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Active Transport of Carbon to Demersal Fish Communities in Shelf-Slope-Abyssal Systems of the North Atlantic Ocean

Daniel Ottmann[1,2], **Ken H. Andersen**[1], **Yixin Zhao**[1], **Colleen M. Petrik**[3], **Charles A. Stock**[4], **Clive Trueman**[5], and **P. Daniël van Denderen**[1]

[1]Center for Ocean Life, National Institute of Aquatic Resources, Technical University of Denmark (DTU-Aqua), Kgs. Lyngby, Denmark, [2]Institute of Marine Sciences of Andalusia, Spanish Research Council, Puerto Real, Spain, [3]Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA, [4]Geophysical Fluid Dynamics Laboratory, NOAA, Princeton, NJ, USA, [5]University of Southampton, Southampton, UK

Key Points:

- Benthic-pelagic coupling provides on average 813 kg carbon km^{-2} yr^{-1} to demersal fishes of North Atlantic shelf-slope-abyssal systems
- Fish-mediated benthic-pelagic coupling can transport carbon to the seafloor in amounts equivalent to up to 20% of the detrital carbon flux
- Midwater fishes are critical in mediating carbon transport to demersal fishes, despite regional differences in the fish food webs

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

D. Ottmann,
daniel.ottmann.riera@gmail.com

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Author Contributions:

Conceptualization: P. Daniël van Denderen
Data curation: P. Daniël van Denderen
Formal analysis: Daniel Ottmann
Funding acquisition: Ken H. Andersen
Investigation: Daniel Ottmann, Ken H. Andersen, Yixin Zhao, Colleen M. Petrik, Charles A. Stock, P. Daniël van Denderen
Methodology: Daniel Ottmann, Ken H. Andersen, Yixin Zhao, Colleen M. Petrik, Charles A. Stock, P. Daniël van Denderen
Project administration: Ken H. Andersen

Abstract

The biological carbon pump sequesters carbon through passive fluxes of biologically derived carbon, and by active vertical movement of marine organisms. Trophic coupling between pelagic and benthic communities increases the efficiency of the biological carbon pump as less carbon is lost to remineralization. Such fish-mediated benthic-pelagic coupling, which can be described as the sum of carbon fluxes that is "passed on" when predators eat prey that occupy different vertical habitats in the water column, remains highly uncertain. Here, we applied a size- and trait-based food web model to estimate the amount of carbon that fish actively transport through benthic-pelagic coupling to the seafloor across the shelf-slope-abyssal continuum in different systems of the North Atlantic. The model estimates that benthic-pelagic coupling transports on average 813 kg C km^{-2} yr^{-1} to the demersal fish communities in North Atlantic shelf-slope-abyssal systems, which is equivalent to 5% of the modeled detritus flux reaching the sea floor. In some slopes, midwater fishes mediate up to 50% of the carbon transported downwards via benthic-pelagic fish coupling. We validated model-estimated biomasses of demersal fishes with biomass estimates of bottom trawl-surveys in the same area. Both modeling and survey approaches show that demersal fish biomass estimates are at the same order of magnitude and decrease with bottom depth following a similar trend. Our study shows that benthic-pelagic coupling is an important mechanism transporting carbon to demersal communities, supplying energy to sustain abundant seafloor fish fauna and fueling commercially valuable fisheries.

Plain Language Summary

Marine organisms move carbon from the atmosphere to the seafloor in different ways. Using a mathematical model, we simulated how carbon flows from small fish and zooplankton to big fish, and from fish that live near the sea surface to fish that live near the seafloor. We find that groundfishes in the North Atlantic up to around 2,000 m depth obtain an average of 813 kg C km^{-2} yr^{-1} from fishes dwelling in midwaters or near the surface. On average, this fish-mediated carbon flux is equivalent to approximately 5% of the carbon reaching the seafloor through sinking particles of organic matter from phytoplankton, microbes, or animals. In some areas, fishes dwelling in midwaters are a key stepping-stone in the carbon flowing to the seafloor. We compare the amount of groundfish that the model predicts with observed estimates from scientific bottom-trawl surveys off Western Ireland and the Mid-Atlantic Bight. The amount of fish in both cases is of the same order of magnitude and follows a similar trend with depth. We show that the vertical movement of carbon driven by fish as they move up and down in the water column is an important process fueling seafloor ecosystems and commercially valuable groundfishes.

1. Introduction

Marine organisms transport carbon from surface waters to the deep ocean through complex natural processes (Boyd, 2019). Combined, this set of processes is called the biological carbon pump, and it contributes to the sequestration of ~1,300 Pg yr^{-1} of atmospheric carbon in the ocean for hundreds or thousands of years (reviewed in Siegel et al., 2023). Most research on the biological carbon pump has focused on phyto- and zooplanktonic organisms (Archibald et al., 2019; Serra-Pompei et al., 2022; Siegel et al., 2023; Steinberg & Landry, 2017; Turner, 2015), and only recently has there been an effort to quantify the importance of upper trophic-level organisms like fishes (Davison et al., 2013; Mariani et al., 2020; McMonagle et al., 2024; Pinti et al., 2023; Saba et al., 2021), whales (Pearson et al., 2023; Roman & McCarthy, 2010) and cephalopods (Hoving et al., 2017; Ottmann et al., 2024).

Software: Yixin Zhao, P. Daniël van Denderen
Supervision: Ken H. Andersen
Validation: Daniel Ottmann
Visualization: Daniel Ottmann
Writing – original draft: Daniel Ottmann
Writing – review & editing: Ken H. Andersen, Yixin Zhao, Colleen M. Petrik, Charles A. Stock, P. Daniël van Denderen

The biological carbon pump fuels benthic production in the deep ocean, supporting near-seafloor (from now on seafloor) communities including fishes. Therefore, bottom dwelling (i.e., demersal) fish obtain organic carbon following two paths (Figure 1):

(i) *Passive flux*: carbon arrives on the seafloor through gravitational sinking of particulate organic carbon (detritus). It is then consumed by benthic organisms making it available as food for demersal fishes. Here, we focus on detritus generated by phyto- and zooplankton.
(ii) *Active flux*: carbon arrives to the seafloor as the result of benthic-pelagic coupling. We define *benthic-pelagic coupling* as the sum of carbon fluxes that is "passed on" as fish biomass through ingestion of prey by predators that occupy different vertical habitats in the water column (Trueman et al., 2014). Note that this definition of active flux differs from other studies (e.g., Saba et al., 2021) in that it ignores carbon injection processes in the water column (e.g., respiration, excretion). To estimate the net carbon flux to the seafloor, we assume that demersal fish respire and excrete the carbon near the seafloor while they rest and digest their food. Although this assumption has limitations, particularly if some demersal fishes rise from the sea floor to feed in the water column, it provides a first-order estimate of active flux that can be compared to the passive flux.

An often overlooked pathway of the biological carbon pump is the benthic-pelagic coupling through active transport of carbon to the seafloor. We hypothesize that active transport of carbon to the seafloor fuels an important portion of the demersal fish communities and that midwater fishes play a key role in mediating benthic-pelagic fish coupling in slope systems. The importance of midwater fishes in mediating benthic-pelagic coupling in slope systems has previously been explored (Trueman et al., 2014), but the extent to which various predators depend on this mid-trophic level and how benthic-pelagic fish coupling varies among regions that differ in environmental conditions remain unknown (reviewed in Boyd, 2019). Additionally, there is growing interest in commercially fishing midwater fishes, despite the limited understanding of their ecological role (Fjeld, 2023; Hidalgo & Browman, 2019; Martin et al., 2020). Demersal fishes in some continental slope areas between 200 and 1,000 m depth are also subject to high fishing intensity (Amoroso et al., 2018). All these factors highlight the importance of studying benthic-pelagic coupling processes in shelf and slope ecosystems and how active carbon flux relies on spatial variations in ocean productivity, seabed depth and fish food web structure.

Previous work (Mauchline & Gordon, 1991; Ricci et al., 2022; Trueman et al., 2014; Walters et al., 2025) has shown that the amount of carbon transported to the demersal community through benthic-pelagic coupling is heavily influenced by the system productivity and bottom depth, which determines the degree of vertical overlap between functional groups in the water column (i.e., epipelagic, midwater, demersals). Demersal fishes can feed directly on epipelagic organisms in shallow (<250 m) systems (Figure 1a; Walters et al., 2025), but they rely on midwater fishes in deeper (250–2,200 m) systems (Figure 1b). Benthic-pelagic coupling becomes decoupled in very deep systems (>2,200 m) where the vertical distance is too large for demersal fishes to feed on midwater organisms (Figure 1c; Trueman et al., 2014). These factors add complexity to this process, making it difficult to quantify active carbon flux through benthic-pelagic coupling. Although an increasing number of studies have attempted to quantify benthic-pelagic coupling of carbon (e.g., Kiljunen et al., 2020; Ricci et al., 2022; Trueman et al., 2014), high uncertainty remains around how important it is in providing carbon to demersal fish communities, and how it compares to the passive flux of carbon.

Van Denderen et al. (2021) resolved the basic transitions in the fish food web structure along the shelf-slope-abyssal transition of large marine systems by applying a process-based food web model. Here, we used an extension of this model to quantify fish-mediated benthic-pelagic trophic coupling of carbon across shelf-slope-abyssal systems of the North Atlantic. We then quantified the amount of carbon that this mechanism transports to the seafloor and compared it to the passive flux of detritus.

2. Materials and Methods

2.1. Approach

We used the FishErIes Size and functional TYpe model (FEISTY; Petrik et al., 2019; van Denderen et al., 2021; Zhao et al., 2025) to simulate food webs in areas distributed over the North Atlantic shelf-slope-abyssal systems at a ¼° grid-cell resolution (Figure 2). We arbitrarily delimited these areas to include the continental slopes between 10°N and 70°N, as well as their adjacent shelf and abyssal plain areas. We further delimited five case-study areas

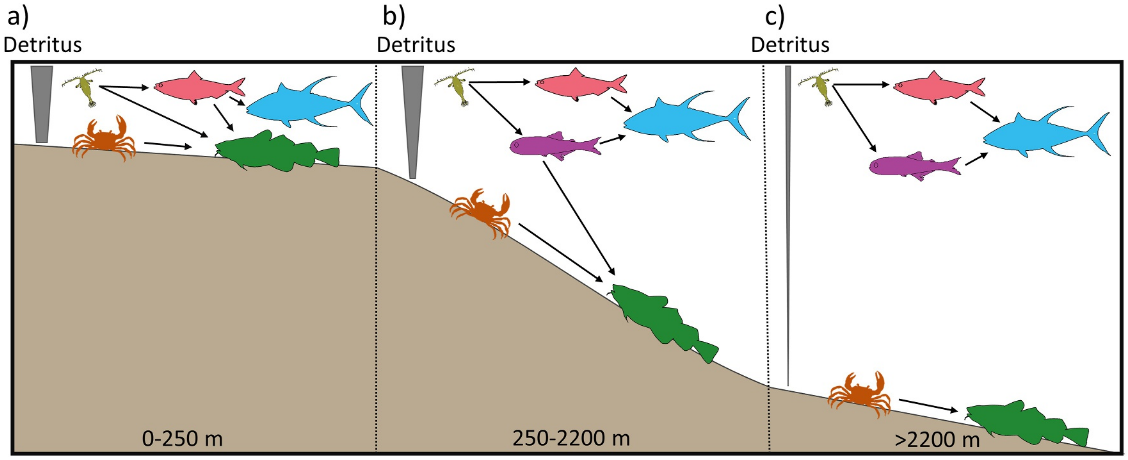

Figure 1. Simplified schematic of (a) shelf, (b) slope, and (c) abyssal systems with respective fish food webs. Arrows indicate the flux of carbon between functional groups through predation (active flux). The copepod and the crab represent zooplankton and benthic production available for fish communities, respectively. Fish pictograms represent functional groups of small and large pelagics (pink and blue, respectively), midwater fishes (purple), and demersal fishes (green). Simulated detritus flux (gray) decreases with depth as it sinks (passive flux) and serves as food for benthic organisms.

exemplifying different secondary productivities and food web structures (Figure 2). In each grid-cell, FEISTY simulated the biomass of each functional group (resolved at a size-class level) and the carbon fluxes among different groups. Finally, we validated the model estimates of demersal fish biomass with biomass estimates of bottom-trawl surveys and evaluated how sensitive model estimated biomass and active carbon flux are to key model parameters.

2.2. Food Web Model Approach

FEISTY is a mechanistic model that simulates fish ecosystem structure across trophic levels by organizing fish communities into functional types based on traits rather than specific species. This approach allows FEISTY to

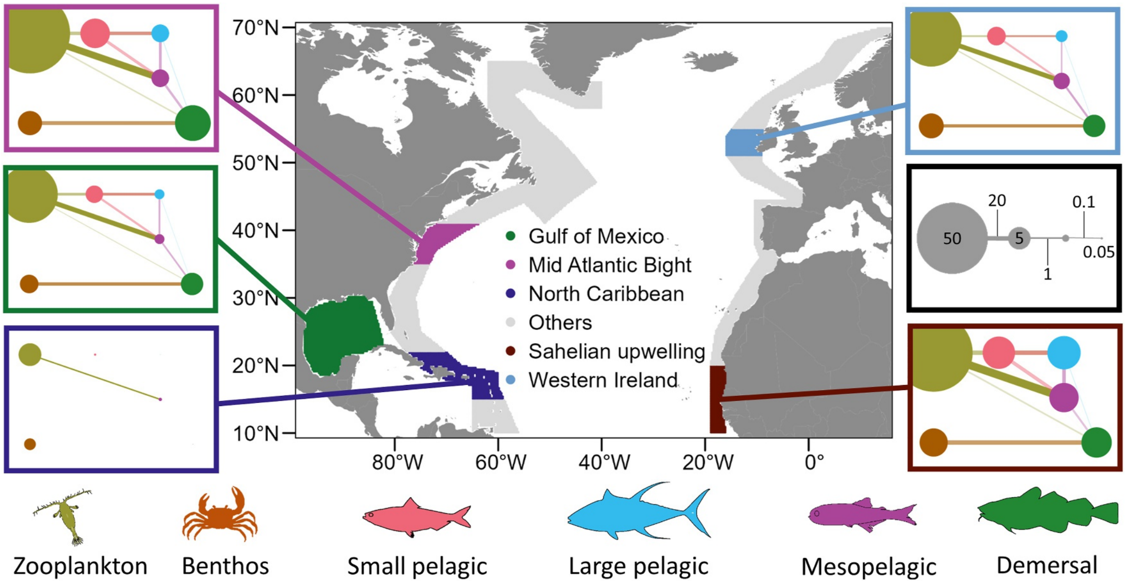

Figure 2. Map with shaded areas denoting the shelf-slope-abyssal systems of the North Atlantic Ocean with colored areas indicating each case study. In each grid cell (1/4° resolution), we resolved carbon fluxes of the benthic-pelagic coupling in the FEISTY food web model forced by the MOM6-COBALT ocean-biogeochemistry model (Stock et al., 2020). Networks represent mean biomass of functional groups (circles; g ww [wet weight] m^{-2}) and biomass fluxes (lines; g ww m^{-2} yr^{-1}) through the food web of each case study (see Results section). The size of the circles and lines (color-coded as for pictograms) in the black panel in the right reflect the scaling of biomass (g ww m^{-2}) and flux (g ww m^{-2} yr^{-1}). In the oligotrophic north Caribbean system, some functional groups and fluxes are too small to be seen in the network plot.

make generalizable predictions by simplifying complex species-specific interactions. The model uses ordinary differential equations and mass conservation to represent predator-prey interactions between fishes, with larger fishes feeding on smaller fishes, zooplankton or benthos that share the same water-column habitat. Fish biomass emerges from these trophic interactions and is governed by an underlying energy budget. A full description of the model can be found in Supporting Information S1.

The functional types which are resolved in FEISTY are: small and large pelagic fishes, demersal fishes, and midwater fishes, and as resources the pelagic zooplankton and benthic biomass (see Figures 1 and 2). The model computes two functional groups of midwater fishes: mesopelagic fishes and midwater predators (which differ in the asymptotic size they achieve). Because the biomass of midwater predators is very small (on average 7% of both groups combined) and they occupy a similar vertical niche, we pooled their biomasses together. Individual fish dynamics, defined by body size and temperature, scale to population-level dynamics of each functional group, with the energy budget driving growth, reproduction, and biomass fluxes. Unlike many fish food web models that rely on species-specific parameters, such as stock-recruitment relationships, FEISTY represents energy invested directly in egg production of fish functional types, as in physiologically structured population models (de Roos & Persson, 2013). The modeled change in biomass over time includes the biomass flux between size classes, accounting for growth, reproduction, and mortality:

$$\frac{dB_i}{dt} = J_i - J_{i+1} + \left(\nu_i - \rho_i - \mu_i\right) \cdot B_i \tag{1}$$

where J_i and J_{i+1} are the fluxes of biomass in the size class i [g m^{-2} time^{-1}] and out to the next size class, B_i is the biomass [g m^{-2}] in the ith size class, ρ_i is the biomass-specific reproduction rate [time^{-1}], and μ_i is the biomass-specific mortality rate [time^{-1}]. The biomass-specific rate of energy available from predation, ν_i [time^{-1}], accounts for assimilation efficiency and basal metabolic losses (Equation 2). The terms $B_i\left(\nu_i - \rho_i - \mu_i\right)$ reflect the change in biomass that results from feeding, reproducing and natural mortality (μ_i) within a size class (see Supporting Information S1 for details on model design and parametrization). We assume that there is no fishing mortality, so simulations represent food webs under natural conditions.

Biomass-specific available energy rate is calculated as

$$\nu_i = \epsilon_\alpha \cdot I_i - M_i, \tag{2}$$

where ϵ_α is the food assimilation efficiency [unitless], I_i is the mass-specific consumption rate [time^{-1}] and M_i is the biomass-specific basal metabolic costs [time^{-1}]:

$$M_i = \exp\left(k_M \cdot (T - T_0)\right) \cdot a_m \cdot w_i^{b_m} \tag{3}$$

Here, k_M [°C^{-1}] governs temperature sensitivity, a_m is the standard metabolic coefficient [g$^{\mathrm{bm}-1}$ time^{-1}], m_i is the mass of size class i [g], and b_m [unitless] dictates size-dependence.

Mass-specific consumption is calculated as

$$I_i = \sum_{j \in J} \frac{C_i \cdot E_{i,j}}{C_i + \sum_j^J E_{i,j}}, \tag{4}$$

where j is the prey in diet J, $E_{i,j}$ is the predator-prey encounter rate [time^{-1}] and C_i is the maximum consumption rate [time^{-1}]:

$$C_i = \exp\left(k \cdot (T - T_0)\right) \cdot a_C \cdot m_i^{b_C} \tag{5}$$

Here, k governs temperature sensitivity [°C^{-1}], a_C is the maximum consumption intercept [g^{bc-1} time^{-1}] and b_C is an allometric scaling constant determining body-size dependence [unitless].

Besides differences in body size, trophic interactions are determined by the vertical overlap between predators and prey, which results from the vertical preference of each group, including their implicit vertical migration pattern. We used the FEISTY-Vertical2 setup that automates the interaction between the functional types based on their vertical overlap (van Denderen et al., 2021; Zhao et al., 2025). The vertical position of each functional group is conditioned by the euphotic zone, the seafloor depth and the development stage of each fish. It is modeled following a normal distribution in a discretized water column ranging from the sea surface to the seafloor at a 1-m resolution. Demersal fish feed on benthic organisms as well as on midwater and pelagic organisms, depending on the bottom depth (Figure 1). Zooplankton and pelagic fish concentrate near the surface, benthos at the bottom, and demersal fish shift habitats through ontogeny—larvae feed near the surface, older juveniles at the bottom, and adults across both layers. In slope (250–2,000 m) and open ocean (>2,000 m) regions, part of the zooplankton community performs diel vertical migrations, affecting prey availability for midwater and epipelagic fishes. Midwater fishes begin life near the surface but move deeper as they grow, following the migrating zooplankton. The temperature-dependence of physiological rates uses the mean temperature in the different vertical habitats of each functional type. FEISTY does not currently resolve horizontal movement of fishes and it assumes that reproduction is continuous if energy is available.

2.3. Input Variables

We forced FEISTY with temperature, flux of detritus to the seafloor, and biomass and productivity of medium and large zooplankton. These variables were generated by the Carbon, Ocean Biogeochemistry and Lower Trophics version 2 (COBALTv2) ecosystem model developed by the Geophysical Fluid Dynamics Laboratory (Stock et al., 2020) that was embedded in the MOM6 ocean model (Adcroft et al., 2019). COBALT represents planktonic food web dynamics (including detritus production) by resolving bacteria, diazotrophs, small and large phytoplankton, and three zooplankton groups that feed on phytoplankton, bacteria, and each other (Stock et al., 2020). The small zooplankton group corresponds to microzooplankton (<0.2 mm). The medium zooplankton are parameterized as small- to medium-sized copepods (0.2–2.0 mm), while the large zooplankton represent large copepods and krill (2.0–20 mm). For the medium and large zooplankton, FEISTY uses biomass and the productivity lost to higher predators, both integrated over the top 100 m. Zooplankton productivity, which in COBALT represents the loss of energy to higher trophic level predators, is simulated with a density dependent closure term (Stock et al., 2020). Medium and large zooplankton serve as prey for epipelagic and mesopelagic fishes and the larvae of demersal fishes. The seafloor detritus flux is converted into benthic invertebrate biomass using a coefficient for benthic trophic transfer efficiency (β) (Petrik et al., 2019), and the resulting benthic invertebrate biomass serves as prey for demersal fishes. β reflects both the respiration costs of the benthic invertebrates and the fraction of the detrital flux that is, buried or remineralized directly by bacteria. The ocean-only MOM6-COBALT hindcast simulation included boundary conditions from the Japanese global atmospheric reanalysis project (JRA-55; Tsujino et al., 2018) and dynamic river freshwater and nitrogen inputs observed over the historical period (Liu et al., 2021). We averaged monthly COBALT outputs from 1990 to 1995 to annual means, and then averaged the annual means to a final mean. We ran FEISTY to steady state conditions using this final mean. The 1990–1995 timeframe was chosen to align with two previous studies (Petrik et al., 2019; van Denderen et al., 2021).

2.4. Model Run and Carbon Calculation

We ran FEISTY for 200 annual time steps in each ¼ degree grid cell, the native horizontal resolution of the MOM6-COBALT model, across the North Atlantic shelf-slope-abyssal systems (Figure 2) and used average outputs of the last 80 time steps in steady state. For each run, FEISTY produced outputs that include biomass of each functional group [g ww (wet weight) m^{-2}], and the mass-specific consumption rate among each functional group [year^{-1}] as calculated in Equation 4. By multiplying these two terms, we computed the flux [g ww m^{-2} yr^{-1}] flowing from each functional group to demersal fishes (including that of other demersal fishes). To evaluate the overall changes in dominance of fish groups with bottom depth, we estimated the mean biomass of each functional group down to 2,500 m.

Regional differences in the food web structure can alter the main pathways of carbon flowing from different functional groups to the demersal community. To evaluate these differences, we quantified how relative carbon fluxes from each functional group vary with bottom depth in each case study. For this exercise, we pooled all fluxes of epipelagic functional groups together (zooplankton, and small and large pelagic fishes). Finally, for each grid cell, we used the COBALT detritus flux to the seafloor as a benchmark for assessing how the magnitude of active flux relative to the passive sinking of particulate organic carbon (100 × active flux/passive flux) varies over space.

In the Results section, we show results of both wet weight and dry carbon weight, applying a ratio of 9:1 wet weight:dry carbon (Pauly & Christensen, 1995). We used the model output of each grid cell to calculate area-weighted averages of biomass and carbon flux. The results only include estimates of the downward flux of carbon mediated by fish, as the upward flux—that is, pelagic and mid-water predators feeding on demersal fish—is negligible in comparison, and the model does not resolve marine mammals or other non-fish predators.

2.5. Model Validation

The FEISTY model has been previously validated by comparing its outputs to peak historical global fisheries catches (Petrik et al., 2019), historical time series of fish catches (van Denderen et al., 2023), and several ecosystem food web structures as represented in published EcoPath models (van Denderen et al., 2021). These comparisons indicate that FEISTY's global results align with both catch and food-web data. So far, FEISTY's fish biomass estimates have not been validated as this is more challenging.

Fisheries-independent survey data have become increasingly available and cover parts of the Atlantic region included in our study (Maureaud, 2024). While these surveys are valuable, they sample fish communities already affected by fishing, which can significantly distort biomass estimates. Furthermore, comparisons with FEISTY require standardization for sampling area (Maureaud, 2024) and corrections for gear catchability (van Denderen et al., 2023), both of which introduce uncertainty. As a result, direct comparisons between model-simulated and survey-based demersal fish biomass estimates are imprecise and make it difficult to determine whether discrepancies reflect limitations in the survey data or the model outputs. Further, commercial trawling depths rarely exceed 800 m in the North Atlantic region, therefore covering only a fraction of the depth range evaluated here. Consequently, the challenge of fish biomass validation in this study is compounded by the limited availability of systematic scientific demersal trawl surveys in continental slope regions, the primary focus of our study.

Survey data corrected for sampling area and gear catchability were available for three of our case study regions: the Gulf of Mexico, Western Ireland, and the Mid-Atlantic Bight (van Denderen et al., 2023). In the Gulf of Mexico, survey sampling did not extend beyond 220 m depth, limiting its relevance for our study, which focuses on deeper continental shelf and slope regions. In the Mid-Atlantic Bight, available data spanned depths from 0 to 400 m, while the Western Ireland surveys covered a broader depth range of 0–650 m. As such, the Western Ireland data, consisting of 1,639 survey hauls sampled between 1990 and 2009, were the most relevant for our analysis. Additionally, estimates of carbon flux to the seafloor via benthic–pelagic coupling in this region can be compared to those from a previous study based on stable isotope data (Trueman et al., 2014), providing a second independent line of validation. While more restricted in depth, we also compared FEISTY's demersal fish biomass estimates and survey data for the Mid-Atlantic Bight, where data consisted of 19,239 survey hauls. All species classified as demersal fish in the trawl survey data are given in Table S1 of the Supporting Information S1.

2.6. Sensitivity Analysis

Sensitivity analyses can help identify which parameters would most benefit from further empirical measurement to reduce uncertainty in biomass and carbon flux estimates of the model. Petrik et al. (2019) found that the simulated biomass of demersal fishes was most sensitive to the trophic transfer efficiency from detritus flux to benthic invertebrates (β), as well as the assimilation efficiency (ϵ_α), standard metabolism coefficient (a_M), and mass scaling of the maximum consumption rate (b_C). To evaluate the sensitivity of active carbon flux to these parameters, we ran the model with a ±10% variation to each of them individually and recalculated demersal fish biomass and active carbon flux of the Western Ireland case study at 500–1,800 m bottom depth. We chose this depth range and case study to make it comparable to Trueman et al. (2014).

3. Results

3.1. Survey Estimates of Demersal Fish Biomass Off Western Ireland

Modeled and observed biomass estimates of demersal fishes across the Western Ireland system shallower than 700 m are similar in magnitude and decline with bottom depth following a similar pattern (Figure 3b). However,

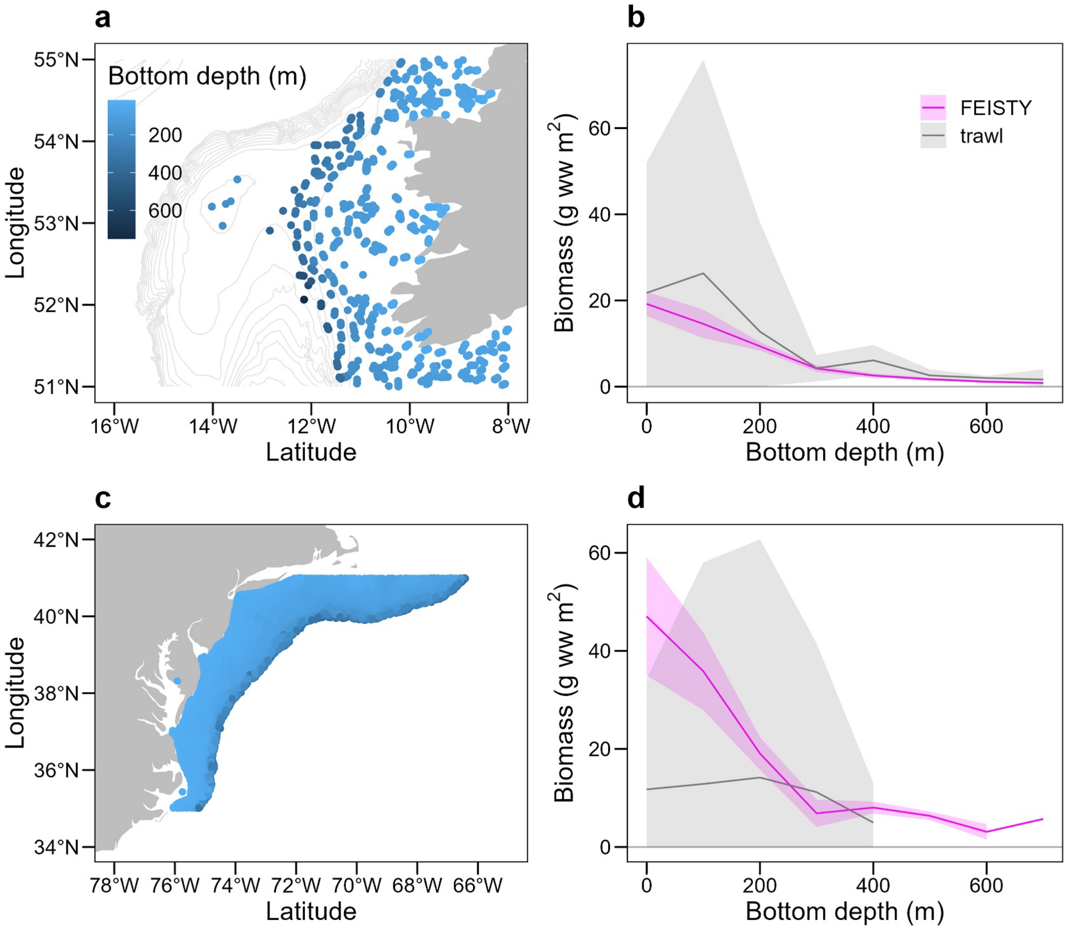

Figure 3. Comparison between modeled and survey estimates of demersal fish biomass at every 100 m bottom depth. Location of bottom trawls sampled off Western Ireland (a) and the Mid-Atlantic- Bight (c). Depth distribution of the mean biomass of demersal fish (g ww m^{-2}) from FEISTY (magenta) and from survey data (black) with their respective standard deviations (shading) sampled off Western Ireland (b) and the Mid-Atlantic- Bight (d).

the mean modeled biomass is consistently lower than the mean observed biomass at all depths. At depths where the bottom is <50 m deep, mean modeled and observed estimates are 19.2 and 23.9 g ww m^{-2}, respectively, and modeled biomasses are within the standard deviation of the observations at all depths. The greater standard deviation around the mean of observed estimates indicates that field biomasses are more variable per depth strata than simulated ones. This was expected because observations include sampling and data processing uncertainty, interannual variability and fish migratory behavior, along with other sources of stochasticity. In contrast, the model simulations use average environmental conditions from 1990 to 1995 and simulations do not resolve horizontal movement of fishes.

In the Mid-Atlantic Bight (Figure 3d), the comparison between simulated and surveyed biomass estimates shows that FEISTY estimates much higher demersal biomass in shallow waters (0–100 m), while model and survey estimates are closely aligned at greater depths (200–400 m). The standard deviation of observations is quite large at depths shallower than 300 m, with FEISTY biomass estimates falling within the observed standard deviation for depths >0 m (0–50 m interval).

3.2. Model Sensitivity to Parameter Variation

The sensitivity analysis indicates that changes in metabolic parameters have a stronger effect on demersal fish biomass and active carbon flux than changes in transfer efficiency from detrital flux to benthic production in the Western Ireland region (Table 1). A 10% increase in the transfer efficiency from detrital flux to benthic production (β), yielded 13.6% and 11.1% increases in the biomass and active carbon flux, respectively. Metabolic parameters

Table 1
Sensitivity of Model Predictions to a 10% Variation of Sensitive Parameters Identified in Petrik et al. (2019)

	Biomass		Active C flux	
Parameter modification	x1.1	x0.9	x1.1	x0.9
Transfer efficiency from detritus to benthic production (β)	13.6	−13.5	11.1	−11.5
Assimilation efficiency (ϵ_α)	103.1	−71.9	87.3	−69.3
Standard Metabolism coefficient (a_m)	−55.2	68.0	−51.8	54.7
Weight-dependence of maximum consumption rate (b_C)	28.6	−35.7	28.7	−35.1

Note. The table shows % change of estimated biomass of demersal fishes (g ww m^{-2}) and active carbon flux (kg C km^{-2} $year^{-1}$) at 500–1,800 m bottom depth of the slope off Western Ireland. Red and blue colors indicate an increase and decrease in biomass and active C flux, respectively, with color intensity proportional to the amount of change.

have a stronger and asymmetric effect, meaning that modifying the parameter 10% in one direction has a stronger effect on biomass and active carbon flux than modifying it in the opposite direction. Fish assimilation efficiency (ϵ_α) is the most influential parameter, with an increase in demersal fish biomass by 103% and active carbon flux by 87% in response to a 10% increase in ϵ_α. Modifying the weight dependence of the maximum consumption rate (b_C) by 10% has almost the same effect on demersal fish biomass as in active carbon flux. The negative effect of the standard metabolism coefficient (a_m) means that biomass and carbon flux decrease with higher metabolism, as the fishes need to spend more carbon to sustain basic metabolic processes, and therefore have less carbon available to store as biomass.

3.3. North Atlantic Fish Biomass and Distributions

Different food web structures emerged from the model in each case study area (network panels in Figure 2). As expected, the biomass of secondary producers (zooplankton and benthos) is greater in the most productive systems (Sahelian Upwelling and Mid Atlantic Bight) than in the less productive ones (North Caribbean), and this relationship propagates through the fish food web. The Mid Atlantic Bight and the Sahelian Upwelling system were the two most productive case-study systems, but the shelf area where demersal fishes have access to both epipelagic and benthic resources is greater in the Mid Atlantic Bight than in the Sahelian Upwelling system. Thus, simulated demersal fishes are more abundant in the Mid Atlantic Bight than in the Sahelian Upwelling system, whereas pelagic fish groups are more abundant in the Sahelian Upwelling system than in the Mid Atlantic Bight (Figure 2). In the oligotrophic North Caribbean system, the fish food web is heavily depressed (making the circles representing biomass of large pelagic and demersal fish groups in Figure 2 difficult to see). Likewise, most biomass fluxes among fish groups are relatively small, and only that from zooplankton to mesopelagic fishes is apparent in Figure 2. The food web structure of the Gulf of Mexico and Western Ireland shelf-slope-abyssal systems are largely similar, yet spatial heterogeneity and river inputs of the Gulf of Mexico result in greater variability (wider standard deviations in Figure 5c below).

The model estimates that the total fish biomass of North Atlantic shelf-slope-abyssal systems is highest in shallow waters and decreases with bottom depth until stabilizing at about 500 m (Figure 4). The biomass of each fish functional group follows different patterns along the shelf-slope-abyssal continuum: demersal fishes decrease sharply with depth from 25.0 to 1×10^{-6} g ww m^{-2}. Small pelagics decrease from 11.0 to 2.5 g ww m^{-2} in the first 700 m and remain relatively stable afterward. The opposite trend is observed for large pelagics, which increase from 0.6 to 2.3 g ww m^{-2} in the first 400 m and remain relatively stable afterward. Midwater fishes (mesopelagics and midwater predators combined) appear once seafloor depths reach 250 m and their biomass remains between 3.0 and 5.0 g ww m^{-2}.

The relative biomass of each functional group depends on their location across the shelf-slope-abyssal system (Figure S1 in Supporting Information S1): while demersal fishes dominate the shelves, midwater fishes dominate the slopes and continental rises. The proportion of epipelagic fish biomass is relatively even across the shelf-slope-abyssal system. The model estimates that midwater fishes are particularly abundant relative to the other fish types in oligotrophic waters of the southeast Caribbean and Gulf of Mexico. In the most oligotrophic waters of the north Caribbean, demersal fishes dominate the shelf-slope-abyssal system, but note that the biomass of each functional type is very low.

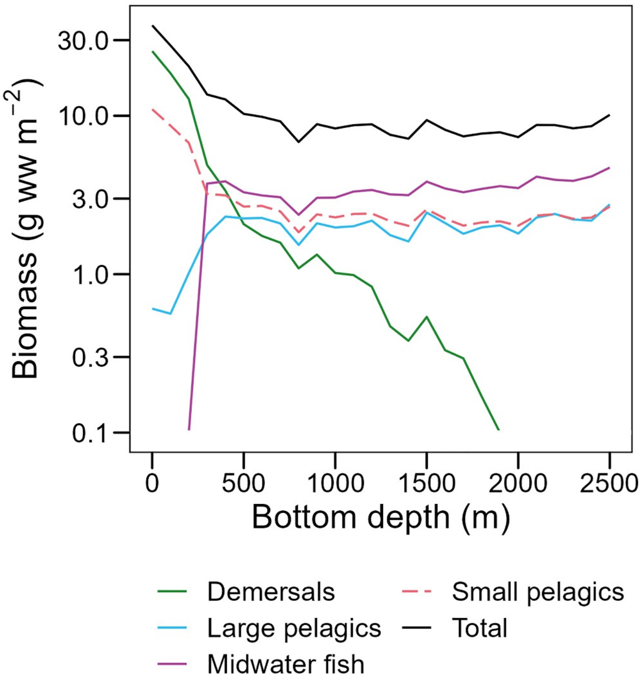

Figure 4. Modeled fish functional type biomass with respect to seafloor depth in shelf-slope-abyssal systems of the North Atlantic Ocean. Lines are mean values (g ww m^{-2} binned at 100-m intervals) truncated at 0.1 g ww m^{-2} for better visualization.

3.4. Benthic-Pelagic Coupling

Relative carbon fluxes from each functional group to demersal fishes are heavily influenced by bottom depth (Figure 5; Figure S2 in Supporting Information S1). Benthic organisms are the overall most important source of carbon for demersal fish throughout the entire shelf-slope-abyssal system, though their dominance varies with depth and among systems. Midwater fishes are almost as important as benthos on the slopes, particularly in eastern Atlantic systems (Figure 5a). The proportion of active carbon flow to demersal fishes from epipelagic and other demersal fishes is greatest in shelf systems, and it decreases with depth to less than 5% at depths below 300 and 1,300 m, respectively (Figure 5a). The proportion of flux from midwater to demersal fishes drops rapidly at depths ~2,000 m because the midwater and demersal fishes no longer overlap in their vertical habitats (as parameterized in the model). Past 2,000 m depth, demersal fishes rely mainly on benthic organisms that feed on detritus.

Different patterns of active carbon flux to demersal fishes emerged among each case study region depending on the characteristics of each system (Figures 5b–5f). In general, benthos and midwater fishes are the most important sources of carbon to the demersal community, and their relative contributions often mirror each other. With the exception of the North Caribbean, the benthos contribution in waters ≤100 m deep is 37%–50% and it steadily increases to 56%–80% at 1,500 m depth before increasing to almost 100% as bottom depths approach 2,100 m. Epipelagic functional groups contribute 25%–38% of carbon flux to demersal fishes in shelf areas ≤250 m depth, and their contributions drop rapidly with increasing depths to almost zero at deeper depths. Similarly, demersal fishes in most systems provided about 25% of carbon to other demersal fishes in regions ≤100 m deep, and this proportion drops to almost zero as the bottom depth becomes deeper. This decline is slower in the most productive systems, where demersal fishes still contribute more than 10% of the flux to other demersal fishes at 1,000 m depth (Figures 5d and 5f). Midwater fishes are most important in transporting carbon to demersal fishes between 250 and 2,000 m depths, particularly in the Western Ireland slope, where they contribute up to 47% at 1,000 m depth.

The North Caribbean (Figure 5c) is the least productive system evaluated in this study and sustains only a small community of fish. The low biomass of epipelagic and midwater fishes results in weak benthic-pelagic coupling with demersal fishes. Thus, demersal fishes rely largely on the meager benthic community.

3.5. Active Carbon Flux to the Seafloor

We estimate that benthic-pelagic coupling transports on average 921 and 771 kg C km^{-2} year^{-1} to the seafloor in the eastern and western shelf-slope-abyssal systems of the North Atlantic Ocean, respectively (Table 2). This corresponds to 4.6% and 5.3%, respectively, of the carbon that is, passively transported to the seafloor by the simulated gravitational detritus flux. Active transport rates averaged over each case study range between 1 mg C km^{-2} year^{-1} in the North Caribbean slope and 2.2 t (metric ton) C km^{-2} year^{-1} in the Sahelian upwelling system. Focusing on the slope area alone (500–1,800 m), fish communities are responsible for an average 180 and 46 kg C km^{-2} year^{-1} in the eastern and western slopes, respectively (Table 2). The proportion of active carbon flux is greatest in shallow, productive shelf systems like the northern Mid-Atlantic BIght or in systems with a very high zooplankton productivity like the Sahelian Upwelling system (Figure 6, Table 2).

4. Discussion

By coupling a food web model to an ocean-biogeochemistry model, we have resolved fish communities across the shelf-slope-abyssal continuum of North Atlantic ecosystems and quantified how much carbon fish functional groups transport to the seafloor as they feed and migrate in the water column (benthic-pelagic coupling).

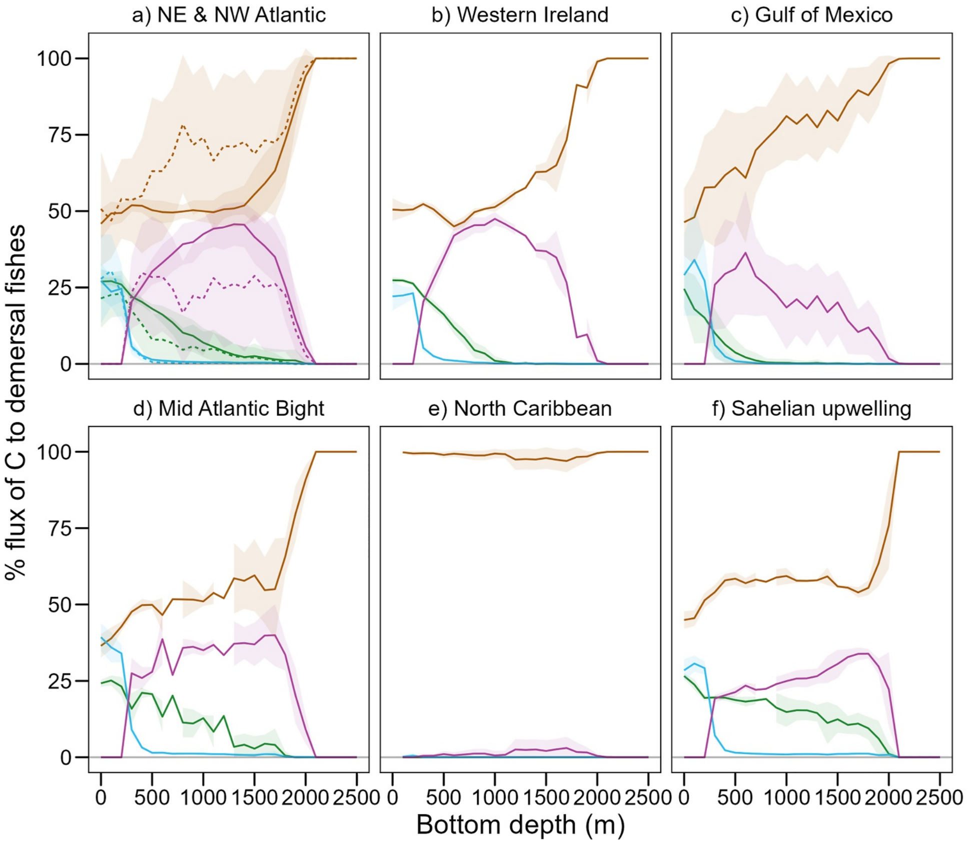

Figure 5. Proportion of active carbon flux towards demersal fishes in shelf-slope-abyssal systems of the North Atlantic Ocean (including demersal fishes feeding on other demersal fishes [green line] and on benthic organisms [brown line]). Solid and dotted lines represent mean relative flux values (binned at 100-m intervals) from the eastern and western shelf-slope-abyssal systems, respectively. Shadings are standard deviations.

4.1. Demersal Fish Biomass

Comparing biomass estimates of both methodologies in the Mid-Atlantic Bight is constrained by depth limitation of the survey data at 400 m. Here, field-observed biomass of demersal fishes is lower than estimated by the simulation in the 0 (0–50) and 100 (50–150) m depth intervals, and biomasses of both estimates converge in the 200 (150–250), 300 (250–350) and 400 (350–450) m depth intervals, suggesting that the biomass estimates used to quantify carbon fluxes in these deeper regions are plausible. The difference in demersal fish biomass in the shallower part of the continental shelf may reflect the collapse of the cod population (Hutchings & Baum, 2005).

Our predictions of demersal fish biomass off Western Ireland match relatively well with biomass estimates obtained from bottom trawl surveys in the same area. In both cases, biomass decreases with depth following a similar pattern, but the drop of modeled biomass is stronger than that of bottom trawls—modeled mean biomass is about half that of observed mean biomass at depths greater than 300 m. A stronger drop in modeled biomass compared to observed biomass was already documented in a previous study (van Denderen et al., 2021). Modeled biomass is also lower than it was estimated from observations at depths >1,000 m in another survey study off Western Ireland (Godbold et al., 2012). This difference between modeled and observed biomass can be attributed to potential ontogenetic migrations by adult demersal fishes (Macpherson & Duarte, 1991) that are not accounted for in our model or by similarly lacking juvenile diel vertical migration. This could also be attributed to underestimating the prey resources for demersal fishes, such as the lack of midwater zooplankton that feeds on detrital particles in the COBALT model (Stock et al., 2020) or the simplistic benthic transfer efficiency used to convert detritus to benthic invertebrate biomass (Figure S3 in Supporting Information S1). Further, adaptations of demersal fishes to exploit resources in deep-sea systems that are not resolved in the model may also result in lower modeled biomasses compared to observed ones (Killen et al., 2009; Koslow, 1996; Seibel & Drazen, 2007). It is also plausible that survey biomasses are overestimated because of underestimating gear catchability (Walker

Table 2
Active Like Flux of Carbon Transported to the Seafloor via Predator-Prey Trophic Interactions Between Fishes Across the Water Column

	Shelf-slope-abyssal system				Slope (500–1,800 m)			
	Area (thousand km^2)	*C* flux (thousand t C year^{-1})	*C* flux per area (kg C km^{-2} year^{-1})	% relative to detritus flux	Area (thousand km^2)	*C* flux (thousand t C year^{-1})	*C* flux per area (kg C km^{-2} year^{-1})	% relative to detritus flux
N Atlantic	7,309	5,940	813	5.0	1,579	139	88	1.7
NE Atlantic	2,035	1,875	921	4.6	501	90	180	2.0
NW Atlantic	5,274	4,066	771	5.3	1,078	49	46	1.4
Mid Atlantic Bight	295	644	2,186	9.4	28	7	252	3.2
North Caribbean	536	7×10^{-7}	1×10^{-6}	1×10^{-7}	132	6×10^{-7}	4×10^{-6}	3×10^{-7}
Gulf of Mexico	1,361	1,930	1,416	8.4	264	4	14	0.5
Western Ireland	184	88	477	3.3	40	2	55	1.5
Sahelian Upwelling	302	675	2,234	6.3	40	28	688	2.2

Note. Estimated values are averages weighted by the size of each grid-cell and then pooled within each of the areas defined in Figure 2. Estimates for the N Atlantic combine all the areas defined in Figure 2. The symbol *t* stands for metric ton.

et al., 2017). Nonetheless, the similarity between empirical and modeled demersal biomass estimates with depth off Western Ireland is encouraging.

Our sensitivity analysis (Table 1) reveals that changes in transfer efficiency from detritus to benthic production have an almost proportional effect on demersal fish biomass (and active transport of carbon) on continental slopes. Little is known about how benthic transfer efficiency is affected by benthic species traits and adaptations to deep-sea conditions (reviewed by Eddy et al., 2021). It is possible that benthic transfer efficiency may vary with depth or among regions similar to the emergent trophic transfer efficiency of planktonic (Stock et al., 2014) and fish (Petrik et al., 2019) food webs. By doubling this parameter value in the Western Ireland case study, demersal fish biomass increases across the entire shelf-slope-abyssal system, matching the empirical biomass estimates from survey data (Figure S3 in Supporting Information S1). If correct, this suggests that active carbon flux in slope depths of 500–1,800 m could be double as high as currently estimated (15% rather than 7.5%).

4.2. Transport of Carbon to the Seafloor

Transport of carbon in the ocean by fish has mainly been studied as the injection of carbon at depth through respiration, egestion, and excretion (reviewed in Saba et al., 2021). The combination of these mechanisms with diel vertical migration patterns is often used for estimating carbon export out of the euphotic zone (tipically 200 m; Boyd, 2019; McMonagle et al., 2024; Pinti et al., 2023; Saba et al., 2021). However, active carbon transport to the seafloor in the form of biomass through trophic transfer, that is, benthic-pelagic coupling, has largely been neglected (Mauchline & Gordon, 1991; but see Pinti et al., 2023; Trueman et al., 2014). In this work, we focus on the portion of active carbon flux that is, “passed on” as fish biomass to demersal fishes through ingestion of prey by predators that occupy different vertical habitats in the water column, ignoring injection mechanisms in the water column. This information is necessary for understanding the origin of carbon that fuels demersal communities and for quantifying the carbon actively transported to the seafloor assuming that the carbon contained in demersal fish biomass is injected near the seafloor as they rest and digest their food. On average, we estimate that benthic-pelagic coupling can transport an equivalent 5% of the passive detrital carbon flux reaching the seafloor. This flux is greater in shallower systems because the greater vertical overlap between functional groups increases demersal predator encounters with midwater and epipelagic fishes (Kopp et al., 2015; Walters et al., 2025).

Using isotopic methods, Trueman et al. (2014) estimated that benthic-pelagic fish coupling supplies over 50% of carbon to demersal fishes at slope depths between 500 and 1,800 m off Western Ireland. Consistent with this, our model simulations estimated that benthic–pelagic coupling accounts for almost 50% of the carbon supply to demersal fishes in slope systems (Figure 5b). The convergence of these independent approaches—stable isotope

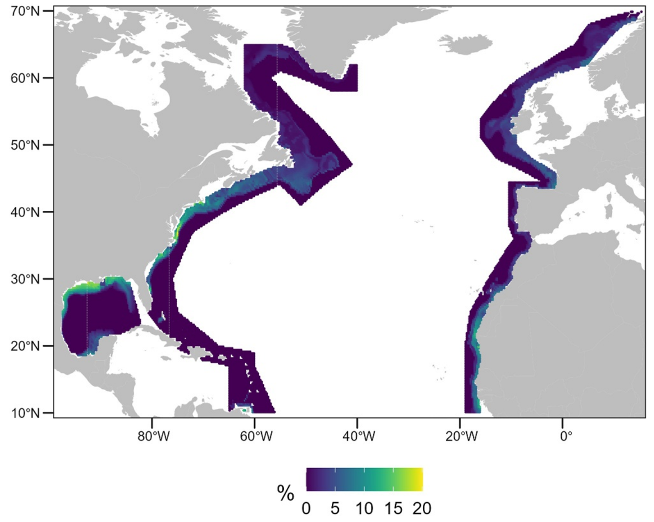

Figure 6. Proportion of active carbon flux to the seafloor through benthic-pelagic fish coupling (active flux) relative to passive detrital flux in shelf-slope-abyssal systems of the North Atlantic Ocean.

analysis and ecosystem modeling—provides reinforcing evidence for the substantial role of benthic–pelagic coupling in supporting demersal fish production in these environments.

In absolute terms, Trueman et al. (2014) estimated that benthic-pelagic fish coupling transport 776–1,375 (mean = 900) kg C km^{-2} yr^{-1}. In comparison, the model estimates that benthic-pelagic coupling only transports 55 kg C km^{-2} yr^{-1}. We hypothesize that these differences originate as our estimate of simulated mean demersal fish biomass at 500–1,800 m depth is 10 times lower (0.5 g ww m^{-2}) than the biomass estimated by Trueman et al. (2014) from trawl catch data (5 g ww m^{-2}). Further, Trueman et al. (2014) assume that demersal fishes consume 3.6 times their biomass yr^{-1}, while the consumption rate of demersal fishes that emerged from our model simulations is 2.1 times their biomass yr^{-1}. The sensitivity analysis (Table 1) shows that estimates of active carbon flux are sensitive to consumption parameters. If we use our biomass estimates (0.5 g ww m^{-2}) and consumption/biomass ratio (Section 2.1) to calculate carbon flux as in Trueman et al. (2014), we get a flux of 53 kg C yr^{-1}, which is similar to our 55 kg C yr^{-1} estimated with the food web model. Such tight estimates highlight that the fundamental principles of both approaches converge, and that biomass estimates and metabolic parameters (Table 1) are major sources of uncertainty. Future empirical work seeking to constrain uncertainty around metabolic parameters can improve estimates of benthic-pelagic coupling with both modeling and isotopic techniques. We expect that the real amount of active carbon flux lies somewhere between both estimates as the survey estimates of demersal fish biomass in slope areas (black line in Figure 3b) lay between our model estimates (magenta line in Figure 3b) and the value used by Trueman et al. (2014). Further, the consumption rate of 3.6 times their biomass yr^{-1} estimated with isotopic methods by Trueman et al. (2014) is a conservative median for fishes with low-quality prey, whereas fishes with high-quality prey consume an estimated median of 1.6 times their biomass yr^{-1}. It is likely that overall consumption of all demersal fishes would include both low- and high-quality prey, and therefore be closer to the value of 2.1 times their biomass yr^{-1} estimated by the food web model.

Our estimations of the active fluxes of carbon heavily rely on the fish food web representation. Uncertainty exists in this food web due to uncertainty in the parameterization of predator-prey feeding interactions and lower trophic level forcings. In addition, FEISTY misses some regional specificities. For example, zooplankton productivity is very high in the northern Gulf of Mexico, resulting in high values of carbon flux through benthic-pelagic coupling. However, such high productivity is often driven by river eutrophication, which creates hypoxic zones that typically have a negative impact on benthic invertebrates and demersal fishes (Diaz & Rosenberg, 2008; Rabalais et al., 2002). Since FEISTY does not use oxygen as a forcing term, we are missing this mechanism and likely overestimate demersal fish biomass and active carbon flux. Similarly, neither COBALT nor FEISTY can adequately represent the productivity of coral reef ecosystems in regions such as the North Caribbean Sea, and may therefore underestimate fish production in this system.

4.3. Fueling the Demersal Fish Community

Benthos is the main source of carbon of demersal fish communities across the North Atlantic shelf-slope-abyssal system, albeit with regional variability. This general trend coincides with empirical studies based on stomach content and isotope analyses (Dolbeth et al., 2008; Eriksen, 2021; Mindel et al., 2016; Trueman et al., 2014; Walters et al., 2025). On shelves (<250 m; Figure 1a), we find that epipelagic and demersal fish sources combined are equally important as benthos. On slopes (Figure 1b), midwater fishes become more important, highlighting the importance of midwater fishes as a stepping stone to transfer carbon from the epipelagic zone to demersal fishes in slope systems (reviewed in Drazen & Sutton, 2016). In deep (>2,200 m; Figure 1c) or very oligotrophic systems (e.g., North Caribbean), benthic-pelagic coupling breaks and demersal fishes depend mainly on detrital sources of carbon that sustain the benthic community. Crabtree et al. (1991) pointed out that the food scarcity of the Caribbean Sea limits the presence of benthic-pelagic fishes in favor of smaller fishes with sedentary feeding strategies. Such a different strategy of how demersal fishes of the Caribbean obtain food matches with our model simulations. The high abundance of midwater fishes relative to the other fish types in oligotrophic waters of the southeast Caribbean and Gulf of Mexico highlights an effective strategy for such oligotrophic systems, complementing other adaptations of mesopelagic fishes to the open ocean (Irigoien et al., 2014).

This study shows that benthic-pelagic coupling is an important mechanism fueling demersal fish in shelf-slope-abyssal systems of the North Atlantic. These systems sustain abundant seafloor biodiversity and commercially valuable fisheries (Amoroso et al., 2018; EU, 2023; NOAA, 2007). We show that midwater fishes are particularly important for mediating benthic-pelagic coupling in slope systems. A recent push to explore the viability and sustainability of mesopelagic fisheries (Fjeld, 2023; Hidalgo & Browman, 2019; Martin et al., 2020) is revealing that developing such fisheries could risk carbon sequestration in the oceans (Iglesias et al., 2023; Pinti et al., 2023; Saba et al., 2021). Because mesopelagic fishes account for up to 50% of demersal fish diets in the slope system, mesopelagic fisheries may also compromise these vertically connected food webs, reducing the supply of energy to sustain an abundant seafloor fish fauna and potential demersal fisheries production. Current biomass estimates of mesopelagic fish remain highly uncertain. Constraining these estimates can help clarify tradeoffs involved in developing mesopelagic fish fisheries.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data and R code to run the model simulations, plot the outputs and compare them to fishery data are available on Zenodo: https://doi.org/10.5281/zenodo.18175996. The data on which this article is based are available in van Denderen et al. (2023) and Maureaud (2024).

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