different distances before and after commencement of hydrocarbon production. The incorporation of a buffer treatment acknowledges that there is no definitive threshold at which the effects of oil contamination can be deemed to have completely dissipated. This is because the precise zone of influence is contingent upon the magnitude of production, infrastructure characteristics, and oceanographic conditions (Terlizzi et al., 2008). To address uncertainties in delineating specific distance-based treatments, previous studies either advocated for a continuous distance analysis to examine various zones of influence for hazardous chemicals and ecological effects (Davies et al., 1984; Kingston, 1992; Olsgard & Gray, 1995) , or adopted distance-based zone analysis (e.g., near-field < 1 km or far-field > 1 km) to examine whether benthic communities exhibited detectable changes from platform exploitation activities in comparison to the reference (Currie & Isaacs, 2005; Henry et al., 2017). Our method simplified the analysis by including the buffer treatment in the distance zones, which not only accounts for the spatial intricacies of the transition zone from high oil contamination to background levels but also assesses whether intermediate oil contamination alters benthic biodiversity and food web structure. The absence of clear chemical or ecological effects within the buffer sites indicates that the main impacts of oil and gas platforms are consistently found much closer to the structures and thus future studies and regulation guidelines could focus on this impact site.

Established threshold values of contaminants could be used to explain the detectability of changes in the benthic communities in these distance-based treatments around platforms (Fig. 4-5). For example, the OSPAR Coordinated Environmental Monitoring Programme utilises the lower tenth percentile of Effect Range Levels (ERLs) to identify the transition from acceptable to unacceptable environmental status associated with deleterious biological effects on organisms (Long, Macdonald, Smith, & Calder, 1995; OSPAR Commission, 2000). When compared to ERLs, median concentrations of heavy metals and hydrocarbons in the buffer and control sites were below the threshold values (Table S5), but median concentrations of some PAHs (e.g., benzo[ghi]perylene, dibenzothiophene) and Pb were close to or exceeded the ERL values in the impact sites. This supports the consistently negative effects of PAHs on all trophic groups and the strong negative correlation between Pb and the detritivores and filter feeders (Fig. 6). Negative impacts on these feeding groups could also be attributed to mixtures of metals and hydrocarbons as their combinations could result in synergistic and antagonistic effects on benthic community (K. Carman, Fleeger, & Pomarico, 2000; Millward, Carman, Fleeger, Gambrell, & Portier, 2004). Whilst previous studies have identified hydrocarbons as the main source of sediment toxicity to benthic invertebrates in the North Sea (Grant & Briggs, 2002), our findings help to identify which individual compounds may make the strongest contribution to ecological impacts in the surrounding sediments.

2.5.2 Biomass and diversity

Elevated contamination of hydrocarbons and heavy metals in the impact sites elicited clear ecological impacts, with reductions in both components of biomass (abundance and mean body size) and biodiversity (species richness and Pielou's evenness), supporting our second hypothesis (Fig. 4). Similar reductions in biomass and biodiversity of benthic communities have been observed from previous assessments of hydrocarbon exploitation in the North Sea and elsewhere (Ellis et al., 2012; Paine et al., 2014). Importantly, these impacts were not consistent throughout the food web, with declining species richness and abundance only observed for the filter feeder, predator, grazer, and detritivore groups (Figs. S2-S3). Elevated sediment toxicity could impose adverse physiological stress on organisms across multiple trophic groups including detritivores (e.g., brittle star *Amphioplus sp*.), grazers (e.g., copepod *Cletocamptus sp*.) and filter feeders (e.g., bivalve *Lucinidae*) (K. R. Carman, Fleeger, & Pomarico, 1997; Honda & Suzuki, 2020; Menzie, D., & Leathem W. A., 1980). The reduction in species richness of predators could be either a direct consequence of contaminants, or through secondary extinction due to lower prey availability (both in terms of abundance and diversity of prey) following general defaunation of the impacted sites (Venturini & Tommasi, 2004). The success of detritivorous polychaetes in the impacted sites (Fig. S5) characterizes environments contaminated with anthropogenic discharges including hydrocarbons and metals (Pearson & Rosenberg, 1978; Rosenberg, 2001; Stark, Kim, & Oliver, 2014). Some of benefitting taxa included capitellids, cirratulids, and dorvilleids, which are known to be resilient to contamination with detoxification mechanisms and opportunistic traits (Stark, 2022; Suriya, Bharathiraja, Sekar, & Rajasekaran, 2012). The associated changes in functional diversity of the broader community could have consequences for ecosystem functioning, including altered bioturbation, energy fluxes to higher trophic levels, decomposing rates of organic matter, and secondary production (Danovaro et al., 2008).

Notably, there was a reduction in the individual mean body mass of benthic invertebrates in the contaminated sites compared to those further away from platforms, which implies that larger organisms are generally more susceptible to the environmental impacts of oil and gas platforms (Fig. 4b). This follows the pattern of benthic succession following exposure to organic enrichment and metal pollution described in early studies (Pearson & Rosenberg, 1978; Ryu et al., 2011). These are two mainstream theories that explain changes in community size structure in response to contamination: size-plasticity and size-dispersal (Farjalla et al., 2012). The size-plasticity theory suggests that organisms have adaptive survival mechanisms to the presence of contamination, as smaller organisms can relocate limited energy resources from individual development (e.g., growth) to metabolic costs of detoxification (Hadfield & Strathmann, 1996; Y. Liu et al., 2017). Nevertheless, the size-dispersal theory argues that smaller organisms are more susceptible to contamination, as their spatial distribution is governed more by environmental filtering mechanisms than dispersal limitation (Cottenie, 2005; Isabwe et al., 2022). Our findings support the size-plasticity theory, as larger organisms are disproportionately affected by elevated oil contamination. The dominance of opportunistic species in the impact sites also supports this theory given that they have relatively small size, short life span, and rapid maturation (Ryu et al., 2011).

In addition, marine ecosystems are highly size structured, with larger organisms typically occupying higher trophic levels and preying on smaller species (M. Nordström, Aarnio, Törnroos, & Bonsdorff, 2015; O. L. Petchey et al., 2008). In a classic Eltonian biomass pyramid, top predators are only sustained when the ecosystem is in a productive state (Elton, 1927). Limited supply of resources, including the loss of primary consumers, may limit the energy fluxes needed to support large organisms at higher trophic levels.

The random forest model identified top benthic species that could be potential bioindicators of hydrocarbon exploitation by distinguishing benthic environments between the impact and control sites. *Capitella capitata* was the most important species, dramatically increasing in abundance in the impact compared to the control (Fig. S5). *C. capitata* is a typical bioindicator in disturbed environments (Pearson & Rosenberg, 1978; Ryu et al., 2011; Tomassetti et al., 2016), particularly following discharges of organic matter from fish farms or oil and gas platforms (Henry et al., 2017; Keeley, Macleod, Hopkins, & Forrest, 2014). Its opportunistic life history allows its adaptation to organically enriched environment, including rapid re-establishment after disturbance, high population increase, and resilience to anaerobic and excessive loading of organic matter (Tsutsumi, 1990). Nevertheless, its limited intraspecific competition, coupled with the association and interaction with bacteria in the decomposition of the organic matter, contribute to its displacement in less contaminated areas (Kunihiro et al., 2011). As for *Capitellidae*, polychate species from the *Spionidae* family thrived in the impact treatment, which aligns with previous observations (Croquer, Bone, Bastidas, Ramos, & Garcia, 2016; Tsutsumi, 1987; Washburn, Rhodes, & Montagna, 2016). In addition to polychaetes, the echinoderm *Amphiura filiformis* and the hatchet bivalve *Thyasira* spp. showed high importance in the model. *Amphiura filiformis* was intolerant to oil contamination (Olsgard & Gray, 1995), with a 60% mean abundance reduction in the impact treatment relative to the control. The *Thyasira* spp. are known to be associated with oil drill cuttings with high resilience to hydrocarbon contamination (Connor et al., 2004; Kingston, Dixon, Hamilton, & Moore, 1995; Ugland, Bjørgesæter, Bakke, Fredheim, & Gray, 2008), showing mean abundance increase in the impact (Fig. S5).

2.5.3 Benthic food web structure

Changes in biodiversity patterns are intricately linked to altered structure of benthic food webs (Sokołowski et al., 2012). The observed reduction in mean trophic level in the impact sites (Fig. 5d) was associated with a disproportionate loss of larger organisms (Fig. 4b). Mean trophic level estimates the mean number of energy transfer steps from the base to higher-level organisms, reflecting the efficiency of trophic transfer (J. E. Duffy et al., 2007). For communities adjacent to oil and gas platforms, a decrease in mean trophic level signifies inefficient energy transfer, implying that longer food chains can only be sustained in healthy and productive ecosystems, whereas impaired ecosystems with contamination exhibit shorter food chains (S. Pimm & Lawton, 1977). A decrease in mean trophic level is thus a typical manifestation of predator collapse (Arim, Marquet, & Jaksic, 2007; Branch et al., 2010). When organisms are lost from the top level of the food web, intermediate consumers could become top-level species in new food webs if they lose all their predators. Thus, the increased proportion of top species in the impact sites in this study is unlikely to reflect the introduction of new top predators, but rather a reallocation of intermediate species that were resilient to the contamination (Figs. 4a-b; (M. C. Nordström & Bonsdorff, 2017)).

The third hypothesis is strongly supported by the decreased number of trophic links and linkage density in the impact sites (Figs. 5g-h). Both metrics are descriptors of food web complexity reflecting decreased number and density of energy pathways (Jennifer A Dunne et al., 2004). In the impacted sites, food web structure exhibits greater homogeneity, given that lower generalitySD and vulnerabilitySD demonstrates reduced variability in diet breadth of predators and predation pressure on prey (Figs. 5e-f) (Galiana, Lurgi, Montoya, & López, 2014). This may relate to decreased mean body size as species in contaminated environments are likely to share common life-history traits (in this case, smaller body size). Variations in diet breadth are associated with life-history traits, especially body size in an allometrically scaling system (Moya-Larano, 2011; Quevedo, Svanback, & Eklov, 2009; Rooney, McCann, Gellner, & Moore, 2006). Although no discernible changes were observed in the mean generality and vulnerability, these results suggest that most remaining species in the community maintain an intermediate number of trophic links. The loss of specialist species in the impacted sites could be attributed to their lack of alternative resources or the inability to rewire their trophic interactions. (Feder & Pearson, 1988; Thierry et al., 2011). In contrast, generalist species exhibit a reduction in links within impacted environments due to a diminished pool of resource species. However, they are able to exploit alternative prey for sustenance and potentially establish new trophic links by capitalizing on novel resources. Such diet switching of generalist species in response to disturbances is well documented as an important dynamical feature of food webs in prior studies (Ostfeld & Keesing, 2000; Polis & Strong, 1996; Shaner & Macko, 2011).

The increase in connectance in the impact sites is counterintuitive, with connectance often shown to decline when food webs are exposed to increasing stress (O'Gorman et al., 2019; Windsor, Pereira, Tyler, & Ormerod, 2019). This may be driven by the homogenisation of diets (i.e., reduced standard deviations of generality and vulnerability). Diets of smaller predators typically consist of a narrower prey body-mass range (Yvon-Durocher, Montoya, Emmerson, & Woodward, 2008). The inverse relationship between diet breadth and predator size is well-established across aquatic ecosystems (Digel, Riede, & Brose, 2011). Owing to limited prey availability, specialists were lost and generalists converged on similar diets by feeding on the same, albeit fewer, remaining prey (M. Nordström et al., 2015). Fewer species in the impact sites are thus much more tightly connected, which may be a stabilising mechanism to maintain community persistence in response to disturbances. For example, more connected food webs tend to be more robust to secondary extinctions and more resistant to biotic invasions (J. A. Dunne, R. J. Williams, & N. D. Martinez, 2002; Gilbert, 2009; Smith-Ramesh, Moore, & Schmitz, 2017). Thus, homogenised food webs and increased connectance could help mitigate fluctuations and benefit long-term stability of complex networks, acting as a stabilizing mechanism for a rapid return to equilibrium following a disturbance (Allesina & Pascual, 2008; Kondoh, 2003).

2.6 Conclusion

This study contributes new evidence for the effects of oil and gas platforms on marine benthic biodiversity by revealing negative causal links between contamination and food web properties, primarily through the disproportionate loss of large organisms from high trophic levels, the homogeneity of consumer-resource interactions, and a more connected food web. The integration of community structure and food web properties provides a more holistic view of how contamination can affect benthic communities, simplifying food web structure vertically through reductions in larger species, and horizontally through reductions in species richness. The comparison between observed concentrations of hydrocarbons and heavy metals, established guideline thresholds, and ecological responses across a spatial gradient in the vicinity of oil and gas platforms also provides an objective means of determining the scale of their environmental impacts. Our BACI framework was key in determining causal links between contamination and changes in the benthos and offers a robust methodological basis for future studies assessing the effects of platform decommissioning. Ecological responses can be compared between actively operating and decommissioned platforms, for example, to ascertain whether the magnitude of ecological recovery at decommissioned platforms is sufficient for any of the structure to be left in place. Insights from this study inform ecological best practices in managing offshore oil and gas exploitation worldwide and the design of associated monitoring programmes to better investigated anthropogenic pressures on marine ecosystem.

Acknowledgements

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Conflict of Interest Statement

The authors declare no conflict of interest.

Data Availability Statement

Sources of previously published and publicly available data are listed in the Methods. A full list of taxa and their trophic interactions will be uploaded to the open access Essex Research Data Repository when the manuscript is accepted.

Appendix: Supplementary materials for chapter 2

S2.1 List of oil and gas platforms

Table S1: A total of 9 oil and gas platforms included in the study. The start date corresponds to the commencement of oil and gas exploration and production from the platforms. It delineates the timeframe prior to the commencement of drilling activities ('before') and subsequent to it ('after') within the context of the BACI design.

Name	Start date	Gear & Mesh	Operator	Production
Alba North	1994/01	Van Veen; 0.5 & 1 mm	Chevron	Oil
Andrew	1996/06	Van Veen; 0.5 & 1 mm	BP	Oil
Beatrice AD	1981/09	Day grab; 1 mm	Ithaca	Oil
Bruce CR	1993/05	Van Veen; 0.5 & 1 mm	BP	Condensate/Oil
Clair	2005/02	Van Veen, Day grab, Hammo; 0.5 & 1 mm	BP	Oil
Forties Echo	1986/07	Day grab, Van Veen; 1 mm	Apache	Oil
Lomond	1993/07	Day grab; 0.5 mm	BG	Condensate
Murdoch drilling	1993/01	Van Veen; 0.5 mm	ConocoPhilips	Gas
Vulcan 1	1987/01	Van Veen; 0.5 mm	ConocoPhilips	Gas

The start date of each platform was derived from the data repository of the North Sea Transition Authority. While the commencement date might not exactly match the start of exploitation activities or subsequent installation construction, it was the best available information to consistently identify the moment that oil and gas production began at each platform.

S2.2 Diet information of benthos

A total of six trophic groups were used based on the feeding ecology of benthic invertebrate taxa, including predator, parasite, detritivore, filter feeder, grazer, and scavenger. For detritivore, filter feeder, grazer, and scavenger, we assumed that taxa within these four trophic groups share the same broad basal resources (Table S2). For predator and parasites, we used literature review to identify preys / hosts of corresponding taxa. Predator-prey /parasite-host interactions were integrated with trophic interactions between basal resources and the other four trophic groups. The study assumed that a trophic interaction was established when two species were present within a same sampling site. This approach has been widely used in the construction of food webs (Garrison, Nordstrom, Albertsson, & Nascimento, 2022; C. Gray et al., 2015; M. S. Thompson et al., 2018).

Prey / host data for predator and parasite were based on literature search with references given at the species level. We used the following protocols to address the absence of diet data: a) When species level was not possible, preys were recorded at a broader (i.e., genus) taxonomic level; b) If a prey cannot be found for a specific species but can for a different species within the same genus, the same prey was assumed for this species with this inference recorded; c) Species recorded at a higher taxonomic level (i.e., family) had their prey recorded as those recorded from other species lower down the taxonomic rank; d) preys were based on taxa at a higher taxonomic level or inferred from other species within the same genus when no diet information can be found; e) If none of above criteria provide dietary information, we used the morphology of feeding apparatus to infer most plausible trophic group.

The assignment of trophic group for each taxon was based on its dominant feeding behaviors. For omnivore taxa showing more than one feeding behaviors, we chose the trophic group that best represents their primary feeding ecology. Juvenile and adult benthic macrofauna were considered indifferently due to very rare age-based feeding differences in identified species. The taxonomic information excludes fish, plants, and pelagic species.

Table S2: Resources for predators and parasites were identified using literature search. The study assumed that a set of basal resources were diet sources for detritivore, filter feeder, grazer, and scavenger.

Trophic group	**Prey or Basal Resources**
Detritivore	FPOM, bacteria, fungi, protists, microalgae, faeces
Filter feeder	FPOM, bacteria, fungi, microalgae
Grazer	microalgae, macroalgae
Scavenger	carrion, CPOM, faeces

Considering that diet information for benthic invertebrates could be scarce for some taxa, we identified feeding guilds for each taxon based on their primary feeding source. Diet information was collected from published literature, available databases including but not limited to Marine Register of Marine Species, The Conchological Society of Great Britain and Ireland, World list of Marine, Freshwater and Terrestrial Isopod Crustaceans, and British Myriapod and Isopod Group, and antidotal evidence inferred from their feeding apparatus or phylogenetic related taxa.

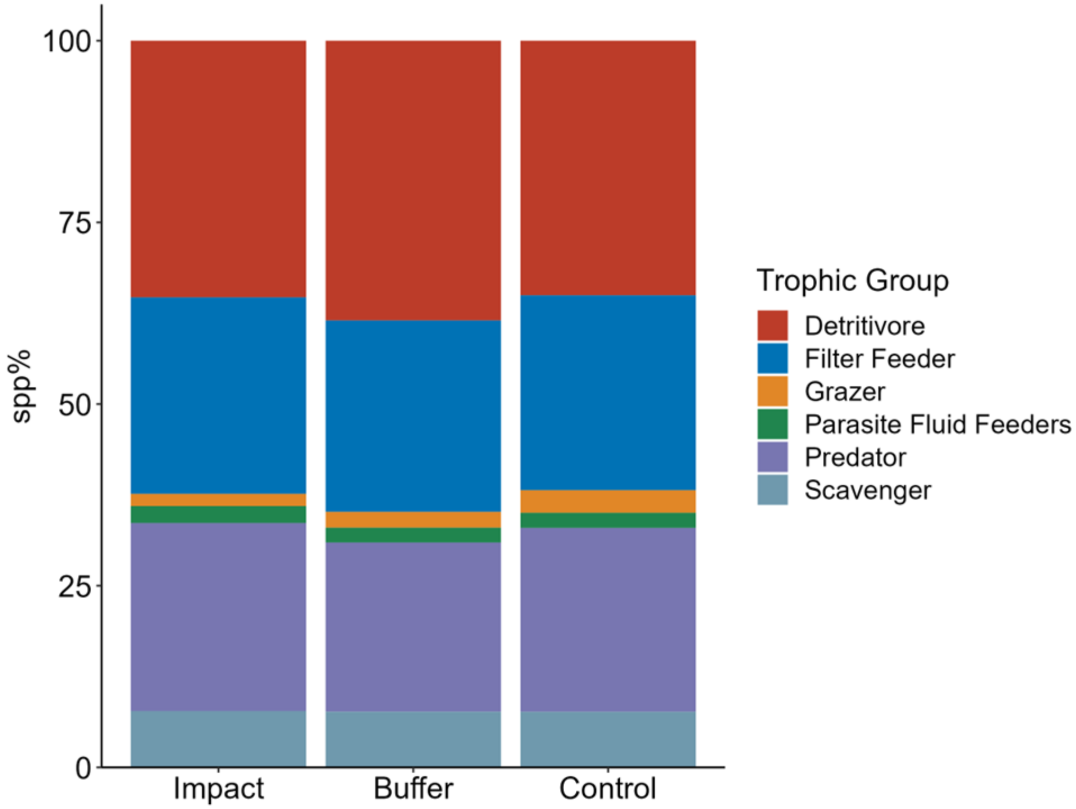

Figure S1: Percent of species richness of each trophic group in each BACI treatment.

Predators: benthic invertebrates that are active carnivory and utilize other benthic invertebrates as their food sources. We consider taxa as predators only when their diet information supports its feeding interactions with another benthic invertebrate(s). For taxa feeding on small suspended animals (i.e., copepods, zooplankton), they will be listed in the filter feeding guild.

Detritivore: Detritus as its main diet; Benthic deposit-feeding or tuberculous feeding invertebrates living in the surface or sub-surface sediment environment, unless specific feeding behaviors listed.

Filter feeder: Benthic invertebrates feed on suspended organic particles in the water column. It is characterized by bivalve, hydrozoa, ciliate, foraminifera, drag powered swimming amphipods. For taxa with little diet information, certain families are assumed to be filter feeder: Hydrozoa (feeding via polyp), Tanaidacea, Phyllophoridae filter-feeding with tentacles, Mysidae family (presumed deep-sea filter feeding swimming shrimp), Phylum Foraminifera.

Scavenger: Benthic invertebrates feed on dead animal remains or large (compared to particles fed by detritivore) organic particles in the sediment. Certain families are assumed to be scavenger: Janiroidea, Lysianassida, Cumacea. It also includes carnivorous invertebrates without identifiable gut content information (e.g., *Protodorvillea kefersteini*, *Dorvilieidae* family)

Grazer: Herbivore benthic invertebrates relies on plant materials (i.e., macroalgae). For taxa (e.g., sea urchin) feeding on kelps (although sea urchins feed on sponges but we consider its herbivorous primary feeding as the basis for this feeding guild. Certain families are assumed to be grazer: Oedicerotidae feeding on Ulva lactuca (sea lettuce)

Parasites: Benthos at certain or entire life stages absorb nutrients or form a symbiotic relationship with another benthic invertebrate host. Fish parasites are generally excluded in this feeding guild. It includes micro-predation (i.e., amphipods feed on sea cucumber's surface tissues; The diet of *Acidostoma nodiferum* contains nematocysts of sea anemone).

Table S3: List of food web metrics, their definitions, ecological implications and references.

Metrics	**Definition**	**Implications**	**Reference**
Proportion of basal	The fraction of basal nodes in the community that feed on no resources but have one or more consumers.	The proportion of taxa that form a major part of total resource pool determining the base structure of food webs.	(J. E. Cohen & Briand, 1984; Owen L Petchey et al., 2004)

Proportion of intermediate	The fraction of intermediate nodes in the community that feed on one or more resources and have one or more consumers.	The proportion of taxa that are mostly basal feeders reflecting the components of primary consumers in food webs.	(J. E. Cohen & Briand, 1984; Owen L Petchey et al., 2004)
Proportion of top	The fraction of top nodes (species) in the community that feed on one or more resources but have no consumers.	The proportion of top predators that impose top-down controls on lower parts of food webs.	(J. E. Cohen & Briand, 1984; Owen L Petchey et al., 2004)
Mean trophic level	Mean trophic level of all the consumer's trophic resources plus 1	Trophic level describes the position of organisms at which the transfer of energy from the beginning of the food chain. Mean trophic level reflects overall trophic structure and number of organisms from high trophic level.	(Levine, 1980; R. M. Thompson, Hemberg, Starzomski, & Shurin, 2007; Williams & Martinez, 2004)
GeneralitySD	A measure of variability in terms of number of preys per consumer in	Generality indicates the amount of prey species does the average	(Bersier, Banašek-Richter, & Cattin, 2002)

	the food web normalized by linkage density	consumer eat as a proportion of total resource pool. Its standard deviation describes the dispersion of the number of trophic links out of nodes in a network.	
VulnerabilitySD	A measure of variability in terms of number of predators per prey in the food web normalized by linkage density.	Vulnerability indicates the amount of predator species does the average prey have. Its standard deviation describes the dispersion of the number of trophic links in to nodes in a network.	(Bersier et al., 2002)
Link richness	Total number of trophic interactions in the food web	Trophic interactions describe the number of energy pathways of the food web.	(Jennifer A Dunne, Richard J Williams, & Neo D Martinez, 2002)
Linkage density	Average number of trophic interactions per species in a food web.	Average number of trophic links per species infers the density of	(Jennifer A Dunne et al., 2002)

		energy pathways in the network.	
Connectance	The fraction of possible trophic interactions that are realized in a food web.	It measures the complexity and robustness of the interactions within the food web	(Jennifer A Dunne et al., 2002; E. J. O'Gorman et al., 2012)

S2.3 Trophic groups

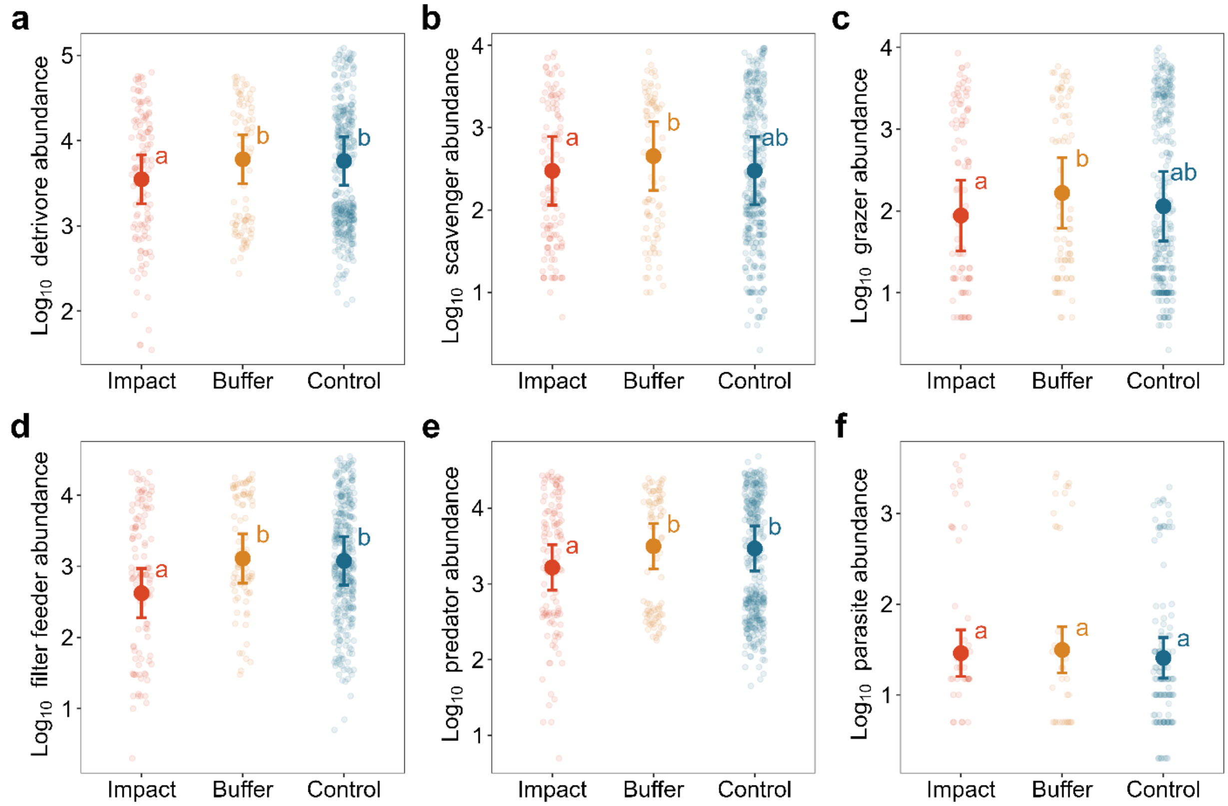

Figure S2: Log10 transformed abundance by trophic group. Mean and error bar were calculated using LMEs. Compact display letters show significant difference across BACI treatment (Tukey's HSD treatment, $p<0.05$)

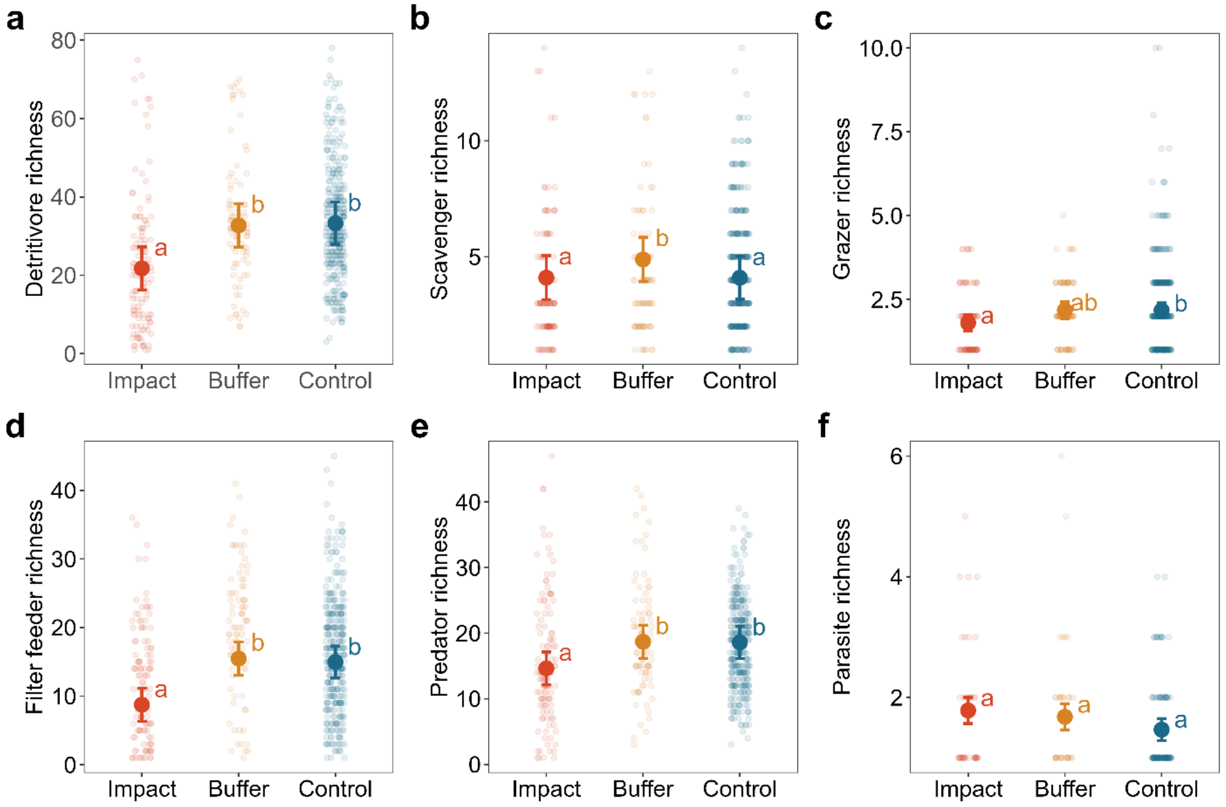

Figure S3: Species richness by trophic group. Mean and error bar were calculated using LMEs. Compact display letters show significant difference across BACI treatment (Tukey's HSD treatment, p<0.05).

S2.4 Random Forest analysis

We conducted a random forest analysis to predict the classification of BACI experimental treatments using a macrofauna abundance matrix. The decision tree n was set to 1000, and the accuracy rate of the model was 82.12%. Using mean decrease accuracy, the top 10 taxa identified as the most important contributors to the model were detritivores and filter feeders. These results suggested that the abundance data of these taxa have highest contribution to the separation of model classes, which can be used to accurately predict the classification of BACI treatments. It suggested detritivores and filter feeders may impose significant responses to exploitation.

Table S4: Number of predicted outcomes in the random forest model that are consistent with the actual treatments.

Actual/Predicted	Predicted.Impact	Predicted.Buffer	Predicted.Control
Impact	32	4	1
Buffer	2	22	2
Control	0	1	103

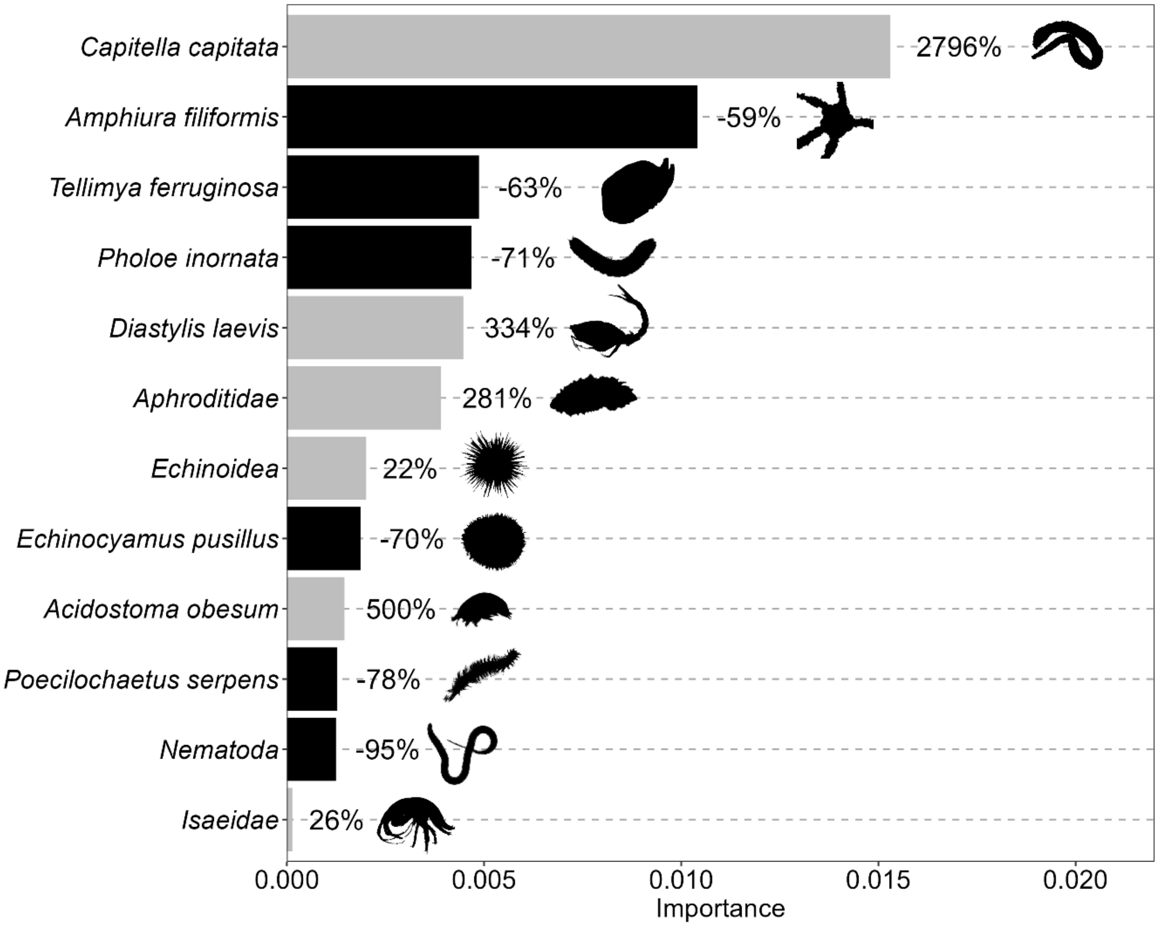

Figure S4: Top 2 taxon at each trophic group ranked by the contribution of predictive power of the classification of BACI treatments. Detritivore: *Capitella capitata*, *Thyasira flexuosa*; Predator:

Pholoe inornata, *Nephtys* spp.; Scavenger: *Cirratulidae* spp, *Poecilochaetus serpens*; Filter feeder: *Fabulina fabula, Virgularia mirabilis*; Grazer: *Westwoodilla caecula*, *Echinocardium* spp.; Parasite: *Acidostoma obesum*, *Isaeidae* spp. Gray bars indicate that the abundance of this species increase in the impact treatment compared to the control. Black bars indicate that the abundance of this species decrease in the impact treatment in relation to the control. Proportions of change in abundance were affiliated behind each bar.

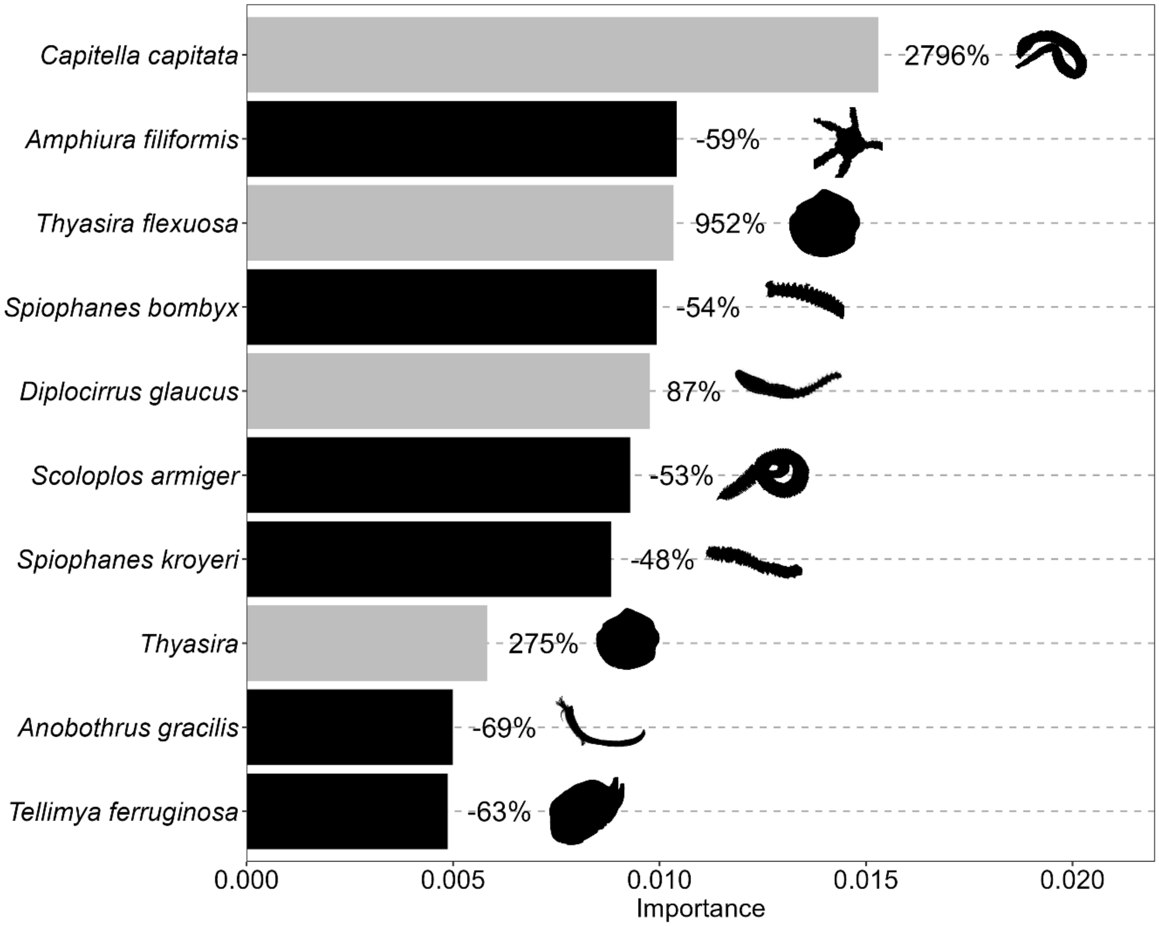

Figure S5: Top 10 species ranked by the contribution of predictive power of the classification of BACI treatment. It consists of detritivores and a filter feeder. The detritivore includes *Capitella capitata*, *Thyasira flexuosa*, *Spiophanes bombyx*, *Diplocirrus glaucus*, *Scoloplos armiger*, *Spiophanes kroyeri*, *Thyasira*, and *Anobothrus gracilis*. The filter feeder include *Tellimya* *ferruginosa* and *Amphiura filiformis*. Gray bars indicate that the abundance of this species increase in the impact treatment compared to the control. Black bars indicate that the abundance of this species decrease in the impact treatment in related to the control. Proportions of change in abundance were affiliated behind each bar.

S2.5 Oil-associated contaminant concentrations

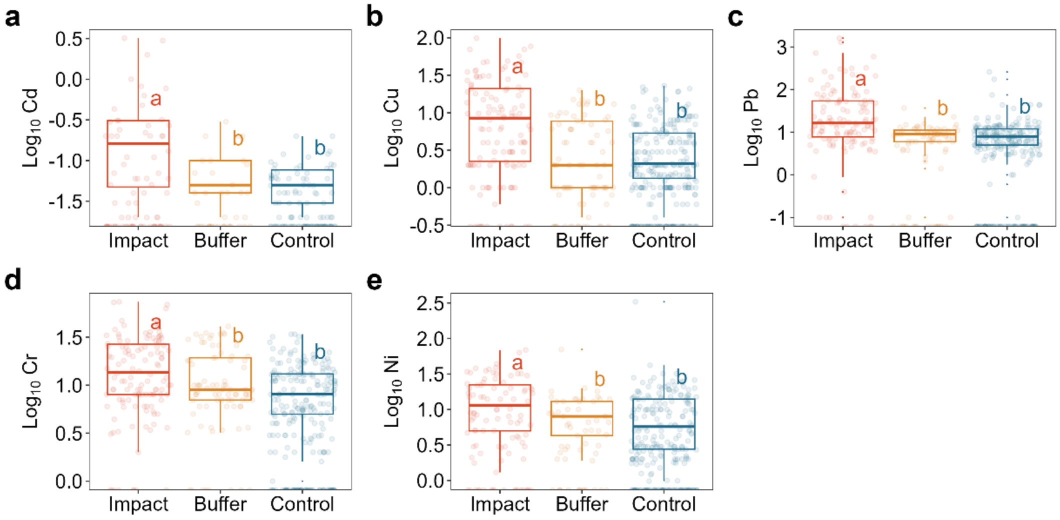

Figure S6: Log_{10} transformed concentrations of (a) Cadmium, (b) Chromium, (c) Copper, (d) Nickel, and (e) Lead in samples within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from platforms. Compact display letters show significant differences between treatments (Tukey's HSD test, $p<0.05$).

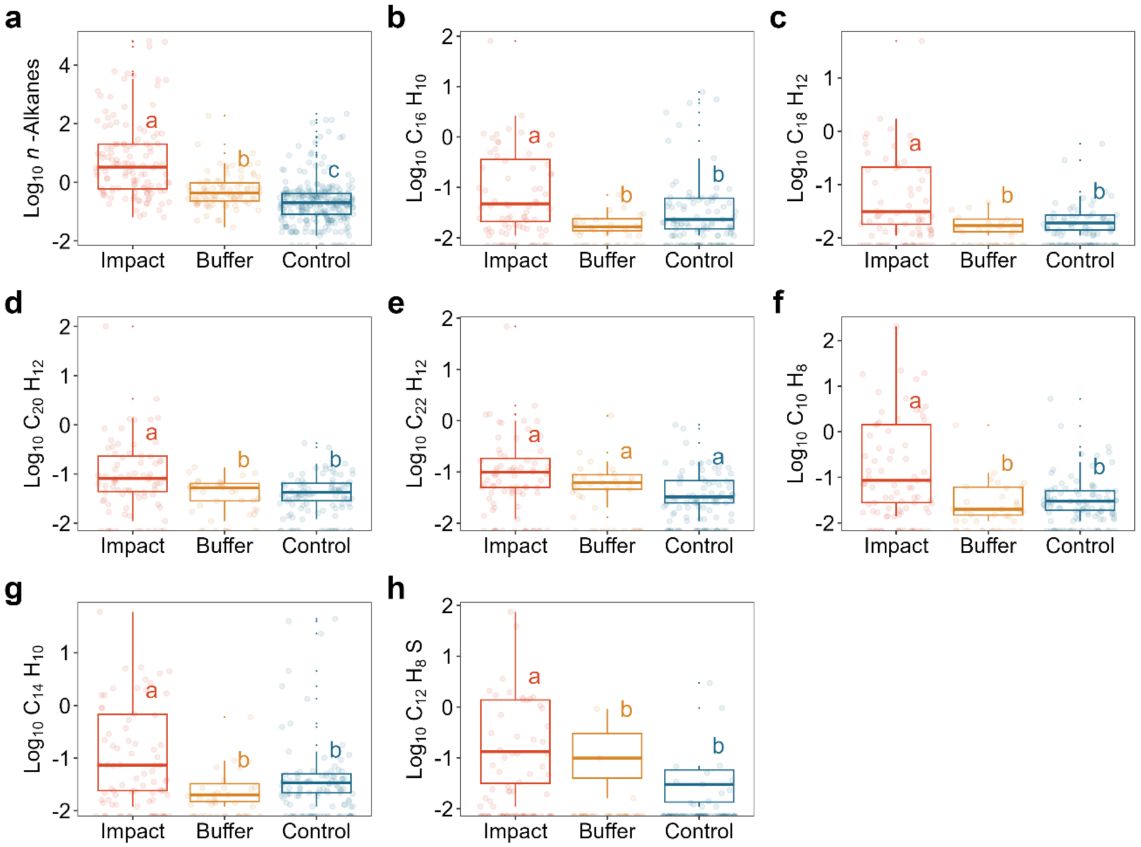

Figure S7: Log_{10} transformed concentrations of (a) normal Alkanes (*n*-Alkanes), (b) pyrene $C_{16}H_{10}$, (c) tetraphene $C_{18}H_{12}$, (d) benzo[a]pyrene $C_{20}H_{12}$, (e) benzo[ghi]perylene $C_{22}H_{12}$, (f) naphthalene $C_{10}H_8$, (g) Phenanthrene $C_{14}H_{10}$, and (h) Dibenzothiophenes $C_{12}H_8S$ in samples within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from MMS. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

Table S5: Threshold values for PAHs and heavy metals established in the OSPAR's Co-ordinated Environmental Monitoring Programme. Groups of contamination compounds include heavy metal (metal), high molecular weight PAHs (HMW), and low molecular weight PAHs (LMW). Effect Range Lows (ERLs) shows the low 10 percentile associated with concentrations (µg/kg dry weight) causing biological effects. All values are round to integer. Summary statistics removes NAs and values below detection limit (less than 0.1 ppm). 25th, median, and 75th percentiles in each BACI treatment are provided for individual compound.

Compound	**Group**	**ERL**	**Impact**			**Buffer**			**Control**		
			Q1	**median**	**Q3**	**Q1**	**median**	**Q3**	**Q1**	**median**	**Q3**
Cd	Metal	1200	40	165	310	40	50	100	30	50	79
Cu	Metal	34000	2200	8500	21000	1000	2000	7800	1300	2100	5400
Pb	Metal	47000	7090	16500	54000	6000	9000	11200	5000	8000	12000
Cr	Metal	81000	8000	13650	27000	7000	9000	19400	5000	8100	13100
Ni	Metal	21000	5000	11600	22000	4300	8000	13000	2760	5750	14000
$C_{16}H_{10}$	HMW	665	18	47	337	13	17	23	15	23	61
$C_{18}H_{12}$	HMW	384	18	31	214	13	17	22	14	19	27
$C_{20}H_{12}$	HMW	430	43	81	235	28	53	65	28	43	65
$C_{22}H_{12}$	HMW	85	50	99	200	46	62	88	25	33	66
$C_{14}H_{10}$	LMW	240	24	74	685	15	20	38	22	34	50
$C_{10}H_8$	LMW	160	28	86	1472	15	20	61	19	30	51
$C_{12}H_8S$	LMW	190	27	133	1365	16	99	920	13	30	67

S2.6 Linear mixed effect model

Table S6: Tukey’s all-pairwise comparisons of contamination among impact, buffer, and control using linear mixed effect model (LMM) Significant findings highlighted in bold.

Metrics	**Test**	**Estimate**	**SE**	**z value**	***p***
Log_{10} *n*-alkanes	Buffer-Impact	-1.1292	0.1020	-11.067	**<0.001**
	Control-Impact	-1.4348	0.1065	-13.471	**<0.001**
	Control-Buffer	-0.3057	0.1132	-2.701	**0.0187**

Log$_{10}$ HMW-PAHs	Buffer-Impact	-0.42258	0.10999	-3.842	**<0.001**
	Control-Impact	-0.3785	0.11085	-3.414	**0.00185**
	Control-Buffer	0.04409	0.12559	0.351	0.93405
Log$_{10}$ LMW-PAHs	Buffer-Impact	-0.93959	0.16566	-5.672	**<0.00001**
	Control-Impact	-0.89910	0.15783	-5.697	**<0.00001**
	Control-Buffer	0.04048	0.18474	0.219	0.974
Log$_{10}$ Heavy Metal	Buffer-Impact	-0.36528	0.06151	-5.939	**<0.0001**
	Control-Impact	-0.43457	0.06346	-6.847	**<0.0001**
	Control-Buffer	-0.06929	0.06774	-1.023	0.562

Table S7: Tukey’s all-pairwise comparisons of biodiversity metrics among impact, buffer, and control following linear mixed effect model (LMM) Significant findings highlighted in bold.

Metrics	**Test**	**Estimate**	**SE**	**z value**	***p***
Log$_{10}$ abundance	Buffer-Impact	0.58398	0.08743	6.679	**<0.0001**
	Control-Impact	0.48829	0.09545	5.116	**<0.0001**
	Control-Buffer	-0.09569	0.10052	-0.952	0.607
Log$_{10}$ individual body mass	Buffer-Impact	0.3372	0.1519	2.221	0.0675
	Control-Impact	0.7465	0.1610	4.638	**<0.001**
	Control-Buffer	0.4092	0.1706	2.399	0.0432
Species richness	Buffer-Impact	23.9146	3.0500	7.841	**<1e-06**
	Control-Impact	23.2204	3.2318	7.185	**<1e-06**
	Control-Buffer	-0.6942	3.4136	-0.203	0.977
Pielou’s evenness	Buffer-Impact	0.09409	0.01414	6.656	**<0.0001**
	Control-Impact	0.10990	0.01304	8.429	**<0.0001**

	Control-Buffer	0.01581	0.01424	1.110	0.507

Table S8: Tukey's all-pairwise comparisons of food web metrics among impact, buffer, and control following linear mixed effect model (LMM) Significant findings highlighted in bold.

Metrics	**Test**	**Estimate**	**SE**	**z value**	***p***
Proportion of basal	Buffer-Impact	-0.079032	0.008904	-8.876	**<0.0001**
	Control-Impact	-0.087460	0.009188	-9.519	**<0.0001**
	Control-Buffer	-0.008428	0.009755	-0.864	0.663
Proportion of intermediate	Buffer-Impact	0.12667	0.01542	8.217	**<0.0001**
	Control-Impact	0.14160	0.01590	8.904	**<0.0001**
	Control-Buffer	0.01493	0.01688	0.884	0.65
Proportion of top	Buffer-Impact	-0.021914	0.005688	-3.852	**0.000361**
	Control-Impact	-0.024872	0.005585	-4.453	**<0.0001**
	Control-Buffer	-0.002958	0.005998	-0.493	0.874426
Mean trophic level	Buffer-Impact	0.11235	0.01802	6.236	**<0.00001**
	Control-Impact	0.12724	0.01827	6.963	**<0.00001**
	Control-Buffer	0.01489	0.01941	0.767	0.723
GeneralitySD	Buffer-Impact	0.093978	0.033400	2.814	**0.0135**
	Control-Impact	0.092592	0.032842	2.819	**0.0133**
	Control-Buffer	-0.001386	0.035244	-0.039	0.9991
VulnerabilitySD	Buffer-Impact	0.09219	0.03033	3.040	**0.00658**
	Control-Impact	0.14563	0.03060	4.759	**<0.001**
	Control-Buffer	0.05344	0.03267	1.636	0.23027
Link richness	Buffer-Impact	288.63	49.17	5.870	**<0.00001**

	Control-Impact	276.91	52.93	5.231	**<0.00001**
	Control-Buffer	-11.73	55.79	-0.210	0.976
Linkage density	Buffer-Impact	2.04064	0.28318	7.206	**<1e-06**
	Control-Impact	1.96143	0.30154	6.505	**<1e-06**
	Control-Buffer	-0.07921	0.31804	-0.249	0.966
Connectance	Buffer-Impact	-0.009170	0.002851	-3.216	**0.00372**
	Control-Impact	-0.012743	0.002773	-4.596	**<0.001**
	Control-Buffer	-0.003573	0.002982	-1.198	0.45399

S2.7 Food web supplementary figures

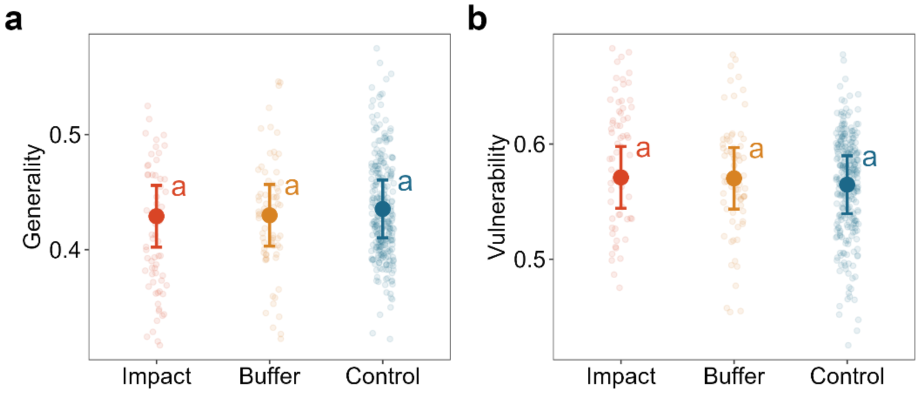

Figure S8: (a) generality and (b) vulnerability within 500 m (impact), at 500-1,500 m (buffer), or >1,500 m (control) from platforms. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

CHAPTER THREE

Benthic biodiversity and food web recovery after decommissioning of oil and gas infrastructure

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Abstract

There is a global increase in the decommissioning of offshore oil and gas (O&G) infrastructure at the end of its operating lifetime. However, there is strikingly limited empirical evidence for the environmental and ecological impacts of decommissioning. Here, we investigate the benthic biodiversity and food web properties of structures sampled in the short term (<1 year; scenario 1), medium term (1-5 years; scenario 2), and long term (>5 years; scenario 3) after decommissioning. We found reduced species richness and simplified food webs in scenario 1, followed by the first signs of recovery in scenario 2, with a slightly higher proportion of intermediate species and density of food web connections. Food webs recovered further in scenario 3, with a much greater density of interactions, but also more links and longer food chains, whilst a reduction in generality and connectance indicated an increased prevalence of specialist species. Our findings demonstrate disturbance risks associated with the decommissioning process in the short term, but a positive recovery trajectory over longer timescales. We highlight the importance of industry collecting more extensive and long-term data at multiple time points and covering different decommissioning types, establishing a standardised data workflow for integrating with available monitoring efforts, and improving stakeholder participation and data accessibility to support an environmentally sound decommissioning process.

Keywords: decommissioning; man-made structures; seabed; food web; biodiversity; marine ecosystem; North Sea

3.1 Introduction

Offshore oil and gas (O&G) infrastructure has a major presence in the global shelf seas, with >12,000 documented structures operating in 2022 (McLean et al. 2022, Martins et al. 2023). As O&G reserves are depleted, >7,500 O&G structures are approaching the end of their economic and operational purposes (Parente et al. 2006, Knights et al. 2024a). The term "decommissioning" generally refers to the process from cessation of production to the removal of obsolete infrastructure (Melbourne-Thomas et al. 2021). In many regions, legislation prohibits the dumping of whole or partial O&G infrastructure and thus removal is required (Fowler et al. 2020). Despite the pressing need of decommissioning of O&G infrastructure in the near future, there is limited understanding of environmental and ecological consequences, calling for a greater evidence base to support best practice in decommissioning (Fortune and Paterson 2018).

Although removal policies regard O&G infrastructure as redundant resources and aim at restoring the marine environment to its pristine state prior to exploitation, there is little empirical evidence for whether this is possible at all given the potential disturbance to marine ecosystems caused by O&G decommissioning (Fowler et al. 2020).The long-term presence of infrastructure has integrated hard-substrate habitats into environments dominated by soft sediment, supporting the settlement of epifaunal communities and associated biodiversity and ecosystem services not originally present locally (van der Stap et al. 2016, Coolen et al. 2020). For example, O&G infrastructure enhances biodeposition processes from epifaunal organisms which increase organic materials in the sediment near the structure, potentially leading to a higher density and diversity of macrofaunal communities (Coates et al. 2014). Furthermore, the exclusion of fishing activities around O&G infrastructure provides shelter for fish assemblages, which in turn attracts marine mammals and other top predators as foraging grounds (Jørgensen 2012, Russell et al. 2014, Fujii

2015). O&G structures can act as stepping stones for native and non−native species, modifying the connectivity of planktonic larvae (van der Molen et al. 2018). What is clear is that the removal of O&G infrastructure will likely alter associated physical and ecological processes currently occurring in and across marine areas impacted by O&G exploitation, and it is not fully clear that removal is more desirable than the pre−infrastructure state.

The environmental and ecological impacts from operational O&G infrastructure are well recognised, especially regarding contamination associated with O&G exploitation (MacIntosh et al. 2021). The primary source of contaminants are discharges of produced water and drill cuttings (Bakke et al. 2013). Produced water is a byproduct derived from O&G extraction and contains a range of contaminants including hydrocarbons and heavy metals (Neff et al. 2011). Drill cuttings consist of petroleum-soaked piles and drilling lubricants, which also contain hydrocarbons, heavy metals, and barite (BaSO4) (Ellis et al. 2012). Depending on the local hydrodynamics and volume discharged, the accumulation of contaminants could extend up to 6,000 m from the infrastructure (Olsgard and Gray 1995). Elevated concentrations of hydrocarbons, heavy metals (Cu, Ni, Pb, and Zn) and barium (Ba) have been observed above the environmental quality guidelines for threshold concentrations (Gray et al. 1990, Altin et al. 2009). Major negative impacts on biotic communities often occur within 500 m of the infrastructure, with modified community composition and simplified food webs (Davies et al. 1984, Chen et al. 2024).

The expected trajectory for benthic biota following decommissioning where this involved removal of hard infrastructure is to progressively modify towards a background community typical of local habitats, i.e., a soft bottom benthic community with little impact from O&G exploitation (Fortune and Paterson 2018). However, there are limited quantitative assessments on environmental and ecological dynamics following decommissioning or the risks associated with the decommissioning process. For example, the use of explosives and cutting tools to dismantle the infrastructure can potentially disturb marine organisms and resuspend contaminated sediment to the marine environment (Burdon et al. 2018). While most of the environmental impact assessments reported no significant environmental impact caused by the decommissioning process, it is contentious how activities with localised and short-lived impacts potentially disturb marine biota near the infrastructure (Lakhal et al. 2009). For recovering soft-sediment communities, recovery rates depend on the ecological state at the onset of decommissioning, larval and adult species dispersal, the degree of residual contamination, and other disturbances (e.g., trawling) (Schroeder and Love 2004). Related studies of biological recovery in the aftermath of O&G exploitation indicated that the recovery of ecosystem functionality typically requires 5-10 years to take effect (Gates and Jones 2012, Henry et al. 2017, Schwing et al. 2020).

In this study, we quantified the effects of decommissioning on sediment contamination and ecological responses of benthic invertebrate communities in a before-after-control-impact design. Marine benthic invertebrates have been widely used as biological indicators to measure ecological quality in the marine environment and assess the consequences and magnitude of a variety of natural and anthropogenic disturbances (Borja et al. 2000, Couce et al. 2020). Their relatively sedentary characteristics and variable tolerances to stress make benthic invertebrates ideal to examine the gradient of decommissioning impacts. Since decommissioning marks the end of O&G exploitation and associated operational disturbances, we expect an improved chemical status in benthic sediment and a shift in benthic biodiversity and food web structure towards the background environment. Considering that decommissioning involves physical disturbance, we expect benthic recovery to be more likely detected in the medium to long term rather than short term after decommissioning. Therefore, we hypothesise that decommissioning of O&G infrastructure will cause: (1) reduced concentrations of hydrocarbons and heavy metals in the sediment; (2) increased total abundance and species richness; and (3) greater food web complexity; but with effects realised in the longer term after decommissioning.

3.2 Materials and methods

3.2.1 Data compilation

We adopted an integrated dataset compiled by Chen et al. (2024) to investigate the effects of decommissioning and post-decommissioning recovery on benthic contamination, diversity, and food web topology. For each sample, this dataset contains mean abundance of each benthic taxon across typically 3-5 replicates and concentrations of hydrocarbons and heavy metals. We assigned individual body mass of each taxon using a biological trait database of Northwest Europe benthos (Clare et al. 2022). We then calculated three diversity metrics of interest: total abundance, species richness, and Pielou's evenness. The mean individual body mass at each sample was calculated by dividing total biomass by total abundance.

Each taxon in our dataset was assigned to one of six feeding groups based on their primary prey and distinct feeding characteristics: detritivore, filter feeder, grazer, scavenger, parasite, and predator. We assumed pervasive existence of nine basal resources at all sampling sites (i.e., carrion, bacteria, CPOM, faeces, FPOM, fungi, macroalgae, microalgae, and protists) and assigned subsets of those basal resources to primary consumers: detritivores, filter feeders, grazers, and scavengers (see Figure S1). We then adopted the inventory of predator prey / parasite host feeding interactions compiled by Chen et al. (2024). Feeding interactions were established for predators and parasites when their preys or hosts were also present in the same samples. For any predator or parasite with no diet information, its feeding interactions were inferred from taxa with available trophic data in the same taxonomic level. We calculated the following nine food web metrics using the '*cheddar*' package in R: proportions of basal, intermediate, and top species, mean trophic level, standard deviations of normalised generality and vulnerability (herein refer as generality and vulnerability), link richness, linkage density, and connectance (Hudson et al. 2013).

Concentrations of hydrocarbons and heavy metals in sediment were measured in the same sample of benthic taxa (micrograms per gram sediment, $\mu g g^{-1}$). Total hydrocarbon concentrations were determined by gas chromatography. Five metals were determined, including barium, copper, nickel, lead, and zinc. We summed up concentrations of cooper, nickel, lead, and zinc as a proxy of total metal concentration, while barium, extracted by sodium fusion and other similar methods, represent total concentration present in environment regardless of its chemical form or availability to marine organisms and was therefore considered in separation. Any concentration values of hydrocarbons and heavy metals below the threshold for detection of 0.01 $\mu g g^{-1}$ were assigned a value of 0.

3.2.2 Scenario defining

Since no single O&G structure in the dataset has been consistently sampled before and at multiple time points after decommissioning, we defined three scenarios that allow us to infer the general trajectory of benthic recovery across multiple structures (Table 1). Three scenarios group structures with the same sampling design (i.e., scenarios 1 & 3: before and after decommissioning; scenario 2: multiple time points post decommissioning) and timescale between decommissioning and sampling dates (i.e., short, medium, and long term). Decommissioning dates were determined from operational status of O&G structures published in North Sea Transition Authority (North Sea Transition Authority 2024) (Table S1).

Each scenarios used samples within 500 m as an impact treatment and those beyond 500 m as a control treatment. Inclusion criteria for scenario 1 were that samples must have been collected within one year of full removal in both impact and control treatments to compare with samples at both impact and control treatments before decommissioning. This allowed us to assess decommissioning effects in the short term on response variables relative to their status during the active period, while controlling for background variability over time using a BACI design. Inclusion criteria for scenario 2 were that samples must have been collected over at least two separate time points following full removal in both impact and control treatments. This allowed us to assess the medium-term recovery of our response variables, while accounting for background variability over time. Inclusion criteria for scenario 3 were that samples must have been collected more than five years after decommissioning in both impact and control treatments to compare with samples at both impact and control treatments before decommissioning. This allowed us to utilise the only structure in the database with available samples showing decommissioning effects in the long term on response variables, despite its decommissioning involving part of the structure being left in place, in contrast to the other two scenarios. We acknowledge that this precludes a perfect comparison across scenarios, but this is currently the best available data to infer the chemical and biological impacts of decommissioning through time.

Table 1: Definitions of the three scenarios used in the study

Scenario	**Interpretations**
Scenario 1	Short term: before and <1 year after full removal, i.e. O&G structures that were sampled soon after decommissioning compared to samples taken when the structures were still active.
Scenario 2	Medium term: post-decommissioning recovery 1 to 5 years following full removal, i.e. O&G structures that were sampled at early and later time points following decommissioning to examine their recovery through time.
Scenario 3	Long term: before and >5 years after partial removal, i.e. O&G structures that were sampled over five years after decommissioning compared to samples taken while the structures were still active.

A total of 17 O&G structures were analysed (Figure 1). Two O&G structures (29/07- 10Y and Single Well 44/12) met the criteria for scenario 1 (Table S2). Fourteen structures were sampled over at least two different time points after decommissioning in scenario 2 (Table S3). Only one structure (NW Hutton) was sampled more than five years after decommissioning to meet the criteria for scenario 3 (Table S2).

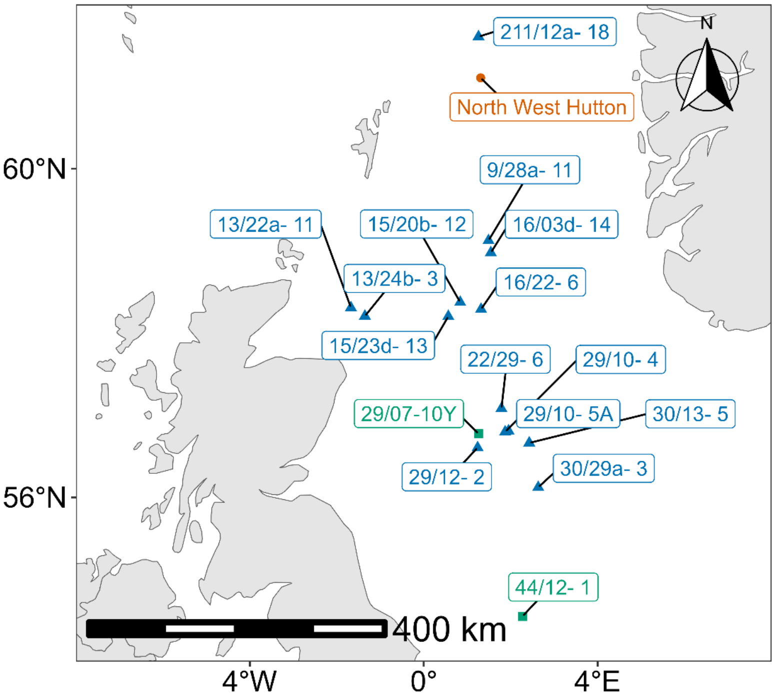

Figure 1: Locations of O&G structures that were used to compare pre- and post-decommissioning in the short term (green squares), post-decommissioning recovery (blue triangles), and pre- and post- partial decommissioning in the long term (orange circles)

3.2.3 Experimental design

We used a difference in differences quasi-experimental design to test the decommissioning effects on our response (Wing et al. 2018; Figure 2). This method compares mean changes in the impact and control, both before and after decommissioning (or in both the early and later stages post-decommissioning), to assess the effects of decommissioning whilst taking account of background variability through time. The net intervention effects (Δ) of decommissioning or post-decommissioning recovery were calculated as follow:

$$\Delta = \left(\overline{impact}_{after} - \overline{impact}_{before}\right) - \left(\overline{control}_{after} - \overline{control}_{before}\right) \tag{1}$$

where $\overline{impact}_{before}$ and $\overline{impact}_{after}$ represent means of the impact before and after intervention, while $\overline{control}_{before}$ and $\overline{control}_{after}$ represent means of the control before and after intervention. Hedge's *g* effect size was then calculated as a standardised measure to quantify the significance and magnitude of the net intervention effects, while considering a correction for small sample sizes at each O&G structure ($n < 30$) (Cohen 2013).

$$Hedge's\ g = \frac{\Delta}{Variance_{pooled}} * \left(1 - \frac{3}{4(N-2)-1}\right) \tag{2}$$

where N is the total number of samples across the impact before, impact after, control before, and control after decommissioning, and $Variance_{pooled}$ is the pooled standard deviation calculated as:

$$Variance_{pooled} = \sqrt{\frac{(n_{i,b}-1)*S_{i,b}^2+(n_{i,a}-1)*S_{i,a}^2+(n_{c,b}-1)*S_{c,b}^2+(n_{c,a}-1)*S_{c,a}^2}{n_{i,b}+n_{i,af}+n_{c,b}+n_{c,i}-4}} \tag{3}$$

where $n_{i,b}$ and $s_{i,b}$ are sample size and variance of the impact before the intervention, $n_{i,a}$ and $s_{i,a}$ are sample size and variance of the impact after the intervention, $n_{c,b}$ and $s_{c,b}$ are sample size and variance of the control before the intervention, and $n_{c,a}$ and $s_{c,a}$ are sample size and variance of the control after the intervention.

The standard error (SE) of the Hedge's g effect size was calculated as follows:

$$SE_{hedge'sg} = \sqrt{\frac{(n_{i.b}+n_{i,a}+n_{c,b}+n_{c,a})}{(n_{i,b}+n_{i,a})*(n_{c,b}+n_{c,a})} + \frac{Hedge's\ g^2}{2*(n_{i.b}+n_{i,a}+n_{c,b}+n_{c,a})}} \tag{4}$$

We then simulated 1000 bias-corrected bootstrap samples to calculate the 95% confidence intervals (CIs) assuming a *t*-distribution centred on the Hedge's g and its SE.

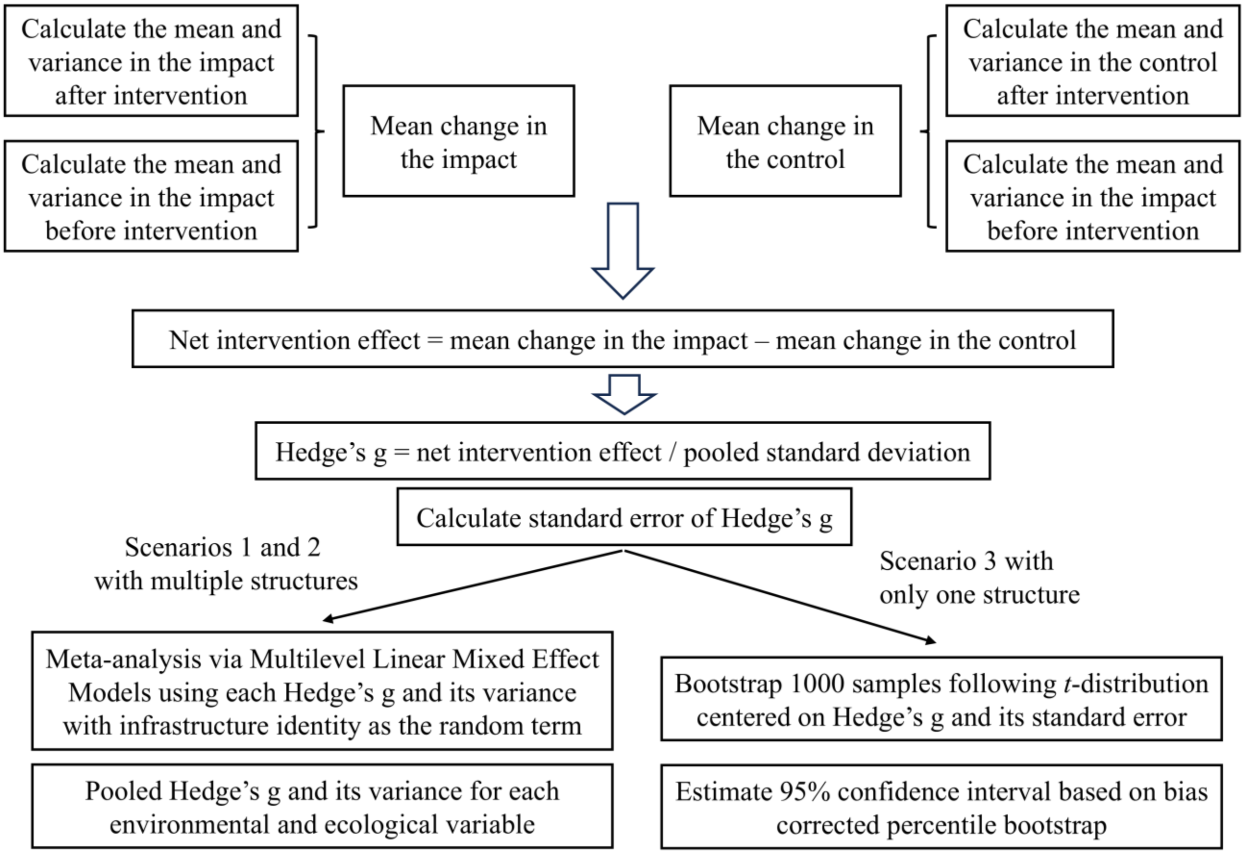

Figure 2: Workflow illustrating how environmental and ecological data were processed and analysed to examine the overall effects of decommissioning on each response variable.

3.2.4 Statistical analysis

We applied this method to a consistent set of response variables at each scenario, including environmental variables, three alpha diversity metrics, mean individual body mass, and nine food web topological metrics. All analyses were conducted in R v4.4.1 (R Core Team 2024). For scenarios 1 and 2 with multiple structures, we used the '*metafor*' package to calculate pooled Hedge's *g* effect sizes and 95% CIs for each response variable using individual estimates at each structure (Viechtbauer 2010). For scenario 3 with only one structure, Hedge's *g* and its 95% CIs at each response variable were based on its net intervention effect. Multilevel linear mixed models were applied for scenarios 1 and 2, with the same variety of response variables as moderators and infrastructure identity as a random term. Test statistics and CIs for the fixed effects were computed using a *t*-distribution. Significance was determined when 95% CIs did not overlap with zero. The magnitude of Hedge's *g* effect sizes follows the thresholds: $|g| \leq 0.2$ (small); $|g| \leq 0.5$ (moderate); $|g| > 0.5$ (large) (Durlak 2009). All results were visualised using orchard plots (Nakagawa et al. 2023).

We identified the most important taxa as bioindicators from phyla and feeding groups with significant effect sizes for abundance data. Representative bioindicators were identified when their mean abundance changes in the impact were substantially influenced by decommissioning or post-decommissioning recovery. Taxa within phyla or feeding groups that exhibited the same directionality as the overall effect size of their group were selected as the most representative members. Taxa with the highest mean abundance changes were identified as the ones contributing the most to the net intervention effects.

We applied Permutational Multivariate Analysis of Variance (PERMANOVA) to examine the independent and combined spatial (impact vs control) and temporal (before vs after decommissioning and early vs later period post-decommissioning) effects on benthic community composition. O&G structure identity was used as a blocking factor in the permutation procedure to account for non-independence of samples at the same structure. We used the "*betadisper*" function to perform a beta dispersion ANOVA, which complements PERMANOVA by testing variation within groups (Anderson 2006). This helps distinguish whether significant differences in community composition (PERMANOVA: $p < 0.05$) are due to true shifts in centroids or differences in within-group variability (spread or dispersion). We then validated the results using Analysis of Similarity (ANOSIM) to test the significance and strength of separation between groups (Clarke and Green 1988). We compared the sample medians of pairwise Bray-Curtis distances between groups using a Wilcoxon test. The Hellinger transformation was used to standardise abundance data to reduce the influence of the most abundant taxa in the ordination analysis (Legendre and Gallagher 2001). We visualised the results using Non-Metric Multidimensional Scaling (NMDS). All community composition analyses were conducted using the '*vegan*' package (Oksanen et al. 2013).

3.3 Results

3.3.1 Chemical variables

In the short term of scenario 1, there were no significant effects of decommissioning on concentrations of either total hydrocarbons or heavy metals (Figure 3a). In scenario 2, post-decommissioning recovery had a moderate significant effect on the concentration of total hydrocarbons (Hedge's $g = -0.44$; $p < 0.05$; Figure 3b), with a greater reduction in median concentration in the impact (from 1,835 to 635 µg/g) than in the control (from 14 to 6 µg/g; Table S4). In the long term of scenario 3, decommissioning had a large significant effect on concentrations of total hydrocarbons (Hedge's *g* = -1.74; *p* < 0.001; Figure 3c), with a large reduction in median concentration in the impact (from 21,500 to 876 µg/g) and little change in the control (from 8.2 to 35 µg/g; Table S4). For individual metals, decommissioning in the long term had a large significant effect on the concentration of total barium (Hedge's *g* = 3.01; *p* < 0.001; Figure S2c), with a much greater increase in median concentration in the impact (from 3,505 to 19,088 µg/g) than in the control (from 1,352 to 4,200 µg/g; Table S4). Decommissioning in the long term also had a large significant effect on the concentration of copper (Hedge's *g* = -0.99; *p* < 0.05; Figure S2c), with a reduction in the impact (from 43 to 24.4 µg/g) and little change in the control (from 3 to 4 µg/g; Table S4).

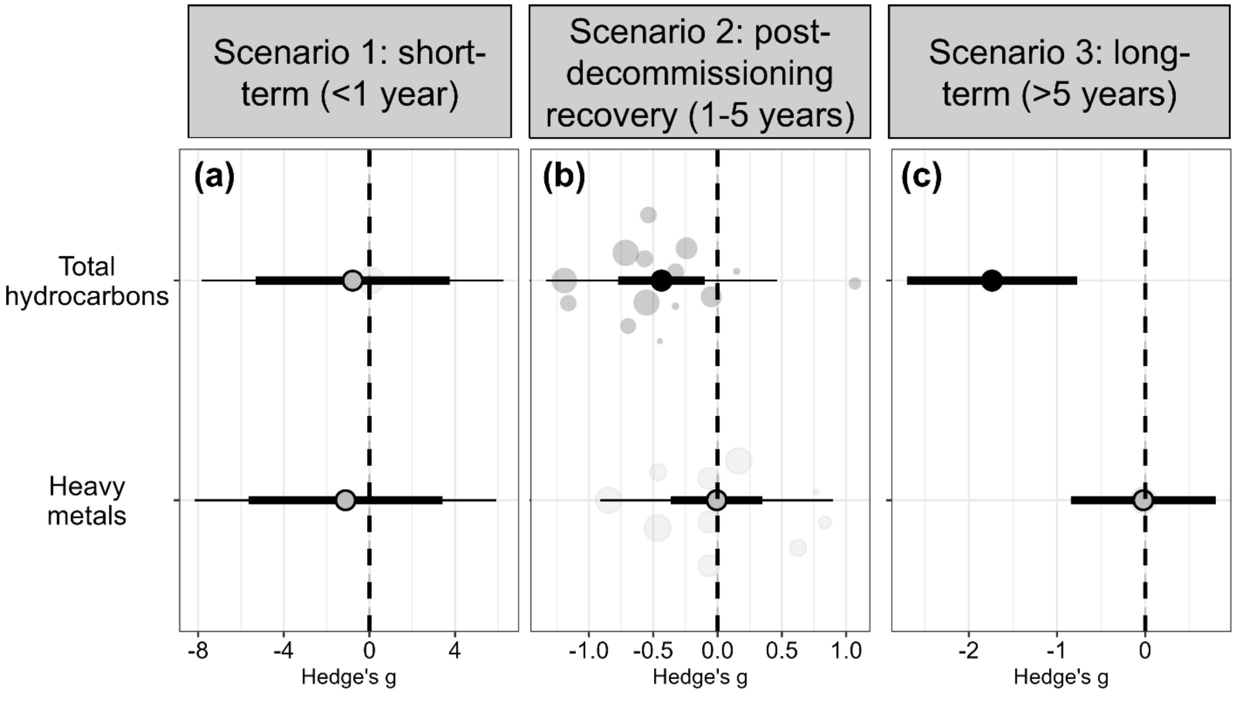

Figure 3: (a-c) Orchard plots of decommissioning effects and post-decommissioning recovery on total hydrocarbons and heavy metals for scenarios 1, 2, and 3. The circles are the pooled Hedge's *g* for each response variable, with significant effects shown in white (positive) or black (negative), and non-significant effects in grey. The thick error bars are 95% CIs, while the think

error bars are prediction intervals (PIs). Note that CIs and PIs overlap in scenario 3 because there was only one Hedge's *g* for each response variable.

3.3.2 Benthic biodiversity and composition

In the short term of scenario 1, decommissioning had a small significant effect on total abundance (Hedge's $g = 0.03$; $p < 0.05$; Figure 4a), with a smaller increase in the mean number of invertebrates in the impact (from 5,728 to 10,427) than in the control (4,388 to 11,808; Table S5). Decommissioning also had a small significant effect on species richness (Hedge's $g = 0.01$; $p < 0.05$; Figure 4a), with a reduction in the mean number of species in the impact (from 26 to 21) compared to an increase in the control (from 28 to 32; Table S5). In scenario 2, post-decommissioning recovery had a large significant effect on total abundance (Hedge's $g = 0.53$; $p < 0.001$; Figure 4b), with a smaller reduction in the mean number of invertebrates in the impact (from 23,835 to 16,134) than in the control (48,008 to 24,423; Table S5). Post-decommissioning recovery also had a moderate significant effect on mean individual body mass (Hedge's $g = -0.39$; $p < 0.01$; Figure 4b), with a greater reduction in mean body mass in the impact (from 0.119 to 0.1 g) than in the control (0.129 to 0.102; Table S5). In the long term of scenario 3, decommissioning had large significant effects on total abundance (Hedge's $g = 1.84$; $p < 0.001$), species richness (Hedge's $g = 1.42$; $p < 0.01$), and Pielou's evenness (Hedge's $g = 0.97$; $p < 0.05$; Figure 4c), with greater increases in all three metrics in the impact compared to the control (Table S5).

In the short term of scenario 1, the PERMANOVA explained 11.9% of the total variation in combined effects of spatial (impact vs control) and temporal (before vs after decommissioning) treatments. There was a significant temporal effect (PERMANOVA: $R^2 = 0.075$; $p < 0.001$) but no significant spatial effect (PERMANOVA: $R^2 = 0.034$; $p > 0.05$) on community composition

(Figure 4d). Differences in within group variation were not significant (beta dispersal ANOVA: $F = 2.46$; $p > 0.05$), which suggested that significant differences reflected true shifts in community structure, which were nevertheless quite small in size (ANOSIM: $R = 0.076$; $p < 0.05$). In the post-decommissioning recovery of scenario 2, there was significant temporal effect (PERMANOVA: $R^2 = 0.008$; $p < 0.001$) but no significant spatial effect (PERMANOVA: $R^2 = 0.005$; $p > 0.05$) on community composition (Figure 4e). There was significant within-group variation, suggesting excessive dispersal in communities (beta dispersal ANOVA: $F = 5.3$; $p < 0.001$). The separation of communities between groups was not significant, which did not support strong compositional changes (ANOSIM: $R = 0.03$; $p > 0.05$). Thus, whilst PERMANOVA showed significant results, the low variance explained (1.2%) suggested subtle shifts in communities in the recovery, which were likely due to large within-group variations. In the long term of scenario 3, the PERMANOVA explained 58.9% of the total variation and had significant spatial effects (PERMANOVA: $R^2 = 0.20$; $p < 0.01$) and temporal effects (PERMANOVA: $R^2 = 0.33$; $p < 0.001$) on community composition (Figure 4f). There were no significant differences in within-group variations (beta dispersal ANOVA: $F = 0.27$; $p > 0.05$), suggesting that decommissioning substantially altered communities between groups. This was also validated by a high separation of communities between groups (ANOSIM: $R = 0.87$; $p < 0.001$). In terms of beta diversity between groups, the comparisons of median Bray-Curtis dissimilarity demonstrated that communities witnessed a slow and subtle shift over time, and eventually became more similar between impact and control in the long term after decommissioning (Figure S3).

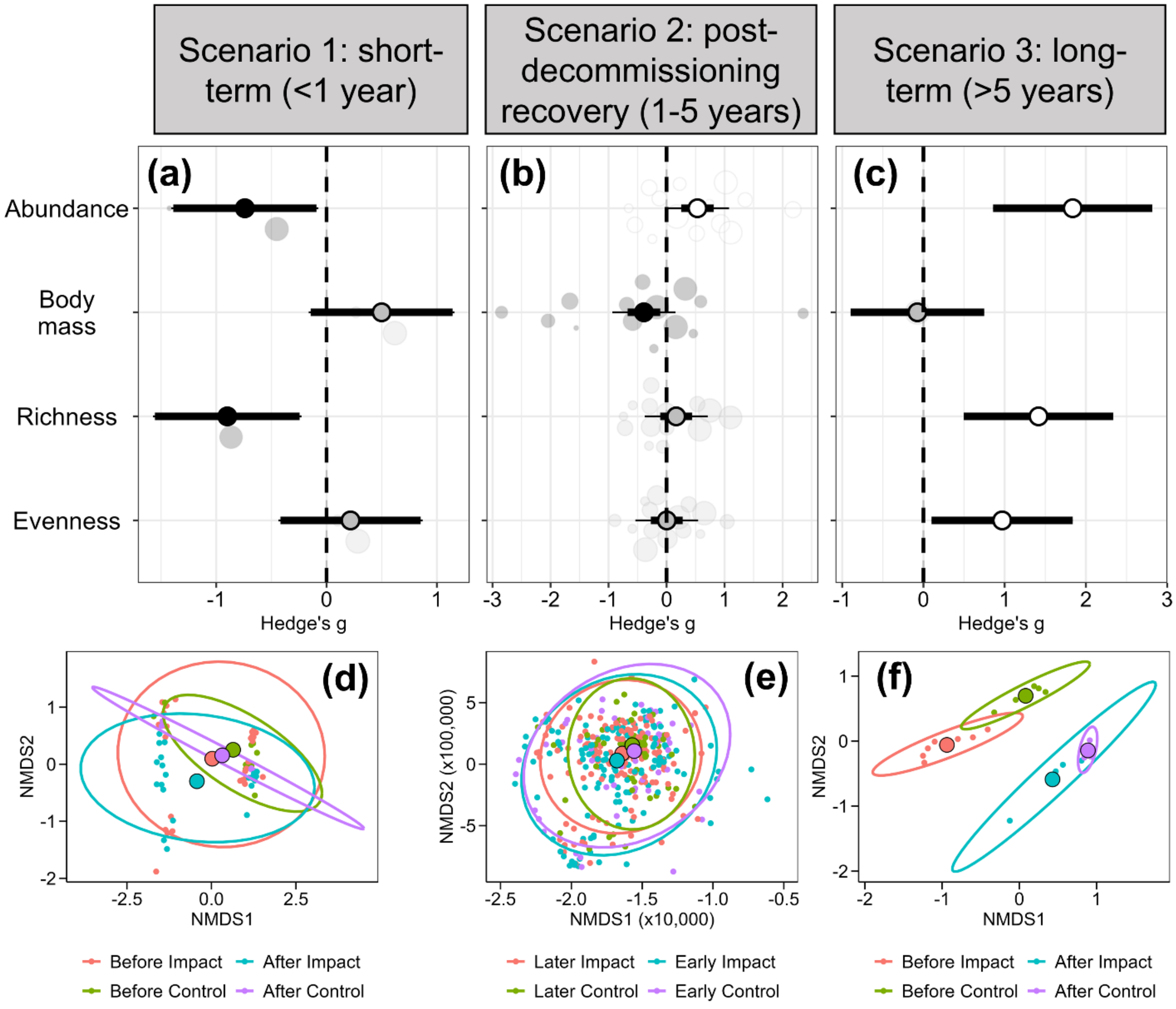

Figure 4: (a-c) Orchard plots of the effects of decommissioning or post-decommissioning recovery on benthic diversity metrics for scenarios 1, 2, and 3. The circles are the pooled Hedge's g for each metric, with significant effects shown in white (positive) or black (negative), and non-significant effects in grey. The thick error bars are the 95% CIs, while the thin error bars are the PIs. (d-f) Ordinations of community composition across the four groups in each scenario, with samples represented by small circles, centroids of each group represented by large circles, and ellipses showing 95% CIs.

Both phyla and feeding groups experienced substantial changes in abundance after decommissioning and post-decommissioning recovery (Figures S4-S5). In the short term of scenario 1, there was a large negative significant effect of decommissioning on arthropods (Hedge's $g = -1.5$; $p < 0.05$), filter feeders (Hedge's $g = -0.77$; $p < 0.05$), and grazers (Hedge's $g = -0.99$; $p < 0.05$), but a large positive significant effect on scavengers (Hedge's $g = 0.83$; $p < 0.05$) and parasites (Hedge's $g = 0.88$; $p < 0.05$). In scenario 2, post-decommissioning recovery had a moderate positive significant effect on arthropods (Hedge's $g = 0.50$; $p < 0.05$) and filter feeders (Hedge's $g = 0.43$; $p < 0.05$), and a large positive significant effect on molluscs (Hedge's $g = 0.64$; $p < 0.01$), detritivores (Hedge's $g = 0.74$; $p < 0.001$), and predators (Hedge's $g = 0.55$; $p < 0.01$). In the long term of scenario 3, there were large positive significant effects on annelids (Hedge's $g = 1.71$; $p < 0.001$), echinoderms (Hedge's $g = 2.20$; $p < 0.001$), and molluscs (Hedge's $g = 1.62$; $p < 0.001$), but a large negative significant effect on phoronids (Hedge's $g = -2.01$; $p < 0.001$). For feeding groups, decommissioning in the long term had large positive significant effects on detritivores (Hedge's $g = 1.98$; $p < 0.001$), filter feeders (Hedge's $g = 1.51$; $p < 0.01$) and scavengers (Hedge's $g = 0.95$; $p < 0.05$), but a large significant negative effect on parasites (Hedge's $g = -0.95$; $p < 0.05$). A detailed comparison of changes in mean abundance of phyla and feeding groups in the impact and control can be found in Tables S6 and S7.

3.3.3 Food web structure

In the short term of scenario 1, decommissioning had large positive significant effects on the proportion of basal species (Hedge's $g = 0.73$; $p < 0.05$; Figure 5a) and connectance (Hedge's $g = 0.55$; $p < 0.05$; Figure 5a), but large negative significant effects on mean trophic level (Hedge's = -0.77; $p < 0.05$; Figure 5a), link richness (Hedge's $g = -0.96$; $p < 0.01$; Figure 5a) and linkage density (Hedge's = -0.71; $p < 0.05$; Figure 5a). In scenario 2, post-decommissioning recovery had moderate positive significant effects on the proportion of intermediate species (Hedge's $g = 0.38$; $p < 0.01$; Figure 5b) and linkage density (Hedge's $g = 0.33$; $p < 0.05$; Figure 5b). In the long term of scenario 3, decommissioning had large positive significant effects on the proportion of intermediate species (Hedge's $g = 1.09$; $p < 0.01$; Figure 5c), mean trophic level (Hedge's $g = 1.68$; $p < 0.001$; Figure 5c), vulnerability (Hedge's $g = 1.32$; $p < 0.01$; Figure 5c), link richness (Hedge's $g = 1.77$; $p < 0.001$; Figure 5c), and linkage density (Hedge's $g = 2.35$; $p < 0.001$; Figure 5c), but large negative significant effects on the proportion of basal species (Hedge's $g = -1.38$; $p < 0.01$; Figure 5c), generality (Hedge's $g = -1.29$; $p < 0.01$; Figure 5c), and connectance (Hedge's $g = -1.60$; $p < 0.001$; Figure 5c). A detailed comparison of changes in food web properties in the impact and control can be found in Table S5.

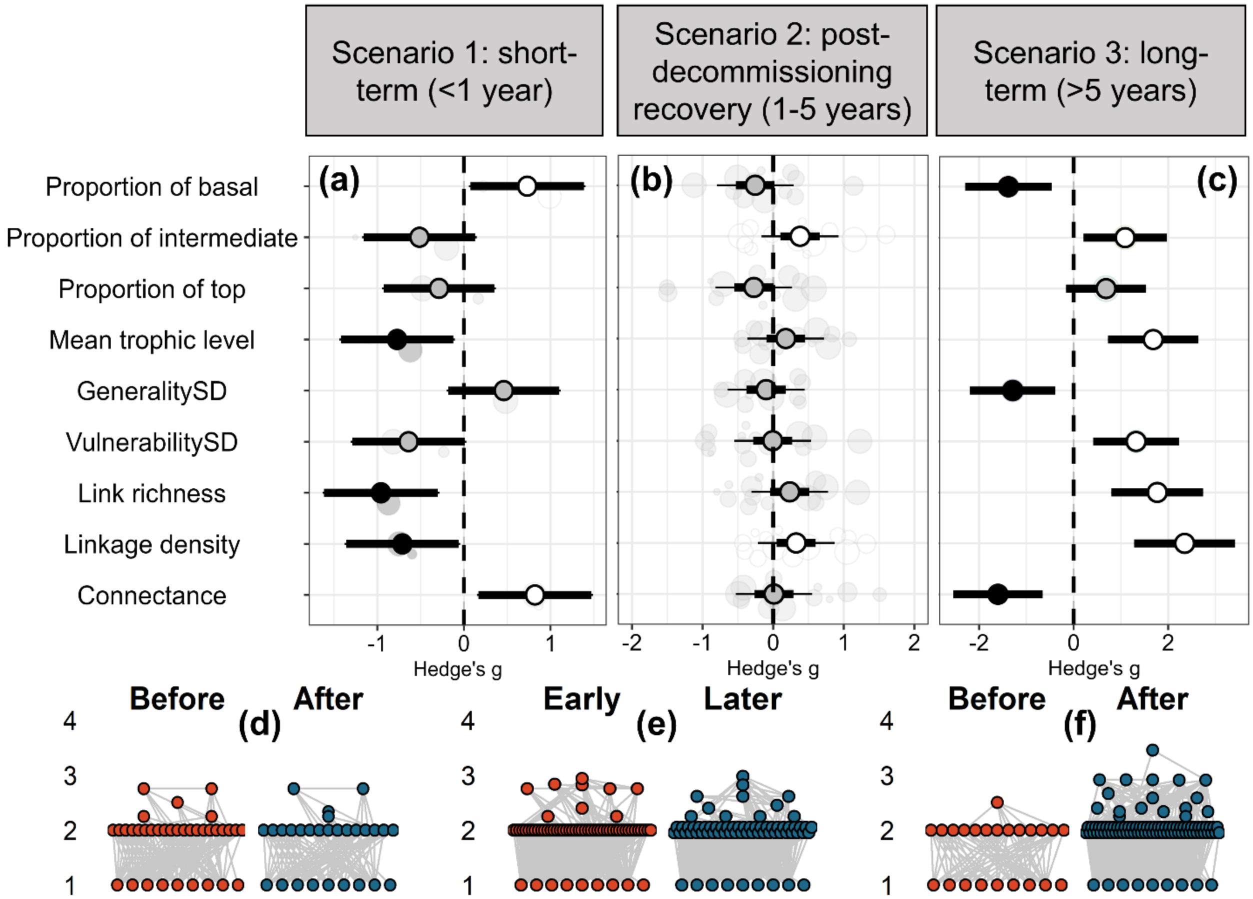

Figure 5: (a-c) Orchard plots of the effects of decommissioning or post-decommissioning recovery on benthic food web topological metrics for scenarios 1,2, and 3. The circles are the pooled Hedge's *g* for each metric, with significant effects shown in white (positive) or black (negative), and non-significant effects in grey. The thick error bars are the 95% CIs, while the thin error bars are the PIs. Examples are also given of a food web (d) before and after decommissioning in the short term, (e) in the early and later period of post-decommissioning recovery, and (f) before and after decommissioning in the long term. Circles are different taxa as nodes, grey lines are feeding interactions. Note that the decrease of trophic complexity in the short term after decommissioning, greater proportion of intermediate species but fewer proportion of top taxa in the post−decommissioning recovery, and greater trophic complexity in the long term after decommissioning.

3.4 Discussion

Assessing potential environmental impacts and marine sensitivities near decommissioning activities is a regulatory requirement that provides essential environmental evidence to justify the chosen decommissioning option and supports risk−based approaches for post−decommissioning management (OPRED 2018). Environmental assessments are usually proportionate to the scale of decommissioning activities on a case−by−case basis, but there has been a paucity of provisions detailing the duration and frequency of monitoring plans contributing to an incomplete understanding of the likely responses of soft sediment environment and benthic communities to O&G decommissioning. With limited long−term monitoring data, it is challenging for the current knowledge base to address whether and how the decommissioning of O&G infrastructure achieves environmental targets, e.g., biodiversity net gains (Knights et al. 2024b). Leveraging the best currently available industrial benthic monitoring database, this study found negative impacts of fully decommissioned O&G structures within the first year, followed by a subtle recovery process after full decommissioning over 1-5 years, and some positive effects of a partially removed structure in the longer term. Differences in the availability of before/after sampling, the extent of decommissioning, and the number of structures involved at each timescale make it difficult to disentangle the trajectory of recovery from potential confounding effects of the sampling design. Thus, our study also highlights the importance of gathering more environmental and ecological data around decommissioned O&G infrastructure to better understand potential impacts associated with the removal process and the long-term trajectory of recovery across different decommissioning options (e.g. partial or full removal). This is important to guide ecologically robust management strategies for future decommissioning practices.

3.4.1 Decommissioning effects on oil-associated contamination

The study found mixed results with regard to sediment contaminants. Specifically, there was a reduction in total hydrocarbon concentration, supporting the hypothesis of lower sediment contamination in the long term after decommissioning, albeit with no change in heavy metals. The decline in total hydrocarbon concentration could be attributed to a number of factors, including the loss of low molecular weight compounds through volatilisation (Chen et al. 2021), dispersion, emulsification, and solubilisation in the water column (Zhao et al. 2015), and sinking to benthic sediments to biodegrade or become buried (Leahy and Colwell 1990, Xu et al. 2018). With the cessation of hydrocarbon production in the decommissioning phase, oil spills and discharges are no longer a major issue, though metals appear to persist in the environment in the long term after decommissioning. The sediment quality guideline was used to assess the toxicity of hydrocarbons and metals present in the sediment (Long et al. 1995). Even in the long term of scenario 3, the median concentrations of lead and zinc were above the threshold values of the lower tenth percentile of concentration levels associated with adverse biological impacts (Table S4), which suggests potential environmental risks for benthic organisms and the environment. Barium, in the form of barite, is frequently used as a weighting material for drilling fluids and therefore has a substantial presence in the drill cuttings (Hartley 1996, Ellis et al. 2012). Even after cessation of production, barium (together with other metals including lead, zinc, and copper) may still have residual concentrations present near drilling sites (Olsgard and Gray 1995). This might be due to their absorption to sediment particles or organic compounds near drilling sites, allowing them to accumulate in the benthic environment (Zhang et al. 2014).

3.4.2 Decommissioning effects on benthic biodiversity

Our results supported the hypothesis that total abundance and species richness increased in the long term after decommissioning. The overall trend showed a complex response from adverse effects on species richness in the short term after decommissioning, followed by a partial recovery post-decommissioning, to more diversified communities in the impact similar to those in the control in the long term after decommissioning (Figures 4 and S2). One possible explanation for negative impacts in the short term could be due to the debilitating nature of decommissioning activities (Odum et al. 1979). For example, dismantling of infrastructure components is likely to cause detrimental impacts to the surrounding benthic environment and organisms, e.g., through resuspension of drill cuttings and other oil-associated contaminants from the sediment back into the water column and interacting directly with the seabed and organisms living on or in the sediments. In this period, ecosystems may experience further degradation rather than intermediate recovery following decommissioning (Odum 1969, Rapport and Whitford 1999). In addition to that, decommissioning also alters the ecology of local ecosystems into which O&G infrastructure has become integrated (Spielmann et al. 2023). Removal of infrastructure means losing hard complex substratum colonised by fouling communities. This will reduce the volume of organic matter falling to and enriching the sediment nearby (Hiscock et al. 2002), which may have cascading effects on local benthic communities adapted to utilising different resources.

Contrasting ecological responses in benthic communities between the short and long term after decommissioning suggest temporal dependence of recovery in benthic communities. Yet, limited studies described the characteristics of benthic succession in the context of O&G decommissioning. Pearson and Rosenberg (1978) provided a useful framework to describe benthic recovery patterns in response to organic enrichment, showing an initial dominance of opportunistic organisms, followed by increasingly more diverse communities with greater fluctuations and progressing toward a state of equilibrium containing many more sensitive species. In our case, decommissioning also indicated the abatement of organic inputs, whereas there exists a variety of unique complexities that influence benthic successional trajectory and a novel state of equilibrium that is different from the pre-infrastructure one. These include the persistence of legacy contamination in the sediment (Gates and Jones 2012), alteration of local hydrodynamics, hard substratum, and fouling communities associated with removal (Nicolette et al. 2023), and potential disturbances associated with the removal process (Fortune et al. 2024). These stressors associated with O&G decommissioning confound a predictable and gradual recovery process, which differs from previous recovery studies in dredging (Cooper et al. 2007) and trawling (Wang et al. 2021). Before the surrounding environment experiences full recovery, it is possible for marine benthos to experience further degradation. Notably, a significant reduction in mean body mass in the impact zone post−decommissioning recovery suggests that initial colonisers tend to be small opportunists with rapid reproduction and a short life span (Ryu et al. 2011), with larger organisms only establishing in the longer term (Rosenberg 2001). Henry et al. (2017) found that benthic recovery after the cessation of drilling in the northern North Sea required over 6.8 years, while recovery in the central North Sea took over 8 years.

Partial recovery was detected in the long term after decommissioning with a significant increase in both total abundance and species richness in the impact (Figure 4). Changes in benthic community composition were most stark in the long term of scenario 3, whereby impact and control communities were homogenised following decommissioning with no significant difference in beta diversity (Figure S3). The opportunistic polychaete *Capitella spp.* was the most abundant species in the impact before decommissioning (Figure S6), which are typical pollution bioindicators in organic enriched and disturbed environments (Keeley et al. 2014, Tomassetti et al. 2016). Communities in the long term of scenario 3 became more diverse with the colonisation of more pollution sensitive species, including the brittle stars *Amphiura* spp. and *Ophiuridae* spp, the scavenging isopod *Iphinoe serrata*, and the heart urchin *Echinocardium cordatum* (Figures S4-S5), reflecting improved benthic habitat quality (Borja et al. 2000, Rosenberg et al. 2002). Our results align with previous assessments showing a decrease in polychaete and concurrent increase in pollution intolerant taxa after decommissioning (OSPAR Commission 2019). This highlights the potential for recovery of benthic communities after decommissioning, albeit only at a single O&G structure due to the absence of long-term monitoring in current industry datasets.

3.4.3 Reorganisation of trophic architecture: gains or losses?

The significant increase in link richness, linkage density, and mean trophic level supported our hypothesis of greater food web complexity in the long term after decommissioning (Figure 5). The significant decrease in connectance and generality seems counterintuitive at first glance, but actually indicates a greater proportion of specialist consumers in the food web. Since less connected dietary specialists are more prone to extinction and dietary generalists are more likely to thrive under environmentally stressful conditions (Laske et al. 2018), the decreasing connectance and generality in the long term after decommissioning suggests an improved environment that can cater to a wider range of trophic niches. The improved communities were also consistent with a more diversified community composition with increased abundance of annelids, echinoderms, molluscs, detritivores, filter feeders, and scavengers (Figures S4-S6). The increase in vulnerability also indicates a greater number of predators in the community, which consistent with the higher mean trophic level. The increase in link richness and linkage density demonstrates increased energy availability and more redundancy in energy flow (Scotti et al. 2009). Nevertheless, the decrease in connectance may be associated with reduced resilience to disturbances through an increased risk of secondary extinctions or invasions (Dunne et al. 2002b, Gilbert 2009, Smith-Ramesh et al. 2017). However, the dearth of available data for fully decommissioned structures makes it difficult to ascribe beneficial effects on long timescales given the partial removal used in this scenario, which contrasts with the full removal in scenarios 1 and 2. Therefore, it is unclear if the beneficial effects on diversity and food webs in scenario 3 are down to the longer timescale allowed for recovery, or the lower initial disturbance to the surrounding sediment from leaving the footings of the decommissioned platform in place. Future studies are encouraged to examine how different decommissioning options affect ecological responses in the long term.

In the short term after decommissioning, completely opposing patterns to the long-term recovery were found, with a significant increase in the proportion of basal species and connectance, and a significant decrease in mean trophic level, link richness, and linkage density (Figure 5). The reduction in mean trophic level indicates a greater dominance of basal species, which suggests inadequate resources to support energy transfer to higher trophic levels (Kaunzinger and Morin 1998). The decrease in the number and density of food web interactions reconciles with the loss of species richness, which leads to lower trophic redundancy. Higher connectance suggests increased resilience against disturbances (Dunne et al. 2002a), however, whereby a simplified but more tightly connected food web may act as a stabilising mechanism that prevents communities from experiencing secondary extinctions following a perturbation (Gilbert 2009, Nordström and Bonsdorff 2017), which is also a typical manifestation in a stressed ecosystem (Duffy et al. 2007, O'Gorman et al. 2019, Nagelkerken et al. 2020). Despite the lack of pre-infrastructure surveys to inform baseline conditions at the structures, the trajectory of benthic recovery was found with positive effects on the proportion of intermediate species and linkage density (Figure 5). However, the lack of significant distinction in community compositions suggests that benthic recovery is relatively subtle in the 1-5 year timeframe (Figure 4).

3.5 Recommendations for monitoring of decommissioning

The preparation and implementation of decommissioning in the North Sea is a lengthy regulatory process that requires environmental appraisals to support proposed decommissioning options and their potential impacts on the marine environment. Environmental surveys are needed to fulfil regulatory requirements, provide an evidence base prior to cessation of production for potential impacts and their consequences to the environment, and to justify the chosen option having minimal environmental impacts (OPRED 2018). Currently, there is no statutory requirement specifying the implementation of long-term monitoring and recommended frequency of key time points, which means there is a lack of consistent environmental and ecological data for monitoring the impacts of decommissioning on marine ecosystems. Using survey data before and after decommissioning at different temporal scales, we attempted to show a variability in benthic diversity and food web responses. To better accommodate the needs of investigating long−term decommissioning effects, we propose the following recommendations concerning (i) the prioritisation of monitoring long-term decommissioning consequences; (ii) a standardised data workflow to integrate with available databases, and (iii) enhanced stakeholder participation in the decommissioning decision-making and accessibility and transparency of monitoring data.

(i) The absence of continuous long−term monitoring surveys post−decommissioning made it difficult to implement a trend−based approach to understand the trajectory of benthic recovery at different successional stages. Our results found that negative effects on benthic biodiversity and food webs persisted in the short timescale (within 12 months), followed by signals of recovery in the medium (1-5 years) and long term (over 5 years). This illustrates how future post−decommissioning sampling strategies should account for monitoring at key timepoints (e.g., within 12 months, then after 2, 3, 5, and 10 years) to provide adequate temporal range to detect the potential environmental and ecological consequences of decommissioning.

(ii) Standardisation in the sampling protocol would be beneficial not only to the comparative analysis between historical baseline data with planned monitoring, but also to allow the integration of existing surveys beyond the industrial sector, including government agencies and research institutions. The methodologies and principles established by existing standardised benthic sampling protocols, e.g. the regional seabed monitoring programme developed by Cooper and Barry (2017), could be further improved by accounting for the uniqueness and difficulties of sampling O&G infrastructure. For example, the distinction of sampling should consider different operational phases of O&G infrastructure, including baseline sampling prior to exploitation, sampling during the operational stage, and post−decommissioning sampling. Important factors should be recorded at each sampling location, such as the transect, angle in direction, and water depth. It would be beneficial to establish an integrated framework to unify the efforts of industry, research institutions, and government to participate in benthic monitoring, which would improve knowledge and decision-making around decommissioning (Froján et al. 2016).

(iii) It is essential to collect environmental and ecological information to identify the optimal decommissioning scenario that brings environmental and societal gains. Without the evidence, there is a risk that the substantial costs in decommissioning do not yield desirable outcomes for the industry and the public. There is also a need for improving data transparency of environmental appraisals submitted for decommissioning approvals, as these assessments tend to be summarised in reports, with raw survey data remaining inaccessible, particularly for decommissioned O&G infrastructure. The UK Benthos database offers valuable historical data to understand the impacts of offshore hydrocarbon exploitation. However, a lack of post−decommissioning data constrains the ability to compare benthic conditions before and after decommissioning, as well as to evaluate post−decommissioning recovery relative to baseline conditions prior to hydrocarbon exploitation. Our scenario−based approach requires comprehensive and long−term benthic monitoring to validate the trajectory of post−decommissioning recovery of benthic communities.

3.6 Conclusion

The study reveals environmental and ecological impacts of O&G decommissioning on marine ecosystems. Hydrocarbons, especially those with lower molecular weight, degrade relatively rapidly after decommissioning, while heavy metals may persist longer in the sediment at levels that could impact benthic organisms. There were detrimental impacts of decommissioning in the short term, with a loss of species richness and simplified food webs. Increases in the proportion of intermediate species and linkage density in the medium term post-decommissioning suggest some recovery is happening, but community composition exhibits greater inertia over this timescale. The greater food web complexity in the long term after decommissioning indicated longer pathways of energy flux and more trophic redundancy in the face of further perturbations, with impact zone communities sharing a similar composition to those of background controls. Given that the data underpinning our findings are limited to scenarios with different structures and decommissioning options, the study highlights the critical need for more systematic long-term monitoring of O&G decommissioning to better inform future practices.

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Appendix: Supplementary materials for chapter 3

S3.1 Simplified North Sea benthic invertebrate food web

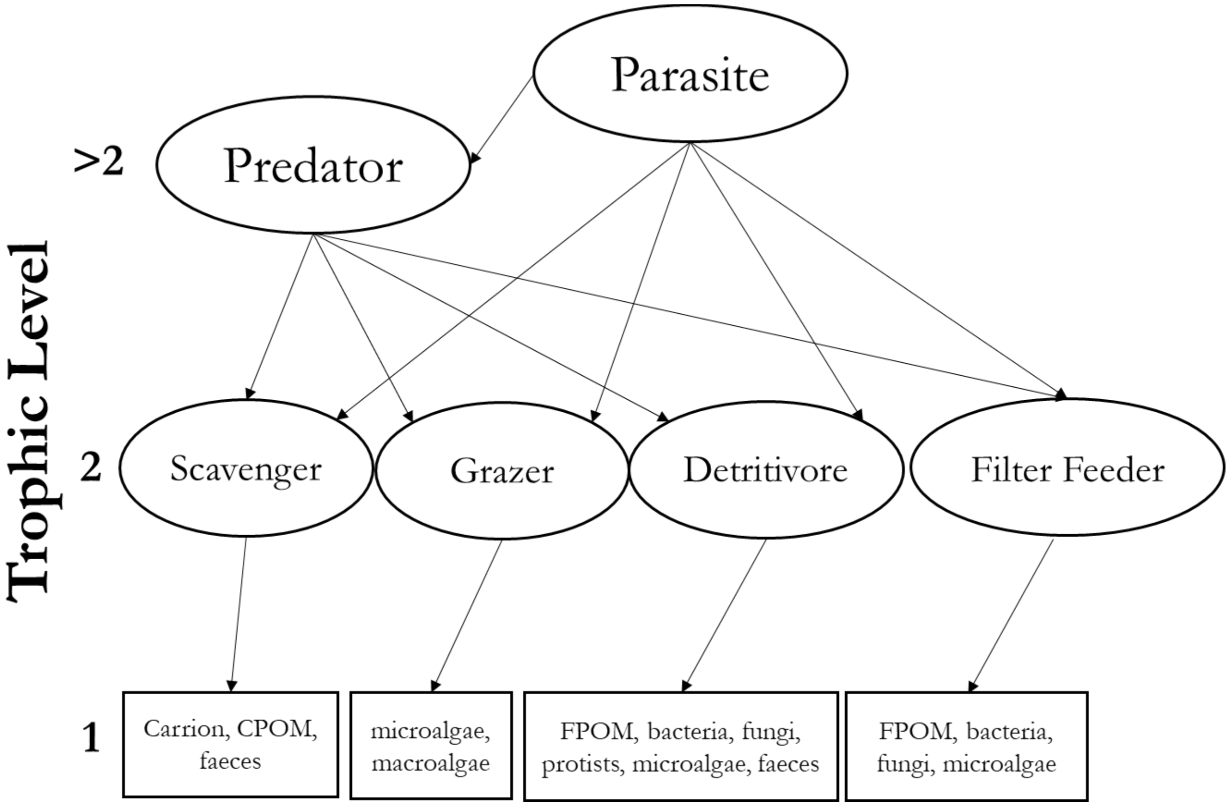

Figure S1: Basal resources were assumed to be present at all samples. Subsets of basal resources were assigned to scavengers, grazers, detritivores, and filter feeders as primary consumers (trophic level = 2). Feeding interactions of predators and parasites were compiled from published literature and databases. Feeding interactions occurred when both predators and preys / parasites and hosts were present in the same sample.

S3.2 Operational status of O&G infrastructure

Table S1: The operational status and definitions for offshore O&G infrastructures were listed with information from North Sea Transition Authority (https://www.nstauthority.co.uk/) and published industry reports. The status of decommissioning for drilling wells were well established while that for fixed steel O&G platforms was not available. For wells, we considered “Abandoned Phase 3” as decommissioning and used their corresponding dates to select eligible surveys. For platforms, we broadly split their life cycle into main phases and used the end of decommissioning programme to select eligible surveys.

Operational status	**Definitions**
Well	
Spudding	The early stage when the well penetrates the earth to remove rock and other sedimentary materials with a drill bit.
Completion	The well has been drilled for the purposes of bringing the well into use (e.g., production or injection). There will be completion activities carried out afterwards, including installing the completion string and associated equipment, installing sand control equipment, perforating, hydraulic fracturing, well stimulation, and installing the tree.
Completed (Shut In)	An active well in which all completion activities have taken place, and the well is shut-in at the tree valves or subsurface safety valve but can be operated by the control system. It is generally applied when this well is intended to be shut-in for more than 90 days.
Plugged	It includes the well that were temporarily plugged with a plug rather than a permanent isolation barrier and the inactive wells where the well is effectively plugged with the subsurface safety valve and tree valves.
Abandoned Phase 1	A well where the reservoir has been permanently isolated. The well below the barrier is no longer accessible.
Abandoned Phase 2	All required permanent isolation barriers have been installed and verified (including environmental barriers). There will be no “in-well” work.
Abandoned Phase 2 (derogated)	All “in-well” isolation work is completed. The Offshore Petroleum Regulator for Environment and Decommissioning (OPRED) granted derogation to leave the well origin or well equipment.
Abandoned Phase 3	The well origin and all conductor above the well origin have been removed.
Platform	

Discovery	Explorative activities to discover potential oil and gas fields through appraisal drilling to assess the characteristics and amount of petroleum deposit.
Installation	A fixed platform being introduced to extract oil and gas by building concrete and/or steel infrastructure directly onto the seabed to support operational activities above the sea.
Commissioning	The preparation stage of assembling pipeline to test whether extracted oil and gas products can be transported to designed destinations.
Operating	The routine procedure of extracting oil and gas from reservoirs, processing hydrocarbon products on the facilities, storing and transporting the products, as well as all associated operational activities.
Shut-In	The platform being temporarily closed and suspending production due to maintenance or other needs.
Cessation of production	The preparation stage before entering into decommissioning when a fixed platform stops production activities.
Decommissioned	Drilling wells being plugged, components of a fixed platform being dismantled and transported to shore for recycle and/or re-use.

S3.3 List of eligible oil and gas structures

Table S2: A total of 3 O&G infrastructure that were sampled before and after decommissioning. For NW Hutton, the start date used the installation date when the structure was built. The end date used the date of removal. For 29/10-10Y and 44/12-1, the start date was determined as the spudding date when the drill was initialized to remove surface sediment. The end date used the regulatory completion date, which is the published date of "Abandoned Phase 3" that represent the cessation of production in the mechanical status in the NSTA. We delineated the samples collected prior to the decommissioning ("Active", marked as "A" in the sampling date) and samples after the decommissioning ("Decommissioned", marked as "D" in the sampling date).

MMS ID	# samples	Start date	End date	Sampling date	Status at sampling

29/07- 10Y	30	1997/04	1997/07	1997/07 (A) 1998/08 (D)	Abandoned Phase 3
NW Hutton	21	1981/09	2009/07	1992/08 (A) 2013/08 (D)	Decommissioned
44/12- 1	36	1988/07	1988/10	1988/07 (A) 1988/10 (A) 1989/11 (D)	Abandoned Phase 3

Table S3: A total of 14 O&G infrastructure that were sampled twice at their post-decommissioning periods. We used “Abandoned Phase 3” as their mechanical status at sampling to ensure all eligible wells to be permanently decommissioned rather than shut in temporarily. The start date used the spudding date when the drill initialized the drilling process to remove surface sediment materials. The end date used the regulatory completion date which is the published date of “Abandoned Phase 1/2/3” or “Completed (Shut In)” that represent the cessation of production in the mechanical status in the NSTA. We delineated the post-decommissioning samples at the early stage (“Early”, marked as “E” in the sampling date) and post-decommissioning samples at the later stage (“Later”, marked as “L” in the sampling date).

MMS ID	# sample	Start date	End date	Sampling date	Status at sampling
13/22a- 11	21	1993/03	1993/04	1996/02 (E) 1996/12 (L)	Abandoned Phase 3
9/28a- 11	40	1988/04	1988/05	1991/07 (E) 1994/09 (L)	Abandoned Phase 3
15/20b- 12	16	1995/01	1995/02	1995/08 (E) 1997/07 (L)	Abandoned Phase 3
15/23d- 13	40	1996/11	1997/03	1997/08 (E) 1998/08 (L)	Abandoned Phase 3
211/12a- 18	23	1994/09	1994/10	1996/06 (E) 1997/07 (L)	Abandoned Phase 3
16/22- 6	34	1996/01	1996/04	1996/11 (E) 1997/07 (L)	Abandoned Phase 3
16/03d- 14	14	1996/04	1996/06	1996/07 (E) 1997/05 (L)	Abandoned Phase 3
22/29- 6	29	1995/08	1995/11	1996/08 (E) 1997/07 (L)	Abandoned Phase 3
30/29a- 3	15	1996/04	1996/05	1996/06 (E)	Abandoned Phase 3

				1997/07 (L)	
29/10- 4	32	1995/03	1995/04	1995/07 (E) 1996/08 (L)	Abandoned Phase 3
29/10- 5A	30	1996/03	1996/04	1996/08 (E) 1997/07 (L)	Abandoned Phase 3
30/13- 5	16	1996/02	1996/03	1996/06 (E) 1997/07 (L)	Abandoned Phase 3
13/24b- 3	40	1997/03	1997/05	1997/08 (E) 1998/08 (L)	Abandoned Phase 3
29/12- 2	26	1992/05	1992/06	1992/09 (E) 1993/09 (L) 1997/05 (L)	Abandoned Phase 3

S3.4 Individual metals

Table S4: 25th, median, and 75th percentiles in the concentrations (µg/g) of total hydrocarbons, metals and individual metal in the impact and control treatment at active and decommissioning period / early and later post-decommissioning period. Effect Range Lows (ERLs) established in the OSPAR's Co-ordinated Environmental Monitoring Programme. Metals with median concentrations exceeding the ERLs were highlighted in red.

Scenario 1: Short term							
Active period							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	262	3795	7463	23	24	25
Metals	NA	335	409	896	26	27	27
Total Barium	NA	22680	74040	231500	8988	14552	20116
Copper	34	8	14	37	2	2	2
Nickel	21	11	13	32	5	5	5
Lead	47	29	35	172	6	6	6
Zinc	150	276	359	656	14	14	15
Decommissioning period							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	5	575	7611	35	61	86
Metals	NA	160	621	749	41	58	74
Total Barium	NA	25625	31875	109375	1875	1875	1875
Copper	34	9	18	34	6	6	7
Nickel	21	17	23	56	12	19	25
Lead	47	35	178	255	2	4	6
Zinc	150	93	287	353	22	29	37
Scenario 2: Post−decommissioning recovery							

Early period post decommissioning							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	117	1835	13916	3	14	32
Metals	NA	50	81	168	38	46	76
Total Barium	NA	1605	5005	18987	385	524	722
Copper	34	5	7	18	3	4	6
Nickel	21	8	12	21	7	10	13
Lead	47	13	18	35	10	12	16
Zinc	150	23	38	94	15	18	45
Later period post decommissioning							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	36	635	5428	3	6	12
Metals	NA	47	83	224	40	47	102
Total Barium	NA	1008	8552	31821	393	490	667
Copper	34	4	7	20	3	4	9
Nickel	21	7	11	27	5	7	20
Lead	47	11	17	47	8	12	17
Zinc	150	24	46	129	17	25	50
Scenario 3: Long term							
Active period							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	5315	21500	28900	4.2	8.2	36
Metals	NA	250.5	449	697	27	36	42
Total Barium	NA	1246	3505	3995	863	1352	1514
Copper	34	20	43	72	2	3	3
Nickel	21	12	17	23	3	6	6
Lead	47	112	183	224	9	12	12
Zinc	150	99.5	143	292	13	15	21
Decommissioning period							
Chemical	ERL	Impact			Control		
		Q1	Median	Q3	Q1	Median	Q3
Hydrocarbons	NA	150	876	2271	19	35	42
Metals	NA	101	356	726	30.1	29.2	32
Total Barium	NA	15906	19088	20283	4010	4200	4270
Copper	34	13	24	37	4	4	4
Nickel	21	9	15	26	7.2	7.5	7.9
Lead	47	26.6	109	197	6.7	6.8	6.9
Zinc	150	53	207	465	11	12	14

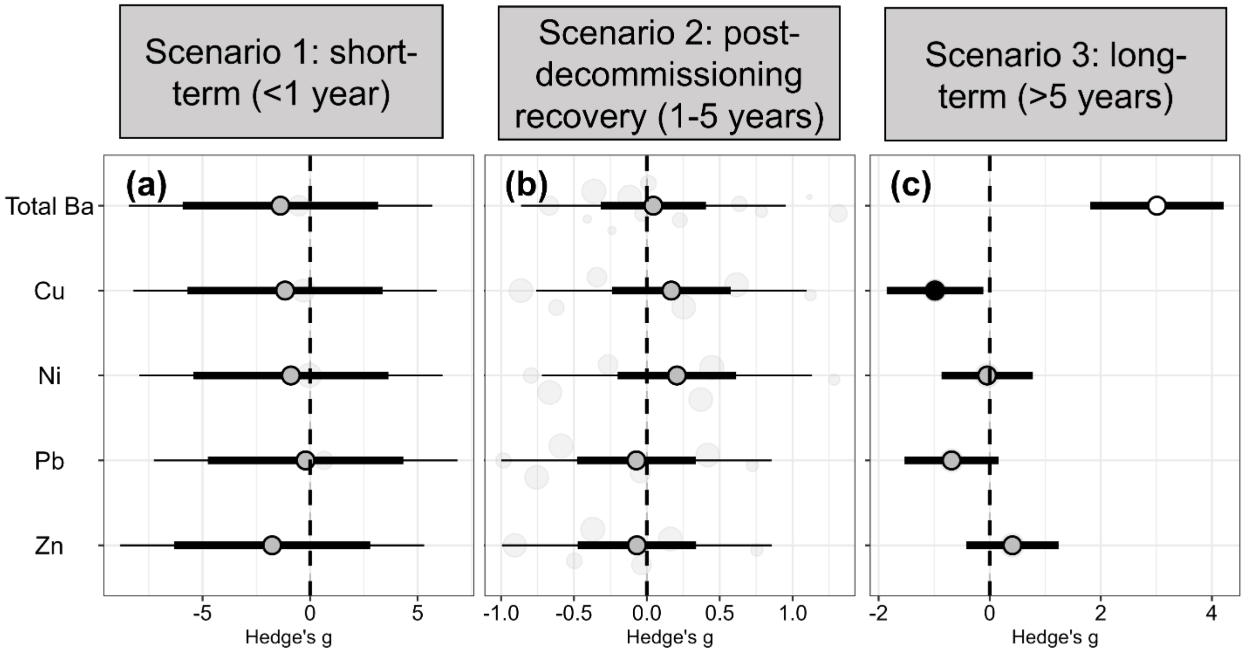

Figure S2: Orchard plots of the effects of decommissioning or post-decommissioning recovery on individual metals. The circles are the pooled Hedge's g for each metric, with significant effects shown in white (positive), black (negative) and grey (non−significant). The thick error bars are 95% CIs, while the thin error bars are prediction intervals (PIs). Note that CIs and PIs are overlapped in scenario 1 because of only 1 Hedge's g for each metric.

S3.5 Ecological metrics across groups

Table S5: Mean values of diversity and food web metrics in impact and control before and after decommissioning and/or at the early and later post-decommissioning periods.

Scenario 1: Short term		
Before decommissioning		
Metrics	Impact	Control
Abundance	5728	4388
Mean body mass	0.184	0.324
Species richness	26	28
Pielou's evenness	0.625	0.690
Proportion of basal	0.275	0.248
Proportion of intermediate	0.149	0.165
Proportion of top	0.553	0.574

Mean trophic level	1.76	1.81
generalitySD	0.768	0.691
vulnerabilitySD	1.657	1.80
Link richness	117	128
Linkage density	3.18	3.39
Connectance	0.0958	0.0933
After decommissioning		
Metrics	Impact	Control
Abundance	10427	11808
Mean body mass	0.356	0.222
Species richness	21	32
Pielou's evenness	0.753	0.791
Proportion of basal	0.310	0.226
Proportion of intermediate	0.121	0.178
Proportion of top	0.536	0.588
Mean trophic level	1.71	1.84
generalitySD	0.841	0.668
vulnerabilitySD	1.60	1.88
Link richness	95	152
Linkage density	3.04	3.67
Connectance	0.106	0.091
Scenario 2: Post−decommissioning recovery		
Early period post decommissioning		
Metrics	Impact	Control
Abundance	23835	48008
Mean body mass	0.119	0.129
Species richness	40	60
Pielou's evenness	0.663	0.768
Proportion of basal	0.266	0.174
Proportion of intermediate	0.196	0.230
Proportion of top	0.506	0.577
Mean trophic level	1.77	1.88
generalitySD	0.862	0.658
vulnerabilitySD	1.97	2.43
Link richness	205	313
Linkage density	3.57	4.15
Connectance	0.0851	0.0726
Later period post decommissioning		
Metrics	Impact	Control
Abundance	16134	24423
Mean body mass	0.100	0.102
Species richness	40	60
Pielou's evenness	0.623	0.743
Proportion of basal	0.259	0.180
Proportion of intermediate	0.193	0.204
Proportion of top	0.509	0.593
Mean trophic level	1.77	1.86
generalitySD	0.878	0.661
vulnerabilitySD	1.98	2.47
Link richness	202	303
Linkage density	3.53	4.03
Connectance	0.0854	0.0732
Scenario 3: Long term		

Before decommissioning		
Metrics	Impact	Control
Abundance	36879	87052
Mean body mass	0.0468	0.0729
Species richness	29	77
Pielou’s evenness	0.72	0.82
Proportion of basal	0.231	0.104
Proportion of intermediate	0.218	0.265
Proportion of top	0.505	0.611
Mean trophic level	1.79	1.963
generalitySD	0.725	0.537
vulnerabilitySD	1.776	2.858
Link richness	144	408
Linkage density	3.66	4.72
Connectance	0.102	0.055
After decommissioning		
Metrics	Impact	Control
Abundance	46098	61920
Mean body mass	0.0178	0.0479
Species richness	73	97
Pielou’s evenness	0.79	0.83
Proportion of basal	0.132	0.085
Proportion of intermediate	0.281	0.264
Proportion of top	0.552	0.626
Mean trophic level	1.963	1.996
generalitySD	0.709	0.632
vulnerabilitySD	2.45	3.073
Link richness	390	491
Linkage density	4.6	4.64
Connectance	0.064	0.044

S3.6 Pairwise community composition, phyla and feeding groups

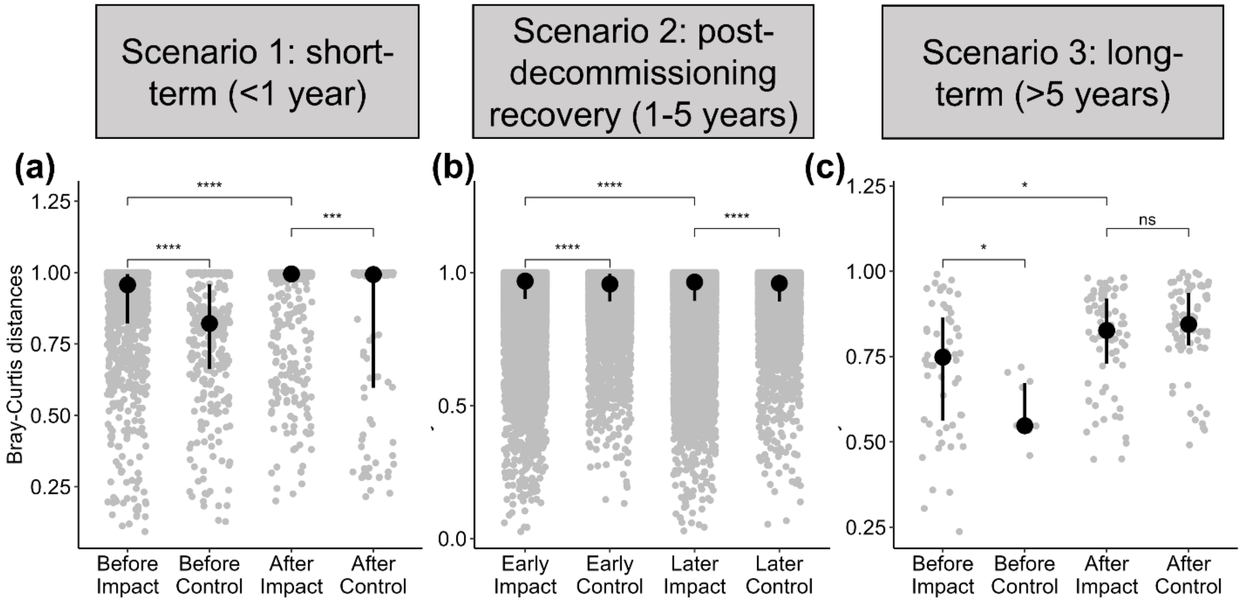

Figure S3: Pairwise comparisons of Bray–Curtis dissimilarity between the impact and the control before and after decommissioning or post−decommissioning recovery. The dots and two–side lines represent the medians and its 25% to 75% interquartile ranges. Each pairwise comparisons of means used Wilcoxon rank sum test with their p value shown in the table. Statistically significant comparisons were marked with asteroids.

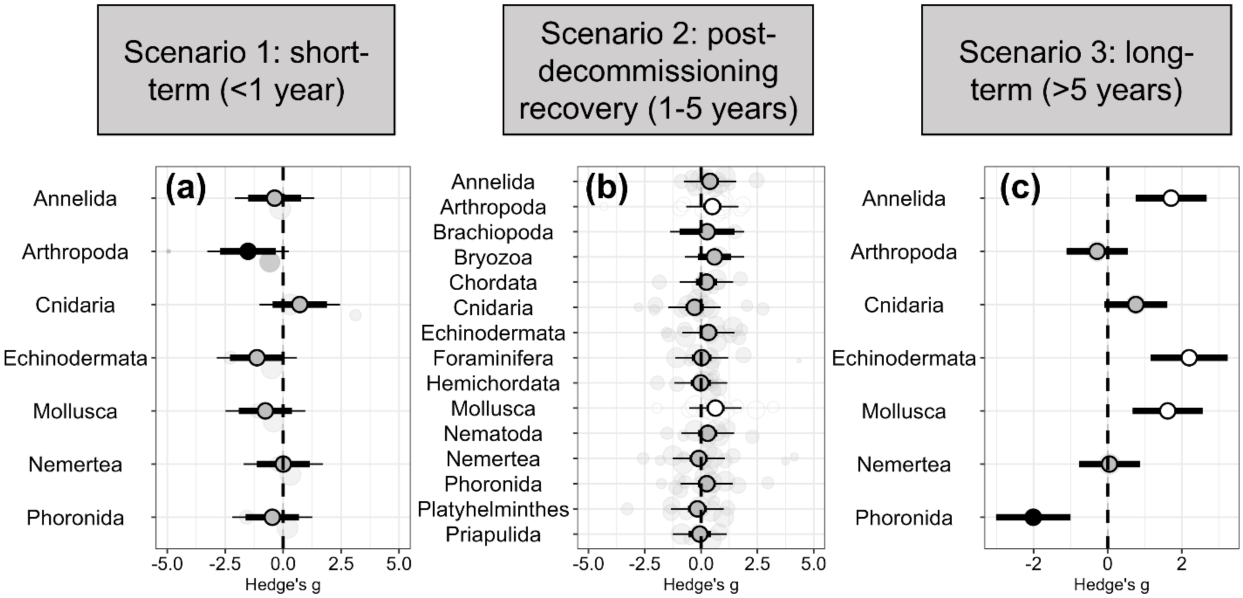

Figure S4: Orchard plots of the effects of decommissioning or post-decommissioning recovery on the abundance of individual phyla. The circles are the pooled Hedge's g for each metric, with significant effect shown in white (positive), black (negative) and grey (non-significant). The thick error bars are the 95% CIs, while the thin errors are the PIs.

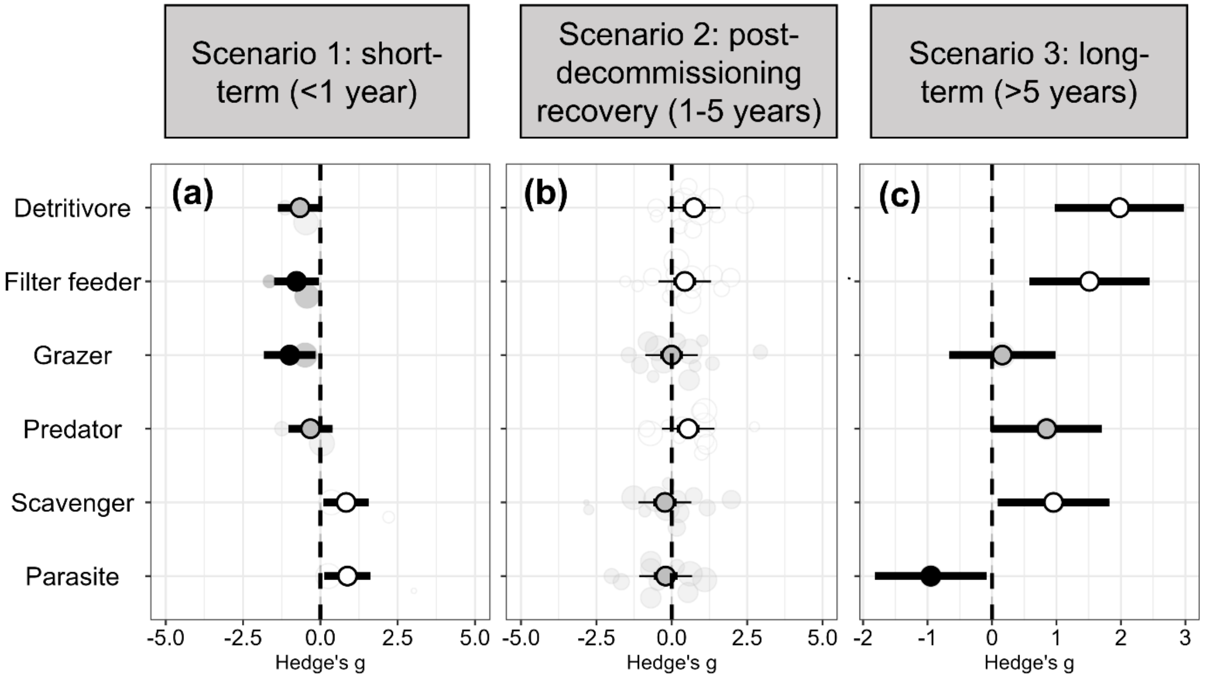

Figure S5: Orchard plots of the effects of decommissioning or post-decommissioning recovery on the abundance of individual feeding groups. The circles are the pooled Hedge's g for each metric, with significant effect shown in white (positive), black (negative) and grey (non-significant). The thick error bars are the 95% CIs, while the thin errors are the PIs.

Table S6: Mean abundance of phyla in impact and control before and after decommissioning and/or at the early and later post-decommissioning periods.

Scenario 1: Short term		
Before decommissioning		
Metrics	Impact	Control
Annelida	288	205
Arthropoda	21	44
Echinodermata	60	49
Mollusca	148	90
Nemertea	23	4
Phoronida	27	26
Platyhelminthes	3	1
Cnidaria	3	12
After decommissioning		
Metrics	Impact	Control
Annelida	530	476
Arthropoda	90	258
Echinodermata	120	164
Mollusca	198	172
Nemertea	59	24
Phoronida	29	83
Platyhelminthes	7	0
Cnidaria	1	3
Scenario 2: Post−decommissioning recovery		
Early period post decommissioning		
Metrics	Impact	Control
Annelida	1494	2760
Arthropoda	110	511
Echinodermata	264	456
Mollusca	301	663
Nematoda	30	70
Nemertea	59	66
Cnidaria	53	74
Hemichordata	0	0
Phoronida	25	61
Priapulida	1	4
Platyhelminthes	1	0

Foraminifera	33	95
Bryozoa	0	0
Chordata	12	37
Brachiopoda	0	0
Later period post decommissioning		
Metrics	Impact	Control
Annelida	827	1223
Arthropoda	116	323
Echinodermata	221	277
Mollusca	283	322
Nematoda	8	29
Nemertea	38	45
Cnidaria	43	63
Hemichordata	3	2
Phoronida	32	39
Priapulida	0	0
Platyhelminthes	2	6
Foraminifera	34	111
Bryozoa	0	0
Chordata	5	0
Brachiopoda	0	0
Scenario 3: Long term		
Before decommissioning		
Metrics	Impact	Control
Annelida	279	509
Arthropoda	16	136
Echinodermata	50	42
Mollusca	124	158
Nemertea	17	11
Phoronida	21	24
Platyhelminthes	2	0
Cnidaria	4	10
After decommissioning		
Metrics	Impact	Control
Annelida	862	353
Arthropoda	154	141
Echinodermata	136	83
Mollusca	368	117
Nemertea	34	13
Phoronida	23	41
Platyhelminthes	7	0
Cnidaria	41	2

Table S7: Mean abundance of feeding groups in impact and control before and after decommissioning and/or at the early and later post-decommissioning periods.

Scenario 1: Short term		
Active period		
Metrics	Impact	Control
Detritivore	265	182

Filter Feeder	155	123
Grazer	46	36
Predator	101	71
Scavenger	5	20
Parasite	0.1	0.3
Decommissioning period		
Metrics	Impact	Control
Detritivore	533	590
Filter Feeder	115	201
Grazer	1	62
Predator	369	323
Scavenger	16	5
Parasite	0.2	0
Scenario 2: Post−decommissioning recovery		
Early period post decommissioning		
Metrics	Impact	Control
Detritivore	1227	2484
Filter Feeder	308	783
Grazer	102	201
Predator	633	1097
Scavenger	111	228
Parasite	3	5
Later period post decommissioning		
Metrics	Impact	Control
Detritivore	817	1186
Filter Feeder	215	426
Grazer	84	119
Predator	441	568
Scavenger	39	127
Parasite	15	14
Scenario 3: Long term		
Active period		
Metrics	Impact	Control
Detritivore	2206	4942
Filter Feeder	331	1579
Grazer	0	79
Predator	1128	1920
Scavenger	23	185
Parasite	0	0
Decommissioning period		
Metrics	Impact	Control
Detritivore	2288	3133
Filter Feeder	273	917
Grazer	147	210
Predator	1396	1532
Scavenger	290	329
Parasite	1.9	16.6

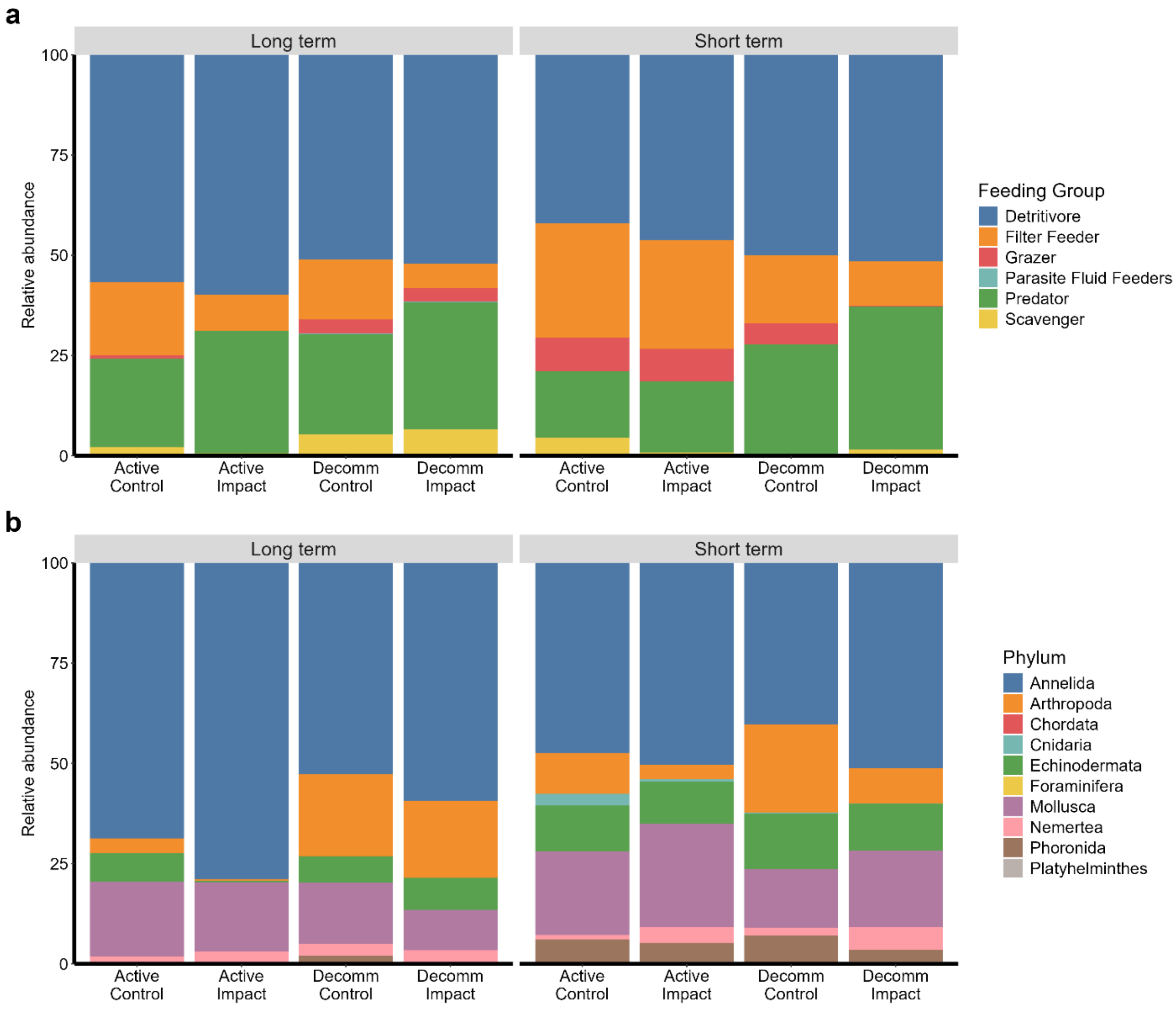

Figure S5: Changes in the benthic community composition before and after decommissioning were shown using relative abundance (%) of feeding groups (a) and phyla (b) across four groups between short term of scenario 1a and long term of scenario 1b.

CHAPTER FOUR

Impacts of offshore marine artificial structures on the biodiversity of marine fish communities

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Abstract

The decommissioning of aging oil and gas infrastructure and the rapid expansion of offshore wind turbines causes a paradigm shift in the ecological impacts of offshore energy structures in the North Sea ecosystem. There is an urgent need to understand cumulative effects of the structures on marine ecosystem functioning and structure. We used Bayesian Integrated Nested Laplace Approximation (INLA) approach to model how O&G platforms and wind turbines influence biodiversity and food web measures of marine fish species across a range of body sizes, feeding guilds and trophic levels. Offshore wind turbines show significant small positive effect in the total fish biomass. Contrasting effects of both structures are identified across feeding guilds, with the decrease in the biomass and typical length higher in the food web (piscivores) but increases for those lower (planktivores). The cumulative impacts on fish biodiversity and food web measures across the North Sea are estimated to quantify total changes attributed to the development of offshore structures. These changes could influence community turnover, energy transfer and food web complexity, which leads to cascading effects on ecosystem stability and structure.

Keywords: Oil and gas platforms; wind turbines; cumulative effects; marine fish; food web; feeding guild; biodiversity; North Sea

4.1 Introduction

The North Sea is experiencing a paradigm shift from oil and gas (O&G) exploitation to renewable infrastructure expansion. Since the 1960s, O&G exploration and development has been an extensive industrial activity, introducing over 470 concrete or steel fixed platforms and related installations (e.g., pipeline, manifolds) (Gourvenec et al., 2022). O&G production peaked in the late 1990s, alongside the installation of fixed platforms which peaked later in 2009 (Craig, Gerali, MacAulay, & Sorkhabi, 2018; Martins et al., 2023). To mitigate global warming and meet international net zero emission target, the development of offshore wind farms (OWFs) was prioritised in the EU's policy agenda in the early 2000s, leading to dramatic increases in their installation in the North Sea in the past decades and continued rapid expansion planned for the future (Lau, Lee, & Mohamed, 2012; Putuhena et al., 2023). The EU's energy and climate objectives laid out regional cumulative offshore goals of 86 GW by 2030 and over 350 GW by 2050, incentivising the installation of a much higher number of OWFs than conventional O&G installations (Paolo et al., 2024). Meanwhile, many O&G platforms are required to be removed in accordance with decommissioning regulations in the OSPAR maritime areas driven by the end of production at many fields (Fortune & Paterson, 2018). There is an urgent need to understand how the transition from O&G platforms to OWFs as the dominant marine artificial structures (MAS) could affect the North Sea ecosystem and marine biodiversity.

Offshore MAS can influence marine fish communities through many impact pathways. First, MAS can enhance primary and secondary production, thereby increasing fish prey and, with it, fish recruitment, biomass and biodiversity (Claisse et al., 2014; Degraer et al., 2020; Dorrell et al., 2022; Ibanez-Erquiaga et al., 2025; van Berkel et al., 2020; Van Elden et al., 2019). Second, where fishing is excluded or reduced near MAS fish gain protection from exploitation, which can enhance biomass production and lead to local fish aggregation around MAS (Love et al., 2006). MAS can also have negative effects on fish communities, including increasing predation by seabirds and marine mammals on aggregated fish prey (Russell et al., 2014), destruction of vulnerable habitats for sensitive and threatened species (Lloret et al., 2022) and O&G associated contamination (i.e. discharge of produced water) that negatively affect fish physiology (J. Neff et al., 2011; Santana et al., 2018). Given that fish exhibit distinct sensitivities and behaviours in response to different MAS stimuli, understanding different impacts between MAS types (O&G platforms vs OWFs) and disproportionate MAS effects that either favour or adversely affect fish groups is crucial to better to assess the ecological roles of MAS in marine ecosystems.

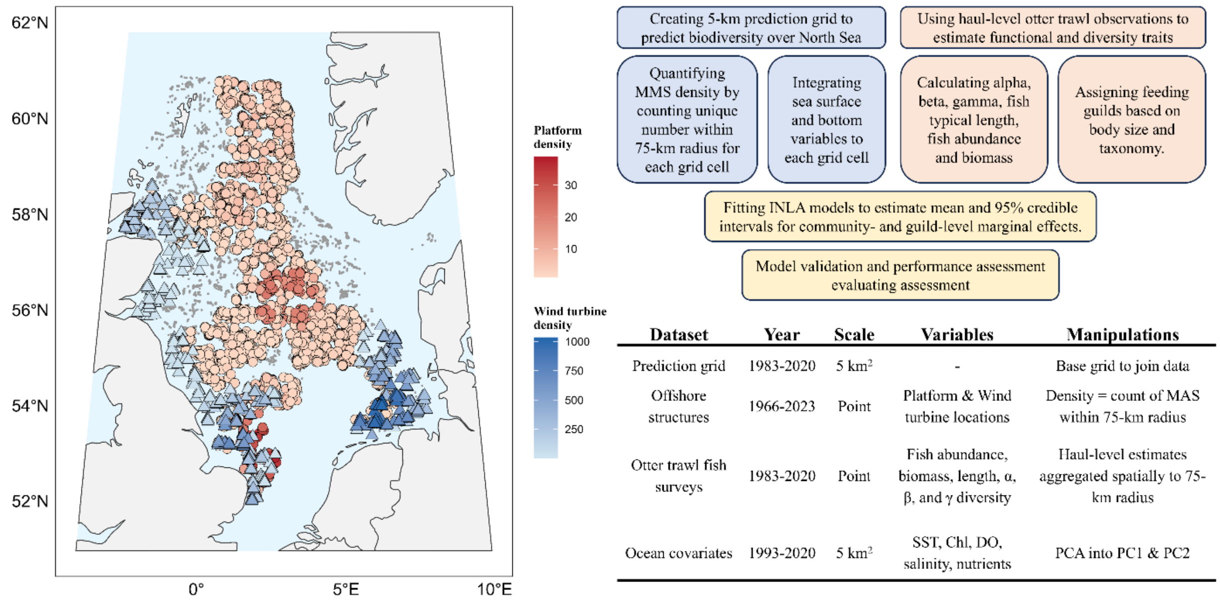
Most existing studies assessed the ecological effects of offshore O&G platforms and wind turbines separately, either through site-specific case studies (J. W. Coolen, Bittner, et al., 2020) or focusing primarily on a limited set of biodiversity indicators like species abundance (Wright et al., 2020). However, it does not provide adequate information relevant to food web assessment on the dynamics of body masses mediated through trophic interactions across functionally distinct groups. Existing research efforts largely neglect how MAS alter food web structure and functioning, especially at large spatial scales for mobile predators like fish (Sadykova et al., 2020). Feeding guilds provide a useful approach to address this knowledge gap and complement traditional biodiversity assessment, as the collation of taxon-specific size classes and dietary information, enabling classification of fish into distinct feeding niches (M. S. Thompson et al., 2020). Changes in fish feeding guilds can inform ecosystem status: planktivores reflect primary production through phytoplankton consumption; benthivores and bentho-piscivores reflect secondary production via fish and invertebrate predation; and piscivores that mainly consume fish reflect fish production (C. P. Lynam et al., 2017).

The main goal of this study was to determine how the aggregations of different MAS cumulatively influence marine fish biodiversity and food web metrics at broad spatial scales. We focused on the North Sea as it is one of the pioneering areas of O&G exploitation and undergoing rapid expansion of OWFs, with spatial and temporal extensive efforts of ecological sampling to enable large-scale diversity and food web assessment. We tested two primary hypotheses: i) MAS exert scale-dependent effects on fish diversity (α-, β-, and γ- diversity), with negative responses near O&G platforms and positive responses near OWFs; ii) MAS effects on fish abundance, biomass, and length vary across fish feeding groups, with smaller, lower-trophic-level fish species benefiting more than larger piscivores. We also conducted two applications: iii) mapping spatial correlations between fish biodiversity change and MAS density to quantify how shifts in the MAS composition, from O&G platform-dominated to OWF-dominated seascape, reshape fish abundance, biomass, length, α-, β-, and γ- diversity from local to regional scales; and iv) projecting the long-term cumulative effects of O&G platforms and OWFs on fish abundance, biomass, length, α-, β-, and γ- diversity. The combination of hypothesis testing and applied analyses provide implications on multifaceted aspects of biodiversity and food web structure across local and regional scales, enabling policy-makers to identify emerging ecological "hotspots", inform marine spatial planning, and predict ecological and environmental outcomes of future MAS expansion scenarios.

4.2 Methods

4.2.1 MAS density data

The spatial distribution of otter trawl hauls and the densities of O&G platforms and OWFs was shown in Figure 1. We focused on the northeast Atlantic shelf seas utilising decadal offshore industrialisation in O&G exploitation and recent development of OWFs. MAS records were accessed from a recently compiled database that corrects previous MAS databases (OSPAR Offshore Installations and EMODnet) for spatial mismatches and omissions (Martins et al., 2023). The metadata including installation dates, removal dates, structure types, and locations were used to select structures fixed to the seabed and extending above the water surface. A total of 684 fixed platforms and 4,295 wind turbines were included in the analysis, with their installation dates ranging from 1966 to 2023.



Creating 5-km prediction grid to predict biodiversity over North Sea

Using haul-level otter trawl observations to estimate functional and diversity traits

Quantifying MMS density by counting unique number within 75-km radius for each grid cell

Integrating sea surface and bottom variables to each grid cell

Calculating alpha, beta, gamma, fish typical length, fish abundance and biomass

Assigning feeding guilds based on body size and taxonomy.

Fitting INLA models to estimate mean and 95% credible intervals for community- and guild-level marginal effects.

Model validation and performance assessment evaluating assessment

Dataset	Year	Scale	Variables	Manipulations
Prediction grid	1983-2020	5 km^2	-	Base grid to join data
Offshore structures	1966-2023	Point	Platform & Wind turbine locations	Density = count of MAS within 75-km radius
Otter trawl fish surveys	1983-2020	Point	Fish abundance, biomass, length, α, β, and γ diversity	Haul-level estimates aggregated spatially to 75-km radius
Ocean covariates	1993-2020	5 km^2	SST, Chl, DO, salinity, nutrients	PCA into PC1 & PC2

Figure 1: Otter trawl fish hauls proximate to wind turbine density (blue triangles) and O&G platform density (red circles) and without MAS nearby (left); A workflow diagram showing how MAS, fish, and environmental data were combined and analysed (right).

We used a 5km^2 prediction grid covering the study region to estimate the density of O&G fixed platforms and wind turbines within a 75 km radius from the centre of each grid cell for each year between 1983 to 2020 (i.e. a sum of individual MAS grouped by type and year within 75 km from the centre of each grid cell). This captured the larger-scale spatial aggregational patterns of offshore MAS in space and time and provides a measure for the cumulative effects of MAS from neighbouring grid cells. Comparing to simply gridding 75 km, this method offers a more accurate representation of spatial heterogeneity for MAS density, fish biodiversity and food web metrics as well as environmental variability in a realistic context.

4.2.2 Fish survey data

Fish survey data were obtained from C. Lynam and Riberio (2022), a data product based on Northeast Atlantic groundfish data using surveys undertaken from 1983 to 2020. Catch records by taxonomic group and by fish length category in terms of biomass and number of fish were standardised to the area swept by the haul. For each fish taxon, we calculated the haul-level estimates of its abundance and biomass at each km^2. A total of 23,798 unique hauls as a subset of total fish survey data from 1993 to 2020 was included in corresponding with temporal span of environmental data. For taxa that were not identified at the species level, their taxonomic levels were assigned with Gobiidae and Ammodytes (Murray S. A. Thompson et al., 2024).

We used fish typical length to assess MAS effects on the size composition of fish communities following the approach adopted by OPSAR to assess the status of food webs (C. P. Lynam, Piet, & Volwater, 2022). For each otter trawl haul, fish typical length was calculated in the unit of centimetres as follows:

$$Fish\ typical\ length = \exp\left(\frac{\sum(DensBiom_i * \log(fish\ length_i))}{\sum DensBiom_i}\right) \tag{1}$$

where $DensBiom_i$ represents fish biomass per km^2 at each haul, while $fish\ length_i$ represents measured body length of corresponding fish taxon at each haul.

4.2.3 Fish feeding guilds

Fish were assigned into feeding guilds following the OSPAR pilot food web indicator (Murray S. A. Thompson et al., 2024) which used a large collation of stomach content data to classify into broad functional feeding groups using fish taxa and body size information. Feeding guilds provide the means to categorise fish into broad functional feeding groups associated with different food web energy pathways: planktivore which have the smallest mean body size of all the guilds and feed nearest the base in the food web, mostly on zooplankton (i.e. most closely linked with local primary production); benthivores which have the second smallest mean body size and feed predominantly on invertebrates dwelling on the seafloor (i.e. most closely linked with benthic secondary production); bentho-piscivores which are the second largest based on mean body size and the most omnivorous, feeding on a combination of benthic invertebrates and fish; and piscivores which have the largest mean body size and feed mostly on fish. Processed survey data with fish classified into feeding guilds per haul are available from Murray S.A. Thompson et al. (2024). We calculated fish abundance, biomass and typical length of each feeding guild for each haul observation.

4.2.4 Fish diversity estimates

We adopted the Whittaker framework and α-, β-, and γ-diversity (i.e. haul-level species richness, change in species composition between hauls within a region and regional species richness, respectively) to assess change in fish diversity in response to MAS (Whittaker, 1972). We used rarefaction and extrapolation with Hill numbers to account for sampling biases associated with spatiotemporal heterogeneity in sampling effort and sampling size (Chao et al., 2014). Estimates of α-diversity rely on individual-based rarefaction and extrapolation to individual numbers (i.e. twice the mean sample count). For γ-diversity, for each haul, 9 other spatially proximate hauls within a radius of 75 km and collected within 182 days were selected for sample-based rarefaction and extrapolation. Estimates of γ-diversity were made by extrapolating to 20 samples. 75 km as a threshold of spatial range was determined in the data exploration of fish otter trawl data because it returned adequate number of samples while small enough to detect regional changes. α- and γ-diversity estimates were made using the iNEXT package (Hsieh, Ma, Chao, & McInerny, 2016). β-diversity was estimated as the ratio of γ and mean α diversity (Jost, 2007; M. S. A. Thompson et al., 2021). The incorporation of three biodiversity metrics allowed us to reveal the relative contributions of local and large-scale processes and thus whether MAS affect regional diversity.

4.2.5 Climate and environmental variables

Environmental data for our study area between 1993 and 2020 were extracted from the Forecasting Ocean Assimilation Model 7km Atlantic Margin model (FOAM AMM7), which integrated version 3.6 of the Nucleus for European Modelling of the Ocean (NEMO) ocean model (Madec, 2016) and assimilated observations from NEMOVar version 6 (Mogensen, Balmaseda, & Weaver, 2012) and European Regional Seas Ecosystem Model (ERSEM) (Butenschön et al., 2016). All data were made publicly available at Copernicus Marine Service (http://marine.copernicus.eu): Atlantic-European North West Shelf of ocean physics reanalysis data (https://doi.org/10.48670/moi-00059) and ocean biogeochemistry reanalysis data (https://doi.org/10.48670/moi-00058).

We used the annual means and standard deviations of temperature, chlorophyII, salinity, nitrate, phosphate, dissolved oxygen, current velocity and mixed layer bathymetry. We also included depth using data from ETOPO 2022 database (NOAA National Centres for Environmental Information, 2022). We extracted using getNOAA.bathy function from the marmap package (Pante & Simon-Bouhet, 2013). All environmental data were processed onto a 5 km^2 grid and then appended to haul-level fish observations.

4.3 Statistical analysis

4.3.1 Data preparation

We utilised the Integrated Nested Laplace approximation (INLA) for Bayesian inference to assess the impacts of offshore platforms and wind turbines over space and time. A total of six fish responses were modelled, including α-, β-, and γ-diversity, fish abundance (individual n km^2) and biomass (kg km^2) as well as fish typical length (cm). Data were then explored using the protocol from Alain F. Zuur, Ieno, and Elphick (2010): the presence of outliers, collinearity between covariates, the relationships between response variables and predictors, potential zero inflation, and dependency was examined using Cleveland dotplots, pairplots, multi-panel scatterplots, the ratio of 0s, as well as UTM-transformed spatial locations by year. We included annual means and standard deviations of all environmental variables and then applied a Principal Component Analysis (PCA) to reduce dimensionality into the first two principal components, PC1 and PC2, which explained over 58% of total variability contained within the environmental data (Figure S1). PC1 characterised an environmental gradient from oceanic, nutrient rich benthic habitats to shallow and highly productive (i.e. high chlorophyll a) a coastal habitats. PC2 captured a gradient from a cold sea surface temperature with strong bottom currents and high oxygen shifting toward a warm and hydrodynamic stable coastal environment. PC1 and PC2 were used as fixed predictors in the INLA models to represent environmental variability.

4.3.2 Model priors

A non-convex area was established around the sampling locations to constraint the spatial domain and minimise the extension beyond the prediction area. A Matérn spatial correlation structure was built over the study domain using a penalised complexity prior. The Matérn correlation parameters include priors of range and sigma. A prior of range was estimated using the histogram of pairwise distances of sampling locations. A prior of sigma depends on the model structure; for models with a log link function (fish abundance, biomass, and typical length), the prior of sigma was estimated based on the residual standard error of a linear model on a constant intercept; for models with an identity function (α, β, and γ diversity), the lower limit of the prior of sigma was estimated based on the standard deviation of the response variable (Alain F Zuur, Ieno, & Saveliev, 2017).

4.3.3 Model selection and comparison

For each fish response metric, we fitted INLA models with Generalised Linear Models (GLMs) with a Gaussian error structure. The fixed variables included the platform and wind turbine number and two principal components, PC1 and PC2. The non-spatial GLM was used as the baseline model, then compared with models adding complexity: i) a spatial GLM with a spatial random field based on the Stochastic Partial Differential Equations (SPDE) approach, ii) a GLM with replicate spatial temporal term, iii) a GLM that allows spatial correlation to change over year according to an auto-regressive (AR1) process. All models were implemented in R 4.4.3 with the INLA version 24.12.11 (Lindgren, Rue, & Lindström, 2011; R Core Team, 2025; Rue, Martino, & Chopin, 2009).

Model comparisons were based on the Deviance Information Criteria (DIC) and Watanabe-Akaike Information Criterion (WAIC), with lower values indicating better fit and parsimonious structure at the mesh size and number of knots. For each fish response tested, we compared models with different spatial temporal structures and selected the best model using the lowest DIC and WAIC value (Table S1). We validated the model by simulating posterior regression parameters 1000 times and fitting them into DHARMa to calculate scaled quantile residuals (Hartig, 2016). The scaled quantile residuals were then tested for uniformity, outliers and dispersion in QQ plots. For each year, spatial autocorrelation was assessed using year-based Moran's I test and variograms (Figure S2).

4.3.4 Posterior estimates of predictors

To understand overall effects of O&G platforms and OWFs on the various fish responses, we extracted estimates and 95% credible intervals from 1000 posterior simulations. The directionality of posterior estimates indicates whether O&G platforms or OWFs had either a positive or negative effect on the corresponding fish responses. Where 95% credible intervals of posterior estimates exclude zero, it means there is a 95% probability that the fixed predictors effected the response being tested against the null hypothesis of the effects being zero.

For each type of MAS, its effect on fish feeding guilds were estimated using the posterior estimates and their 95% credible intervals. Using the spatial temporal structure of the optimal INLA model, the interactions between fish feeding guilds and O&G platforms and OWFs, together with PC1 and PC2, were modelled against $\log_{10}$ transformed fish biomass, abundance and typical length as response variables. We used a Gaussian distribution for fish biomass and abundance and used Bernoulli and Gaussian hurdle model to account for zeros and positive data in the response variable. The effects between MAS on one fish feeding guild were calculated as the sum of coefficients of MAS main term and interaction term based on 1000 posterior sample simulations.

4.3.5 Examining spatial correlation between changes in fish biodiversity and MAS density

To understand cumulative changes over years over space and time, we assessed total changes between 1993 and 2020 by simulating 1000 posterior samples and reprojecting data back to the prediction grid. The simulated fish responses were derived using the mean value of the covariates

(O&G platform and wind turbine density, PC1, and PC2) at the nearest spatial feature multiplied by their coefficients in addition to spatial random fields in 1993 and 2020 respectively. The 95% credible intervals were used to filter out areas without significant change. We used linear regression to model changes across the various fish responses with O&G platform and wind turbine density as well as PC1 and PC2 to assess the impacts of density changes for both types of MAS.

4.3.6 Quantifying cumulative effects of each MAS on fish biodiversity metrics

We assessed cumulative effects of O&G platform and wind turbine densities on fish responses based on the product between estimated coefficients and differences in mean MAS density from the baseline year (i.e. 1993). At each year, we reprojected the mean of O&G platform density, wind turbine density, PC1, and PC2 onto the nearest grid and extracted its spatial random field. To develop a causal quantitative relationship between MAS density and fish response, we separately considered fixed effects and total effects based on three baseline scenarios: (1) the baseline grid with platform density fixed at 1993 while wind turbine density, PC1, and PC2 were as observed; (2) the baseline grid with wind turbine density fixed at 1993 while O&G platform density, PC1, and PC2 were as observed; and (3) both O&G platform and wind turbine density in the baseline grid fixed at 1993 while PC1 and PC2 were as observed. For baseline 1-2, only fixed effects were considered to isolate MAS effects from environmental variability and other latent variables and ensure the causation between differences in fish responses and changes in MAS densities over year. For baseline 3, both fixed and random effects were used to determine total changes relative to the baseline 1993. As estimated coefficients between each MAS structure and each response were constant, we produced a deterministic perspective of cumulative trends that depends on temporal changes in mean number of each structure over time amplified by its coefficient and transformed back to the original measurement scale. The means and 95% credible intervals were summarised at each year.

4.4 Results

4.4.1 Optimal model identification

For fish abundance, biomass, length, and β- diversity, the optimal model is the GLM that allows spatial correlation to change over year according to an auto-regressive (AR1) process; For α- and γ- diversity, the optimal model is the GLM with replicate spatial temporal term (Table S1). We used the optimal model of each variable to estimate the marginal effects, mapping biodiversity changes and quantifying cumulative effects of each structure type.

4.4.2 Marginal effects of each MAS on fish biodiversity metrics

Offshore structures demonstrated limited effects on fish community-level responses. There were no significant effects of platform density on any metric, whilst wind turbine density only had a significant positive effect on $\log_{10}$-transformed fish biomass (Figure 2: posterior estimate = 0.001, 95% CIs = 0.00021 to 0.00188).

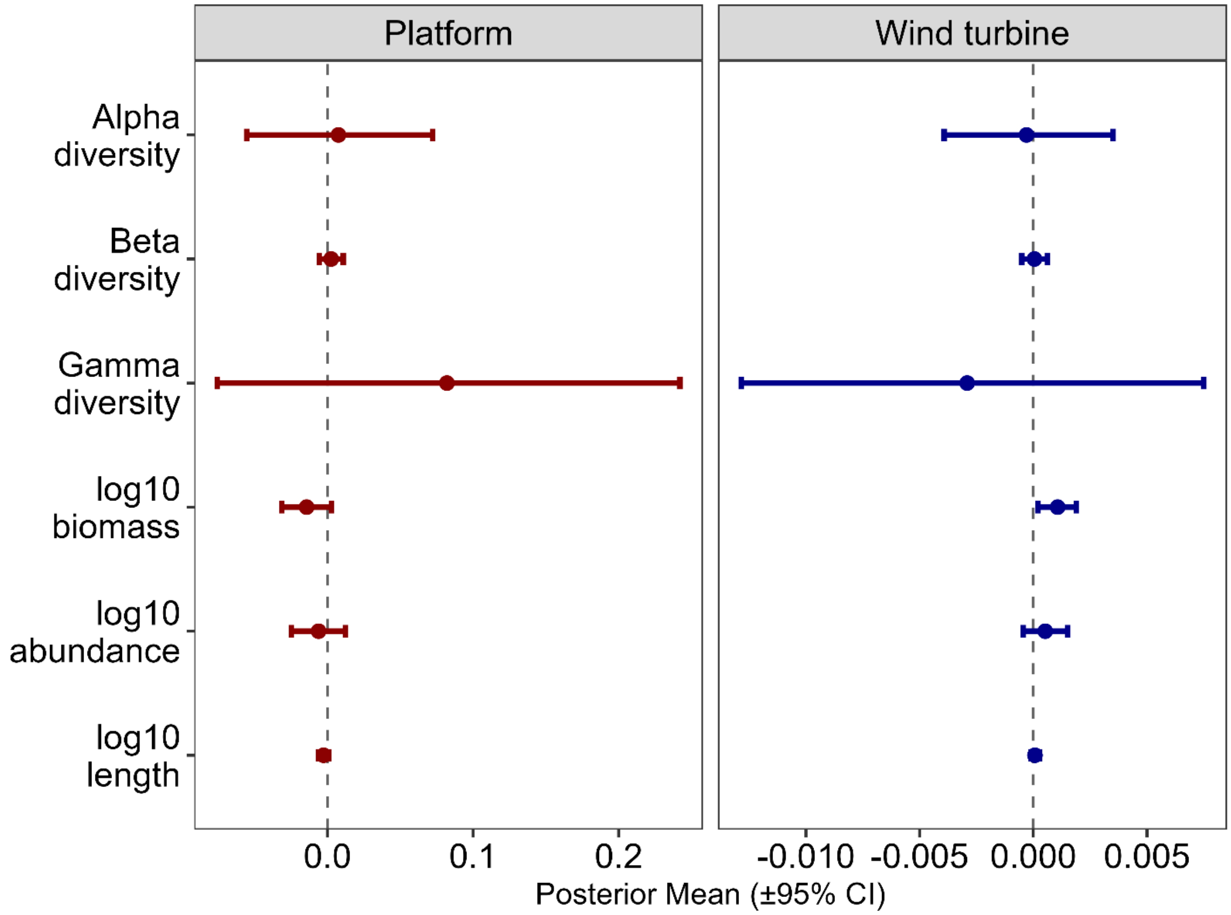


Figure 2: Marginal estimates and their 95% credible intervals of platform and wind turbine number on the six biodiversity response variables. Statistically significant patterns (represented by an asterisk) occur if the credible intervals do not include zero.

4.4.3 Marginal effects of each MAS on guild-specific abundance, biomass and length

O&G platforms and OWFs had contrasting effects on fish feeding guilds. There was a negative effect of platforms and wind turbines on the biomass of both piscivores and bentho-piscivores (Figure 2A). In contrast, OWFs were positively associated with planktivore and benthivore biomass (Figure 2A). Both O&G platforms and OWFs were negatively associated with piscivores abundance, whilst only platforms had negative effect on bentho-piscivore abundance (Figure 2B). OWFs had a positive effect on the abundance of benthivores and planktivores (Figure 2B). For feeding guild typical length, there was a negative effect of O&G platforms on planktivores and of OWFs on piscivores positive effects of OWFs on planktivores and benthivores (Figure 2C).

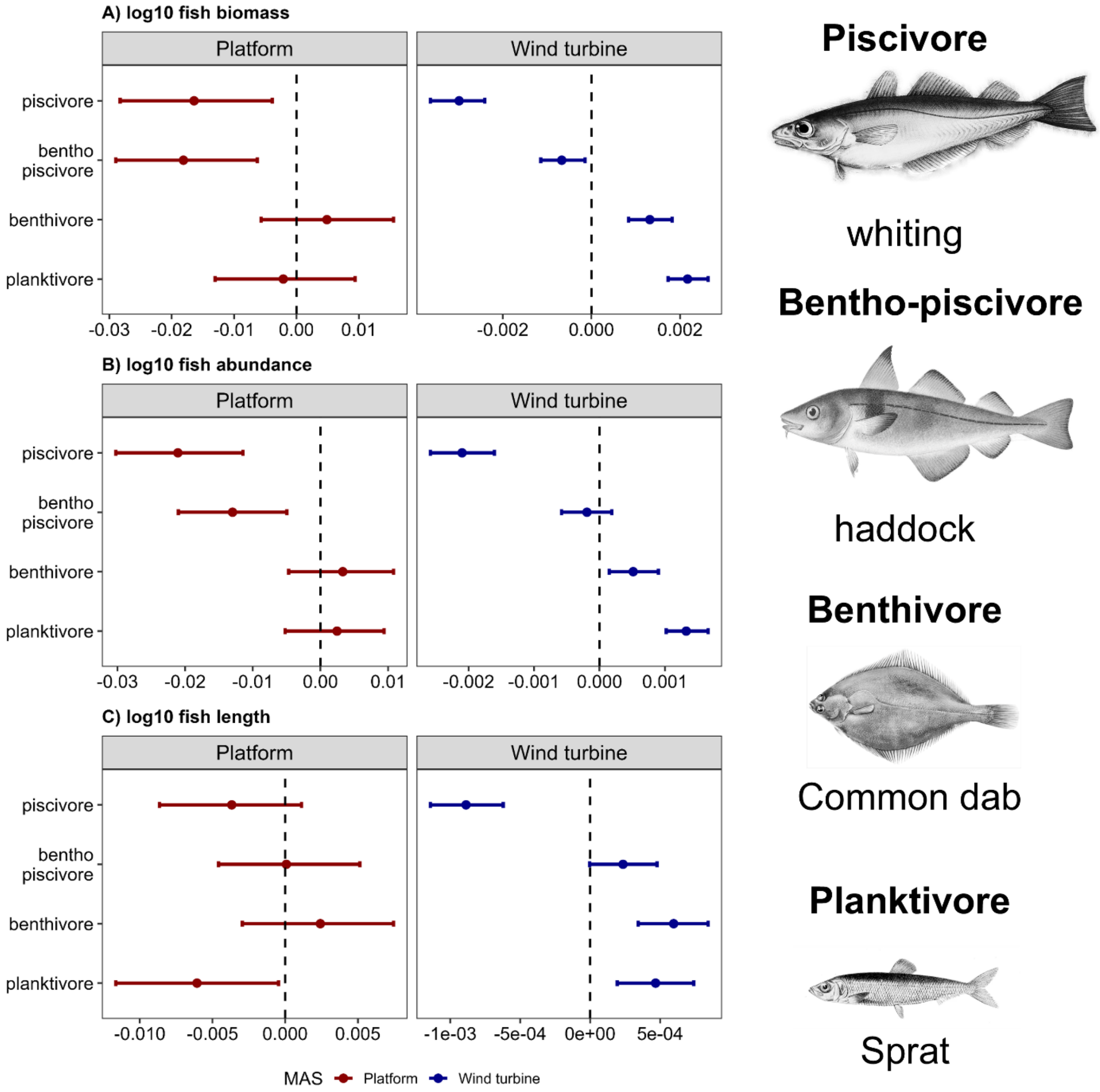


Figure 3: Posterior estimates and their 95% credible intervals of effects between platform or wind turbine and four fish feeding guild based on 1000 posterior simulations.

4.4.4 Spatial correlation of changes in fish biodiversity metrics and MAS densities

Spatial patterns in species richness and gamma diversity were similar, with southeastern areas increasing and northern areas decreasing in both (Figure 4A, C). In contrast, beta diversity decreased at the southern coast and much of the northern areas, indicating greater homogenisation of fish communities (Figure 4B). Fish biomass and abundance declined in the central North Sea, but increased in the southern areas and parts of the northern North Sea (Figure 4D, E). Fish typical length mainly decreased in the central North Sea and southern areas near the continent (Figure 4F). Significant changes in fish biodiversity metrics were shown int eh Figure S2. For species richness, the increase of platform density had a significant negative effect (Estimate = -0.682; 95% CIs = -0.757 to -0.607) while wind turbine density had a significant positive effect (Estimate = 0.009; 95% CIs = 0.005 to 0.012). For beta diversity, the increase of platform density had a significant positive effect (Estimate = 0.046; 95% CIs = 0.019 to 0.073) while no significant effects were observed in the increase of wind turbine density. For gamma diversity, the increase of platform density had a significant negative effect (Estimate = -0.754; 95% CIs = -0.806 to -0.702) while wind turbine density had a significant positive effect (Estimate = 0.005; 95% CIs = 0.004 to 0.007). For fish biomass, the increase of platform density had a significant negative effect (Estimate = -307.5; 95% CIs = -244.6 to -205.9) while wind turbine density had a significant positive effect (Estimate = 13.0; 95% CIs = 11.234 to 14.762). For fish abundance, the increase of platform density had a significant negative effect (on the standard deviation scale: Estimate = -0.072; 95% CIs = -0.085 to -0.058) while wind turbine density had a significant positive effect (on the standard deviation scale: Estimate= 0.003; 95% CIs = 0.003 to 0.004). For fish typical length, the increase in platform and wind turbine densities had significant positive effects (Platform: Estimate = 0.522; 95% CIs = 0.331 to 0.714; Wind turbines: Estimate = 0.008; 95% CIs = 0.006 to 0.011).

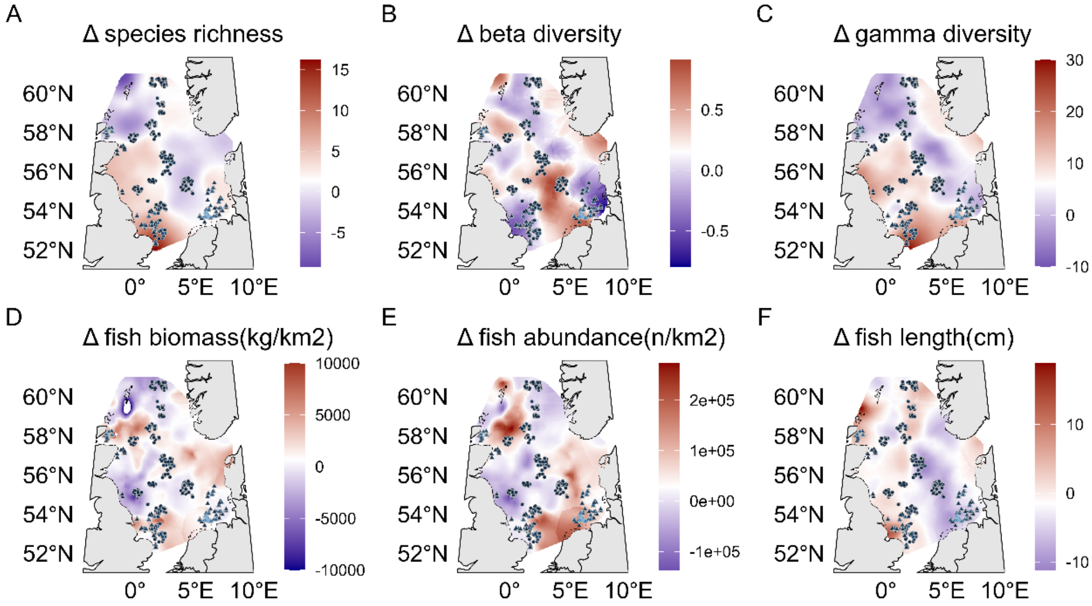


Figure 4: Changes between 1993 and 2020 in fish alpha diversity (A), beta diversity (B), gamma diversity (C), fish biomass (D), fish abundance (E), and fish typical length (F). Red indicates an increase, and blue indicates a decrease in fish responses over time. Black circles and triangles show the locations of platforms and wind turbines, respectively.

4.4.5 Cumulative effects of each MAS type on fish biodiversity metrics

Cumulative effects of platforms and wind turbines at the North Sea scale were detected on all six fish responses over time (Figure 5). Declines in species richness locally and regionally in response to both platforms and wind turbines were detected, based on α- and γ- diversity (Figure 5A, C). There were divergent effects of both MAS types on β- diversity, with increases in response to increasing wind turbine density over time, but a decrease in response to increasing wind turbine density over time, but a decrease in response to platforms (Figure 5B). Fish biomass and abundance increased in response to increases in wind turbine density, with little change due to change in the density of platforms (Figure 5D, E). The increase and decrease in wind turbine and platform densities over time, respectively, both contributed to increased fish typical length (Figure 5F).

While both MAS types supported beta diversity, the increase of wind turbine and the decrease of platform number showed divergent patterns (Figure 5B). Wind turbine number showed positive interactions with fish abundance and biomass number, resulting in an exponential increase over time in parallel to their structure number (Figure 5D and 5E). The loss of platform number benefited the increase of fish abundance and biomass number as it had negative effects on both metrics. As wind turbine number was positively associated with fish typical length while platforms were opposed, the increase of wind turbine and the decrease of platform densities over time both contributed to increased fish length (Figure 5F).

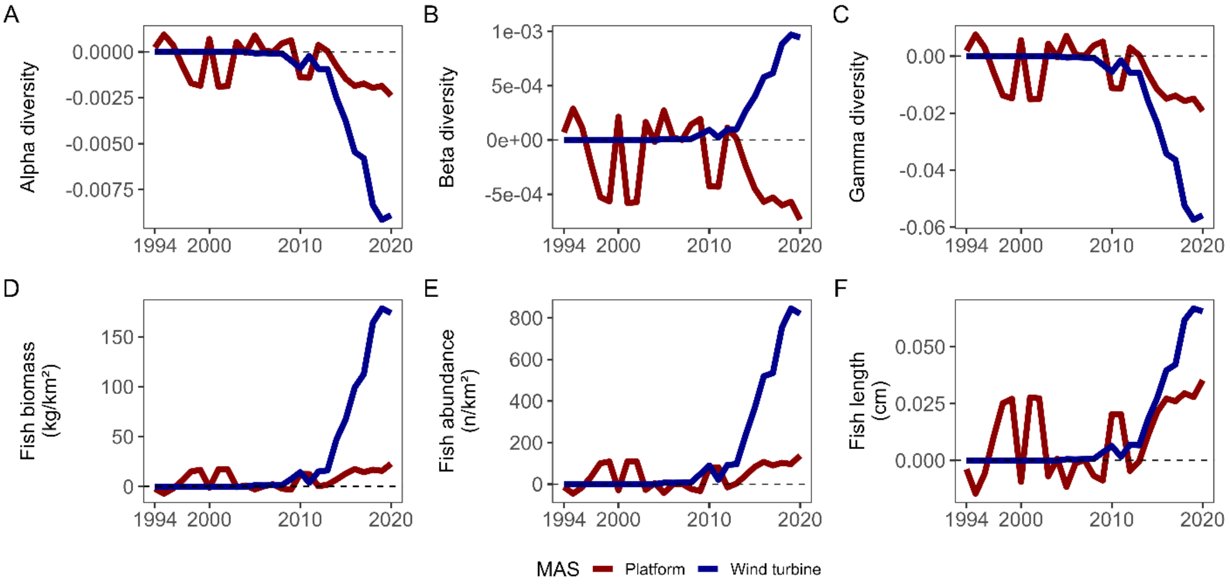


Figure 5: Changes of fixed effects between 1993 and the following 1994 to 2020 being attributed to platform and wind turbine number respectively on fish α- diversity(A), β- diversity (B), γ-diversity (C), fish biomass (D), fish abundance (E), and fish typical length (F).

4.5 Discussion

On average, the contrasting effects of offshore platforms and wind turbines on fish responses showed their distinct ecological roles in the marine environment. Increases in wind turbine density supported higher fish biomass (Figure 2A). Commercial fishing is often restricted or prohibited within wind farms (Fortune & Paterson, 2018) meaning that they could act as a refuge for fish from exploitation and enhance fish biodiversity (Ashley et al., 2014). Increased food availability and structural complexity supports higher fish densities, which use wind turbines as foraging grounds and refuges to avoid predators (Folpp et al., 2020; J. T. Reubens et al., 2011). While both no-take zones and artificial reef effects are also applicable to platforms, the release of drilling muds, cuttings, and produced water during oil and gas exploitation leads to elevated concentrations of pollutants like heavy metals and, hydrocarbons, (Ellis et al., 2012; Olsgard & Gray, 1995) that can disproportionately affect larger organisms at higher trophic levels and dietary specialists in food webs (Chen et al., 2024). The exposure and uptake of these contaminants could impose adverse physiological effects on fish development and growth, including oxidative stress, altered fatty acid composition and genotoxicity (Balk et al., 2011; Sorhus et al., 2016).

Nevetherless, the impacts of MAS on large-scale fish biodiversity patterns across the North Sea were generally limited and statistically insignificant (Figure 2), indicating that the ecological footprint of MAS may be limited in space. A synthesis of UK benthic surveys near oil and gas structures found that the spatial extent of oil-associated contamination and altered community structure for O&G platforms in the North Sea was mostly within 1.2 km (Henry et al., 2017). This is a relatively localised effect compared to marine fish as a more mobile assemblage. For example, Sadykova et al. (2020) showed that fish predators and preys generally had a spatial range over 75 km. Similarly, a modelling study on OWFs also showed a highly localised ecological effect (Halouani et al., 2020). This suggests that effects of MAS are likely to be patchy in areas with a high density of installations. Another possible explanation is that estimating the effects of MAS as the average change across all observations introduces large variability given the broad temporal and spatial scale used in the study. The historical magnitude of exploitation (Cordes et al., 2016), local environmental features (Terlizzi et al., 2008), and other site specific conditions could thus override the effects of Mas on fish communities (S. C. L. Watson et al., 2024), despite our best efforts to account for key environmental factors in our models. In comparison with wind turbines, the marginal effects of platforms had much larger variability (Figure 2), which could be attributed to the broad distribution of platforms across the North Sea and throughout the duration of the dataset. Thus, fish communities associated with platforms experience a wider range of environmental conditions compared to wind turbines, which are primarily located in coastal regions and have only increased dramatically in number since 2010.

The attraction-production hypothesis, whereby fish either aggregate around MAS without increases in local net production (Brickhill et al., 2005; Klima & Wickham, 1971; Smith, Lowry, Champion, & Suthers, 2016) or that MAS boost local fish biomass production via increased carrying capacity and novel habitat (Claisse et al., 2014; McLean et al., 2022; Wu, Tweedley, Loneragan, & Zhang, 2019) is still hotly debated. Yet, attraction and production may not be mutually exclusive, if aggregated fish communities lead to settlement or longer residence, and refuge, enhancing growth, larval recruitment and biomass production (Ninon Mavraki et al., 2021). The extent to which MAS attract marine fish or increase local productivity reflects the capacity of such structures to provide ecosystem functions and services. MAS effects on fish communities are often context dependent, e.g., wind turbines with a longer operational time and more complex structure could impose larger effects on fish biomass and abundance than platforms (Bicknell, Gierhart, & Witt, 2025).

We found that fish community composition changed across feeding guilds though total biomass of fish increased near wind turbines: small fish such as planktivores and benthivores were dominating whereas biggest piscivores were losing (Figure 3). This equates a simplification of food webs with shorter foo chains and a reduction in the typical size of the community, which could have negative effects on ecosystem services like fisheries yield (O’Gorman, Zhao, Kordas, Dudgeon, & Woodward, 2023; Pauly et al., 1998). The positive effects of wind turbines on abundance, biomass and typical length of planktivores and benthivores offer some support for the production hypothesis. They also align with previous field surveys, stomach content analysis and stable isotope data showing that gadoids (i.e., Atlantic cod and pouting) and demersal flatfish (i.e., plaice and dab) exhibit higher food intake of epifaunal prey associated with hard substrate supporting more growth (Buyse et al., 2023; Gimpel et al., 2023; Ninon Mavraki et al., 2021; Jan T Reubens, Vandendriessche, Zenner, Degraer, & Vincx, 2013). The presence of wind turbines facilitates local vertical mixing and results in increased vertical nutrient transport supporting higher primary productivity, which could have trophic cascading effects on supporting higher densities of planktivorous species like herring and sprat (Floeter et al., 2017).

The negative effects of platforms and wind turbines on the abundance, biomass, and typical length of piscivores seem to be counterintuitive. Increased small fish around MAS should be followed by increased predation from top predators (Paxton et al., 2019). A possible reason is that higher density of MAS leads to behaviour changes for piscivores. Studies have found that apex predators such as skates and sharks avoid wind turbines (Maxwell et al., 2022; Van Hal, Griffioen, & van Keeken, 2017). While altered fish behaviours near MAS are poorly understood, the plausible explanations are altered habitat conditions after MAS introduction, increased underwater noise and the generation of electromagnetic fields (Tricas, 2012; Wahlberg & Westerberg, 2005). In contrast to wind turbines, the typical length of planktivorous fish decreased in response to platforms (Figure 3C). It might suggest that platform-associated effects, such as accidental oil leaks and hydrocarbon and heavy metal-contaminated discharges, provide suboptimal habitats for planktivores with adverse impacts on fish growth (Weis, Smith, & Zhou, 1999). Thus, platforms may act as ecological traps by attracting fishes into polluted environments that compromise their fitness and growth (Robertson & Hutto, 2006).

The overall changes in fish responses between 1993 and 2020 were significantly associated with the density of MAS (Figure 4). Areas with a greater platform density had consistent negative effects through time on α-diversity, γ-diversity, fish biomass and abundance, indicating overall adverse impacts of O&G platforms on fish responses. On the contrary, areas with more wind turbines had higher values in those same metrics, indicating an overall beneficial role in boosting local and regional fish diversity. The contribution of MAS effects to the total change in fish responses was smaller than environmental factors (included in the models as PC axes), implying that climatic variables and latent variables (e.g., commercial fishing) played a more important role in explaining spatial and temporal patterns of fish biodiversity and food web metrics. It indicated that the ecological effects of MAS are mediated by local and regional environmental and ecological contexts.

The determination of marginal effects of MAS on each fish response allow for causation attribution between acclimated number changes of each structure type over time and corresponding cumulative effects on fish responses (Figure 5). Observed and counterfactual setting with realistic and localised mean MAS number over space and time while holding other covariates same as observed dataset enables us to disentangle MAS effects from complex interannual variability in fish biodiversity and exclude yearly-varying climatic effects and unobserved latent processes. The current results could be further refined into country's jurisdictions or other geographic boundaries (i.e., northern, central and southern North Sea), which provides important empirical evidence for conservation policy-making and fisheries management. Given the expansion of offshore renewable infrastructure in the near future, our model contributes to a better understanding of ecosystem level environmental and ecological impacts for future scenarios.

Appendix: Supplementary materials for chapter 4

S4.1 Reducing dimensionality via Principal Component Analysis

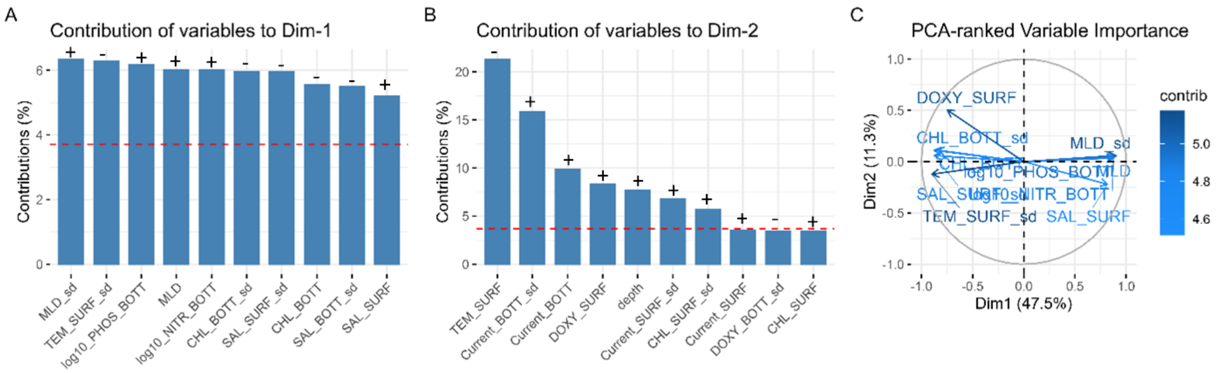


Figure S1: The top 10 variables with their contribution to PC dimensional 1 (A) and PC dimensional 2 (B), and total contribution on explaining the variations by PC1 and PC2 (C). The red line in panel A and B represents the expected average contribution. "+" or "-" on top of each contribution bar shows the directionality of this environmental variable correlating with PC1 (A) and PC2 (B). PC1 is characterised with higher mixed layer depth, higher sea bottom nutrient but lower chlorophyII. PC2 is characterised with cold sea surface temperature, high bottom currents, high surface oxygen and deeper depth.

S4.2 Model comparison, selection and validation

Table S1: INLA model selection of six fish biodiversity and food web metrics based on DIC and WAIC. The lowest DIC/WAIC with the most parsimonious model structure is identified as the best model for further analysis.

Fish biomass density (kg / km^2)		
Formula	DIC	WAIC
Log$_{10}$ biomass ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	15078.89	15079.52
Log$_{10}$ biomass ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	12454.80	12466.43
Log$_{10}$ biomass ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + replicated spatial field (SPDE replicate with year)	12836.93	12896.09
Log$_{10}$ biomass ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	11246.93	11275.47
Fish abundance density (n / km^2)		
Formula	DIC	WAIC
Log$_{10}$ abundance ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	18825.75	18826.29
Log$_{10}$ abundance ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	16784.96	16794.75
Log$_{10}$ abundance ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + replicated spatial field (SPDE replicate with year)	16175.63	16238.31
Log$_{10}$ abundance ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	15160.22	15195.48

Fish typical length (cm)		
Formula	DIC	WAIC
Log$_{10}$ length ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	-16923.04	-16920.16
Log$_{10}$ length ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	-20111.85	-20096.76
Log$_{10}$ length ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + replicated spatial field (SPDE replicate with year)	-21893.18	-21708.60
Log$_{10}$ length ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	-22662.48	-22561.62
Alpha diversity		
Formula	DIC	WAIC
a_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	61185.21	61187.17
a_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	55124.43	55126.43
a_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + replicated spatial field (SPDE replicate with year)	47145.01	47151.55
a_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	47166.05	47178.73
Beta diversity		
Formula	DIC	WAIC
b_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	9273.769	9275.202
b_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	7695.537	7699.187
b_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	4076.511	4143.411

+ replicated spatial field (SPDE replicate with year)		
b_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	4014.602	4078.076
Gamma diversity		
Formula	DIC	WAIC
g_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2	78554.12	78556.39
g_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial field (SPDE)	72039.18	72045.86
g_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + replicated spatial field (SPDE replicate with year)	68390.41	68443.75
g_q0 ~ -1 + Intercept + PlatDensity + WindDensity + PC1 + PC2 + spatial temporal field (SPDE in AR1 correlation)	68442.00	68485.80

S4.3 Fish biodiversity changes between 1993 and 2020

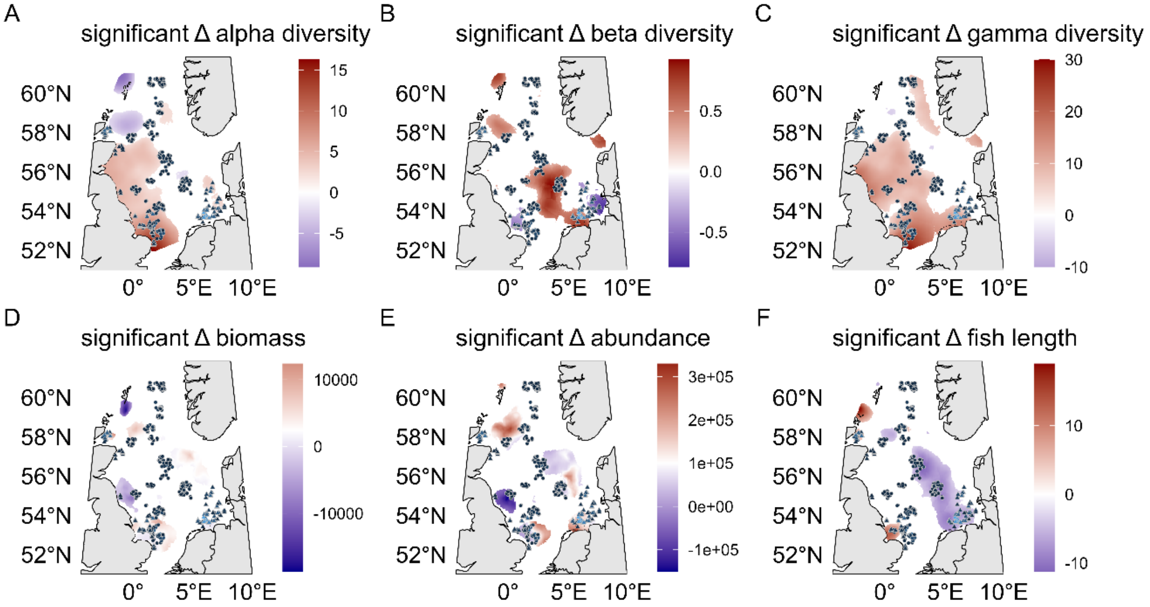


Figure S2: Fish biodiversity metric with 95% credible intervals excluding 0 were shown. Red indicates increase while blue indicates decrease. Black circles and triangles were locations of platforms and wind turbines

CHAPTER FIVE

General discussions on the contributions of each data chapter and future directions

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This chapter is a synthesis of the main findings, novelty and contributions for each data chapter. Future directions cover side projects in parallel to this thesis and future researches to further advance this topic, data compilation and management implications

5.1. Synthesis

Understanding how offshore energy structures affect marine biodiversity and food webs is crucial in determining whether their installation, operation, and decommissioning result in net gains in ecosystem services. Assessing these ecological impacts is also prioritised in the current global and regional legislations and framework to protect the ocean, including Sustainable Development Goal 14 – Life Below Water, the Agreement on Marine Biological Diversity of Areas Beyond National Jurisdiction, the Convention on Biological Diversity Global Biodiversity Framework, and the Oslo and Paris Conventions. Empirical evidence from these assessments is needed to guide ecologically robust management to mitigate potential negative impacts and produce positive outcomes.

The integration of biodiversity and food web metrics provides a holistic approach to evaluate how offshore energy structures reshape marine communities at a functional group and population level. Biodiversity metrics, including total abundance, species richness, mean individual body mass, and Pielou's evenness, describe changes in population size, taxonomic composition, size classes and dominance patterns. These metrics are vital to identify changes in community-level traits. On the other hand, food web metrics complement biodiversity metrics by linking species loss and changes in size structure to trophic architecture. Proportions of basal, intermediate, and top species describe the trophic distribution of taxa in the network; mean trophic level shows the average vertical position of sampled taxa and inform the status of energy pathway; generality and vulnerability reflect the average number of prey and predators, respectively, of each taxon in the food web; the number of links reflects the size of the food web, linkage density is the average number of links per taxon, and connectance is a measure of food web complexity that is often associated with the resilience of the system to external perturbations. The combined use of these metrics enables the detection of community reorganisation and changes in ecosystem functioning. It also contributes to better-calibrated programmes and the assessment of cumulative impact of offshore structures.

The rapid sprawl of offshore energy structures in the marine environment requires an ecosystem-based perspective to assess and predict not only effects on marine species, habitats, and ecosystem functioning, but also to account for natural background variability and concurrent stressors including climate change (Isaksson et al., 2025). The North Sea ecosystem is a particularly important focus given its leading role in O&G exploitation and offshore wind development in the past decades and foreseeable future and that fact it is highly susceptible to climatic variables like warming, circulation, and stratification as a shallow and semi-enclosed coastal shelf sea (Quante & Colijn, 2016). The integration of biodiversity and food web properties of marine fish and benthic invertebrates at both local and regional scales provides a more holistic understanding of how offshore energy structures alter community composition and consequently food web structure. This thesis examined diversity measures, functional traits and food web topology in the North Sea ecosystem to reveal their responses to different activities of offshore energy structures. Chapter 2 used diversity estimates (i.e., Shannon diversity index; Pielou's evenness), functional traits (i.e., individual mean body mass) and food web structural properties to reveal the spatial patterns of benthic communities along the distance away from the operating O&G platforms. Chapter 3 used a same set of diversity and food web indicators and investigated relative differences on benthic ecological responses before and after the decommissioning of O&G platforms to examine benthic succession and recovery. Chapter 4 explored the ecological impacts of both offshore O&G platforms and OWFs across the entire North Sea on fish biomass, diversity, and feeding guild responses. The main contributions of each data chapter are discussed as below, followed by some major research directions I consider as important themes to be explored.

5.2 Chapter contributions

This thesis demonstrates the interdependent relationship between biodiversity changes and food web functioning when marine communities are exposed to the impacts of offshore energy structures. Especially, this thesis explores the size spectrum theory at marine benthic invertebrates and fish communities at the operational and post-decommissioning phases of offshore structures. Chapter 2 describes the general defaunation of benthic communities within 500 m of highly contaminated areas. It shows that larger predators and dietary specialists were disproportionately affected while smaller organisms with opportunistic diets and rapid recruitment benefited in this degraded ecosystem and maintained high connecntance to survive against perturbations, which resulted in a simplified but more connected food web structure in the impact zone. It provides new empirical evidence to guide future biological monitoring programmes of offshore structures given the BACI design comparing the impact and the control and complement traditional biodiversity assessments with food web metrics. Chapter 3 examines post-decommissioning recovery in the benthic communities at the short-, medium-, and long-term. It found an initial decline in species richness and trophic interactions, followed by higher proportion of intermediate species, and further recovery with a greater food web complexity and longer food chain length. It characterises a non-linear recovery process shifting from smaller, opportunistic and pollution tolerant species to larger, more specialist and pollution sensitive species in the benthic communities. It utilised the best available data in the UK industry benthic monitoring surveys to examine three scenarios of benthic recovery. The adaptation of food web metrics can reveal the recovery process characterised with changes in food web complexity and proportions of intermediate species. Chapter 4 modelled fish abundance, biomass, and biomass-weighted length in response to the density of O&G platforms and OWFs. While community-level effects on these biological traits are limited, offshore structures exhibited guild-level effects on marine fishes, with larger piscivores becoming less abundant and smaller in both structures while smaller planktivores becoming more abundant and larger near wind turbines. It is one of the first pioneering studies that models regional level impacts of offshore structures and provide a novel method to quantify cumulative impacts in the marine biodiversity. In the biodiversity-ecosystem functioning framework, this thesis supports that biodiversity loss associated with O&G activities have cascading effects for trophic pathways and ecosystem functioning. Body size as the fundamental trait in the metabolic and size-spectrum theories supports that anthropogenic stressors could shift benthic and fish communities toward smaller size classes, which results in structural alternations in the trophic network.

5.2.1 Chapter 2: Oil and gas platforms degrade benthic invertebrate diversity and food web structure

Chapter 2 pioneered the integration of food web assessment into offshore O&G platforms by first compiling an extensive meta food web for over 4,000 benthic invertebrate taxa sampled around the O&G platforms and grouping them into feeding guilds using stomach content data, morphological traits of feeding apparatus, and taxonomical hierarchy. This is a well-established approach to build up meta and local-scale food webs based on taxonomic occurrence and biomass data from the samples, which is often used in aquatic ecosystems at large spatial scales (S. Kortsch et al., 2021; M. Nordström et al., 2015; E. J. O'Gorman et al., 2012; Planque et al., 2014). Trophic interactions between consumers and resources are supplemented with individual mean body mass estimates, which links biological traits to taxonomy identity and allows for ecological inference of allometries of foraging, trophic niches, and life-history behaviours (Clare et al., 2022; O. L. Petchey et al., 2008). Though a subset of the overall benthic data available across the North Sea was used for this chapter to meet the requirements of the Before-After-Control-Impact (BACI), the compiled metaweb and a full list of benthic invertebrate body masses could be extended into studies on other O&G structures in the UK Benthos database or other benthic databases.

The availability of sediment chemical contaminant data provides an objective measure to establish a distance-based experimental design (impact, buffer and control treatments) and quantify spatially explicit patterns in community composition, size spectrum, and food web topology. The multiple BACI design is commonly used in assessing ecological responses when an anthropogenic disturbance occurs across multiple sites and research goals focus on disentangling the "true" impact effects from background variability (Dos Santos et al., 2022; M. S. Thompson et al., 2018; Underwood & Chapman, 2003). By comparing distance-decaying patterns of total hydrocarbon concentrations to the baseline hydrocarbon concentration prior to O&G exploitation commenced, Chapter 2 identified the samples in the reference distance category and used them as the baselines to compare ecological responses (i.e., benthic diversity measures, individual mean body mass and food web topological metrics) in the impact distance category. The O&G associated contamination at each distance treatment was also examined using median concentrations of individual PAHs and metals in reference to OSPAR's sediment toxicity guidelines. The linking between contaminations and diversity or food web metrics provides empirical evidence of O&G localised adverse effects propagating through ecological networks. The absence of significant difference between the buffer and the control treatment emphasised that future studies should focus on the impacted sites within 500 m of the structure.

Chapter 2 highlighted the importance of adopting a multi-dimensional approach to assess diversity changes through a series of distinct but complementary aspects. At the individual level, changes in mean body mass provide insights into the effects of O&G exploitation on organismal size distributions, i.e., an overall shift towards smaller or larger organisms around the offshore structures. As marine ecosystems are highly size-structured, individual body size is generally positively correlated with trophic level (Jennings, Pinnegar, Polunin, & Warr, 2002), with larger organisms more likely to occupy higher trophic levels. At the feeding group level, the abundance, biomass, and species richness for each benthic feeding group were estimated at each distance-based treatment. This allows for a group-level understanding about the disproportionate effects of O&G exploitation on predators, filter feeders, and grazers and shifts in benthic community composition at different distances from offshore structures. At the community level, total abundance, species richness and Pielou's evenness respectively show the number of individuals across all populations, total taxonomic diversity, and the abundance distribution of individuals in a community. Simultaneously analysing all these metrics helps develop a holistic picture of biodiversity change as these metrics can exhibit contrasting responses under environmental and anthropogenic stressors. For example, only tolerant and opportunistic species are likely to dominate in the heavily polluted environment while species richness experiences a reduction (J. S. Gray, Clarke, Warwick, & Hobbs, 1990; Pearson & Rosenberg, 1978). This could lead to higher abundance in a few dominant species but a general defaunation with smaller body size.

Quantifying altered trophic interaction structure is a key element of assessing external stressors on ecosystem functions. The *Cheddar* package in R offers a useful tool for managing predator-prey interactions from collections of communities and allowing inter-web comparisons along spatial, temporal and environmental gradients (Hudson et al., 2013). Analysing changes in food web structural properties as a result of environmental and anthropogenic stressors provides implications on the community productivity, diversity, and stability changes within and across trophic levels (Arim et al., 2007; Eoin J O'Gorman & Emmerson, 2009). Chapter 2 investigated the effects of O&G exploitation on food web structural properties including proportions of basal, intermediate, and top species, mean food chain length, generality and vulnerability, number of trophic links, linkage density, and connectance. These metrics are well-established in previous studies (Martinez, 1993; Navia, Cruz-Escalona, Giraldo, & Barausse, 2016) and able to capture signals in biological communities such as nonrandom species loss (Xu et al., 2022), increased robustness to secondary extinctions (E. J. O'Gorman et al., 2012), complexity of trophic interactions (M. C. Nordström & Bonsdorff, 2017) and a redistribution of generalists and specialists in the heavily impacted areas. There is currently a dearth of food web approaches in environmental monitoring and this is a challenge that needs to be overcome to provide greater insight into the impacts of environmental stressors on our ecosystems (Bohan et al., 2017; C. Gray et al., 2014)

5.2.2 Chapter 3: Benthic biodiversity and food web recovery after decommissioning of oil and gas infrastructure

The decommissioning of O&G infrastructure is currently ongoing but there are limited studies on assessing environmental and ecological consequences of decommissioning O&G structures as well as how impacted communities and environments developed post-decommissioning. Chapter 3 thus filled in this research gap by examining changes in the benthic community structure and food web structure before and after O&G decommissioning. The integration of community structure and ecosystem functional aspects provides a more comprehensive framework to assess expected effects of decommissioning offshore energy structures including offshore wind turbines in the next couple of decades. It is vital for the current decision-making process for offshore decommissioning to account for environmental and ecological consequences to formulate better decommissioning programmes that best suits infrastructure conditions and local ecosystem context.

As described in the General Introduction, there are both positive and negative potential impacts associated with offshore energy structures. The increasing number of empirical observations and experiments make it possible to assess the overall ecological effects of offshore structures using meta-analysis approaches to synthesise global evidence (Lemasson et al., 2024). However, the quality of literature reviews and meta-analyse is subject to the number of available published studies qualified for a consistent study design and may encounter heterogeneity issues such as different species, study locations and habitats (Senior et al., 2016). Chapter 3 extended the meta-analytical approach to a standardised monitoring surveys on benthic invertebrates around O&G infrastructure, which maximised the amount of harmonised empirical data for improved statistical power (Gurevitch et al., 1992) and allowed for hypothesis-driven testing using standardised effect size. As decommissioning options and intervals between decommissioning and sampling time vary across structures, Chapter 3 developed three distinct scenarios to accommodate the characteristics of the available data: (1) samples prior to decommissioning as the baseline and within a short time period after full removal; (2) samples only collected after decommissioning but at multiple time points to allow for longitudinal analysis; and (3) samples collected prior to decommissioning as the baseline and a longer time period after partial removal. Using a difference-in-difference quasi-experimental design, treatment effects (O&G decommissioning for scenario 1 and 3; the post-decommissioning recovery for scenario 2) were estimated as the difference between the differences of the impact and the control observations before and after the treatment (Butsic, Lewis, Radeloff, Baumann, & Kuemmerle, 2017). This approach has the advantage of incorporating natural variability to detect the true treatment effects from potential background biases and enhances the scientific rigour of estimating the effect size in the meta-analytical framework.

This chapter quantified the extent and direction of benthic recovery after O&G decommissioning using biodiversity metrics, body mass, and food web topological metrics. The results demonstrated that benthic recovery was not a linear process: O&G decommissioning could be detrimental to benthic communities in the short term, with adverse effects on mean trophic level, number of trophic interactions, and species richness. This was followed by positive effects on the number of intermediate species and a more complex trophic structure at the post-decommissioning recovery. Long-term sampling after O&G decommissioning with partial removal showed positive effects on mean trophic level, the number of trophic interactions, and the proportion of intermediate species. Although scenarios 2 and 3 inferred a positive recovery trajectory, current data limitations compromised a perfect comparison across the same type of decommissioning (complete removal), which confounds the long-term positive outcomes with both benthic successional patterns over time and potential effects of remaining O&G infrastructure. Spielmann et al. (2023) studied epifaunal invertebrates between one complete and two partially removed offshore wind farms and found that partial removal could preserve a high percentage of species. J. W. Coolen, Bittner, et al. (2020) studied the decommissioning of a gravity-based platform and found that 26% of the species would be lost if the foundation was completely removed. While the extent to which epifaunal communities contribute to benthic invertebrate community structure remains unclear, it is necessary for future monitoring efforts to think about short-term and long-term data across different types of decommissioning.

The objective of decommissioning policy is to restore the seabed to its “original” state (Fowler et al., 2020). Although the UK Benthos database does not include a systematic sampling protocol through the entire life cycle of O&G structures, this chapter attempted to compare the benthic state under active operations with that after decommissioning at different timescales and decommissioning options. This chapter highlighted the necessity of continuous long-term monitoring across different phases of O&G infrastructure. The cost-effective approach could be based on key timepoints (e.g., within 12 months, then after 2, 3, 5, and 10 years) so that short-term and long-term localised effects on benthic communities could be sufficiently assessed and then compared for different decommissioning options.

5.2.3 Chapter 4: Impacts of marine artificial structures on the biodiversity of marine fish communities

Understanding cumulative human impacts on the marine environment is important with a growing number and intensity of human pressures around the global oceans (Halpern et al., 2015). Currently, most empirical evidence on the ecological impacts of offshore energy structures is at a localised scale or on a case study basis. The broader spatial patterns and temporal changes in response to the addition or removal of offshore energy structures remain largely unknown. As offshore industrialisation is projected to expand in the coming decades, it is essential to develop an ecosystem-level perspective to assess whether localised changes caused by the presence of MAS can spread to the wider ecosystem and to what extent the projected magnitude of MAS alters changes at the ecosystem level (C. Lynam et al., 2017). Wright et al. (2020) is one of the first studies initialising large-scale ecological assessment of MAS on the abundance of three economic fish species. While this study provided a relatively comprehensive list of MAS and associated environmental data, abundance data derived from historic electronic tagging had limited spatial coverage and a limited set of sampled fish. Chapter 4 utilised the North Atlantic groundfish dataset to provide a better spatial and temporal coverage in the North Sea ecosystem and a more holistic list of species across different trophic levels. MAS predictors in Wright et al. (2020) were measured as a proportion of grids using point location data of each structure divided by prediction grid area.

Chapter 4 also used the unique number of MAS to avoid disentangling the overwhelming fine details of infrastructure (e.g., age, tonnes, number of steel legs) in large-scale ecosystem modelling and smoothed local heterogeneity by estimating MAS density within a spatial radius. In addition, Chapter 4 used the collection of Copernicus whole-ocean physics reanalysis variables, which was able to capture more natural variability compared to a subjective subset.

The data compilation workflow in this chapter provides an important method to extrapolate fisheries-independent data across the North Sea and covers the spatial locations of MAS that generally have access restrictions. This method was previously used to explore predator-prey body mass ratios in marine fish food web in response to future environmental scenarios (M. S. A. Thompson, Couce, Schratzberger, & Lynam, 2023). With a consistent spatial resolution firstly set up to accommodate Copernicus reanalysis data, it was also used to host biodiversity estimates (α, β, and γ diversity), fish functional traits (length, abundance, and biomass) and MAS density as the main predictors. Incorporation of both sea surface and sea bottom variables ensures the relevant environmental variability can be included in the analysis via principal components of an environmental ordination, given that fish in both the pelagic and benthic environment were included in the model. This ultimately allows for statistical analysis between each fish biodiversity and biomass metric and the associated MAS and environmental predictors.

Methodologically, this chapter explored the Generalised Additive Model and sdmTMB package to handle spatial temporal analysis. Both frequentist approaches turned out to be inferior than Bayesian INLA modelling due to the model validation (i.e., unable to handle spatial residuals using a sophisticated structure and the lowest AIC) and heavy computing time (i.e., running the tweedie family model in sdmTMB). This highlighted the advantages of INLA in accounting for spatial autocorrelation with prior knowledge to set up spatial mesh size in the Matern correlation parameters, a more efficient computing program than running complete Bayesian Markov Chain Monte Carlo simulations, and accepting a flexible model structure. INLA has been adopted in modelling mobile predators such as fish, allowing for high-resolution predictions of predator interactions and estimations of cumulative effects from the predictors (Isaksson et al., 2025; Sadykova et al., 2020). In our case, given that MAS distribution is likely to aggregate in certain geographic regions, especially for wind turbines, future studies should consider high local heterogeneity for MAS predictors in the modelling step, which can be in contrast to large-scale environmental variable modelling with a smoother heterogeneity across space.

The results of this chapter demonstrated guild-level effects of both O&G platforms and wind farms, providing a solid foundation for future food web analysis. Our findings were consistent with other empirical studies i.e., Ninon Mavraki et al. (2021), indicating that the presence of MAS benefits certain fish groups and likely those that could utilise available food sources such as epifaunal benthos. This chapter showed that fish at higher trophic levels tended not to have an affinity for MAS, but offshore wind turbines were positively associated with fish at lower trophic levels (i.e., planktivores and benthivores). Shifts in fish community composition and functional traits could be validated in future work using available stomach content data. The otter trawl groundfish biodiversity data will be concatenated with modelled fish stomach content data to test if dietary changes occur in areas were MAS are present and with consistent patterns within feeding groups (Murray S.A. Thompson et al., 2024). The estimation of marginal effects on each biodiversity metric at the community and feeding guild levels are useful for the parameterisation of ecosystem models such as Ecopath with Ecosim (EwE), including revised diet matrix setup and adjusting the forcing and mediating functions (Perryman et al., 2020; Stock et al., 2023).

5.3 Future directions

5.3.1 Alternations in trophic structure around offshore energy structures

Chapter 2 and Chapter 3 have demonstrated that the establishment and decommissioning of O&G platforms changed seabed macrofauna community composition and food web structure. With more offshore wind turbines installed in the global oceans, future studies could utilise the BACI method in a similar manner to analyse macrofauna communities in the impact and control treatments given that baseline data are more likely to collect prior to the commencement of offshore wind turbines. Compared with O&G platforms, offshore wind turbines generally do not have major contamination issues (i.e., large quantity of discharge of hazardous materials) but possess similarly complex hard substrata. Offshore wind turbines might be a better candidate to investigate the effects of different substratum types on marine benthic communities.

Altered community composition and food web structure have consequences on the energy transfer from basal resources to high trophic levels. The taxonomic composition of ecological communities and their dominant energy pathways characterise food webs as predominantly "green" or "brown" (Cebrian et al., 2009). A green food web primarily relies on photosynthesis and subsequent herbivore consumption, representing autotrophic-based energy flow from primary producers (i.e., phytoplankton and algae in pelagic marine food webs). A brown food web mainly utilises the decomposition of detritus (i.e., deposit-feeding and detritivore in benthic marine food webs), characterising heterotrophic-based energy flow from detritus decomposers. Both green and brown food webs are interconnected and associated with ecosystem processes such as stoichiometric constraints on nutrient regulation (Evans-White & Halvorson, 2017), trophic cascades via the top-down or bottom-up control (Zou, Thébault, Lacroix, & Barot, 2016) and food web complexity and stability (Moore et al., 2004; Rooney et al., 2006). Assessing relative contributions of green vs. brown food webs provide important implications on ecosystem stability against external disturbances (Mougi, 2020).

Habitat substratum type is considered as a key environmental driver for marine benthic community composition and food web structure (Cordone et al., 2020). In the soft bottom, marine benthos are characterised by infauna and detritivores (Wilson, 1990), while macroalgae, grazing crustaceans, and filter feeders are dominant in the hard substrata (De Mesel et al., 2015). Changes in the dominance of primary producers or detritus-feeders determine green or brown energy pathways and associated topological properties in different substratum types. In the North Sea where the majority of seabed is characterised by sandy soft bottom, hard substrata provided by offshore wind turbines enable the colonisation of epifauna invertebrates that are characterised by a high dense of filter feeders such as mussels (Degraer et al., 2020). Soft sediments around offshore wind turbines could also be different from natural soft sediment through organic enrichment, changes in sediment grain composition and the exclusion of fishing activities. D. A. Coates et al. (2014) found that there was higher organic matter content potentially driven by a mixture of hydrodynamics and the deposition of fecal pellets egested by filter feeders, which caused a more abundant and diverse macrobenthic community near the turbine. Delphine A Coates, Kapasakali, Vincx, and Vanaverbeke (2016) reported that the exclusion of trawling around the turbine led to an increased abundance of benthic macrofauna that were sensitive to trawling. It is therefore expected that habitat modifications due to the presence of offshore wind turbines affects green and brown energy channels of benthic invertebrate food webs nearby.

The relative contributions of green vs. brown energy pathways to the diet of marine invertebrates were studied in a pilot project. I participated in a research cruise on the Ondine Jule during March

2024 to collect benthic macrofauna samples around Barrow offshore wind farm (54.1°N, 3.2°W) using a NIOZ corer. Benthic samples were taken at an increasing gradient away from the Barrow offshore wind farm 50, 100, 200, 400, 800, 1600, and 3200 m from the edge and three samples between the turbines (Figure 1). Samples were sieved on board using 500-micrometre mesh size and preserved in the 95% ethanol. We examined benthic samples collected in the centre of the wind farm and the reference site (3200 m). Species identification and gut content extraction were conducted in the Sediment Ecology Lab, University of St Andrews. For samples in the centre, we found that both detritivores and filter feeders were abundant, including the brittle star *Amphiura filiformis*, amphipod *Ampelisca spinipes*, nut clam *Nucula nitidosa*, and razor shell bivalve *Phaxas pellucidus*. For samples in the reference, we found that polychaete trumpet worm *Lagis koreni* and tubeworm *Owenia fusiformis,* razor shell bivalve *Phaxas pellucidus*, and nut clam *Nucula nitidosa* were abundant. The results indicated that there were more deposit-feeding bivalves and detritus polychaetes in the reference while filter-feeding brittle stars *Amphiura* spp. and amphipods were more abundant near the turbine.

It was noted that morphological identification was difficult to identify taxonomy from the diet of marine benthos. We extracted over 30 gut samples from *Lagis koreni* in the centre and reference, the majority of which consisted of fine sand particles. This indicated that detritivores like deposit-feeding polychaetes may not be informative in showing the potential source of algae, diatom and plankton in the ambient environment. Filter feeders such as *Amphiura filiformis* might be a better choice. However, brittle stars sampled were generally small in size, with their diets digested in the form of fluid. At a 10X magnification under a microscope, we failed to identify algae and plankton in their diets. Though we preserved extracted stomach content of brittle stars in 90% ethanol in the glass tubes for future DNA metabarcoding to identify and quantify prey items, the current samples for predators (i.e., Nephtys) does not contain at least three individual duplicates to meet statistical robustness for further analysis.

Given the limitations described above, the data collected above were not included as a standalone data chapter in this thesis. Future studies should endeavour to reveal a more comprehensive picture how offshore structures alter marine food web dynamics from hard-substrata habitats to soft seabed communities nearby and natural seabed communities further away. It will require a more intensive and systematic sampling from phytoplankton, zooplankton, macrofauna to pelagic fish across three representative locations attached to the structure, on the surrounding soft sediment and background sediment habitats. If possible, baseline monitoring could be undertaken to collect data prior to the commencement of wind turbines. This will allow for comparison before and after the introduction of wind turbines to assess changes in food web dynamics. A more comprehensive appraisal should also include multiple wind turbines instead of single structure to determine whether observed trend in community shifts and altered food web trophic pathways are reliable and avoid potential biases caused by spatial and temporal heterogeneity. The inclusion of multiple wind turbines could allow the use of multiple BACI framework to increase statistical power in analysis.

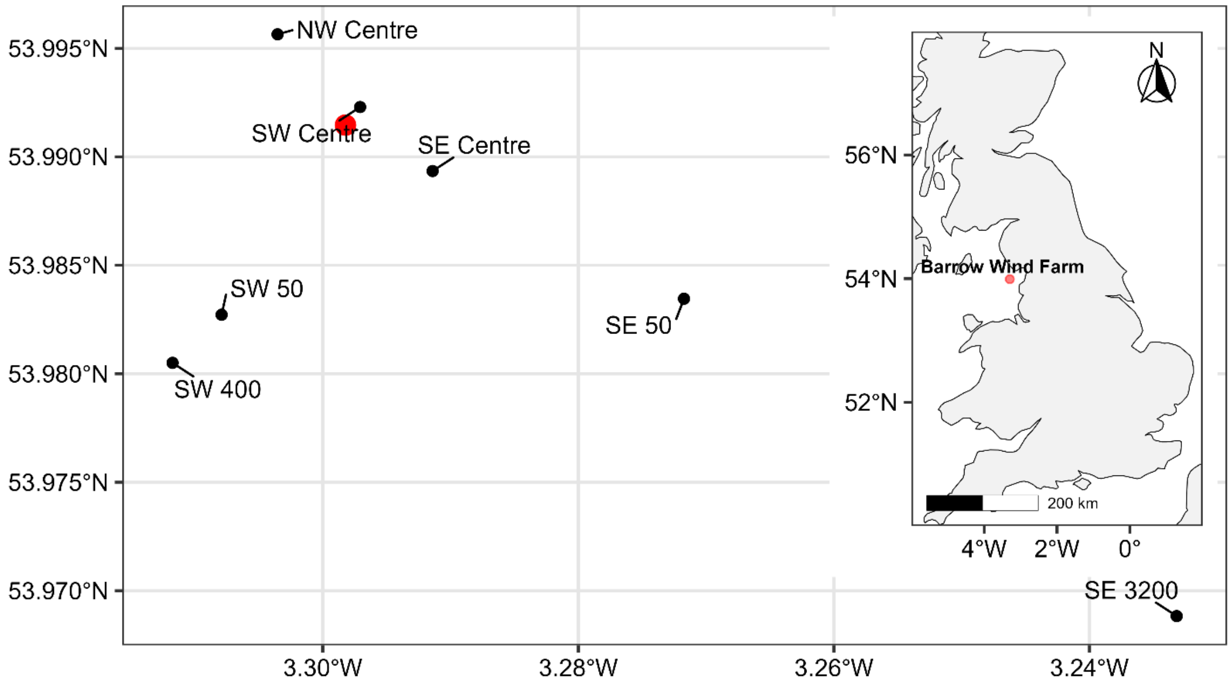

Figure 1. Sampling stations marked in red cross around Barrow wind farm.

5.3.2. Shifts in diet composition in marine fish around offshore energy structures

Chapter 4 has shown that offshore energy structures had significant effects on fish feeding groups, which may be underpinned by alternations to the relative biomass contribution of available prey groups in the environment of offshore energy structures. Similar results were found in Ninon Mavraki et al. (2021), whereby benthopelagic (*Gadus morhua* and *Trisopterus luscus*) and benthic (*Myoxocephalus scorpioides*) fish utilised fouling organisms such as the amphipod *Jassa herdmani* and decapod porcelain crab *Pisidia longicornis*. Therefore, it is expected that fish stomach content can be used to reflect whether fish benefit from additional prey biomass or novel prey groups near offshore energy structures. This expands the existing findings of Chapter 4 toward fish-centred food web analysis to allow for advanced exploration on shifts in diet composition and predator-prey interactions.

Thus, I propose integrating modelled and observed fish feeding dietary data with the existing haul-level estimation of fish biodiversity metrics and functional traits (i.e., abundance, biomass, and typical length). Fish dietary data will use observations of modelled stomach content with estimates of individual prey counts and biomass compiled from different data sources including the DAPSTOM (Pinnegar, Cooper, & Thompson, 2023) and ICES Year of the Stomach (N. Daan, 1989; ICES, 1997) (Murray S.A. Thompson et al., 2024). More than 900,000 fish stomach samples from 227 predator taxa have already been compiled as part of a Cefas database, including predator size, predator taxa and prey functional groups (i.e., zooplankton, benthos, fish, nekton). Combining these data with my work in Chapter 4 could enable predator-prey body mass ratios (PPMRs) to be estimated for each haul-level observation. Together with proportions of prey functional groups, haul-level data will then be interpolated across prediction grids, aligning with fish biodiversity and functional metrics. This would enable spatial and temporal analysis of how the density of offshore energy structures correlates with PPMRs and fish dietary composition, revealing spatio-temporal changes in fish food web structures under varying anthropogenic pressures.

PPMRs provide crucial insights to understand food web structure and dynamics (G Woodward, Warren, Hildrew, Raffaelli, & Edmonds-Brown, 2007). From the metabolic perspective, body mass determines metabolic rates associated with the intraspecific population interactions including consumption and competition (Brown et al., 2004). Body mass thus becomes one of the most fundamental traits for population and food web dynamics (Elton, 1927). Body mass constrains foraging behaviours concerning gape limitation, handling time, attack rate, and interference strength (Ulrich Brose, 2010). The intermediate level of PPMRs tends to yield to optimal foraging as physical constraints on predators limit the lower bound of PPMR to consume prey that are too large (i.e., gape limitation) whereas vital energy intakes limit the upper bound of PPMR for predators to target prey that are too small (U Brose et al., 2008; Tsai, Hsieh, & Nakazawa, 2016). Therefore, PPMRs portray size-dependent food web dynamics and act as a useful indicator to predict food web responses to environmental and anthropogenic stressors. For example, increased temperature results in smaller predator size and an increase in the relative abundance of intermediate-size prey, causing declining PPMRs and interaction strengths for Southern Ocean fish (Eskuche-Keith et al., 2024). However, very few studies have examined whether and how the effects of offshore energy structures alter PPMRs in fish or benthic food webs.

Examining changes in fish dietary composition from fisheries-independent surveys could support stable isotope analysis of a limited number of fish samples close to offshore energy structures. The significant impacts in fish feeding groups indicated that mean relative biomass contribution of prey in the ambient environment might shift toward hard substrata organisms and benefit fish functional groups that are capable of utilising them (M. S. Thompson et al., 2020). With dietary information of prey groups including zooplankton, benthos, fish and nekton (M. S. A. Thompson et al., 2023), future studies can perform not only spatial comparisons for geographic areas affected by offshore energy structures and those with the absence of structures but also temporal comparisons to examine whether dietary shifts occurred over time with the increase of structure age and epifaunal successional patterns. It further provides concrete evidence supporting improved food availability close to offshore energy structures as an important impact pathway for fish attraction for a prolonged residence.

5.3.3 Adopting systematic sampling and integrating evolving datasets in analysing ecological effects of offshore energy structures

This thesis utilised benthic invertebrate data (i.e., UK Benthos database) and otter trawl fisheries data (i.e., Northeast Atlantic groundfish database) to investigate the ecological effects of O&G platforms and/or offshore wind turbines on either benthic and pelagic marine ecosystems. Though this approach has advantages of processing consistent biological data using a standardised approach, the ecological interpretations are confined to benthic or pelagic compartments of marine food webs in isolation. The discontinuous perspective on biotic compartments of food webs hinders integrated understanding of how energy and matter is transferred within and across ecosystems and intrinsic links between trophic complexity and ecosystem functions (Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018). For the pathways of energy flow in marine ecosystems, a large proportion of pelagic matter and energy converts into benthic compartments in the forms of fecal pellets and animal carrion, whereas benthic biomass and energy transfers back to pelagic systems through organism movement, trophic interactions, and biogeochemical cycling (Baustian et al., 2014; Marcus & Boero, 1998). It is therefore important to account for benthic-pelagic coupling mechanisms in future food web studies to better understand cross-ecosystem trophic architecture at the multitrophic scale and a more holistic perspective about the transport from basal organic matter sources to consumers at the higher trophic levels.

Understanding trophic relationships, energy transfer and topological characteristics in the benthic-pelagic coupling requires systematic sampling that includes fish, zooplankton, phytoplankton, benthic invertebrates, and benthic basal resources for wholistic food web analysis. Several methods have been used to establish the coupling links between pelagic and benthic biotic compartments. The first method uses peer-reviewed data compilations of trophic interactions based on the list of taxa and existing stomach content information in certain geographic areas or ecosystems. For example, Pecuchet et al. (2022) used bottom trawl surveys at spatially predetermined stations between 2009 and 2017 in the Barents Sea to collect demersal fish and megabenthos and then linked sampled fish and invertebrate taxa based on an extensive metaweb documenting feeding links in the Barents Sea. The second method uses stable isotope analysis with muscle tissues from fish and invertebrates. For example, Walters, Kopp, Cresson, and Robert (2025) extracted fish tissue samples for $\delta^{13}C$ and $\delta^{15}N$ composition and used $\delta^{13}C$ and $\delta^{15}N$ data of suspension feeding bivalves and zooplankton to determine the relative contribution of benthic and pelagic organic matter in the diet and measure fish trophic position with mixing models. Similarly, Kiljunen et al. (2020) studied carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios and used primary consumers (i.e., pelagic baseline using cladocerans; benthic baseline using the Baltic clam *Limecola balthica*) to adjust isotopic signals over time, which enables the quantification of benthic versus pelagic energy pathway to consumers. Besides that, DNA-based methods (e.g., metabarcoding) could analyse digestive parts of consumers, faeces or regurgitates to detect the occurrence of consumer and prey taxa with high taxonomic resolution (Traugott, Thalinger, Wallinger, & Sint, 2021).

There is an emerging need for growing evidence to assess ecological impacts of offshore structures. To overcome data challenges for ecologically-robust management, active collaboration between the industry, regulatory authorities, academic institutions and other stakeholders is crucial to facilitate data collection and sharing (F. Murray et al., 2018). Such joint efforts will advance better data quality and accessibility to help develop evidence-based scientific suggestions for planning, managing and predicting the impacts of activities at offshore structures (i.e., environmental assessment; decommissioning). One of the latest outputs, for example, is the BISAR (Biodiversity

Information of benthic Species at Artificial structures) dataset published by the Working Group on Marine Benthal and Renewable Energy Developments (Jennifer Dannheim et al., 2025). It contains 4,000 samples and 890 taxa from various environmental impact assessments and scientific projects across 34 offshore structures from 2003 and 2019 and includes both seabed macrofauna and hard substrata epifauna data, which will be a great source for future marine benthic studies on substrate impacts (hard substrate versus soft bottom) and recently installed structures (e.g., offshore wind turbines) as well as comparisons with historical benthic monitoring surveys (i.e., UK Benthos) in different geographic areas.

5.3.4 Life cycle impact assessment methods to assess effects of offshore energy structures on marine biodiversity

Life cycle assessment (LCA) provides a method to quantify potential environmental impacts of a product or process over its full life cycle from raw material acquisition to end-of-life management (International Organization for Standardization, 2006). There is an increasing number of LCA uses to estimate the pressures of anthropogenic activities on biodiversity (Winter, Lehmann, Finogenova, & Finkbeiner, 2017). In a LCA system, the inventory data will be transferred into midpoint impact indicator results for a midpoint impact category, allowing for further interpretation via impact assessment models into the endpoint impact indicator results. For example, the emissions generated (measured in kg CO_2) and resource consumed (kWatt of electricity used) are converted to impact scores for designated environmental categories (i.e. climate change) using category-specific characterisation assessment models. These impact scores measures the end point of biodiversity impacts attributed to an anthropogenic intervention and are represent by characterisation factors (CFs). CFs measure the fate (spatial distribution and intensity of the pressure induced by the intervention of interest) and the impact (a quantifiable loss in biodiversity such as the fraction of species that could potentially disappear) through well-established environmental fate models (Curran et al., 2011). This draws a cause-effect link between the stressor of interest and biodiversity attributes.

However, LCA is still in its infantry in the context of marine ecological impacts, as it was originally used to assess the impacts of land-based industries on mainly terrestrial and freshwater ecosystems (Woods, Veltman, Huijbregts, Verones, & Hertwich, 2016). There is a lack of quantitative approaches to describe impact pathways on marine biodiversity and a lack of characterisation of environmental impact categories specifically tailored to O&G exploitation or offshore wind farms. Research attempts have emerged in recent decades though, such as Veltman, Huijbregts, Rye, and Hertwich (2011) who parameterised CFs for particulate emissions for O&G exploitation and showed that the discharge of drill cuttings had major impacts on marine sediment through physical burial of benthic communities. However, CFs for toxic stressors including metals and organic chemicals (i.e., PAHs) regarding their acute and chronic effects on marine organisms in the seawater environment remained unclear. C. Li et al. (2023) assessed the consequences of seabed occupation, artificial reefs and trawl avoidance due to the operating of offshore wind turbines and found net positive effects in species richness and abundance from artificial reefs, both positive and negative effects from seabed occupation, and limited effects on trawling avoidance. However, this study did not consider the partial life cycle of the structures (i.e., overlooked the decommissioning and the construction phases) and utilised a limited number of biodiversity attributes (i.e., richness and abundance only).

LCA has advantages of quantitatively synthesising major intervention-environment processes into biodiversity impact assessment measures with comprehensive understanding of impact pathways linking each life cycle phase and its associated effects on marine biodiversity. However, it requires more quantitative studies and empirical data to support linkage formulation and parameterisation, a clearly defined baseline to compare biodiversity changes, and a more comprehensive inclusion of biodiversity metrics to represent hierarchical aspects (i.e., genes to ecosystems) and the level of scale and complexity in the multifaceted characteristics (i.e., compositional, structural, and functional) (Curran et al., 2011; Stranddorf, Colley, Delefosse, Svendsen, & Olsen, 2024). As highlighted in the General Introduction, data scarcity is a major limitation, given that biodiversity monitoring surveys were either collected in a non-MAS-targeted manner (i.e., general fisheries independent surveys) or covering a subset of life cycle phases and an incomplete set of scenarios (i.e., complete removal versus partial removal). Experimental studies are also required to validate impact pathways of environmental mechanisms such as toxic effects on marine organisms in support of quantitative understandings. To build up a more rounded characterisation of end point biodiversity impact measures, the inclusion of food web properties is strongly recommended in the future LCA to incorporate shifts in energy transfer and trophic interaction topologies.

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