

Offshore wind farm development alters food web structure and carbon flows: Insights from a 14-year data-driven study

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ABSTRACT

Offshore wind farms (OWFs) introduce artificial hard-substrates into generally soft-bottom environments and are rapidly colonized by suspension feeders. The new biomass attracts fish and top predators and enriches macrobenthos in the surrounding area. However, these changes are dynamic, evolving over time through shifts in community composition and dominance. Using a unique 14-year dataset (2009–2023) from the C-Power OWF (Belgium), spanning both early colonization and mature operational stages of OWF development, we present the first long-term, data-driven assessment of OWF impacts on the marine food web and its carbon flows. By combining qualitative and quantitative food web (Linear Inverse Model) modelling approaches, we demonstrate that OWF development enhances carbon flow through the system and reshapes how energy is distributed among trophic pathways. A shift towards a suspension-feeding-dominated community lowers connectance, trophic level, and omnivory, thereby reducing trophic flexibility. Over time, a greater number of hard-substrate organisms emerge as module connectors, decreasing overall modularity and facilitating the spread of potential perturbations. Overall secondary production does not show increasing trends with time. Our findings suggest that OWF development alters the marine food web in a dynamic process that evolves through time, with several food web indices pointing towards a potential reduction in ecosystem stability over time. Our insights emphasize the value of using food web indices for monitoring ecosystem functioning under anthropogenic pressures.

1. Introduction

Human-induced climate change, driven primarily by greenhouse gas emissions, has raised global temperatures to 1.5 °C above pre-industrial levels (Copernicus, 2025). The Paris Agreement aims to limit warming below 2 °C, requiring a rapid shift to renewable energy. Offshore wind is a major contributor, with global capacity projected to reach 2000 GW by 2050, covering 500,000 km² of ocean surface (Putuhen et al., 2023). This expansion raises concerns about its impacts on the marine environment, particularly the challenge of balancing renewable energy development with the protection of marine biodiversity and ecosystem functioning (Degraer et al., 2020; Lindeboom et al., 2011, 2015).

One of the major long-term ecological consequences of offshore wind farms (OWFs) is the artificial reef effect. In the North Sea biogeographic region, turbine foundations and scour protection layers (SPL) provide

hard-substrates in sandy seabeds, rapidly colonized by suspension-feeders such as *Mytilus edulis*, *Metridium senile*, and *Jassa herdmani* (Coolen et al., 2022; Degraer et al., 2020; Zupan et al., 2023). As these hard-substrate communities establish, they attract consumers of higher trophic levels (i.e. fish, seabirds), serving as key prey for mobile predators (De Backer and Hostens, 2018; Buyse et al., 2022a; Galparsoro et al., 2022; Reubens et al., 2014; ter Hofstede and van Koningsveld, 2024) and enhancing benthic biodiversity in surrounding sediments by increasing organic matter availability and fining grain size (Coates et al., 2014; De Borger et al., 2021; Jamar et al., 2025). As a result, OWFs support more diverse faunal communities enhancing carbon cycling and deposition in the local ecosystem (De Borger et al., 2025). However, these ecological processes are dynamic, with shifts in species composition, abundance, and dominance over time (Zupan et al., 2023).

Most studies dealing with OWF impacts focus on specific taxa such as

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benthos (De Backer and Hostens, 2018; Coates et al., 2014, 2016; Hutchison et al., 2020; Jammam et al., 2025; Lefaible et al., 2023), hard-substrate communities (Voet et al., 2022; Zupan et al., 2023), fish (Buyse et al., 2023; Reubens et al., 2013; Stenberg et al., 2015), seabirds (Galparsoro et al., 2022; Garthe et al., 2017; Vanermen et al., 2020) and marine mammals (Benhemma-Le Gall et al., 2021; Graham et al., 2019) but often overlook the broader ecological context in which these organisms interact. Alterations to primary producers, benthic communities or fish populations can trigger cascading effects across trophic levels influencing ecosystem functioning, stability, and ultimately affecting ecosystem services (Cardinale et al., 2006; Soliveres et al., 2016).

Food web analysis captures interactions across multiple trophic levels (e.g. Cardinale et al., 2006; Soliveres et al., 2016) and provides a framework for ecosystem-based management. This aligns with the EU Marine Strategy Framework Directive (MSFD) (EU, 2008; EU, 2017), which emphasizes maintaining food webs in Good Environmental Status (Directive 2008/56/EC) and testing indicators for their effectiveness (Machado et al., 2021).

Food webs can be characterized using qualitative (presence/absence of trophic interactions) or quantitative (flux-based interactions) approaches. Qualitative approaches provide high taxonomic resolution and dominate food web studies (e.g. Cordone et al., 2020; Funes et al., 2022; Kortsch et al., 2015; Marina et al., 2018; Nauta et al., 2023), while quantitative approaches capture energy flows and subtle changes, often requiring aggregation into functional groups (e.g. De Borger et al., 2025; De Smet et al., 2016; Van Oevelen et al., 2009). Derived food web indices from these approaches (e.g., omnivory, trophic level, recycling) summarize key aspects of ecosystem structure and functioning (Brito et al., 2024; Fath et al., 2019; Safi et al., 2019; Schückel et al., 2023) and have been applied in the MSFD and cited by OSPAR as plausible indicators for ecosystem-based management (Niquil et al., 2014; Safi et al., 2019) or used to assess human impacts on marine ecosystems (Funes et al., 2022; Nogues et al., 2021; Pauly et al., 1998).

Most OWF food web studies rely on scenario-based or before-after impact designs, with limited empirical validation and short post-construction datasets (Adgé et al., 2024; Nauta et al., 2023; Raoux et al., 2017, 2019; Wang et al., 2019). OWFs can alter predator-prey dynamics as fish exploit hard-substrate fauna, and suspension-feeding organisms can enhance local carbon flows (Buyse et al., 2023; De Borger et al., 2025). Yet, conclusions regarding OWF ecosystem stability and maturity remain inconsistent, highlighting a persistent lack of long-term, empirical food web studies in operational OWFs (Watson et al., 2025).

To address this gap, we built 5 qualitative and quantitative year-specific food web models (2009, 2012, 2016, 2019 and 2022/23) using empirical data collected over 14 years (2009–2023) from the operational phase of a Belgian OWF. These models allowed us to investigate how community shifts influence food web structure, carbon flows, and ecosystem functioning. We tested three hypotheses: (1) OWF-induced community changes alter food web structure by introducing new species, modifying connectance and predator-prey dynamics. (2) Because turbine foundations and SPL establish a persistent link between the water column and the benthic compartment, hard-substrate fauna increasingly serves as prey for mobile predators, generating new feeding links and acting as module connectors (species linking different parts of the food web). (3) Introduced habitats (SPL and turbine) and increased resource availability enhance carbon flows and recycling, supporting higher secondary production in the OWF food web.

2. Methodology

2.1. Study area

Belgium has emerged as a key player in OWF development. Despite its small marine area, nine operational OWFs supply 10% of the

country's electricity demand, with this share expected to reach 25% by 2030 (Global Offshore Wind, 2024). Together, these projects create a 238 km² non-take zone in the Belgian Part of the North Sea (BPNS).

Our study area is the C-Power OWF, located 27 km from the coast on the Thornton Bank, where depths range from 18–24 m (MUMM, WinMon, 2026) (Fig. 1.A). Construction began in 2008 with 6 gravity-based foundations (GBF) and was finalized in 2013 with the construction of 48 jacket foundations (C-Power, n.d.) (Fig. 1.A). GBFs are composed of a SPL spanning 55.5 m diameter with rocks of 0.5 diameter average (Zupan et al., 2024). Jacket foundations, in contrast, do not have a SPL. As one of Belgium's oldest OWFs, C-Power has been extensively monitored, providing long-term, standardized data across multiple trophic levels (Buyse et al., 2022b; Coates et al., 2015; De Borger et al., 2025; De Mesel et al., 2015; Jammam et al., 2025; Kerckhof et al., 2009; Lefaible et al., 2025; Mavraki et al., 2020; Zupan et al., 2023).

2.2. Data collection

Using data from the WinMon.BE program, we constructed five year-specific food web models (2009, 2012, 2016, 2019, 2022/23) representing a GBF unit within the C-Power OWF. Because turbine and SPL data were missing for 2023 and macrobenthos for 2022, we combined 2022 hard-substrate and fish data with 2023 macrobenthos, justified by their lower temporal variability (Fig. S1). We applied two food web approaches: (1) qualitative, including all species and their trophic interactions from phytoplankton to top predators, and

(2) quantitative, focusing on carbon flows for compartments with area-standardized biomass (plankton, hard-substrate fauna, macrobenthos, epibenthos, and demersal fish).

2.2.1. Changes in community structure

We assessed temporal changes in community composition and biomass using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities. Species were grouped by habitat (turbine, SPL, epibenthos, demersal fish, macrobenthos), with 2–4 replicates per habitat per year, totaling 440 turbine, 348 SPL, 307 epibenthos, 245 fish, and 256 macrobenthos samples. The Bray-Curtis matrix was used for nMDS and analysis of similarities (ANOSIM) using R software 4.3.1 and the Vegan package v2.6.8 (Oksanen et al., 2025).

2.2.2. Qualitative approach

We used annual species list to build year-specific qualitative food webs (Table S1.1). Hard-substrate and macrobenthos data were collected around turbines D5 and D6 (Fig. 1), while epibenthos, fish, marine mammals, and seabirds were compiled at the OWF scale. We included pelagic fish based on their known presence in the area (Reubens, pers. comm., Reubens et al., 2013) and incorporated marine mammals and seabirds based on long-term monitoring data collected intermittently over the OWF concession zone (Aoufi, pers. comm., Vanermen et al., 2017).

We identified trophic interactions through a systematic literature review, prioritizing field observations and region-specific studies (Text S1). We constructed a binary interaction matrix, assigning 1 or 0 depending on whether species *j* consumes species *i* (Table S1.2). We constructed year-specific webs by subsampling the matrix according to the species present in the corresponding year and transformed it into a food web where nodes represent trophic species and links indicate predator-prey interactions using the package *igraph* v2.1.4 (Csardi et al., 2025).

2.2.3. Quantitative approach

We built five year-specific Linear Inverse Models (LIMs) to quantify carbon flows. LIMs require standardized area-biomass measures of species. To reduce computational complexity, we aggregated species into trophic species (i.e. species that share the same predators and prey

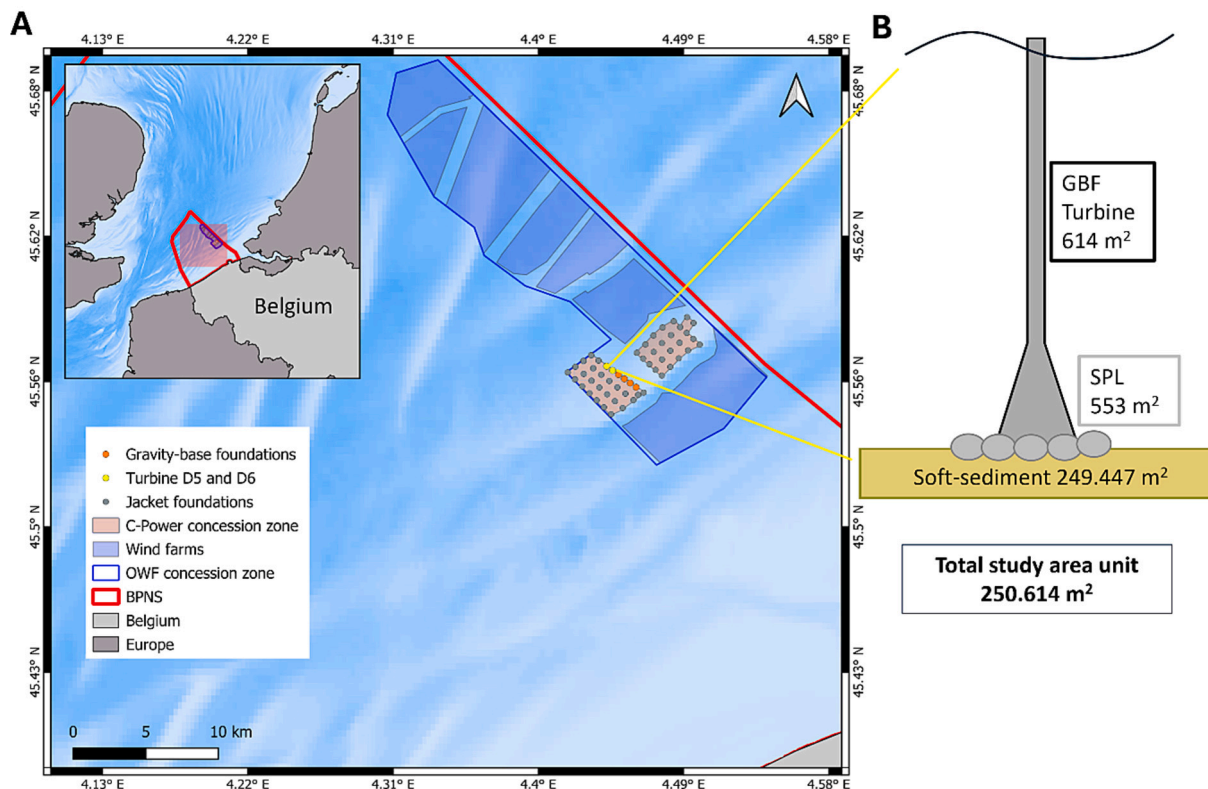


Fig. 1. Study area. (A) Belgian Part of the North Sea showing OWF concession zones: C-Power in orange, Jacket foundations as grey points, GBFs as orange dots, and turbines D5–D6 in yellow. Other wind farms are in light blue. Projection: EPSG:32631 – WGS84 / UTM Zone 31 N. Data: OD Nature (MUMM) and GEBCO (2023). (B) Area units used to standardize species biomass for the quantitative food web models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in a food web) (Yodzis and Winemiller, 1999). Hereafter, we refer to these trophic species as compartments. We classified compartments by habitat (turbine, SPL, soft sediment, ubiquitous) ensuring biologically realistic representation of trophic interactions (i.e. organisms from soft-sediments could not prey upon hard-substrate fauna (De Borger et al., 2025)). We scaled the biomass of each compartment to the relative area of its corresponding habitat within the OWF food web unit to avoid overrepresenting taxa that occupy only a small portion of the food web unit (De Borger et al., 2025) (Fig. 1.B, Table S3.4).

2.2.3.1. Stock data. We collected data on all faunal compartments for the C-Power OWF following WinMon.BE protocols. Hard-substrate and SPL fauna were sampled by divers scraping turbines D5 and D6 and collecting rocks, respectively (Mavraki et al., 2020). As only density was available for hard-substrate communities, biomass was estimated using average individual biomasses from the Princess Amalia zone (Vanagt, 2014). Fish and epibenthos were sampled with a beam trawl between turbines (~200 m from structures) with individuals identified, measured and counted on board (Buyse et al., 2022b). Fish and epibenthos biomass was then calculated using length–weight relationships and established conversion factors (Froese and Pauly, 2024; Ikeda et al., 2011). Macrobenthos were sampled 200–1000 m from turbines with a Van Veen grab, and samples were counted, blotted wet-weighted, and identified to the lowest taxonomic level before conversion to model units (Jammam et al., 2025; Brey et al., 2010). Full details on sampling design and protocols for all compartments are provided in Text S2.

We derived phytoplankton stocks from the Copernicus database (European Regional Seas Ecosystem Model (ERSEM), NEMO-NEMOVAR, 7 km horizontal grid resolution). We extracted averaged daily chlorophyll-*a* concentrations from August–September across five depth layers for the grid cell encompassing turbine D5 (51.75–51.5° N,

2.75–3.0° E) and transformed to model units using published Carbon-to-chlorophyll ratio (Jakobsen and Markager, 2016). For zooplankton, direct biomass measurements were not available for the study years and given their temporal variability and patchiness (Klais et al., 2016), point estimates would not have been representative. Therefore, we derived zooplankton biomass based on model estimates specific to our study area (Schrump et al., 2006).

To complete the models, we introduced a set of additional compartments representing carbon pools and fluxes that were not resolved with the biological sampling: sediment and water-column bacteria (SedBACT, WatBACT), sediment and suspended detritus (SedOM, WatPOM), dissolved inorganic carbon (DIC), burial (BUR), and export (EXP). We derived SedOM stocks from the Total Organic Matter content (Loss on Ignition, 500 °C) of the macrobenthos monitoring program (Jammam et al., 2025) and converted them to model units using the TOM/TOC relationship for our study area (Toussaint et al., 2021). We estimated SedBACT stocks based on the relationship between organic matter content and sediment bacterial biomass for our study area (Billen et al., 1990). Given the absence of long-term, site-specific WatPOM data and the relatively stable background conditions in the offshore BPNS (Desmit et al., 2024; Fettweis and Lee, 2017) we extrapolated WatPOM concentrations sampled at a nearby coarse sandy station (st. 330, 8.2 NM) (Van Oevelen et al., 2009) for all years. For WatBACT we also considered constant stocks across our time series, with a fixed average value of 30 µg C L⁻¹ for the BPNS (Billen et al., 1990). We defined burial as an external process representing the net flow of carbon from detrital pools to the buried carbon pool. The value for the net flow was taken from Toussaint et al. (2021), where this flow was quantified through mass budget modelling (Fig. S2). We applied these burial rates uniformly across the time series. We treated DIC and EXP as externals in our models and therefore no standing stocks were assigned to these

compartments. DIC represented respiratory carbon losses from biological compartments, whereas EXP accounted for physically exported carbon and trophic transfer to higher-level consumers not explicitly quantified in our quantitative models. For more information on the sampling design of these components, we refer to [De Borger et al. \(2025\)](#).

2.2.3.2. Respiration data. We incorporated respiration rates using the respiration coefficient (r , d^{-1}) (Eq. 1), derived from average individual weight (W) in mg C ([Mahaut et al., 1995](#)). For fish and larger organisms, we used a constant measure of respiration rate (1% of the individual biomass per day, [De Smet et al., 2016](#)). To account for variability, we assigned respiration rates a range, with lower and upper bounds set at 75% and 125% of the baseline respiration value.

$$r = 0.017 \bullet W^{-0.156} \left(d^{-1} \right)$$

1)

2.2.3.3. Stable isotope data. We used nitrogen stable isotopic values ($\delta^{15}N$) as indicators of trophic position, as they reflect the enrichment of nitrogen with each trophic level and provide a long-term signal of dietary assimilation ([Perkins et al., 2014](#)). Because $\delta^{15}N$ increases by 2.5 to 3.4‰ from diet to consumer, we used these values to constrain food web flows in the quantitative models. Due to the absence of year-specific

data we applied isotopic signatures consistently across all five food webs, based on values previously measured in our study area (see [De Borger et al., 2025](#) for more details on isotope sampling processing).

2.3. Data analysis

2.3.1. Qualitative approach

To characterize the qualitative food web, we calculated three standard complexity indices —number of nodes (S), link density (LD) and connectance (C) ([Dunne et al., 2002](#); [Williams and Martinez, 2004](#))— and three widely used indices reflecting ecosystem structure and functioning: trophic level (TL), omnivory ($LOmn$), and modularity (Mod). All indices were computed using the *multiweb* R package v0.7.4 ([Saravia, 2024](#)) (Fig. 2: methodological figure, Table 1: index descriptions; Table S2: index calculation).

We applied the Strona Curve-ball algorithm to enable statistical comparisons on qualitative food web indices (TL , $LOmn$, Mod). This algorithm randomizes the food web while keeping ecological relevance by preserving the number of prey and predators for each species and can be used to mimic natural variability ([Strona et al., 2014](#)). We performed 1000 randomizations for each year-specific food web and calculated the food web indices described above, except connectance because it remains unchanged under this randomization. If the empirical value for a

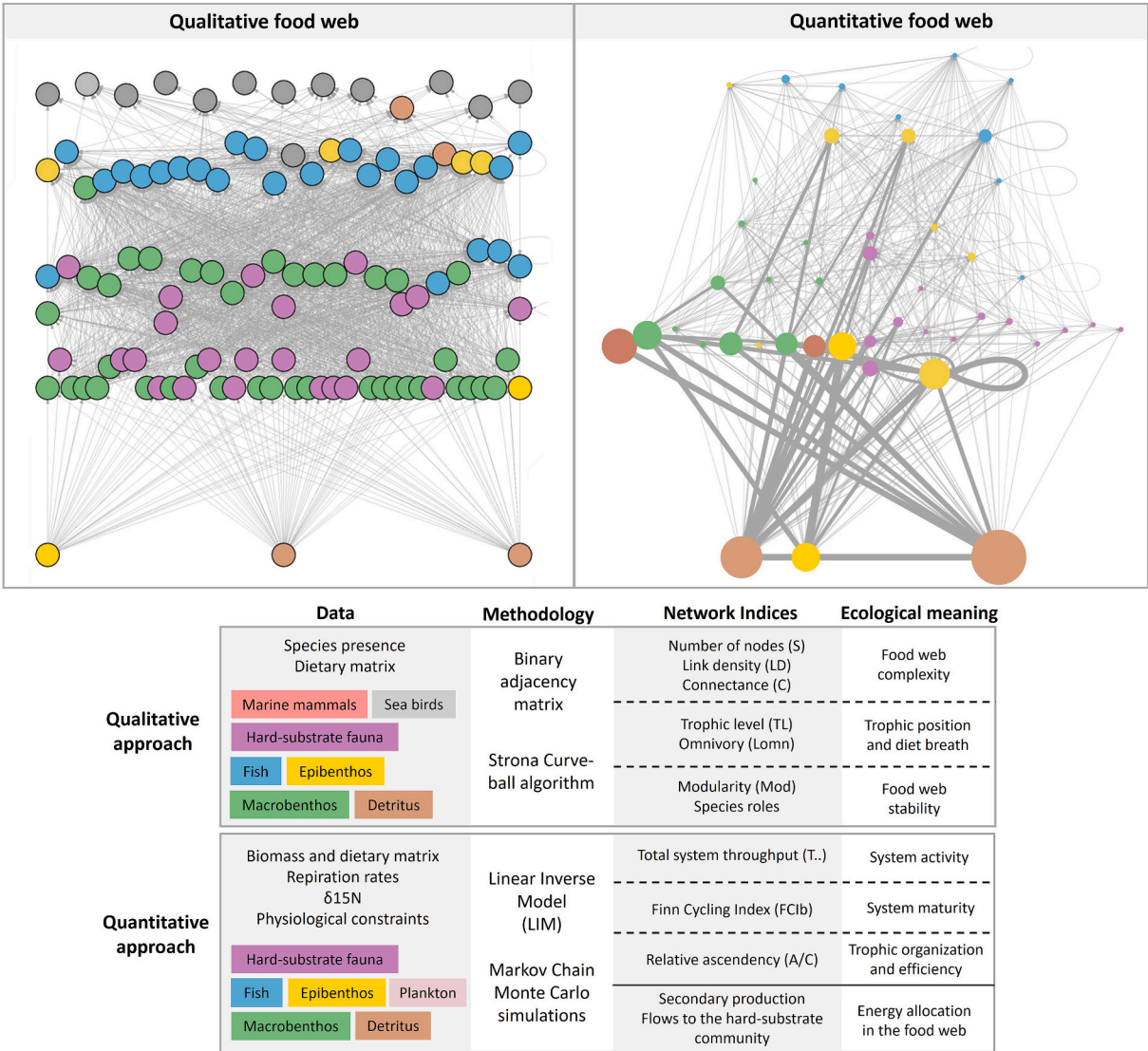


Fig. 2. Conceptual and methodological overview of the qualitative and quantitative food web approaches applied in this study.

Table 1
Food web indices used in this study.

Index	Definition and ecological relevance	Reference
Qualitative approach		
Number of nodes (S)	Number of species in the food web.	(Dunne, 2009)
Link density (LD)	Average number of interactions for each species in the food web.	(Dunne, 2009)
Connectance (C)	Proportion of realized links out of the maximum possible links. It constitutes a key descriptor of the food web complexity and reflects general aspects of food web structure.	(Dunne et al., 2002; Montoya et al., 2006)
Trophic level (TL)	Mean trophic level of the food web, averaged over all species. Measures energy transfer from basal resources to consumers. Indicates species positions in the food web and is related to food chain length and ecosystem health.	(Williams and Martinez, 2004)
Omnivory (LOmn)	Mean omnivory level of the food web. Ranges from 0 (non-omnivores) to 1 (high omnivory). Reflects vertical complexity of the food web and trophic flexibility.	(Dunne et al., 2002; McCann and Hastings, 1997; Williams and Martinez, 2004)
Modularity (Mod)	Presence of subgroups (modules) of species that interact often or strongly with one-another but have few or weak connections to species outside their subgroup. Values near 1 indicate a high modular food web, promoting food web stability by containing perturbations within modules.	(Grilli et al., 2016; Stouffer and Bascompte, 2011)
Species topological role	Participation of species in connecting its own module and/or different modules. Four roles are defined: network connector, module connector, module hub, and module specialist (see 2.3.1.1).	(Guimerà and Amaral, 2005; Kortsch et al., 2015; Rodriguez et al., 2022)
Quantitative approach		
Total system throughput (T _s)	The sum of all flows of the system.	(Finn, 1976; Kazanci and Ma, 2015; Ulanowicz, 1986)
Finn Cycling Index (FCIb)	The fraction of energy recycled in the system. High recycling ratio typically suggests that an ecosystem is mature, resilient, and stable.	(Finn, 1976; Kazanci and Ma, 2015)
Relative ascendancy (A/C)	It is an information-theory index measuring the organization and efficiency of energy flows in a food web, ranging from 0 to 1. High values indicate energy concentrated along few dominant pathways, while low values reflect more evenly distributed flows.	(Ståhl et al., 2025; Ulanowicz, 1986, 2004)

given index falls within the distribution generated by the randomization, the distribution is considered representative for the empirical index value and could be used for comparing food webs. As the data did not conform to normality and homogeneity of residuals, we used the non-parametric test Kruskal-Wallis to test differences in index values between years (Kruskal and Wallis, 1952). If the test was significant, the Pairwise Wilcoxon Test was computed (Wilcoxon, 1945). To quantify the magnitude of these differences, we applied the beta (β) dissimilarity formula to each index (Kortsch et al., 2015; Whittaker, 1972) defined by (Eq. 2), where A represents the value for one year and B represents the

value for the following consecutive year in our time series. We also reported the Curve-ball simulated food web values as the median and the 2.5 - 97.5% quantile values.

$$\beta = \left(\frac{B - A}{A} \right) \times 100 \quad (2)$$

2.3.1.1. Species roles. Food webs exhibit non-random modular structures, where groups of species interact more strongly within their own subgroup than with species outside of it (Grilli et al., 2016). Modularity quantifies the extent to which species from these subgroups or modules interact with each other compared to species from other modules. Species can be classified according to the links they have within their own module and/or across modules: module hubs (highly connected within their own module), module specialists (few links, mostly within their own module), module connectors (few links, mainly bridging different modules), and network connectors (highly connected both within and across modules) (Guimerà and Amaral, 2005) (Table 1). To assess changes in hard-substrate species roles during OWF development, we computed their topological roles and the number and proportion of module connectors across years using the *multiweb* R package v0.7.4 (Saravia, 2024).

2.3.2. Quantitative approach

We used LIMs to quantify carbon flows between compartments in the food web while accounting for dietary uncertainties (De Borger et al., 2025; Soetaert and Van Oevelen, 2009; Van Oevelen et al., 2006). LIMs integrate three components; (1) a qualitative food web describing consumer-source interactions (see section 2.2.2); (2) physiological constraints such as growth rates and assimilation efficiency (Soetaert and Van Oevelen, 2009) and (3) site-specific data including biomass data, stable isotopes and respiration rates. These elements form a mathematical system of equalities and inequalities, and steady state is assumed (i.e. the rate of change of the mass balances of the compartments is zero) (for more information on the LIM methodology we refer to Text S3 and Table S3.3).

The solution to the LIM models is a set of values for each flow in the food web that are consistent with the set of equations and inequalities. Since the LIMs were underdetermined (i.e., the number of equations was smaller than the number of flows to be estimated), multiple solutions were possible. To explore the solution space, we used Markov Chain Monte Carlo simulations (MCMC). For each food web, we performed MCMCs over 5000 iterations. To assess how well the solution space was sampled, we used the diagnostics and visual plots from the *AutoLIMR* package v3.0.1 (Gerber et al., 2023). We verified the diagnostics of stationarity (whether the statistical properties (i.e. mean) no longer change as more samples are collected and therefore the correct distribution is sampled), mixing (whether the sampling is moving through the entire solution space) and sampling efficiency (whether a sufficient number of iterations has been performed) (Gerber et al., 2023). We build and solve the LIMs using the R packages *LIM* v1.4.7.1 (Soetaert and Van Oevelen, 2009) and *sampleLIM* v0.1 (Bréhélin et al., 2024) (Table S3).

To evaluate ecosystem functioning, we selected a set of quantitative indices, focusing on those identified as potential indicators for ecosystem-based management (Fath et al., 2019; Safi et al., 2019). For each LIM, indices were calculated across 5000 MCMC iterations, producing distributions for each year from which summary statistics were derived. We calculated total system throughput (T_s; Ulanowicz, 1986), the revised Finn's cycling index (FCIb; Finn, 1976) and the relative ascendancy index (A/C; Ulanowicz, 1986) using the *NetIndices* R package v1.4.7.1 (Kones et al., 2022) (Table 1). Additionally, we calculated three variables specific for the C-flows in the OWF food web: (1) total flows to and from the hard-substrate community (sum of all turbine and SPL compartments' flows), (2) total secondary production (sum of all faunal compartments production), and (3) total hard-substrate community production (sum of all turbine and SPL compartments'

production). We reported all quantitative food web indices, LIM variables and flows as mean, standard deviations, minimum, maximum and 95% credible intervals (CI) (Table S3). We compared the indices and variables derived from the five LIMs (5000 iterations) with the Kruskal-Wallis test due to non-normality and heteroscedasticity (Kruskal and Wallis, 1952) combined with the Pairwise Wilcoxon Test for pairwise comparisons (Wilcoxon, 1945). To quantify the magnitude of change, we applied the beta (β) dissimilarity formula to each index value (eq. 1).

3. Results

3.1. General community changes

We observed changes in community composition across years for all habitats (Fig. 3, NMDS Bray-Curtis, stress = 0.04–0.15). Hard-substrate communities showed strong turnover, with SPL changing more

(ANOSIM $R = 0.790$, $p = 0.005$) than turbine foundations ($R = 0.632$, $p = 0.001$). Epibenthos, fish, and macrobenthos also showed significant temporal changes with R values ranging from 0.676 to 0.671 ($p = 0.001$).

3.2. Qualitative changes in the food web

Food web complexity increased over time: number of nodes increased 25%, link density 15%, while connectance decreased 8% (Table 2). We statistically compared trophic level (TL), omnivory ($LOmn$) and Modularity (Mod) as all empirical index values fell within the null distributions generated by the Curve-ball randomizations (Fig. 4.B–D, Table S4 for Curve-ball model distribution). TL declined from 3.01 to 2.80 (7%), $LOmn$ from 0.22 to 0.16 (27%), and Mod fluctuated, with an overall 5% decrease by 2022/23. (Fig. 4.D, Table 2). All indices showed significant temporal differences (Kruskal-Wallis, $p <$

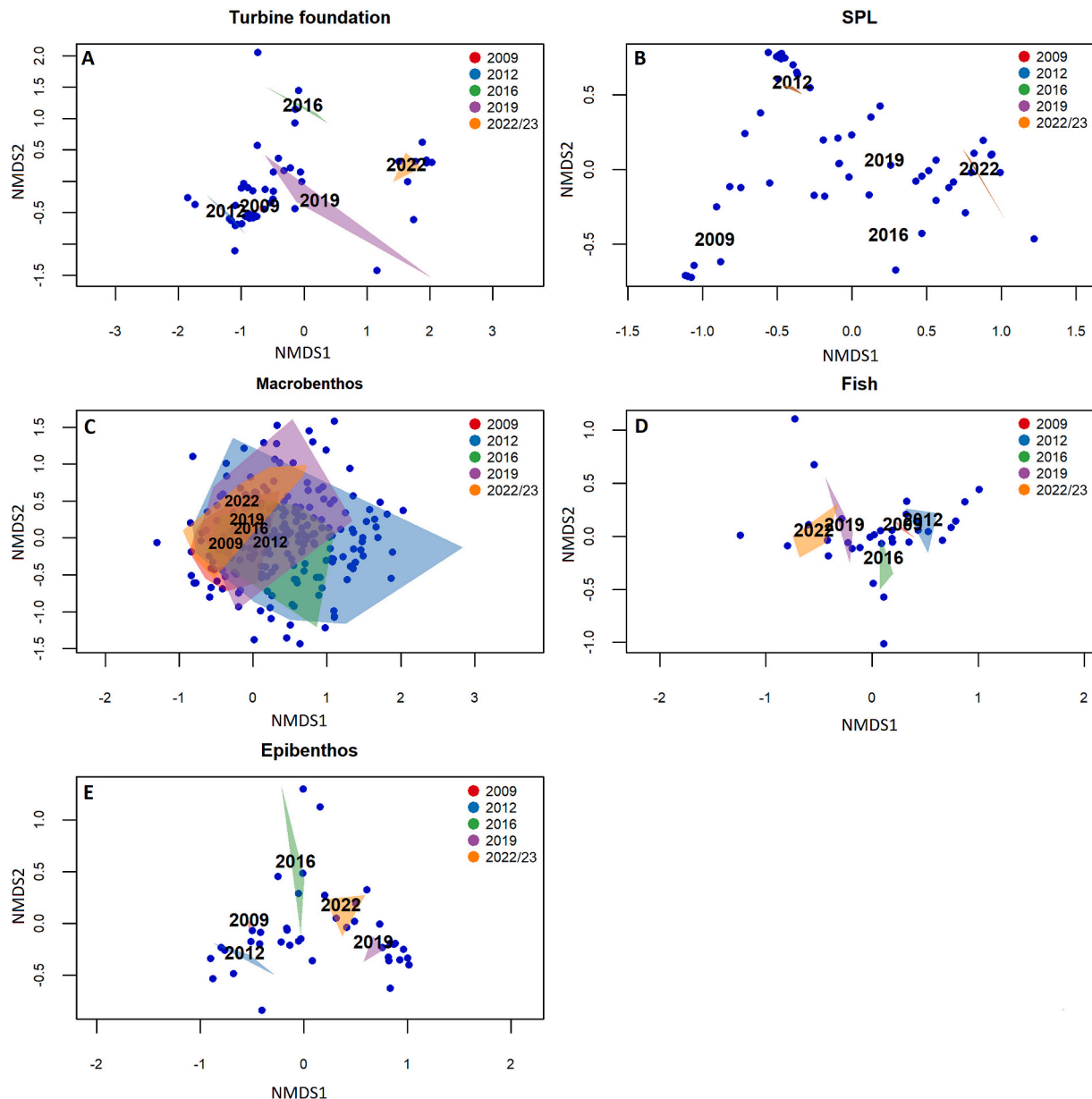


Fig. 3. NMDS ordinations showing yearly changes in community composition for five habitats, based on Bray–Curtis dissimilarity of species density. Each panel represents one habitat, with blue points showing the species found there: turbine foundation (A), scour protection layer (B), macrobenthos (C), fish (D), and epibenthos (E). Polygons are convex hulls around yearly samples; overlap indicates similar community composition, while separation reflects differences across years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Qualitative properties for each of the year-specific food webs. The first five columns show the index values per year, while the last four columns display the percentage change (β -dissimilarity) between consecutive years. * Indicates that there is a significant difference (p -value < 0.05) based on the pair-wise test.

Index	2009	2012	2016	2019	2022/23	2009-2012	2012-2016	2016-2019	2019-2022/23
Nodes	110	121	122	141	137	10.00	0.82	15.57	-2.84
LD	17.30	18.70	18.50	21.40	19.90	8.09	-1.07	15.68	-7.01
C	0.153	0.151	0.146	0.148	0.141	-1.34	-3.11	1.42	-4.92
LOmn	0.22	0.18	0.19	0.17	0.16	-18.24 *	4.55 *	-8.80 *	-4.78 *
TL	3.01	2.88	2.90	2.85	2.80	-3.91 *	0.71 *	-1.74 *	-1.85 *
Mod	0.153	0.137	0.142	0.149	0.145	-11.69 *	4.47 *	4.41 *	-2.46 *

0.05), with pairwise comparisons confirming changes between consecutive years.

3.2.1. Species roles

Most of the species in our food webs acted as either module connectors—*Monocorophium acherusicum*, *Crepidula fornicata*—or module specialists—*Metridium senile*—throughout the study period. We detected no module hubs and only two network connectors (Table S5). The number of hard-substrate species increased from 22 to 29 over time, with interannual variability (Table 3, Table S5). Although the number of module connectors—species linking different modules—increased, except for a temporary decline in 2016, the proportion of module connectors (nr. of module connectors over the nr. of total species) fluctuated over time, with the lowest proportion in 2016 and the highest in 2022/23 (55%) (Table 3, Fig. S3, Fig. S4).

3.3. Quantitative changes in the food web

The final five LIM models comprised approximately 50 compartments, including two non-living (WatPOM and SedOM), three external compartments (EXP, DIC, BUR) and multiple faunal compartments. All compartments were expressed in mmol C m⁻² and rates in mmol C m⁻²d⁻¹ (Table S3.2).

3.3.1. Carbon stocks

Total carbon stocks were highest in 2012 (14,995 mmol C m⁻²) and lowest in 2016 (10,560 mmol C m⁻²), with detritus (WatPOM + SedOM) comprising ~95% of the total stocks. Among living compartments, 2019 had the highest biomass (596 mmol C m⁻²), followed by 2022/23 (590 mmol C m⁻²) and 2009 (467 mmol C m⁻²). Sediment and plankton dominated faunal biomass, while hard-substrate and fish compartments contributed to smaller fractions. Hard-substrate biomass increased from 2 to 4% to 8–16% in 2019–2022/23; fish biomass remained low (~1%), with a minimum of 0.1% in 2022/23 (Fig. 5, Table S3.1).

3.3.2. Quantitative indices, secondary production and specific pathways

Total system throughput (T_{t}) increased by 24% over the study period, from 148 mmol C m⁻² d⁻¹ in 2009 (95% CI 113–172 mmol C m⁻² d⁻¹) to 185 mmol C m⁻² d⁻¹ in 2022/23 (95% CI 131–218 mmol C m⁻² d⁻¹, Fig. 6.A). Finn Cycling Index (FCI_b) was lowest in 2009 (median 3%, 95% CI 1–7%), peaked at 6% in 2012 and 2019, and declined to 4.6% in 2022 (95% CI 3–6%; Fig. 6.B), representing a 44% increase relative to 2009 despite interannual fluctuations. Relative ascendancy (A/C) fluctuated over time, peaking at 0.46 in 2012 (95% CI 0.42–0.51), decreasing in 2019, and partially recovering to 0.42 in 2022/23 (95% CI 0.38–0.44). All indices differed significantly over time (Kruskal-Wallis, $p < 0.05$), with pairwise differences between consecutive years except for T_{t} between 2012 and 2016 (Table S6). Exact index values and CIs are provided in Table S6.

Total secondary production fluctuated over time without a consistent trend, whereas production of hard-substrate communities increased with time, peaking at 2.7 ± 0.36 mmol C m⁻² d⁻¹ in 2019 and contributing ~20% of the total production (Fig. 6.D; Table S3.10–11). Flows to and from turbine compartments followed a similar pattern, accounting for 9% of all consumer flows by 2022/23, with a maximum of 16% in

2019. Secondary production by habitat is shown in Fig. S5; detailed flows and values are in Table S3.10–11.

The total carbon exported from the system, calculated as flows directed to the export compartment, increased from 4.27 ± 1.47 mmol C m⁻² d⁻¹ in 2009 to 7.70 ± 2.43 mmol C m⁻² d⁻¹ in 2022/23. Exported flows rose from 2.9% of the total flows in 2009 to 4.6% in 2022/23 (8.41 ± 2.76 mmol C m⁻² d⁻¹). Overall, carbon export roughly doubled, increasing availability to higher trophic levels, but remained a small fraction of T_{t} .

4. Discussion

We integrated both qualitative and quantitative food web indices to show that the establishment of an OWF dynamically restructures the local marine food web. Several indices related to trophic flexibility and compartmentalization suggested a potential reduction in ecosystem stability over a time frame spanning more than a decade. Despite increased hard-substrate fauna production, we did not observe a consistent trend of overall rising secondary production.

4.1. OWFs restructure the marine food web and increase secondary production of hard-substrate communities

Community composition and densities shifted across years which was reflected in the food web properties: nodes and link density increased, while connectance, trophic level, and omnivory declined; modularity fluctuated but generally decreased. These changes are consistent with other long-term studies showing trophic interactions in response to environmental perturbations (Kortsch et al., 2021; Olivier et al., 2019). Declining connectance largely reflects the addition of benthic and hard-substrate species, which increase the number of nodes and potential interactions (Dunne, 2006). Modularity decreased over time, indicating greater integration of hard-substrate communities, evidenced by the increasing number of module connectors—species linking different modules—which likely serve as important prey for predators (Berges et al., 2024; Buyse et al., 2023; Mavraki et al., 2021). Module connectors are defined by their network position and represent a network-based way of assessing keystone species, as these taxa can have a strong influence on food web structure and stability (Andrade et al., 2025; Rodriguez et al., 2022).

Quantitative analyses supported these trends: secondary production of hard-substrate species increased over time, showing that turbine and SPL communities became more integrated into the food web. However, reduced modularity implies decreased compartmentalization and potentially higher vulnerability, as disturbances can propagate more easily through the system (Stouffer and Bascompte, 2011).

Despite OWFs attracting higher trophic levels (Buyse et al., 2022a; Galparsoro et al., 2022; Reubens et al., 2014; ter Hofstede and van Koningsveld, 2024), we observed a decline in TL with time. This reflected the proliferation of low-TL species, mainly filter feeders on hard-substrates and benthos, rather than loss of top predators. We did not include top predators (marine mammals and seabirds) as explicit compartments in the LIM models due to uncertainties in their occurrence, abundance and residence within the OWF area. Monitoring in the BPNS shows strong seasonal, interannual, and spatial variability, especially for

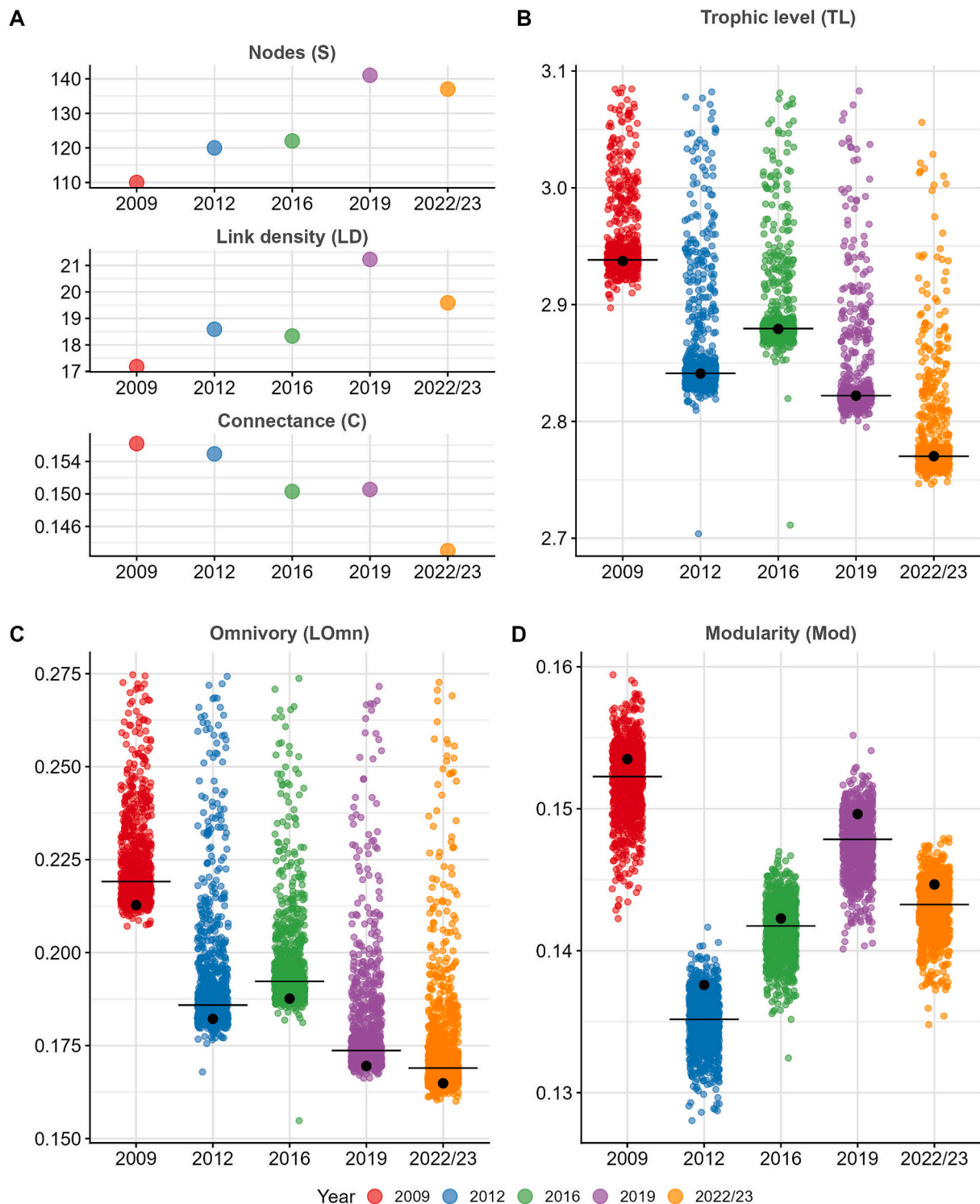


Fig. 4. Temporal variation of qualitative food web indices. A: General food web indices (Number of Nodes, Link Density and Connectance), B: Trophic level, C: Omnivory, D: Modularity. Plots B, C and D show the 1000 Curve-ball simulated values for each food web, the black points denote the value of the empirical food web and the line the median.

marine mammals (e.g., harbor porpoises peak in late winter-spring in the western BPNS) (Haelters et al., 2011, 2013, 2023). Species also differ in responses to OWFs: porpoises mainly transit or forage occasionally, avoiding turbines; seals likely transit and forage but remain unmonitored in the OWF zone (Rumes and Aoufi, pers. comm.); and seabirds show species-specific attraction or avoidance to the structures (Vanermen et al., 2017, 2020). Given this variability and the

uncertainties in their distribution it was not accurate to derive robust, year-specific estimates of top predator standing stocks at the scale of the modelled food web unit. Instead, carbon flows directed to the export (EXP) compartment provide an integrated representation of carbon leaving the system potentially available to top predators. Across years, EXP accounted for approximately 3-5% of total system flows, with exported carbon nearly doubling over the study period. This increase

Table 3

Species individual topological roles of the hard-substrate fauna communities (SPL and turbine) per year. “Nr. of Species” refers to the total number of hard-substrate species; “Nr. of module connectors” refers to the number of species classified as module connectors within hard-substrate communities. “Proportion” is calculated as the number of module connectors divided by the total number of species. Modularity is the modularity value of the food web for that year.

Year	Nr. of Species	Nr. of module connectors	Proportion	Modularity
2009	22	11	0.50	0.154
2012	26	12	0.46	0.137
2016	24	7	0.29	0.142
2019	32	13	0.41	0.149
2022/ 23	29	16	0.55	0.144

confirms that the developing OWF ecosystem enhances carbon production and export beyond the modelled food web boundaries. Therefore, by focusing on EXP, we can assess the carbon flow to top predators without relying on highly uncertain information about top predator biomass.

Although OWFs are expected to increase secondary production by creating artificial reef habitats and restricting fishing within concession zones (Buyse et al., 2022b; Reubens et al., 2013; Reubens et al., 2011), we found no measurable increase in fish production, indicating that operational OWFs have not yet led to measurable ecosystem-wide increases in fish biomass. This absence may reflect the localized nature of the reef effect or the limitations in our sampling design. Beam trawl surveys were conducted approximately 200 m from turbines, with a large gradient of distance from the turbines not captured. Previous studies have shown that fish aggregation effects are highly localized near the turbine (100 m from the structures), with densities up to four times higher than the surrounding area (Berges et al., 2024; Buyse et al., 2022b; dos Santos et al., 2010). Nevertheless, increased hard-substrate fauna production likely enhances food availability and shelter for fish, benefits not fully captured by our study (Bergström et al., 2013; Buyse et al., 2022b, 2023; Carey et al., 2020; Reubens et al., 2013).

4.2. Carbon dynamics and stability are affected by OWF development

Over 14 years, total system throughput ($T_{..}$) increased, indicating enhanced carbon flows in the system, consistent with previous studies showing that both monopile and floating OWFs can enhance carbon cycling via suspension feeders (Adgé et al., 2024; De Borger et al., 2025; Raoux et al., 2017). System activity intensified with OWF community development, with no indication of a stable “climax” community after 14 years (Kerckhof et al., 2019; Zupan et al., 2023). Primary production remained stable, indicating that increased throughput was not driven by higher primary production. While increased $T_{..}$ is often linked to ecosystem maturity (Ulanowicz, 1996), our findings deviate from classical succession theory. In our case, hard-substrates were introduced into an already functioning ecosystem with established top predators. Therefore, enhanced system activity does not necessarily reflect an increase in ecosystem maturity but the introduction of a new system (turbine and SPL structures) into an existing environment.

Relative ascendancy (A/C) showed interannual variability without a clear trend, indicating that enhanced carbon throughput did not correspond to more constrained or specialized energy pathways (Ståhl et al., 2025). Reduced omnivory and modularity suggest that while overall activity increased, the system's resilience may have decreased as perturbations can spread more easily across the network (low modularity), with fewer alternative pathways co-existing (low omnivory) (Gellner and McCann, 2012; Gutgesell et al., 2022; McCann and Hastings, 1997). Recycling ($FCIb$) remained low ($\leq 6\%$), reflecting limited internal matter reuse and further supporting the view that the OWF ecosystem remains relatively immature compared to adjacent natural soft-sediment systems. OWF ecosystems have shown lower recycling rates compared to nearby natural soft-sediment systems (i.e. 1.3% in OWF compared to 1.9% and 2.8% in adjacent sandy habitats (De Borger et al., 2025)) reinforcing our findings that the OWF ecosystem remains in a relatively immature state in contrast to more established habitats. We recommend that monitoring programs move beyond collection of presence-absence data and simple biodiversity metrics towards standardized, quantitative measurements (incl. biomass) that allow estimation of network properties such as total carbon flow, modularity, omnivory, and the distribution of food web flows across compartments. This is particularly relevant for lower trophic levels: fine-scale, site-specific measurements of phytoplankton and zooplankton abundance

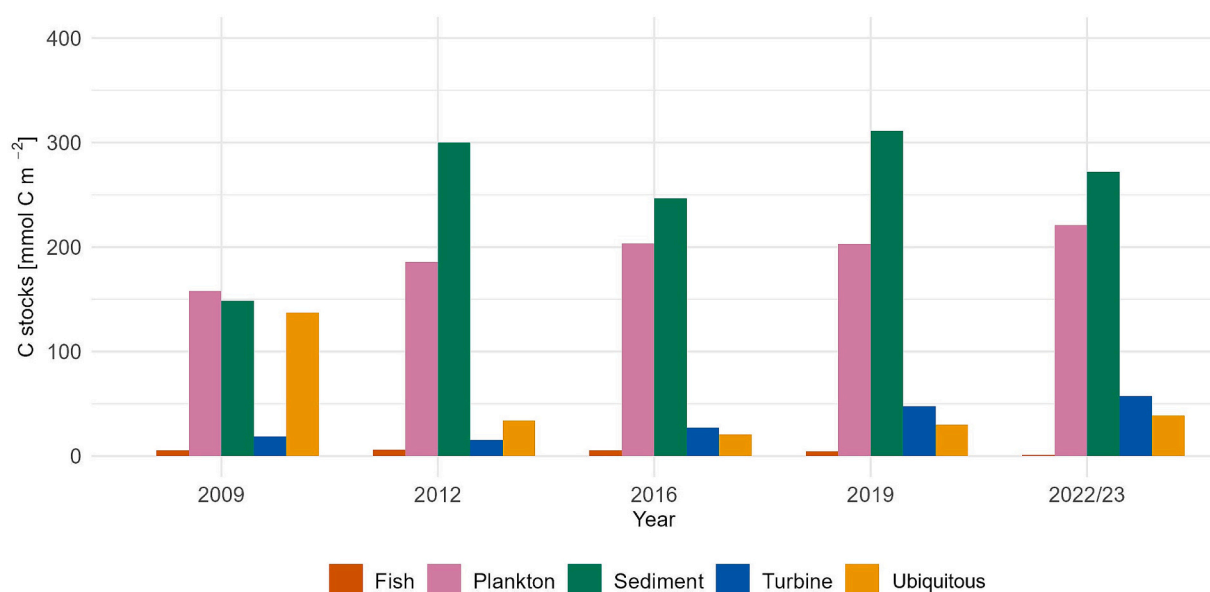


Fig. 5. Carbon stocks for the LIM models across the years. Sediment organic matter, suspended particulate organic matter, and bacteria are excluded for clarity. Fish represents all demersal fish compartments; plankton includes phytoplankton and zooplankton; sediment includes all compartments that inhabit the sediment, comprising epibenthos and macrobenthos; turbine + SPL include hard-substrate compartments and ubiquitous include compartments present across all habitats.

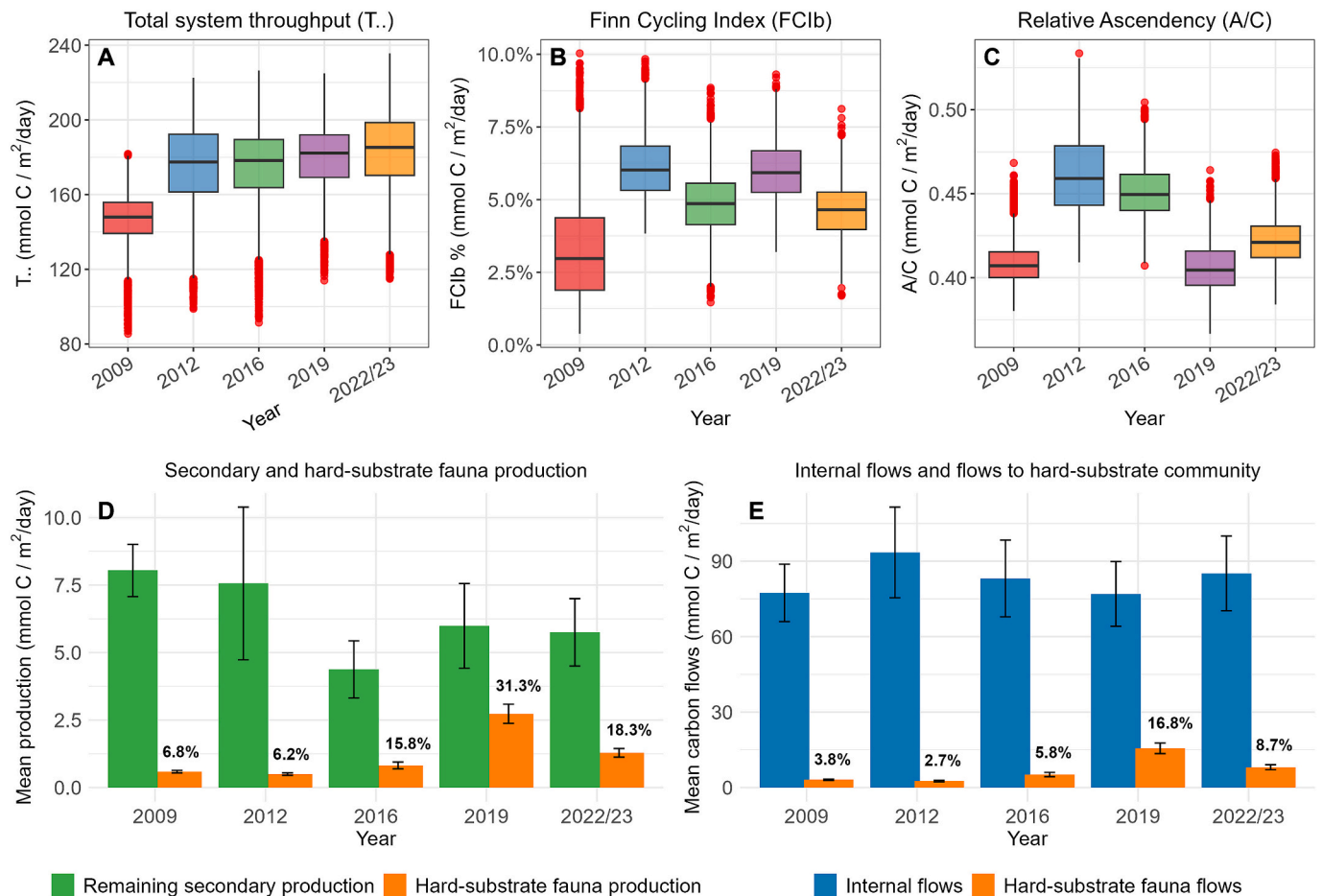


Fig. 6. Temporal trends in quantitative indices and LIM variables. (A) Total system throughput ($T.$), the sum of all C-flows. (B) Finn Cycling Index ($FCIb$), the proportion of recycled carbon. (C) Relative ascendency (A/C), flow distribution and organization. (D) Total secondary production of all consumer compartments and hard-substrate fauna production, with percentages indicating the proportion of hard-substrate fauna production over total production. (E) Sum of internal flows and flows from and to the hard-substrate community, with percentages representing the proportion of turbine and SPL-associated flows. Boxplots (A–C) show distributions from 5000 LIM iterations; error bars (D–E) show standard deviations.

and biomass around OWFs remain scarce, despite their central role in structuring energy supply to higher trophic levels. Future sampling and modelling efforts should incorporate standardized, high-resolution sampling of plankton communities within and around OWFs. Such an approach would enable detection of changes in ecosystem functioning that are not apparent from community composition alone.

In general, the year 2009 stood out in our time series, likely reflecting construction-related disturbance. During turbine installations activities like dredging and drilling resuspend sediments, resembling sand extraction impacts and promoting the proliferation of opportunistic species (Hiscock et al., 2002). These early-stage disturbances have been linked to short-term increases in abundances of opportunistic species and benthic fish, followed by macrobenthos recovery approximately two years after construction (Coates et al., 2014; De Backer et al., 2014). Additionally, the expansion of the OWF after 2012, which introduced Jacket foundations around the initial six GBFs, influenced local hydrodynamics (van Berkel et al., 2020), sediment composition (Coates et al., 2014), and increased the availability of hard-substrate, which could have further influenced the marine food web in the earlier years.

Our system represents a shallow, dynamic North Sea environment typical of many fixed-bottom OWFs. Turbine foundations and associated structures link the water column and benthic communities, promoting hard-substrate assemblages. Because our LIM models represent a single food web unit (turbine foundation + SPL + surrounding sand), extrapolation to other sites should account for local factors such as turbine

density, foundation type, sediment, hydrodynamics, and other anthropogenic pressures (De Borger et al., 2025; Galparsoro et al., 2022; Nogues et al., 2021). Ecosystem responses to OWFs are context-dependent and can vary even over small spatial scales (e.g., plaice and macrobenthic responses differ among sites in the BPNS) (Buyse et al., 2023; Jammár et al., 2025). Nonetheless, OWFs consistently cause measurable local changes, such as increased biomass and reorganization of trophic pathways (De Borger et al., 2025; Raoux et al., 2017). At broader scales, these effects are less consistent and often masked by fishing and climate pressures (Huang et al., 2025; Nogues et al., 2021), though future expansion of OWF infrastructure, including larger fixed-bottom and floating developments, may amplify their influence. Furthermore, as our study is based on a single site, environmental changes due to climate change cannot be fully excluded, therefore, future studies incorporating paired control sites, climate-informed species niche models, and cumulative impact assessments will help disentangle these effects (Nogues et al., 2021, 2023).

4.3. Model assumptions and uncertainty

Several assumptions inherent to our LIM approach should be considered when interpreting the results. Our models assume steady state within each year, implying constant biomass stocks and no intra-annual variability. Some inputs (e.g. stable isotope values and burial rates) were extrapolated across years due to data limitations. Trophic links were derived from literature, with priority given to local studies

from our study area (Text S1). In addition, the 2022/23 food web combines datasets from adjacent years (fish and hard-substrate fauna from 2022; macrobenthos from 2023). However, Bray-Curtis analysis indicated high temporal similarity in macrobenthic communities across years, suggesting that our approach provides a reasonable approximation (Fig. S1). Phytoplankton biomass was derived from satellite-based ERSEM-NEMOVAR outputs (7 km resolution), which do not explicitly resolve OWF-scale impacts on plankton communities (Christiansen et al., 2023; Daewel et al., 2022; Hendriks et al., 2025; Zampollo et al., 2025), and zooplankton biomass was estimated using a literature-based phyto-zooplankton relationship (Schrum et al., 2006). OWFs affect plankton communities through changes in hydrodynamics caused by the blades and the turbines (Christiansen et al., 2023; Daewel et al., 2022). However, induced changes in phytoplankton biomass are typically <1% in shallow, well-mixed systems such as our study site (Daewel et al., 2022), a magnitude that falls within the natural variability already captured by our LIM-MCMC solution space, where phytoplankton uptake varies by 6–10% across iterations for each model year (Table S3.10). As higher-resolution OWF-resolving biogeochemical and zooplankton datasets become available, their integration into food web models will be an important next step (Zampollo et al., 2025). Finally, the absence of control sites means we cannot formally disentangle OWF-driven changes from climate-driven trends; however, available evidence from the BPNS suggests that climate-driven shifts in benthic and fish communities operate over longer timescales (Buyse et al., 2022a; Jamar et al., 2025), and that observed patterns are more strongly associated with turbine-related than climate-related variables (Jamar et al., 2025). Despite these limitations, our results are based on a unique long-term empirical dataset collected within an operational OWF over more than a decade. Our main conclusions are supported by broad temporal trends that are consistent across multiple qualitative and quantitative indicators from different modelling approaches, strengthening the confidence and robustness of our findings.

5. Conclusion

This study provides a long-term, empirically based assessment of food web dynamics in an operational offshore wind farm over more than a decade. Qualitative food web indices detected structural shifts, including lower trophic level and omnivory, caused by the addition of new taxa. Incorporating quantitative data showed that structural reorganization coincided with altered carbon flows. The increasing role of hard-substrate species as module connectors, together with their higher secondary production, indicated a progressive integration of turbine-associated communities into the local food web. This integration, however, was accompanied by indices pointing towards increased vulnerability to disturbance. Combining both approaches in a long-term time series thus revealed complementary insights into ecosystem responses.

Our results demonstrate that food web indices are sensitive to OWF-driven ecosystem changes and have potential for management and monitoring under frameworks such as the Marine Strategy Framework Directive and OSPAR. To fully exploit their potential, we recommend collecting data in a standardized and comparable way across space and time to enable robust comparisons and distinguish site-specific from general OWF effects and climate effects. As first-generation OWFs approach decommissioning, the food web models developed here also provide a basis for evaluating alternative decommissioning scenarios and their implications for ecosystem structure and functioning.

Associated content

The data underlying this study are openly available in <https://doi.org/10.5281/zenodo.22254096>

Supporting information includes (1) qualitative food web files (literature sources for feeding links, species list and interaction matrix);

(2) quantitative food web files (stock data, constraints, LIM input files, flow values and variables values); (3) species topological roles; (4) exact values of qualitative and quantitative food web indices.

CRediT authorship contribution statement

Abril Reynés-Cardona: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Emil De Borger:** Writing – review & editing, Validation, Supervision, Software, Methodology, Investigation, Conceptualization. **Jan Vanaverbeke:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Tomás I. Marina:** Writing – review & editing, Software, Methodology, Conceptualization. **Jolien Buyse:** Writing – review & editing, Resources. **Ulrike Braeckman:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2026.115432>.

Data availability

The code and data underlying this study are openly available in the Zenodo repository: <https://doi.org/10.5281/zenodo.22254096>.

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