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Original Article

Estimating the contribution of the Irish Sea fish community to carbon sink potential

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Abstract

The marine biological carbon cycle plays a crucial role in the sinking and sequestration of atmospheric carbon and in regulating the global climate. Most existing research on biological carbon sequestration has focused on the role of oceanic (off-shelf) species and processes. We know little about how species living on continental shelves contribute to and influence carbon sinks due to the complex dynamics of biological and physical transport processes. However, continental shelves often have high levels of carbon productivity and a high potential for disturbance from human activities such as fishing, which strongly impact fish communities. Fish are important components of ecosystems that interact with the biological carbon cycle. Here, we used an Ecopath with Ecosim food web model of the Irish Sea coupled with biogeochemical equations to provide a novel quantitative assessment of the contribution of the fish community to the annual carbon reaching the continental-shelf seafloor over a four-decade simulation (1973–2016). Similar to the open ocean, faecal pellets dominated estimates of fish-mediated carbon flux in the Irish Sea. Our simulations imply that pelagic fish contribute more than half of the fish-mediated carbon, equivalent to approximately 2% of the plankton-mediated carbon deposited on the seafloor. Our results provide the first quantitative assessment and early insights into the relationship between fish species and the biological carbon sink in a shelf ecosystem.

Keywords biological carbon cycle, fish-mediated carbon, faecal matter, Irish Sea ecosystem, Ecopath with Ecosim

Introduction

The ocean absorbs atmospheric carbon dioxide and stores a substantial fraction of the carbon present in the global carbon cycle (c. 93% of non-geological carbon; DeVries 2022). Marine ecosystems play a crucial role in maintaining the ocean's function as a sink for carbon (Longhurst 1991), which is a key factor in regulating the global climate. The carbon is considered sequestered when it increases a pool or reservoir of carbon other than the atmosphere (Visser 2025). The biological carbon pump drives sequestration of carbon by exporting carbon from the ocean surface to the deep ocean and seafloor sediments (Sigman and Hain 2012, Nowicki et al. 2022). Sinking particles are a main pathway of carbon transport from the surface to the ocean interior and sediments (Henson et al. 2012, Boyd et al. 2019, Bisson et al. 2020). Zooplankton faecal pellets have been highlighted as the most important pathway for carbon export to the deep ocean (Cavan et al. 2015, Nowicki et al. 2022). However, most previous studies on the biological carbon cycle have focused primarily on open-ocean processes (i.e. off the continental shelves) and lower trophic levels, lacking resolution at higher trophic levels.

Recent research found that fish and other nekton make similar contributions to carbon export in the open ocean, each accounting for up to 20%–30% of the carbon sequestered by the biological carbon pump and that this carbon is typically sequestered for timescales in excess of 250 years (Pinti et al. 2023). Previous research on fish has focused on mesopelagic fish contribution to carbon transport (Dişa et al. 2024, McMonagle et al. 2024, 2023). Fish faecal pellets (i.e. passive carbon flux) may represent an important pathway for carbon transport to the seafloor due to their rapid sinking speed and slow dissolution rate, which become increasingly important at greater depths (Bianchi et al. 2021, Saba et al. 2021). Fish species represent a substantial biomass and play key functional roles in marine ecosystems. Fish interact with the biological carbon cycle in multiple ways, including through consumption, respiration, accumulation of carbon in biomass, and release of carbon via egestion, excretion, reproduction, and death (Martin et al. 2021, Liu et al. 2022), as well as trophic interactions (Trueman et al. 2014).

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The global continental shelf supports productive ecosystems and marine sediments that store approximately 266 petagrams of carbon (Pg C) in the top one metre (Atwood et al. 2020). The carbon sequestration in continental shelf systems involves different processes compared to the open ocean due to the relative shallowness of these areas, which are more hydrodynamic, with tides, currents, and storm events, and generally more productive (Sigman and Hain 2012). Continental shelves also tend to have more productive benthic systems (Yool and Fasham 2001, Lessin et al. 2019). Continental shelf systems are areas that exhibit high primary productivity and carbon export potential, which co-occur with regions of high fishing effort (Cavan and Hill 2022). Fishing activities impact fish communities and their ecosystem; therefore, they can affect the biological carbon cycle (ICES 2024). Previous research indicates that exploitation of fish could have important implications for oceanic carbon storage and climate regulation (Mariani et al. 2020, Bianchi et al. 2021, Saba et al. 2021).

Quantifying the contribution of fish species to the on-shelf carbon sink is crucial for understanding their relative importance in carbon sequestration and determining how an improved understanding may be factored into management decisions where appropriate. This study aims to investigate how the shelf-sea fish community contributes to the carbon sink and deposition on the seafloor, considering ecosystem-level processes and interactions, using the Irish Sea as a case study. We used an ecosystem model that integrates trophic interactions, fishing pressure, and environmental variability to disentangle the estimated contributions of fish species to carbon flux through mortality and egestion over the past four decades. We used model simulations to estimate the carbon released by fish and reaching the seafloor over the period 1973–2016 to evaluate how this contribution has changed over time. We performed a sensitivity analysis of key parameters to better understand their influence on model simulations and the associated uncertainties.

Materials and Methods

This study simulated the Irish Sea food web and estimated fish-mediated carbon deposition on the seafloor by coupling an ecosystem model with offline, adapted biogeochemical equations. We estimated the fish-mediated carbon reaching the seafloor per unit area per day and its temporal dynamics over a four-decade period (1973–2016).

Ecosystem model: Ecopath with Ecosim

Ecopath with Ecosim (EwE; Christensen and Walters 2024, 2004) is a trophic dynamic modelling package that has been widely used to simulate marine food webs, interspecific interactions, and how they are impacted by retrospective or predicted environmental and anthropogenic pressures. The approach has been applied globally, primarily to explore fishery management options in the context of their ecosystem impacts (Mackinson et al. 2018), but also to simulate the ecosystem effects of climate change (Serpetti et al. 2017), Marine Protected Areas (Püts et al. 2023), bioaccumulation of contaminants (Serpetti et al. 2021), and infrastructure development such as offshore wind. EwE also has a large collaborative user community that actively documents technical advances (Steenbeek et al. 2018), and protocols for diagnostics and best practices (Link 2010, Heymans et al. 2016). EwE includes three main components: (1) Ecopath—a static snapshot of the system used to initialize the remaining components, (2) Ecosim—a time-dynamic simulation module, and (3) Ecospace—a spatial and temporal dynamic module. In this study, we use only Ecopath and Ecosim.

Ecopath provides a mass-balanced snapshot of the ecosystem for a given year, based on data such as biomass estimates, species diets, life-history parameters (e.g. production and consumption rates), and fisheries catch. Ecopath quantifies energy flow between functional groups, which can represent single species (e.g., cod), life stages (e.g., juvenile or adult), or aggregated groups of ecologically/functionally similar species (e.g., demersal fish). Ecopath is underpinned by master equations for production and consumption (Christensen and Walters 2024). Ecosim provides a dynamic temporal simulation capability with initial conditions inherited from Ecopath. It uses a system of differential equations that expresses biomass flux rates as a function of variation in trophic interactions, harvest rates, and environmental variability (for equations, see Walters, 1997)). Ecosim predictions of consumption account for spatial and temporal constraints which emerge as a result of risk-sensitive foraging behaviour (i.e. Foraging Arena Theory; Ahrens et al. 2012, Bentley et al. 2024). The objective of Ecosim is often to produce simulations that are sufficiently capable of reproducing observed past dynamics to inform retrospective analyses and thereby enhance understanding of potential responses to anthropogenic or environmental change.

The Irish Sea model

This study uses the International Council for the Exploration of the Sea (ICES) key-run configuration of the EwE model for the Irish Sea (Bentley et al. 2019, ICES 2019, 2020). The Irish Sea EwE model was co-designed with fishers and other stakeholders to investigate the ecosystem dynamics of commercially important species, including cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), plaice (*Pleuronectes platessa*), whiting (*Merlangius merlangus*), sole (*Solea solea*), herring (*Clupea harengus*), and nephrops (*Nephrops norvegicus*). The model has been reviewed and used to inform fisheries advice (Bentley et al. 2021).

The modelled area is the Irish Sea, which covers approximately 58 000 km^2 between Ireland and the UK (Vincent et al. 2004, Figure 1). It is a semi-enclosed basin with depths ranging mostly from 20 to 100 m, featuring extensive areas of relatively flat and shallow seafloor, as well as deep channels in the western-central area, where water depths reach up to 230 m (Mellett et al. 2015). The model comprises 41 functional groups ranging from detritus and primary producers to top predators, including marine mammals and seabirds. The Ecopath model provides a snapshot of the Irish Sea ecosystem in 1973. This sets the initial conditions for the Ecosim simulation, which spans 44 years (1973–2016). Material flows, such as prey consumption by predators and detritus production, are expressed in the wet weight km^{-2} year^{-1}. The fish component is well defined with life stages (juvenile and adult) explicitly modelled for key species such as cod, haddock, whiting, and plaice. Unassimilated consumption across all functional groups was initially set to 0.2 (Bentley et al. 2019, ICES 2019, 2020),

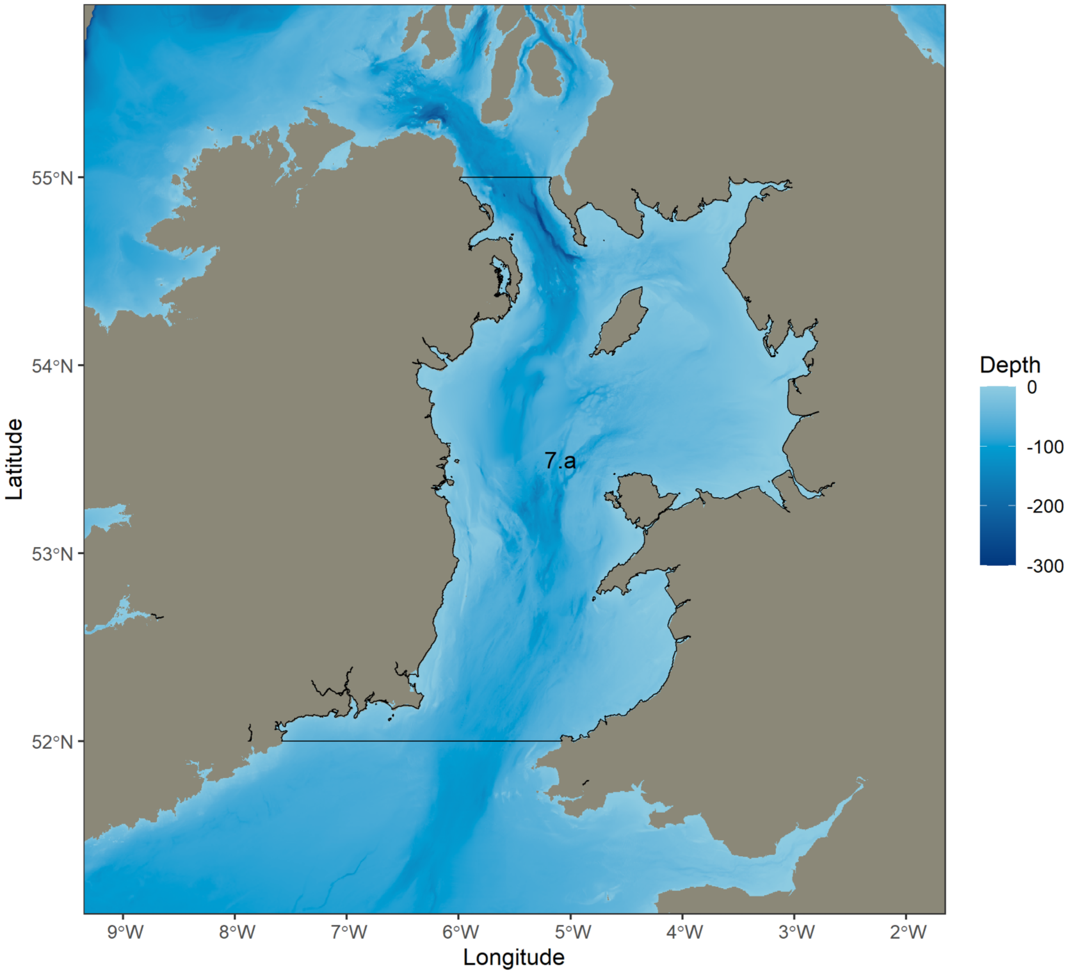

Figure 1. Map of the study's location, the Irish Sea (ICES area 7.a).

i.e. 80% of consumption is physiologically useful, and 20% is directed to detritus. However, for the current analysis, we adjusted the unassimilated consumption for zooplankton groups to 0.4, reflecting their herbivorous diet and the associated lower efficiency. We did not change any other Ecopath parameters (Table SM1). Ecosim was run using EwE version 6.7.

Conversion of Ecosim outputs

In Ecopath, the flow to detritus comprises non-assimilated food or unassimilated production (i.e. urine and faeces) and other mortality (organisms dying due to old age, disease, or starvation, rather than predation or fishing). Other fish-released waste (e.g. respired carbon, dissolved organic carbon, and inorganic carbon) is not modelled in this framework. For each fish functional group, we calculated these flows separately for the simulated time period (1973–2016). We converted Ecosim outputs into the parameters required to estimate fish-mediated carbon in faeces and carcasses. We focus on the non-assimilated food, which comprises the flow to faecal pellets, and the "other mortality" (i.e. that due to old age, disease, or starvation), which comprises the flow to carcasses. We used the following modelled components for each fish group:

(i) Year-specific biomass (B_t) (t km^{-2})
(ii) Year-specific consumption to biomass ($(Q/B)_t$)—the annual intake of food per unit biomass of the group
(iii) Constant unassimilated consumption (U)—the proportion of food consumed that does not cross the gut wall and is typically egested as faecal matter—specified as an Ecopath input
(iv) Year-specific other mortality ($M0_t$)—instantaneous mortality rate, excluding the effects of predation and fishing

Other mortality ($M0$) is not provided as a direct Ecosim output and was therefore calculated from available outputs (biomass, total mortality, predation mortality, and catch). In Ecosim, the mortality rate is a result of predation, fishing, plus other ("unexplained") mortality (Equation 2 in Walters et al. 2008). Thus, the other mortality at year t can then be calculated as

$$M0_i\,(t) = Z_i\,(t) - M2_i\,(t) - \frac{C_i\,(t)}{B_i\,(t)}, \qquad (1)$$

where $Z_i(t)$ is the year-specific total mortality, $M2_i(t)$ is the year-specific predation mortality, and $C_i(t)$ is the year-specific catch, and $B_i(t)$ is the year-specific biomass.

Fish-mediated carbon

Carbon released in the water column

We estimated the rate of carbon released in the water column from faecal matter (pellets) and carcasses. We calculated carbon in faecal pellets from ingested food only. Unlike some planktonic organisms, fish faecal pellets lack an external covering and are bound together with mucus, often remaining as discrete entities for days or weeks (Wotton and Malmqvist 2001). We assumed this is the case for faecal matter produced by fish species in the Irish Sea model.

We used two equations: one for the carcass flux (Equation 2, *Fc*) and one for the faecal pellet flux (Equation 3, *Ff*).

$$Fc_t^i = CF_i \cdot B_t^i \cdot M0_t^i \tag{2}$$

$$Ff_t^i = \overline{CF} \cdot \left(\frac{Q}{B}\right)_t^i \cdot B_t^i \cdot U_i \tag{3}$$

To estimate the carcass flux (Fc_t^i) for fish functional group *i* in year *t*, we used the other mortality rate (*M0*) in year *t* (in yr^{-1}), and the biomass (*B*) in year *t* (in t km^{-2}). We used a conversion factor, CF_i, to convert carcass biomass wet weight to carbon mass. We estimated the conversion factors (Table SM4) using the DM/WM (dry mass to wet mass ratio) and the C/DM (carbon mass to dry mass ratio) conversion factors by taxon extracted from the global database Conversion Factors for Aquatic Organisms—Version 4 (2012) (Brey et al. 2010). The conversion factor was calculated per functional group by multiplying DM/WM and C/DM to obtain the C/WM ratio per taxon, using the genus when available, or higher taxa for the species or assemblage of species constituting that group. The conversion factor for multispecies functional groups was calculated by the weighted mean of the conversion factors for each species in the group.

The faecal carbon flux (Ff_t^i) of fish group *i* in year *t* was calculated using consumption to biomass rate (*Q/B*) in year *t* (in yr^{-1}); the biomass in year *t* (in t km^{-2}), and *U*, the unassimilated consumption (unitless, and assumed to be 0.2 for all teleost fish as in Bentley et al. 2019). The conversion factor to convert the pellet mass to carbon ($\overline{CF}$) is the diet-weighted average of all the prey groups consumed by functional group *i* (Table SM4). These carbon fluxes, initially in t km^{-2} yr^{-1}, were converted to mg m^{-2} d^{-1} to allow comparisons with other studies.

Water column attenuation

Organic carbon released by fish passively sinks until deposited on the seafloor. We measure the deposition flux as the rate at which carbon reaches the seafloor. During the sinking of faecal pellets and carcasses through the water column, remineralisation of carbon by microbial action can reduce the carbon content. The degree of water column attenuation is a function of various factors, including the surface area-to-volume ratio, water temperature, the presence of barriers to microbial colonisation, depth, and sinking speed, which determine the time the pellet or carcass spends in the water column (Yool et al. 2013, Turner 2015). We used the Martin curve (Martin et al. 1987) to estimate the carbon remaining in pellets and carcasses when they reach the seafloor (Equation 4).

$$F\,(z)_t^i = F\,(z0)_t^i \left(\frac{z_0}{z}\right)^{-b} \tag{4}$$

For each year (t), *F(z)*$_i$ is the carbon released by group *i* that reaches the seafloor at depth z, *F(z0)*$_i$ is the starting carbon content at depth z_0, and *b* is the attenuation parameter.

Observations of fish faecal matter are limited; however, those published show that fish pellets sink rapidly (Saba et al. 2021). Measured sinking rates range from 787 m d^{-1} for anchovy (Saba and Steinberg 2012) to 1028 m d^{-1} for mid-water fish (*Stenobrachius leucopsarus*, *Triphoturus mexicanus*, *Leuroglossus stilbius*, *Lampanyctus ritteri*, *Argyropelecus affinis,* and *Parvilux ingens*; Robison and Bailey 1981). The attenuation parameter in Martin's equations represents the combined effect of the particle's remineralisation and sinking rates. Martin et al. (1987) proposed a global average for particulate organic carbon (POC) of $b = 0.86$ (Martin et al. 1987), which applies to particles sinking at rates of 10 to 100 m d^{-1}. We assumed that sinking fish pellets have a relatively low attenuation rate because they sink 10 times faster than POC, i.e., $b = 0.07$ (as used in Bianchi et al. 2021). We assumed that water-column attenuation would be negligible for carcasses and set *b* to 0 because of their very fast sinking speeds, their low surface area-to-volume ratio, and the inclusion of an effective barrier to remineralisation (skin). Seafloor depth (*z*) was set at 50 m, the rounded average depth in the Irish Sea.

To analyse fish community-mediated carbon flux, we grouped the species according to their common positions in the water column. The benthic group included European plaice, common sole, and flatfish: common dab (*Limanda limanda*), solenette (*Buglossidium luteum*), scaldfish (*Arnoglossus laterna*), lemon sole (*Microstomus kitt*), thickback sole (*Microchirus variegatus*), witch (*Glyptocephalus cynoglossus*), brill (*Scophthalmus rhombus*), European flounder (*Platichthys flesus*), and turbot (*Scophthalmus maximus*). This group also comprised monkfish (*Lophius piscatorius*), and gurnards and dragonets, which include grey gurnard (*Eutrigla gurnardus*), red gurnard (*Aspitrigla cuculus*), common dragonet (*Callionymus lyra*), and tub gurnard (*Trigla lucerna*). The demersal group included Atlantic cod, whiting, European hake (*Merluccius merluccius*), sandeels, including greater sandeel (*Hyperoplus lanceolatus*) and lesser sandeel (*Ammodytes tobianus*). This group also comprised other demersal fish, which include saithe (*Pollachius virens*), pollack (*Pollachius pollachius*), lesser weever (*Echiichthys vipera*), shorthorn sculpin (*Myoxocephalus scorpius*), European conger eel (*Conger conger*), John Dory (*Zeus faber*), greater weever (*Trachinus draco*), common ling (*Molva molva*), hooknose (*Agonus cataphractus*), and European seabass (*Dicentrarchus labrax*). The group also included other benthopelagic fish, which include Norway pout (*Trisopterus esmarkii*), poor cod (*Trisopterus minutus*), and bib (*Trisopterus luscus*), and anadromous fish, which include seatrout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). The pelagic comprised Atlantic herring, European sprat (*Sprattus sprattus*), and other pelagic fish: Atlantic mackerel (*Scomber scombrus*), blue whiting (*Micromesistius poutassou*), Atlantic horse mackerel (*Trachurus trachurus*), and European anchovy (*Engraulis encrasicolus*). We set the released depth z_0 for these groups at *z* (i.e. no water column attenuation), 20 m, and 10 m, respectively.

Fish-mediated carbon deposited at the seafloor

The carbon reaching the seafloor was estimated for each year from 1973 to 2016 as the sum of the carbon fluxes via fish carcasses and faeces for each fish functional group in the model, expressed in mg C m^{-2} d^{-1}. To assess the strength of the relationship between biomass and deposited carbon, we fitted a linear model in which deposited carbon was explained by carbon biomass. The total fish-mediated carbon reaching the seafloor was estimated for the entire Irish Sea, in t C yr^{-1}, by summing functional group fluxes and multiplying by the total area (58 000 km^2), number of days per year (365), and an area conversion factor (0.001). The mean carbon reaching the seafloor from 1973 to 2016 was then estimated.

Plankton-mediated carbon

Phytoplankton and zooplankton are known to be major contributors to detritus in ecosystems (Christensen and Walters 2024), and therefore to carbon sinks (Bisson et al. 2020, Nowicki et al. 2022). Using a similar approach to that for the fish-mediated carbon, we estimated the carbon deposited at the seafloor from the planktonic groups, i.e. phytoplankton, small zooplankton, and large zooplankton. We used offline equations to calculate carbon released and water-column attenuation (Equation 4). For phytoplankton, we estimated the rate of carbon released as detritus (dead phytoplankters), and attenuation assuming $b = 0.86$ (POC; Martin et al. 1987). For small zooplankton, we estimated the rates of carbon released as pellets and as carcasses, and attenuation for both, assuming $b = 0.86$ due to their small size. For large zooplankton, we estimated the rates of carbon released in pellets and carcasses, and attenuation for both, assuming $b = 0.3$ (krill; Cavan et al. 2024).

Sensitivity analysis

We conducted a sensitivity analysis to account for the limited availability of parameter data for the Irish Sea and the broader uncertainty surrounding how these parameters vary across species and ecosystems. We explored the relative influence of the nine key parameters used as inputs to the offline equations by varying each parameter by 10% in both directions and evaluating the resulting change on the fish-mediated carbon flux at the seafloor. We further explored the effect of five of these parameters by using the extremes of a plausible range of potential values (Table 1).

Results

The contribution of fish to carbon deposited at the seafloor

Our modelling framework estimated that fish-mediated carbon in the Irish Sea contributed between 71 531 and 103 055 t C yr^{-1} to seafloor deposition during the period 1973–2016, with a mean of 82 460 t C yr^{-1} or 3.89 mg C m^{-2} d^{-1} (Figure 2) .

The model simulations revealed that pelagic fish groups were responsible for c. 58% of carbon deposition (Table 2). Around 70% was contributed by just three of the 20 fish functional groups: European sprat, other pelagic fish (including horse mackerel, anchovy, Atlantic mackerel, and blue whiting), and other benthopelagic fish (including poor cod, pouting, and Norway pout; Figure 2). Although interannual variation differed among fish groups, there was an overall decreasing trend in total estimated fish-mediated carbon, resulting in a 26.44% decline over the simulation period (Figure 2).

The estimated contribution of each functional group to seafloor deposited carbon was strongly related to its biomass (Figure 3, Table 2). This relationship was positive for all fish groups except adult European plaice, and was not significant for European sprat and monkfish (Table 2).

Fish-mediated carbon deposited at the seafloor modelled consisted of 85.12% faecal pellets and 14.88% carcasses (Figure 4); however, this ratio varied among fish groups, with the carcass contribution being higher for groups with higher other mortality, such as adult cod, anadromous fish, adult European plaice, Atlantic herring, and monkfish (Figure SM3). The carbon losses through the water column by attenuation were around 36% of the carbon released in fish faecal pellets.

Overall, the estimated contribution of the fish community to the passive sinking flux of carbon was small compared to other pathways of sinking carbon in the ecosystem (i.e. phytoplankton, small zooplankton, and large zooplankton). The plankton groups accounted for 95.9% of the detritus flux, dominating the biologically mediated carbon fluxes. We estimated that the contribution of fish-mediated carbon in the water column was equivalent to 0.65% of the plankton-mediated flux; however, at the seafloor, the fish-mediated carbon was equivalent to 3.97% (Figure 5). This difference was caused by much higher attenuation of plankton-mediated carbon.

Sensitivity analysis

A 10% change in the most sensitive parameter values (e.g. biomass) results in approximately a 10% change in carbon deposition estimates (Figure 6). Our sensitivity analysis revealed that the modelled carbon deposition at the seafloor was most sensitive to changes in determinants of faecal pellet production (biomass, consumption-to-biomass ratio, unassimilated consumption, and the carbon conversion from wet mass to carbon units). This sensitivity showed greater inter-group variability for conversion factors, the consumption-to-biomass ratio, and unassimilated consumption than for biomass (Figure SM7). Assumptions about assimilation efficiency (U) substantially affect estimates of total deposited carbon; however, this parameter has typically been observed to have little variation among fish (Winberg 1956). However, more recent publications have found greater variation for carbon assimilation depending on food (Liu et al. 2022), which would have a high impact on the estimation of carbon flux. For a shallow continental shelf, assumptions about release depth and seafloor depth had a minimal effect. However, assuming higher water-column attenuation, i.e. $b = 0.3$ used for krill faecal pellets (Cavan et al. 2024), would result in almost 25% less deposited carbon (Figure 6).

Discussion

In this study, we provide a first estimate of the carbon sink to the seafloor produced by the fish community on a continental shelf system, using the Irish Sea as an example. Using EwE enabled us to simulate past changes in the food web that affect biomass and carbon release. We estimate that the Irish Sea fish community contributes to the sinking of c. 82 000 t C yr^{-1} to the seafloor. Our analysis of the Irish Sea food-web simulation suggests that pelagic fish groups (predominantly forage fish) contributed the majority (c. 58%) of fish-mediated carbon deposited on the seafloor, equivalent to approximately 2% of the plankton-mediated carbon, primarily due to fish's high biomass. A strong relationship between biomass and carbon contribution was also found in Cavan et al.

Table 1. Parameter plausible ranges.

	Parameter	max	min	Comments
U	Unassimilated consumption	0.1	0.3	We explored a range from a 50% increase to a 50% decrease relative to the assumed 0.2 total loss of food energy in faeces and urine. Unassimilated consumption was typically assumed to have little interspecies variation (Winberg 1956), but recent studies have found greater variation (Liu et al. 2022).
b	Martin's b attenuation parameter	0	0.03	We explores a range from no attenuation to assumed attenuation for an efficient carbon-sinking pelagic organism, Antarctic krill (Cavan et al. 2024).
Z	Seafloor depth	20	230	We explored a range from shallow water to the maximum depth in the Irish Sea (Mellett et al. 2015).
$\overline{CF}$	Carbon conversion factor of faecal pellets	0.07	0.12	We explored the range of the calculated $\overline{CF}$ based on the diet of our fish functional groups.
CF	Carbon conversion factor of body	0.06	0.14	We explored the range of the CF of our fish functional groups.

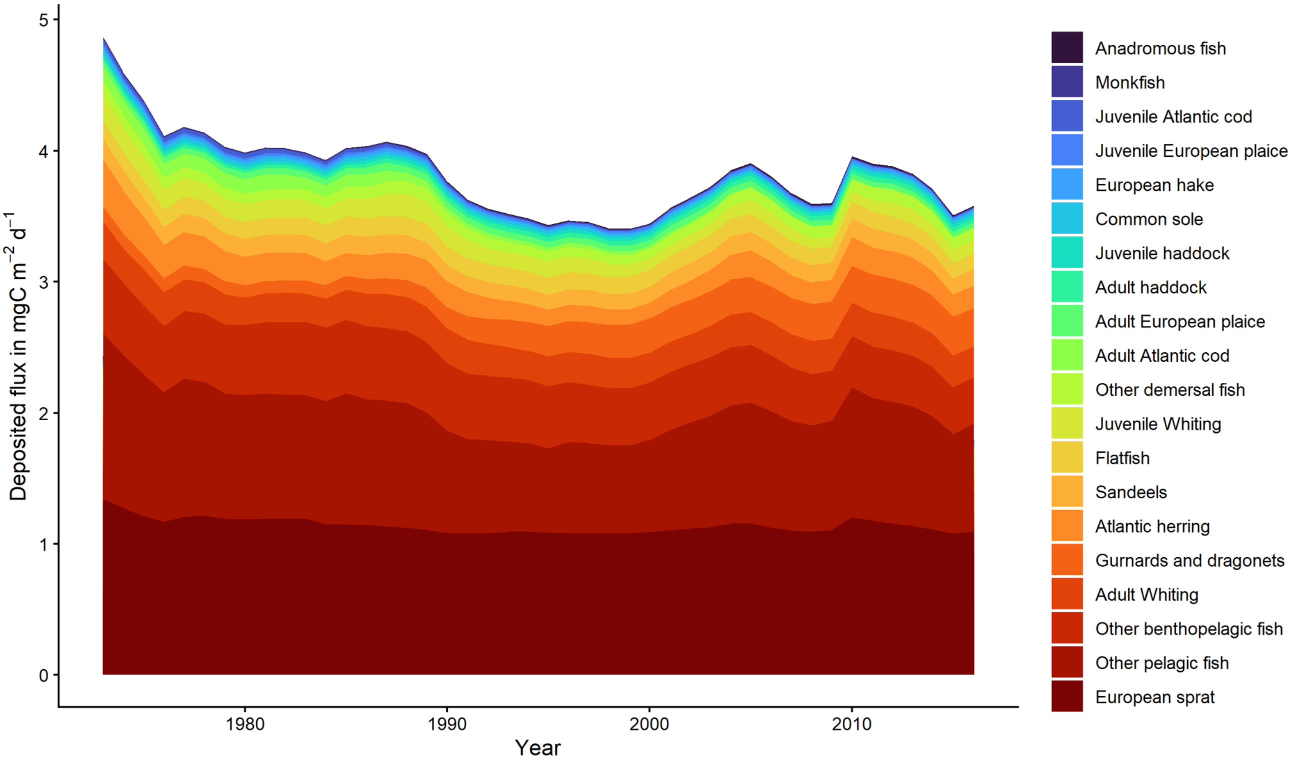

Figure 2. Time series of estimated fish-mediated carbon deposited on the seafloor from the Irish Sea model (1973–2016).

(2024). Our results implied that faecal pellets were the most important pathway for fish-mediated carbon passive flux (c. 85% of fish-mediated carbon deposited on the seafloor). This exceeds the relative importance of faecal pellets compared to carcasses estimated for open-ocean fish by c.15% (Pinti et al. 2023).

In simulations of the period 1973–2016, the Irish Sea fish community's carbon contribution at the seafloor showed a decreasing trend, coinciding with a decline in biomass, highlighting the strong link between biomass and carbon. This decreasing trend in Irish Sea fish biomass has been previously studied by Bentley et al. (2020), who identified several important ecosystem processes that suppressed the overall production of various fish species. For example, demersal species, such as cod and whiting, were affected by temperature in their reproduction, by impacting the growth and survival of juveniles (Rindorf et al. 2020). Pelagic species such as herring and sprat were impacted by the decreasing abundance of large zooplankton, which suppressed the overall production of cod, whiting, and herring. These changes may have led to in-

Table 2. Average rate of carbon deposited in the Irish Sea per fish functional group, coefficient of variation of the time series, and adjusted R^2 of the linear model of the deposited fish-mediated carbon ∼ carbon biomass relationship (asterisk indicates P-value < 0.05).

	Type	**Mean rate of carbon deposited (mg C m^{-2}d^{-1})**	**Irish Sea mean carbon deposited (t C yr^{-1})**	**lm (deposited carbon ∼ fish carbon biomass)**	
				Slope	**Adjusted R^2**
Total fish-mediated carbon	-	3.89	82 460.6	2.93 x 10^{-03}	0.97∗
European sprat	P	1.15	24 334.1	9.45×10^{-04}	0.05
Other pelagic fish	P	0.90	19 042.3	2.07×10^{-03}	0.91*
Other benthopelagic fish	D	0.48	10 186.1	2.25×10^{-03}	0.99*
Adult whiting (age 2+)	D	0.25	5189.3	6.35×10^{-04}	0.13*
Atlantic herring	P	0.20	4231.6	7.38×10^{-04}	0.09*
Gurnards and dragonets	D	0.20	4220.2	2.83×10^{-03}	0.99*
Sandeels	D	0.13	2844.0	4.78×10^{-03}	0.85*
Flatfish	D	0.13	2831.6	4.86×10^{-04}	0.85*
Juvenile whiting (age 0–1)	D	0.13	2652.5	7.60×10^{-03}	0.98*
Other demersal fish	D	0.09	1841.5	6.70×10^{-04}	0.17*
Adult Atlantic cod (age 2+)	D	0.05	1087.3	3.49×10^{-03}	0.98*
Adult European plaice (age 2+)	D	0.05	970.6	-1.69×10^{-03}	0.78*
Adult haddock (age 2+)	D	0.03	679.0	1.27×10^{-03}	0.98*
Juvenile haddock (age 0–1)	D	0.03	542.3	5.16×10^{-03}	0.90*
Common sole	D	0.02	502.5	2.30×10^{-03}	0.85*
European hake		0.02	394.8	2.07×10^{-03}	0.33*
Juvenile European plaice (age 0–1)	D	0.02	320.6	5.63×10^{-03}	0.96*
Juvenile Atlantic cod (age 0–1)	D	0.01	286.6	5.62×10^{-03}	0.99*
Monkfish	D	0.007	151.9	3.21×10^{-04}	0.06
Anadromous fish	D	0.007	151.7	2.28×10^{-03}	0.97*

Type indicates our broad zone-based grouping (D—demersal, P—pelagic).

creased haddock biomass as a result of competitive release, but haddock are a minor contributor to the carbon sink. Additionally, the high fishing effort during the 1980s–1990 s affected the recovery of many fish groups, such as herring and cod (Bentley et al. 2020).

Although a strong relationship between biomass and carbon contribution was evident at the community level and across most fish groups, some exceptions occurred due to the complex interactions among biomass, feeding, and mortality represented in the model. In the case of adult European plaice, for example, both mortality (*M0*) and feeding rate (*Q/B*) decreased as biomass increased (Supplementary Material), leading to a negative relationship between biomass and carbon flux. Decreased feeding rate is a plausible consequence of increasing competition, while decreased natural mortality (*M0*) might reflect a higher predation mortality.

The fish community's relative estimated contribution to carbon deposition at the seafloor was relatively small compared to planktonic groups (c. 98 mg C m^{-2} d^{-1}). This is due to high phytoplankton and zooplankton biomass, which results in large detrital fluxes and thus dominates carbon at the seafloor. Our results compare with field research on the Celtic Seas using snow catchers, which estimated fast sinking POC flux of 96 mg C m^{-2} d^{-1} (Davis et al. 2019). Plankters are small organisms, and the small particles they release are exposed to more remineralization during sinking (Turner 2015). Although the Irish Sea is very shallow, our results suggest that the attenuation of carbon from phytoplankton and zooplankton groups reduces this carbon flux substantially, increasing the relative importance of the fish-mediated carbon at the seafloor. Global open-ocean models also found that fish faecal pellets become increasingly important relative to other particles with depth (Bianchi et al. 2021).

Ecosystem and multi-species models have inherent uncertainty linked to the number of parameters included (parametric uncertainty), the assumptions of individual modelling frameworks (structural uncertainty), and the environmental drivers used in models (climate uncertainty). The parameterization and performance of the Irish Sea model used in this study were previously reviewed by the ICES Working Group on Multispecies Assessment Methods (ICES 2019) as a precursor to the model being used in ICES advice. Nevertheless, modelled simulations from a single simulator (EwE in this case) are constrained by the assumptions underlying the mechanism of the model, leading to structural uncertainty in the modelled outputs. As capacity for ecosystem modelling in the Irish Seas increases, structural uncertainty might be addressed in the future using an ensemble approach, whereby multiple simulators with different underlying structures are to simulate the same scenarios to identify synergies in outcomes and develop a more robust understanding of uncertainty (e.g. Spence et al. 2024).

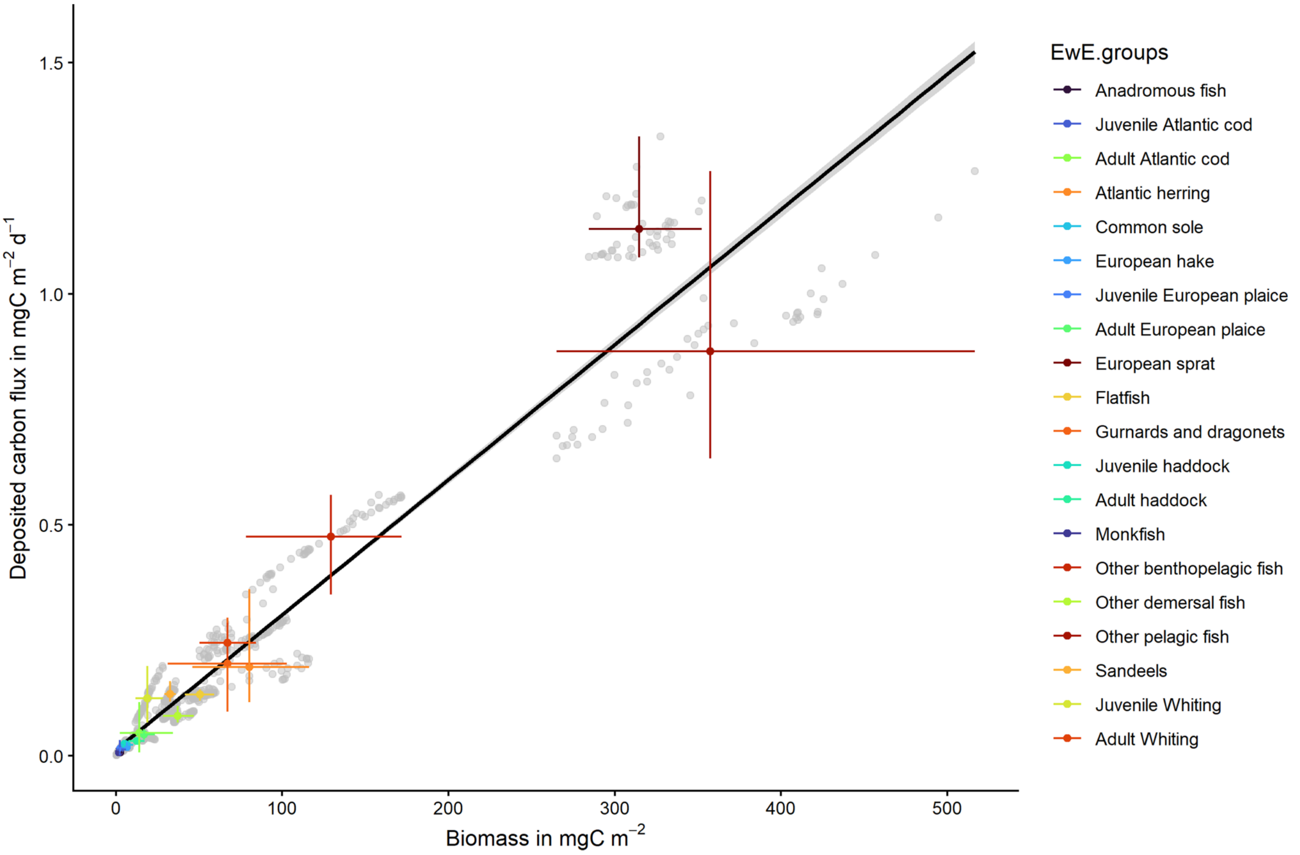

Figure 3. Relationship between deposited carbon (mg C m^{-2} d^{-1}) and carbon biomass per functional group. Grey points represent each annual value of the time series (1973–2016). The colour segments represent the difference between the maximum and minimum values of the time series, and the colour points represent the mean values. Linear model: fish-mediated deposited carbon $\sim$ fish carbon biomass, adjusted $R^2 = 0.97$ (P-value < 0.05).

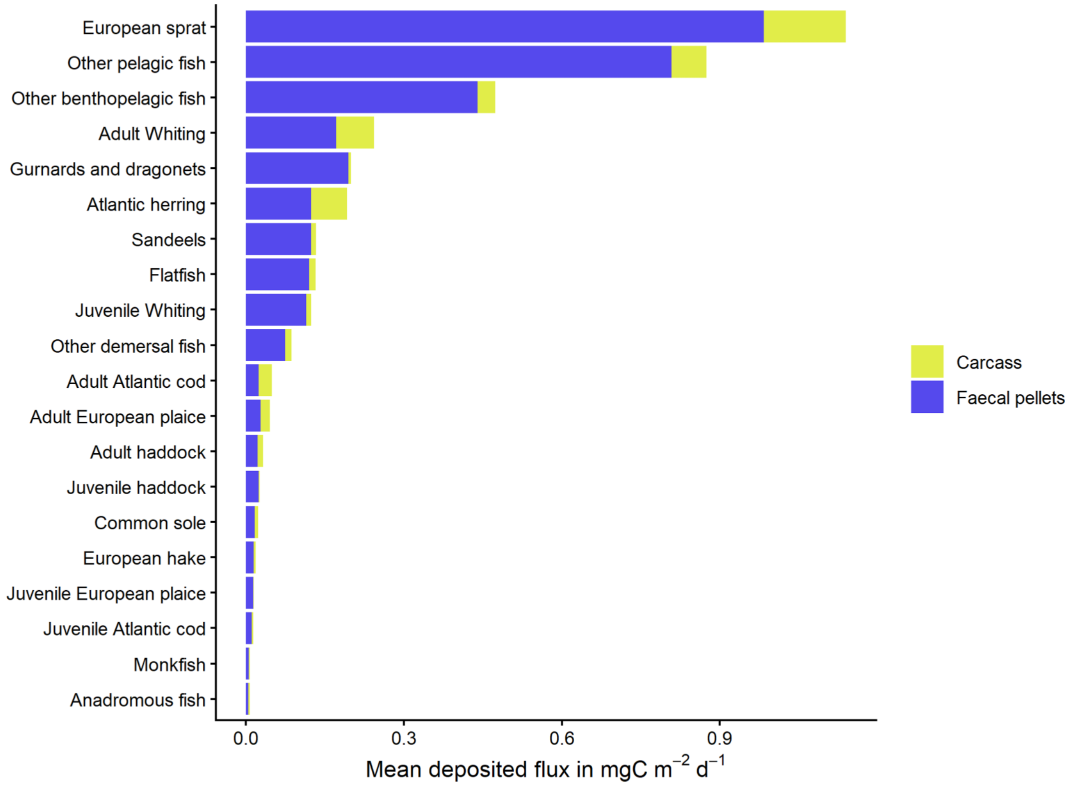

Figure 4. Carbon deposited on the seafloor by each fish functional group in the Irish Sea model.

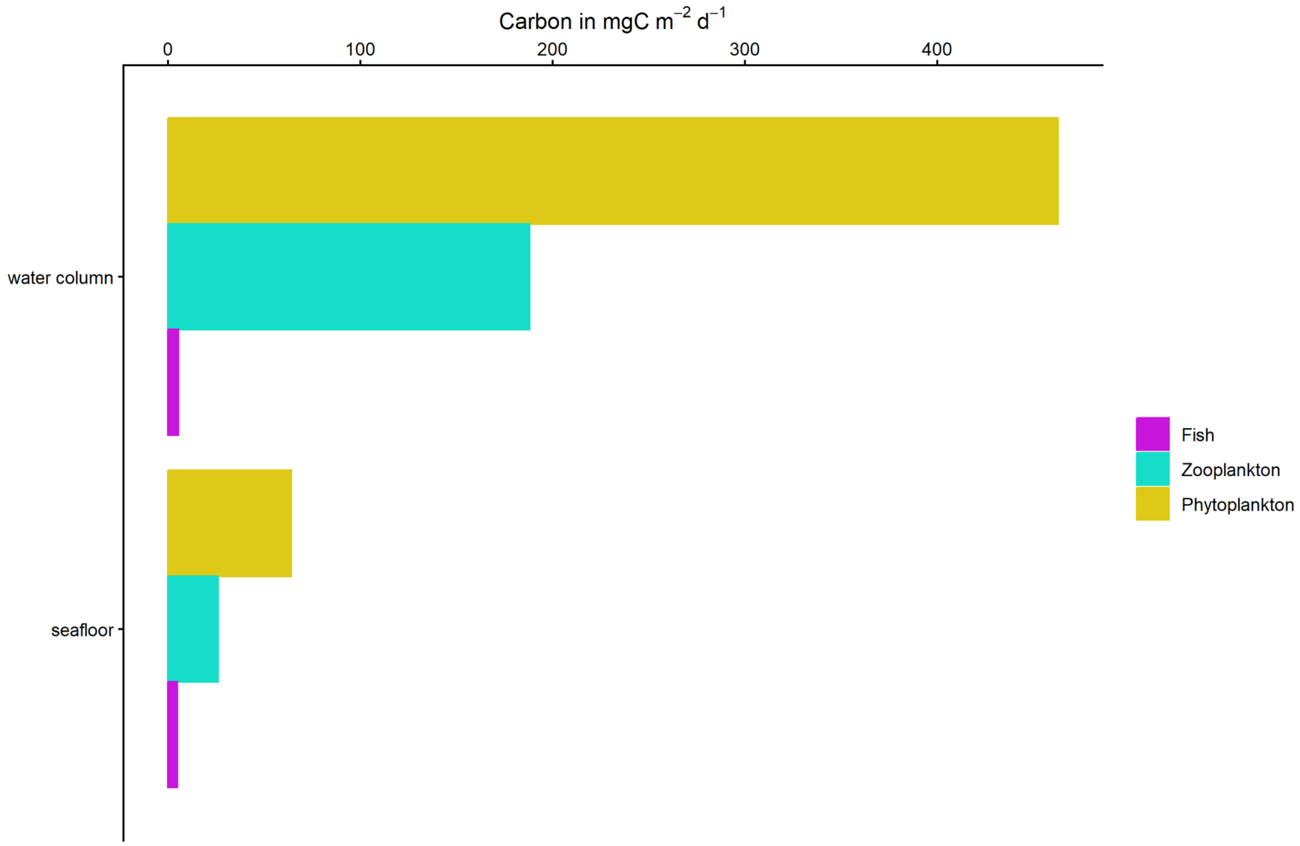

Figure 5. Comparison of fish-, zooplankton- and phytoplankton-mediated carbon flux in the water column (5 m) and at the seafloor (50 m).

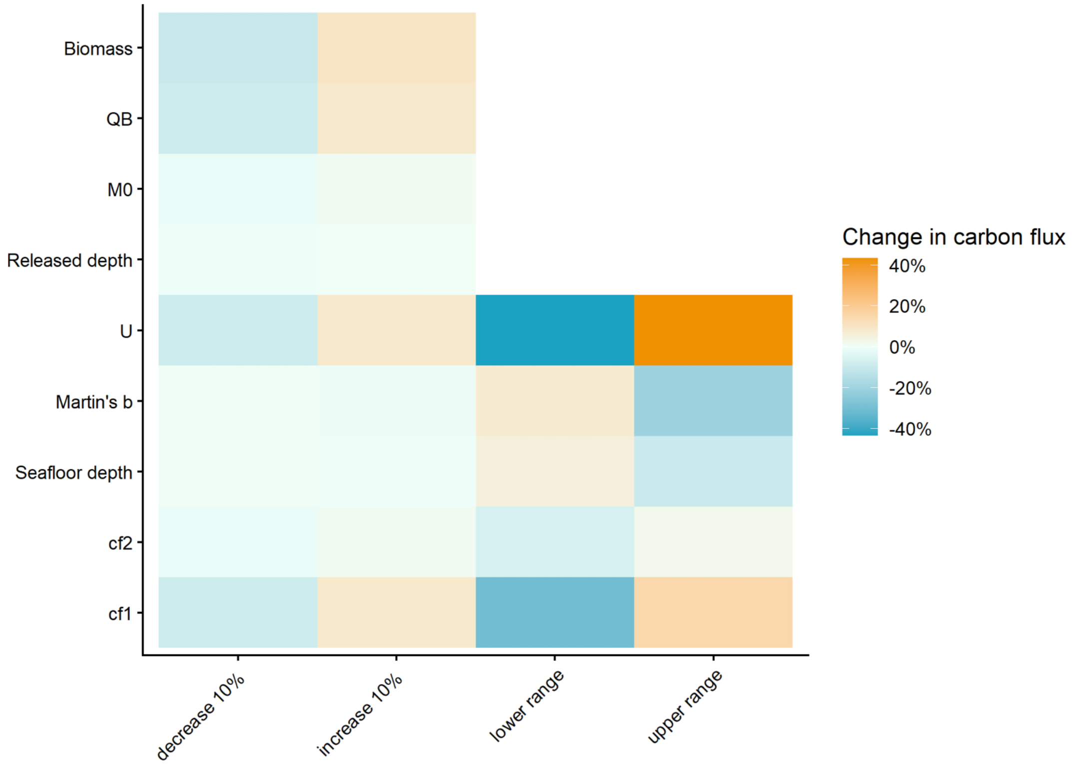

Figure 6. Sensitivity of mean total fish-mediated carbon deposited at the seafloor to a 10% increase and decrease (*Q/B* is consumption to biomass, *U* is unassimilated consumption, *M0* is other mortality). Change in total fish-mediated carbon flux by change in parameter within a plausible range (*U* is unassimilated consumption, cf1 is ($\overline{CF}$) the conversion factor for faecal pellets, and cf2 is (CF) the conversion factor for carcasses.

Assessing fish-mediated carbon sequestration requires further research. The framework to estimate carbon fluxes used in this study has simplified the system. Water dynamics are not taken into account, e.g. advection and tidal flows. Fish species are assumed to inhabit a limited vertical range dependent on their ecology (i.e. pelagic, demersal), yet they might use the entire water column in shallow shelf ecosystems, and have a uniform distribution across the modelled area. We have assumed that the carbon mass of the faecal pellet is a percentage of the total carbon in the biomass of diet items. In addition, our framework does not account for other metabolic and catabolic carbon released by fish (e.g. dissolved organic carbon and carbon dioxide) and thus could underestimate their contribution to carbon flux (Liu et al. 2022). Chemical characterization of carbon released by fish (e.g. organic and inorganic carbon content, lability, dissolution rate) would be key to understanding sequestration potential. Sequestration would also depend on benthic processes, including trophic interactions, as well as on physical processes such as bioturbation (Lessin et al. 2019). The carbon deposited on the seafloor can be recycled into benthic production and may re-enter the food web. Benthic processes are typically captured in biogeochemical models; therefore, coupling higher-trophic-level ecosystem models with biogeochemical models would be the next step to assess the contribution of fish to the biological carbon cycle.

The average rate of fish-mediated carbon deposited at the seafloor was relatively robust to changes in parameter values in this framework and most sensitive to changes in fish biomass. This reiterates the importance of accurate biomass estimates for fish species (Saba et al. 2021, McMonagle et al. 2024). Most commercially targeted fish species have good estimates of the biomass of the stock (e.g. cod, whiting, haddock), but non-target species sometimes lack good biomass estimates (e.g. Norway pout, gurnards, dragonets). Fish-mediated carbon flux estimates were also sensitive to changes in attenuation, assimilation estimates, and conversion factors to translate wet biomass into carbon units. Physiological parameters are another source of uncertainty; the uncertainties related to bioenergetics are nearly equal to those of biomass estimates (McMonagle et al. 2024, 2023). Empirical measurements or estimates of species-specific parameters, e.g. sinking speeds, chemical composition, and remineralization rates of faecal matter for fish species, as well as fish physiological parameters, would reduce uncertainty in future estimates (Saba et al. 2021).

Conclusions

In this study, we investigated fish-mediated carbon deposited on the seafloor using an ecosystem EwE model, coupled with attenuation calculations. Our model simulations suggest that the fish community mediates substantial carbon deposition to the seafloor in continental shelf systems. To our knowledge, this is the first time that fish-mediated carbon fluxes have been estimated for a continental shelf system and that an ecosystem model with high trophic-level representation has been used. Understanding the role of fish in the carbon cycle is crucial for assessing the impact of anthropogenic activities, such as fishing. We conclude that, to improve quantification of fish carbon fluxes, we need to characterize species biomass, assimilation rates, sinking speeds, remineralization rates, and particle composition in the future.

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Author Contributions

Paula Silvar-Viladomiu (Conceptualization [equal], Data curation [lead], Formal Analysis [lead], Methodology [equal], Visualization [lead], Writing – original draft [lead], Writing – review & editing [lead]), Emma L. Cavan (Conceptualization [equal], Methodology [supporting], Visualization [supporting], Writing – original draft [supporting], Writing – review & editing [supporting]), Angela H. Martin (Methodology [supporting], Writing – original draft [supporting], Writing – review & editing [supporting]), Jacob Bentley (Conceptualization [equal], Data curation [supporting], Formal Analysis [supporting], Methodology [supporting], Visualization [supporting], Writing – original draft [supporting], Writing – review & editing [supporting]), Simeon Hill (Conceptualization [supporting], Writing – review & editing [supporting]), David Reid (Conceptualisation [equal], Funding acquisition [lead], Writing – original draft [support]).

Supplementary Material

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflict of Interest

The authors have no conflict of interest to declare.

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Data Availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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