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

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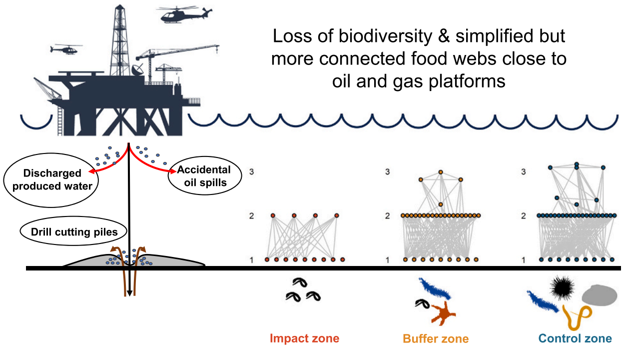
HIGHLIGHTS

- Causal links between hydrocarbon exploitation and ecological responses were studied.
- Chemical and ecological effects were limited to within 500 m of the structure.
- Elevated contamination leads to general defaunation but benefits opportunistic taxa.
- Food webs are degraded through loss of larger predators and dietary specialists.
- New evidence is provided for future monitoring practices to prioritize impact zones.

GRAPHICAL ABSTRACT



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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 >1400 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 chains, 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.

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1. Introduction

Food webs represent the network of trophic interactions among biological organisms in a community (Pimm, 1979; Pimm et al., 1991). Human activities profoundly affect food web architecture and the associated composition of functional traits (Brose et al., 2019; Morin and Lawler, 1995) by altering global patterns of biodiversity and predator-prey interactions (Storch et al., 2022). For example, discharge of organic pollutants could cause declines of species that are sensitive to disturbance inducing community turnover and altering the diet and trophic position of consumer species (Borja et al., 2000; Pearson and Rosenberg, 1978; Xu et al., 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; Lynam et al., 2017; Pauly et al., 1998; 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 (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 et al., 2014; De Mesel et al., 2015; Fujii, 2015; Ronconi et al., 2015). The presence of platforms establishes exclusion zones that may 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 produced water, drill cuttings and accidental spills (Stokke et al., 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 et al., 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 and 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 et al., 2022; O'Gorman et al., 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 et al., 2008; Wang and Rainbow, 2005). Hydrocarbons persist in the marine environment (especially aromatic compounds) and can chronically impair physiological functions, such as respiration, feeding, and reproduction (Adzigbli and Yuewen, 2018). Heavy metals exert toxicity via bioaccumulation, resulting in disrupted enzymatic activities and changes in cellular processes (Chiarelli and Roccheri, 2014). Benthic invertebrate communities close to oil and gas platforms generally exhibit lower biodiversity and altered community composition compared to pristine sites (Daan et al., 1996; Ferrando et al., 2015; Olsgard and Gray, 1995). Even after the cessation of hydrocarbon exploitation, legacy effects on benthic invertebrate communities may persist over years (Gates and Jones, 2012; Jones et al., 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 on benthic communities across multiple oil and gas platforms. 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; Thompson et al., 2018). This study aimed to compare benthic biodiversity and food web metrics in an 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) species richness and community biomass decrease in the contamination sites, with similar effects across trophic groups; and (3) food webs become simpler.

2. Materials and methods

2.1. Data compilation

Biotic and environmental data were collated from the UK Benthos database v5.17, and inventory of UK offshore environmental surveys from 1975 to 2015 (Offshore Energies UK, 2015). Infrastructure data at each structure was extracted from the North Sea Transition Authority (North Sea Transition Authority, 2023). All samples were collected with associated (i) coordinates, sampling year, and distance to the structure, (ii) concentrations of a range of hydrocarbons and heavy metals in the sediment, (iii) mean abundance and taxonomy of benthic invertebrates, and (iv) sediment composition and water depth.

Hydrocarbon and heavy metal concentrations in the sediment were standardised with their extraction method attached. Total hydrocarbon content was measured using gas chromatography. If concentrations of individual hydrocarbon elements were extracted using different methods, we estimated their average value. Hydrocarbons were subdivided 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 had sufficient data across sites to be analysed, including Cadmium (Cd), Chromium (Cr), Copper (Cu), Nickel (Ni), and Lead (Pb). All data provided in the UK Benthos database are comparable in standardised units ($\mu g\ g^{-1}$). Any values of hydrocarbon and heavy metal concentrations below the threshold for detection of 0.01 $\mu g\ g^{-1}$ were assigned a value of 0.

A total of 4216 invertebrate taxa were compiled from the database, with taxonomic data verified against the World Register of Marine Species and identified to the lowest possible level (typically species). All taxa henceforth are referred to as species. The body mass of each species was estimated from the biological trait database of benthic invertebrates in Northwest Europe, which was compiled based on published reports of in situ observations, laboratory measurements, and online databases (Clare et al., 2022). Total biomass at each site was calculated by multiplying mean abundance and body mass for each species. The mean individual body mass at each site was calculated by dividing total biomass by total abundance. Pielou's measure of species evenness was calculated as a ratio of Shannon Weiner diversity to total species richness. Total abundance, mean individual body mass, species richness, and Pielou's evenness were selected as diversity response variables.

Each species was assigned to one of six feeding groups based on their main dietary content and distinct feeding behaviours: detritivore, filter feeder, grazer, scavenger, predator, and parasite. We assumed a total of nine basal resources present at all sites (bacteria, carrion, CPOM, faeces, FPOM, fungi, macroalgae, microalgae, and protists) and then assigned subsets of those basal resources to detritivores, filter feeders, grazers, and scavengers (see Table S1). A literature review was conducted to compile the feeding interactions for predators and parasites. Feeding interactions were only established when there were matches between records from peer-reviewed sources and species present in the UK Benthos database (Garrison et al., 2022; Nordström et al., 2015). Our literature research noted that a high proportion of predators can feed on dead animal prey, and thus we included carrion as a link to predators in our food webs. For any predator or parasite with no diet information, its prey or host would be inferred from other taxa in the same taxonomic level. We identified nine well-established topological metrics to describe the horizontal (e.g., number of species in a trophic level) and vertical (e.g., number of trophic levels) dimensions of food web architecture, including proportions of basal, intermediate, and top species, mean trophic level, standard deviations of normalised generality (generalitySD) and vulnerability (vulnerabilitySD), link richness, linkage density, and connectance. The definitions and ecological implications of all metrics are described in the Table S2. 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).

2.2. Experimental design

The effects of oil and gas platforms on diversity and food web metrics were analysed using a multiple before-after control-impact (MBACI) experiment. Here, we used generalized additive models to examine the relationship between total hydrocarbon concentration and distance to the structure (Fig. 1). This determined three distance-based treatments in the MBACI experiment: (1) the 'impact', which was up to 500 m from the structure until predicted concentrations of total hydrocarbon before and after the commencement of oil and gas production converged, (2) the 'buffer' (500–1500 m), which typically continued to exhibit declining concentrations of total hydrocarbon with increasing distance from the structure, and (3) the 'control' (1500–5000 m), which showed very little change in the concentrations. These treatments were combined with time periods to differentiate samples taken before and after oil and gas began. The true 'impact' and 'buffer' treatments were composed of samples taken after the commencement of oil and gas production in sites within 500 m and 500–1500 m, respectively. All other samples were taken as control treatments, including the samples from baseline surveys in sites within 500 m and 500–1500 m before the commencement of oil and gas production, which acted as temporal controls for the post-exploitation samples (Thompson et al., 2018). This design helps to simplify the statistical model from the interactions between distance categories (<500 m, 500–1500 m, and > 1500 m) and time period (before, after) into one grouping variable (impact, buffer, and control).

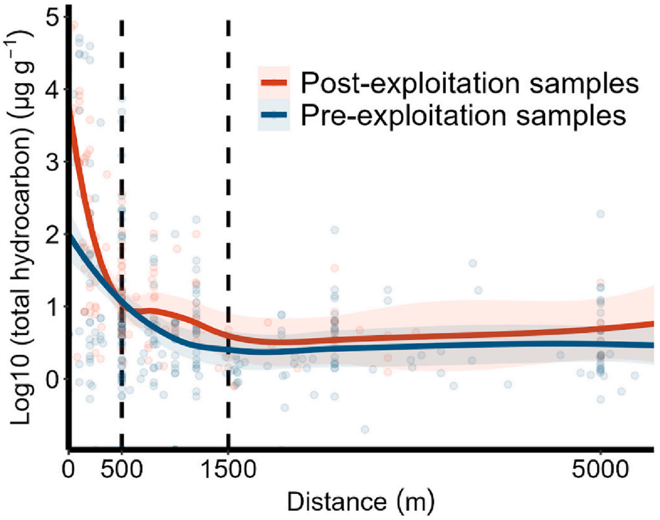

Fig. 1. Log_{10}-transformed concentrations of total hydrocarbon in the sediment along a distance gradient before (blue) and after (red) the commencement of oil and gas production. The "intersect" of the two smoothing curves at approximately 500 m away from the platforms was used to distinguish the 'impact' sites with high levels of total hydrocarbon concentrations. The second cutoff point around 1500 m was used to distinguish the 'control' sites where hydrocarbon concentrations approached the background level.

UK Benthos database v5.17 contains data from 4739 sites across 209 structures including platforms, drilling wells, and other subsea infrastructures. The selection of oil and gas platforms was based on several criteria for the MBACI experiment: (i) the infrastructure type being a platform; (ii) the availability of samples spanning both pre-exploitation to post-exploitation time periods of oil and gas production, characterizing both baseline conditions and those when active operations were underway; (iii) the availability of samples in each of the impact, buffer, and control treatment. 553 samples from a total of nine oil and gas platforms satisfied these criteria, containing over 1,400 invertebrate taxa across a 30-year period of surveys from 1981 to 2012 (Table S3). The distribution of eligible platforms covers the southern and northern North Sea and Atlantic margin (Fig. 2).

2.3. Statistical analysis

Linear mixed effect models were used to assess the influence of predictors on the calculated four diversity metrics and nine food web metrics, resulting in a total of 13 models (Table S4). All mixed effect models were built in R using *lme4* (Bates et al., 2015). Tukey's all-

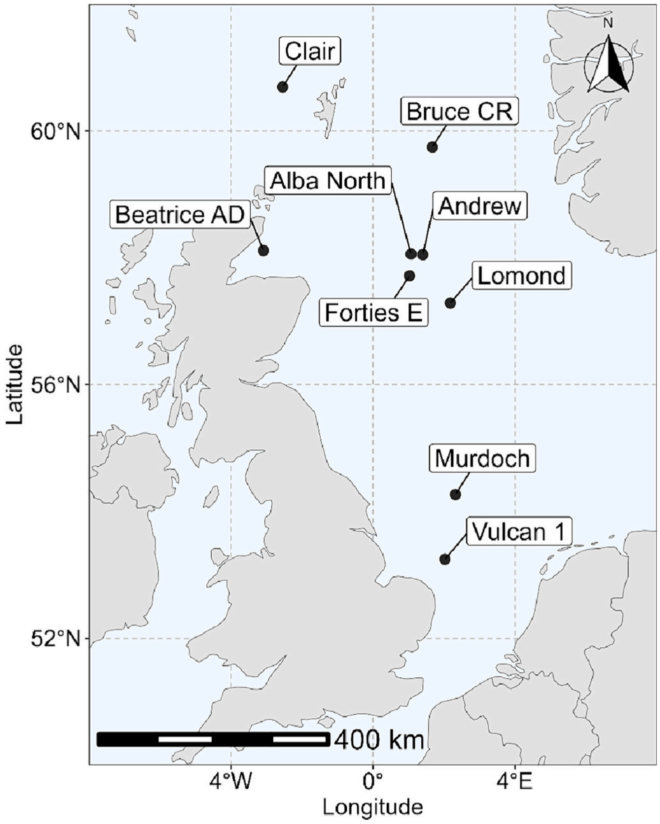

Fig. 2. Locations of nine eligible platforms in the North Sea with sampling before and after the commencement of oil and gas production at a range of distances from the structure.

pairwise comparisons were conducted to compare the means of response variables between the MBACI treatments using *multcomp* (Bretz et al., 2008). Statistically significant differences in means between pairs of MBACI treatments were identified with Tukey's Honest Significant Difference (HSD) and shown in compact display letters using *multcompView* (Graves and Piepho, 2006). Both sieve mesh size (0.5 mm, 1 mm) and gear type (Van Veen, Day grab) were sometimes different between and within platforms (see Table S3). Thus, sieve mesh size and gear type were concatenated into a composite variable 'SieveGear', nested within platform identity, as a random term in initial models. To reflect the temporal non-independence of observations, sampling year was also added in the initial models as a random term. Sediment composition characterized the difference in benthic habitat type, with a median grain size of 0–4 phi units considered as "sand" and 4–10 phi units considered as "mud" (Krumbein, 1934). To account for confounding environmental variability from potential correlating variables, initial models considered the additional fixed terms of habitat type (sand or mud) and water depth. The optimal random structure was determined by Akaike Information Criterion (AIC) comparison of the full fixed structure with all possible combinations of the random structure. The optimal fixed structure was then determined by AIC comparison of the optimal random structure and all possible comabinations of the fixed structure (see Tables S9.1–S9.13).

The importance of individual benthic species in response to MBACI treatment was studied using random forest modelling in R using *Randomforest* (Liaw and Wiener, 2002). Here, 70 % of the data at each treatment was randomly sampled to train the random forest model, with the remaining 30 % used for validation. Species with the highest contribution to the MBACI treatment were identified as indicator species. Pairwise correlations of concentrations of hydrocarbons and individual heavy metals were studied using the Spearman rank coefficient. Pairwise correlations of mean abundance of each feeding group and concentrations of hydrocarbons and individual heavy metals were studied using the Mantel test, with results visualized in R using *LinkET* (Huang, 2021).

3. Results

3.1. Contamination

All contaminants assessed were higher at impact sites relative to buffer and control sites (Fig. 3). There was a significant effect of the MBACI treatment with concentrations of n-alkanes 10,613 % higher ($F_{2,550} = 110.8, p < 0.001$; Fig. 3a), HMW-PAHs 1940 % higher ($F_{2,550} = 8.3$, $p < 0.001$; Fig. 3b), LMW-PAHs 534 % higher ($F_{2,550} = 8.1, p < 0.01$; Fig. 3c), and heavy metals 453 % higher ($F_{2,550} = 23.7$, $p < 0.001$; Fig. 3d) on average in the impact sites relative to the control sites. Similar results were observed for individual hydrocarbon and heavy metal compounds (Figs. S1,S2). Buffer site contaminant levels were not statistically different from control sites. Pairwise comparisons of MBACI treatments are shown in the Table S5.

3.2. Biomass and diversity

For biomass and diversity metrics, there were significant reductions within impacted sites compared to control sites (Fig. 4). There was a significant effect of the MBACI treatment with $\log_{10}$-transformed total abundance 0.9 % lower ($F_{2,550} = 26.1$, $p < 0.001$; Fig. 4a), $\log_{10}$-transformed individual mean body mass 10.0 % lower ($F_{2,550} = 10.8$, $p < 0.001$; Fig. 4b), species richness 28.0 % lower ($F_{2,550} = 40.2$, $p < 0.001$; Fig. 4c), and Pielou's evenness 11.4 % lower ($F_{2,550} = 40.6$, $p < 0.001$; Fig. 4d) on average in the impact sites relative to the control sites. For all metrics, responses in the buffer sites were not statistically different from the control sites. Pairwise comparisons of MBACI treatments for biomass and diversity metrics are shown in Table S6.

3.3. Food web structure

There was a significant effect of the MBACI treatment on community composition and food web structure (Fig. 5). Food webs were more connected and had fewer trophic interactions and lower mean trophic level in the impact treatment (Fig. 5a). Larger top predators were more often present in the buffer and control treatments (Fig. 5b,c). The

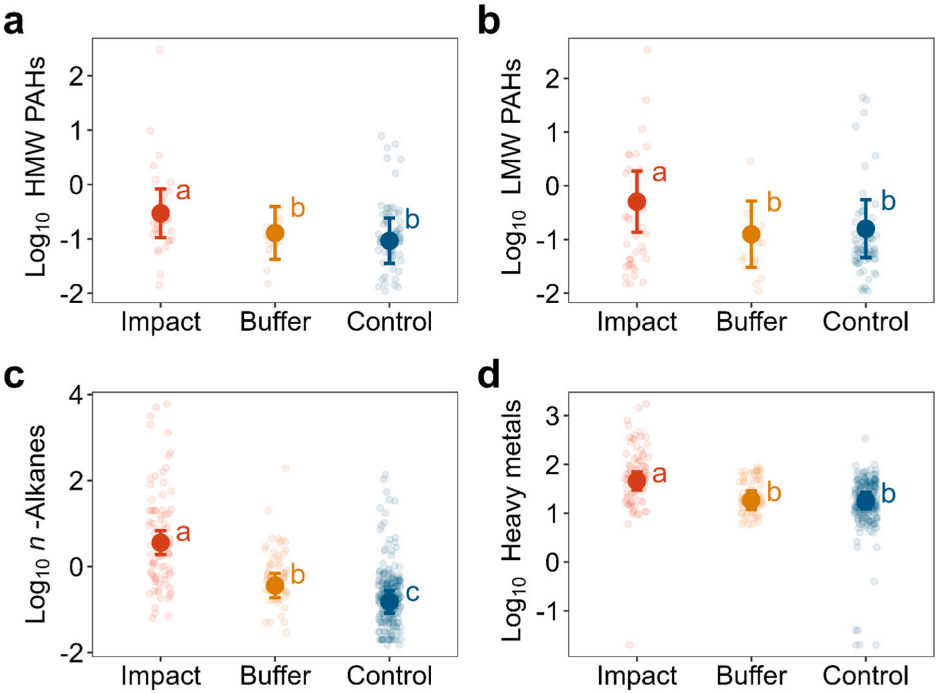

Fig. 3. Log_{10}-transformed concentrations of (a) HMW-PAHs, (b) LMW-PAHs, (c) n-alkanes, and (d) heavy metals within 500 m (impact), at 500–1500 m (buffer), or >1500 m (control) from platforms. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

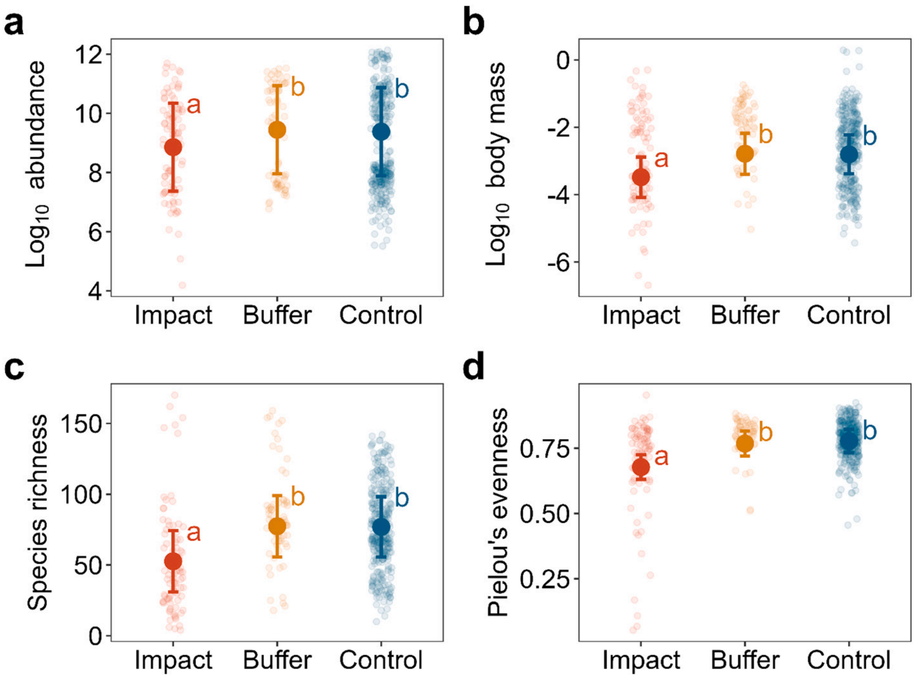

Fig. 4. Log_{10} transformed (a) abundance and (b) individual mean body mass, (c) species richness, and (d) Pielo's evenness of benthic samples within 500 m (impact), at 500–1500 m (buffer), or >1500 m (control) from platforms. Compact display letters show significant differences between MBACI treatments (Tukey's HSD test, $p < 0.05$).

proportion of basal species was 64.5 % higher ($F_{2,550} = 69.6$, $p < 0.001$; Fig. 5d), proportion of intermediate species 3.5 % lower ($F_{2,550} = 12.6$, $p < 0.001$; Fig. 5e), and proportion of top species 12.5 % lower ($F_{2,550} = 18.0$, $p < 0.001$; Fig. 5f) on average in the impact sites relative to the control sites. Mean trophic level was 4.5 % lower ($F_{2,550} = 45.0$, $p < 0.001$; Fig. 5g), link richness 27.5 % lower ($F_{2,550} = 35.0$, $p < 0.001$; Fig. 5j), linkage density 12.2 % lower ($F_{2,550} = 54.2$ $p < 0.001$; Fig. 5k), and connectance 16 % higher ($F_{2,550} = 11.5$, $p < 0.001$; Fig. 5l) on average in the impact sites relative to the control sites. No significant effect of the MBACI treatment was observed on generality and vulnerability (Tukey's HSD, $p > 0.05$; Fig. S3), but generalitySD was 23.0 % higher ($F_{2,550} = 33.2$, $p < 0.001$; Fig. 5h) and vulnerabilitySD 21.2 % lower ($F_{2,550} = 49.4$, $p < 0.001$; Fig. 5i) on average in the impact sites relative to the control sites. Pairwise comparisons of MBACI treatments for food web metrics are shown in Table S7.

3.4. *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 (Figs. S4–S6). 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 (Fig. S5). 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 (Fig. S6). 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 $r < -0.2$; Fig. 6). The *n*-alkanes, however, were positively correlated with filter feeders and detritivores, which contained the top ten indicator species of the MBACI treatment (Fig. S7).

4. Discussion

Anthropogenic activities in the marine environment have profound impacts on biodiversity and ecosystem functioning (Carrier-Belleau et al., 2021). Understanding ecological responses of benthic communities to oil and gas platforms is essential for assessing industrial impacts on marine ecosystems (Birchenough and 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-MBACI 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).

4.1. *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 et al., 2020; Stokke et al., 2022). Elevated hydrocarbon concentrations prior to the commencement might be attributed to exploratory-drilling contamination or high background concentrations near natural seeps (Steichen Jr et al., 1996). For hydrocarbon concentrations after the commencement, the use of oil-based muds such 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

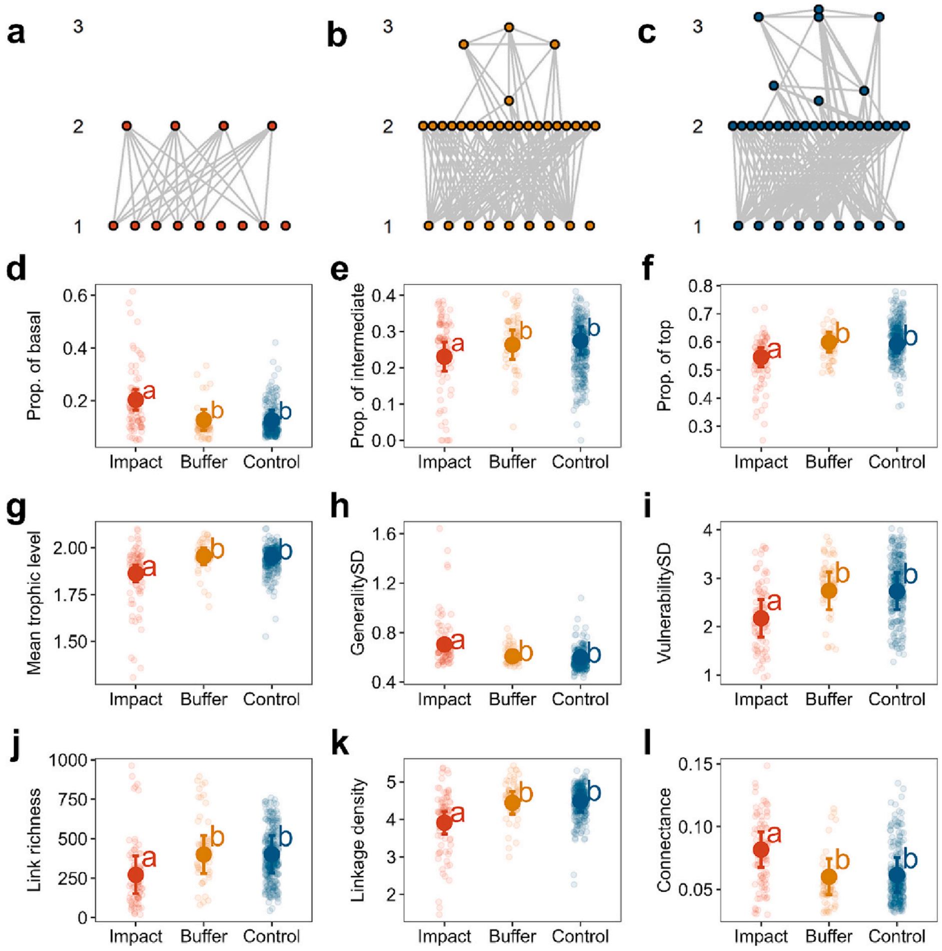

Fig. 5. Food webs are visualized for an impact, buffer and a control treatment. (a) The impact food web has high connectance, low species richness and mean trophic level. (b) (c) The buffer and control food webs have low connectance, high species richness and mean trophic level. (d) Proportion of basal species, (e) proportion of intermediate species, (f) proportion of top species, (g) mean trophic level, (h) generalitySD, (i) vulnerabilitySD, (j) link richness, (k) linkage density, and (l) connectance of benthic food webs within 500 m (impact), at 500–1500 m (buffer), or >1500 m (control) from structures. Compact display letters show significant differences between treatments (Tukey's HSD test, $p < 0.05$).

and naturally occurring PAHs from crude oil (Jacobs et al., 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 (Liu et al., 2015; Shih et al., 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 and 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 and 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 (Figs. 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 et al., 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 S8), 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 effects on the benthic community (Carman et al., 2000; Millward et al., 2004). Whilst previous

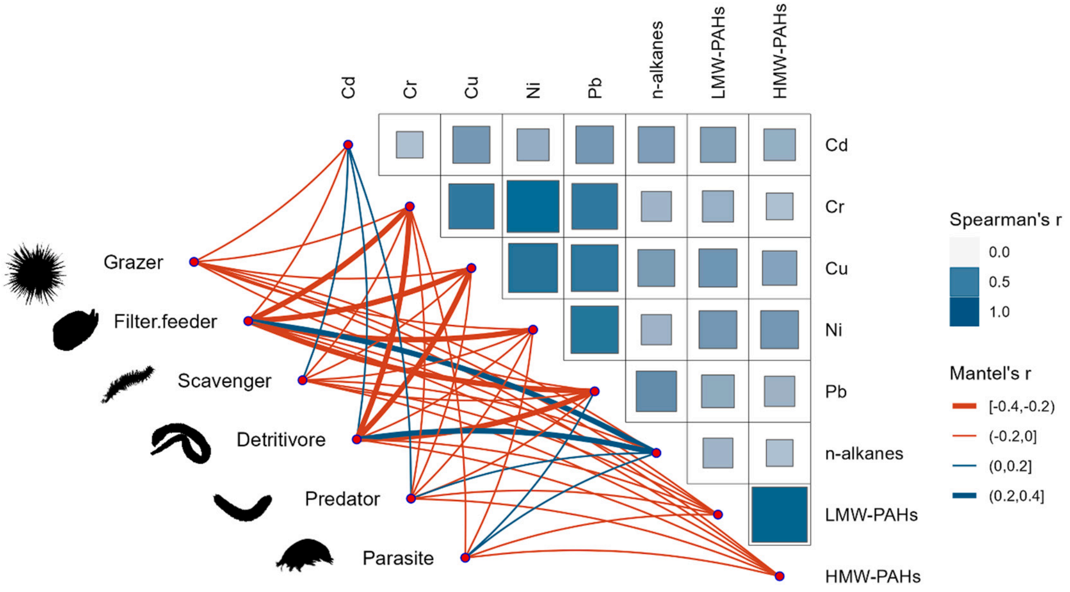

Fig. 6. Correlations among the abundance of six trophic groups, heavy metals, and hydrocarbons. Square size and colour gradient represent correlation strength (Spearman rank correlation: larger square with deeper blue indicate stronger correlation). Only lines with p-values <0.01 are shown. The colour 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 visualised for each trophic group as identified by the random forest model (Fig. S8).

studies have identified hydrocarbons as the main source of sediment toxicity to benthic invertebrates in the North Sea (Grant and Briggs, 2002), our findings help to identify which individual compounds may make the strongest contribution to ecological impacts in the surrounding sediments.

4.2. 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, in contrast to our expectations, with declining species richness and abundance only observed for the filter feeder, predator, grazer, and detritivore groups (Figs. S5, S6). 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*) (Carman et al., 1997; Honda and Suzuki, 2020; Menzie et al., 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 and Tommasi, 2004). Although studies found that oil contamination would alter the composition and abundance of parasites (Centeno-Chale et al., 2015; Perez-del Olmo et al., 2007), their species richness and abundance did not exhibit any significant changes across the MBACI treatments (Figs. S5, S6). This might be due to the absence of direct and intermediate hosts in the UK Benthos database as many parasites were known to parasitize on fish. The success of detritivorous polychaetes in the impacted sites (Fig. S7) characterizes environments contaminated with anthropogenic discharges including hydrocarbons and metals (Pearson and Rosenberg, 1978; Rosenberg, 2001; Stark et al., 2014). Some of the benefitting taxa included capitellids, cirratulids, and dorvilleids, which are known to be resilient to contamination with detoxification mechanisms and opportunistic traits (Stark, 2022; Suriya et al., 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 and Rosenberg, 1978; Ryu et al., 2011). There 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 smaller organisms have adaptive survival mechanisms to the presence of contamination, as they can relocate limited energy resources from individual development (e.g., growth) to the metabolic costs of detoxification (Hadfield and Strathmann, 1996; 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 (Nordström et al., 2015; 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 (Table S9). *Capitella capitata* was the most important species, dramatically increasing in abundance in the impact compared to the control (Fig. S7). *Capitella capitata* is a typical bioindicator in disturbed environments (Pearson and 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 et al., 2014). Its opportunistic life history helps it adapt 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 interspecific competition, coupled with the association and interaction with bacteria in the decomposition of 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 et al., 2016; Tsutsumi, 1987; Washburn et al., 2016). In addition to polychaetes, the echinoderm *Amphiura filiformis* and the hatchet bivalve *Thyasira* spp. showed high importance in the model. As previously observed, *Amphiura filiformis* was intolerant to oil contamination (Olsgard and 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 et al., 1995; Ugland et al., 2008), increasing in mean abundance in the impact zone (Fig. S7).

4.3. 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. 5g) 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 (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 are only sustained in healthy and productive ecosystems, whereas impaired ecosystems with contamination exhibit shorter food chains (Pimm and Lawton, 1977). A decrease in mean trophic level is thus a typical manifestation of predator collapse, which corresponds to the reduction in proportion of top species in the impact sites (Arim et al., 2007; Branch et al., 2010). The concurrent decrease in body size, proportion of top species and mean trophic level reflects the size structure of marine food webs, with top species tending to be the largest organisms and driving the trophic structure of the food web (Dunne et al., 2004).

The third hypothesis is supported by the decreased number of trophic links and linkage density in the impact sites (Fig. 5j–k). Both metrics are descriptors of food web complexity reflecting decreased number and density of energy pathways (Dunne et al., 2004). In the impacted sites, food web structure exhibits greater homogeneity, with lower variability in the number of predators for each species (Fig. 5i) (Galiana et al., 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 et al., 2009; Rooney et al., 2006). The increase in consumer generalism, despite the reduction in the proportion of top species, individual body mass, and mean trophic level, suggests that dietary generalists are dominating over dietary specialists. This is opposite to the scenario that variability in diet breadth tends to increase with larger body size at higher trophic level (Jonsson et al., 2005). The increase in generalism and loss of specialist species in the impacted sites could be attributed to the lack of alternative resources or the ability to rewire their trophic interactions (Feder and Pearson, 1988; Thierry et al., 2011). The generalists 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 and Keesing, 2000; Polis and Strong, 1996; Shaner and 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 et al., 2019). This may be driven by the homogenisation of diets (i.e., general defaunation and reduced predatory pressure). Diets of smaller predators typically consist of a narrower prey body-mass range (Yvon-Durocher et al., 2008) due to the inverse relationship between diet breadth and predator size in aquatic ecosystems (Digel et al., 2011). Owing to limited prey availability, dietary specialists were lost while generalists survived by expanding their diet to the remaining prey (Nordström et al., 2015). The fewer species in the impact sites were thus much more tightly connected, which may be a stabilizing 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 (Dunne et al., 2002; Gilbert, 2009; Smith-Ramesh et al., 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 and Pascual, 2008; Kondoh, 2003).

4.4. Considerations for industry monitoring

The UK Benthos database is a valuable source for understanding the impacts of offshore exploitation activities on the marine environment. The compilation of environmental surveys from separate industry reports in the archives of individual operators and environmental consultancies demonstrates a substantial investment of effort and strong commitments to effective environmental management and improved transparency. Using pooled data from multiple structures, the increased statistical power enables the identification of general patterns of diversity and food web topological changes in benthic invertebrates and variations on the total effects of response variables (Gurevitch et al., 1992). To improve the application of industry monitoring programs toward wider applications, our study proposes three recommendations concerning data collection:

1. The absence of data on the presence and type of drill cuttings makes it impossible to assess their magnitude and persistence in environmental impacts. Historical oil-based mud and its contaminated cuttings was a major source of pollution in the North Sea (Kingston, 1992). It is important to determine whether their adverse effects on biological communities persist and whether current decommissioning practices might alter the concentrations and spatial distribution of contaminants in the marine environment. The inclusion of other data, including oceanic variables and anthropogenic pressure, could help to further disentangle effects from oil and gas platforms from other causes of variability. In addition, the conventional taxonomy-based morphological approach for species identification could be supplemented with evolving assessment techniques including environmental DNA metabarcoding.
2. The integration of the UK Benthos database and future monitoring surveys will be beneficial to examine temporal changes in sediment characteristics, oil-associated chemical concentrations and benthic communities. To accomplish this, detailed protocols of previous sampling designs and measurement approaches should be more transparent to maintain data integrity and consistency. In collaboration with academia and policy makers, the industry can take an active role in building a routine monitoring and assessment system to provide evidence for scientific and policy needs. The standardisation of data collection and analysis could further facilitate knowledge exchange and data sharing.

3. There are emerging needs to understand how decommissioning measures will affect marine ecosystems with an increasing number of oil and gas infrastructures approaching the end of their operational lives. Historical monitoring data primarily covers baseline and operational phrases, with limited samples available for the decommissioning phase. A consistent monitoring effort with an emphasis on the pre- and post-decommissioning phases is encouraged to fill the current data gap and help inform ecologically-sound decommissioning scenarios.

5. 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 MBACI 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 assess the impacts of anthropogenic pressures on marine ecosystems.

CRediT authorship contribution statement

Zelin Chen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Tom C. Cameron:** Writing – review & editing, Supervision. **Elena Couce:** Writing – review & editing, Supervision, Methodology. **Clement Garcia:** Writing – review & editing, Resources, Data curation. **Natalie Hicks:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation. **Gareth E. Thomas:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Murray S.A. Thompson:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Corinne Whitby:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Eoin J. O'Gorman:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

Data availability

Sources of previously published and publicly available data are listed in the Materials and methods. The R code and data that support the findings of this study are available from the University of Essex Research Data Repository at https://dx.doi.org/10.5526/ERDR-00000200.

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Appendix A. Supplementary data

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