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Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes

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Biological transfer of nutrients and materials between linked ecosystems influences global carbon budgets and ecosystem structure and function. Identifying the organisms or functional groups that are responsible for nutrient transfer, and quantifying their influence on ecosystem structure and carbon capture is an essential step for informed management of ecosystems in physically distant, but ecologically linked areas. Here, we combine natural abundance stable isotope tracers and survey data to show that mid-water and benthic–pelagic–feeding demersal fishes play an important role in the ocean carbon cycle, bypassing the detrital particle flux and transferring carbon to deep long-term storage. Global peaks in biomass and diversity of fishes at mid-slope depths are explained by competitive release of the demersal fish predators of mid-water organisms, which in turn support benthic fish production. Over 50% of the biomass of the demersal fish community at depths between 500 and 1800 m is supported by biological rather than detrital nutrient flux processes, and we estimate that benthic–pelagic fishes from the UK–Irish continental slope capture and store a volume of carbon equivalent to over 1 million tonnes of CO₂ every year.

1. Introduction

The upper and middle reaches (water depths of 500–2000 m) of continental slopes, seamounts and mid-ocean ridges comprise approximately 15% of the global ocean area and support diverse communities [1,2]. Upper and mid-slope ecosystems are subjected to increasing anthropogenic disturbance through fisheries, mineral and energy extraction industries, and waste disposal [3–8]. Research interest in the deep ocean ecosystem is growing as biological movement of carbon between the sea surface and deep waters controls atmosphere–ocean CO₂ exchange [9] and fuels all heterotrophic biological production in the deep ocean. Biological active transport of carbon and other nutrients out of surface waters occurs through diel vertical migrations (DVM) of fishes, zooplankton and larger invertebrates such as cephalopods and jellyfish. The DVM community exploits phytoplankton in surface waters at night, returning to depths exceeding 1000 m during daylight [10,11]. Recent advances in biogeochemical modelling have suggested that active biological export is needed to balance global biogeochemical carbon budgets [9,12] and that mesopelagic fishes alone may contribute between 10 and 40% of deep carbon flux [9].

Carbon contained within the DVM community may be recycled within surface waters or exported to depth through deep respiration, settling of faecal particles and predation by deep-living organisms [9,13]. The role of demersal (bottom living) organisms in carbon capture is relatively understudied, partly owing to limited knowledge of trophic linkages between the mesopelagic and demersal communities [9,14]. On a global scale, the biomass of benthic organisms generally declines with depth, implying that most energy is transferred to

the benthos through the passive flux of settling particles [10,15]. Consequently, particulate organic matter (POM) is often assumed to form the most important food input to deep-sea communities [16,17]. However, it has long been recognized that biological interactions such as overlapping vertical migrations provide an additional energy source to demersal organisms, particularly fishes [14,18,19], and thus that deep demersal fishes play a role in carbon capture and long-term storage.

Estimating the carbon sink represented by deep demersal fishes requires quantification of the trophic interactions between deep demersal fishes, mid-water organisms and settling particles. Variations in the stable isotope compositions of animal tissues demonstrate lateral movement of organisms in marine ecosystems, as the isotopic composition of primary production is geographically variable [20,21]. Stable isotopes also provide an effective marker for vertical nutrient export pathways as the isotopic composition of carbon and nitrogen is modified during vertical transport, and the extent of this modification varies between different export mechanisms.

The isotopic composition of passively sinking small particles increases with depth owing to preferential assimilation of light isotopes during microbial metabolism. Predator communities whose prey is primarily fuelled by suspension feeders show depth-dependent increases in carbon and nitrogen isotope compositions (described as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) and are relatively isotopically enriched [17,22–24]. Rapidly settling particles may be less fractionated during passive settling [24–26], but biological processing within the benthos increases $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values [18,22], thus predator communities ultimately dependent on large POM will be relatively isotopically enriched but show less depth-dependent increases in isotope values. Predator communities preying on active migrators, by contrast, will be relatively isotopically depleted [22] and will show limited depth-dependent increases in isotopic composition. A schematic representation of expected isotopic gradients is provided in the electronic supplementary material.

Here, we compare depth-dependent trends in abundance and isotopic composition in demersal fishes primarily consuming prey at or within the sediment surface (benthic feeders), and those primarily consuming prey at some distance above the sea floor (benthic-pelagic feeders). Concentrating on a depth transect between 500 and 1500 m on the North Atlantic continental slope west of Ireland, we explore the relative importance of passive compared to active nutrient transfer mechanisms in exporting carbon and nutrients out of the upper ocean.

2. Material and methods

Demersal fishes from the northeastern North Atlantic continental slope were collected during the Marine Institute fisheries science service deepwater trawl surveys in September 2006 and December 2009. Surveys were conducted on the northern slope of the Porcupine Bank and the Western Continental Slope (figure 1) from the *RV Celtic Explorer* using a BT184 deepwater trawl. In each area, fishes were sampled from 500, 1000 and 1500 m in 2006, with additional samples from 500 and 1800 m recovered in 2009. An implicit assumption of the sampling strategy is that individual fish do not routinely travel between the depth zones analysed. Extensive survey data [4,6,8,27–33] indicate that fish communities

on the northeast Atlantic continental slope are strongly structured by depth, with limited overlap in community composition at depth intervals in excess of 250 m. Consequently, it is extremely unlikely that individual fish sampled in this study routinely migrate over depth intervals of 500 m. Full details of the deep-water surveys sampled in this study are provided in the Irish Fisheries Bulletin Series [29–32]. Four years of survey catch data were analysed to determine the relative abundance of each sampled species within trawl samples (relative abundances given in the electronic supplementary material, compiled from unpublished data, Marine Institute, Galway).

The sampled fishes were assigned to one of two functional groups classified by morphological traits and previously published stomach content analyses [4,6,8,18,27,28,33]. Using literature data, feeding modes were assigned *a priori* to either a benthic or benthic-pelagic foraging strategy [18,33,34]. Benthic-feeding fishes are defined here as those feeding on organisms associated with the sea floor (predominantly epi- or hyper-benthic diet), whereas benthic-pelagic-feeding fishes are defined as those feeding on organisms found at some distance above the seafloor (predominantly benthic-pelagic or pelagic diet). Details of the *a priori* functional group assignments are provided in the electronic supplementary material.

To estimate the relative biomass of benthic and benthic-pelagic feeders from abundance and length data, the average (mean) trawled abundance of each sampled species was calculated for all measured lengths. Mean biomass per length unit was estimated from modal lengths and abundances by applying length–weight relationships derived from repeated trawl surveys in the Rockall Trough region [35], or from www.fishbase.org [34], and calculated by species and depth. Data were then binned into log 5 mass classes.

(a) Sample selection

Samples of white muscle were removed from 527 individuals comprising 30 species. All samples were removed within 1 h of landing on deck. Approximately 1 cm³ of muscle tissue was removed and immediately frozen at -20°C . Insufficient samples were recovered from 1800 m depth trawls, so the statistical analyses of stable isotope data are restricted to fishes sampled at 500, 1000 and 1500 m depths. Relative biomass ratios estimated from survey data were used to calculate the proportional biomass of the trawled community sampled in each log 5 mass class. The smallest and largest mass classes are under-represented in the population sampled for isotopic analyses, but species representing at least 75% of the trawled biomass were sampled in each log 5 mass class at each depth. Proportional species weightings used are provided in the electronic supplementary material.

(b) Stable isotope analyses

Frozen muscle samples were freeze-dried, crushed and approximately 0.7–0.9 mg of powdered muscle was weighed into a tin capsule. Samples from elasmobranchs were additionally washed three times in distilled water to remove any traces of isotopically light ammonia from muscle tissue. Mathematic corrections for the effect of lipid concentration on measured $\delta^{13}\text{C}$ values were performed according to the method of Hoffman & Sutton [36], explicitly derived for deepwater fishes.

The isotopic compositions of C and N were determined using a GEO instruments isotope ratio mass spectrometer at the RLHA at the University of Oxford. Nylon was used as an internal standard. All isotope ratios are reported in delta notation relative to Pee Dee Belemnite and air standards for carbon and nitrogen, respectively. Precision and accuracy monitored through repeat analyses of laboratory standards were less than 0.1 per mil (‰) in C and 0.3‰ in N.

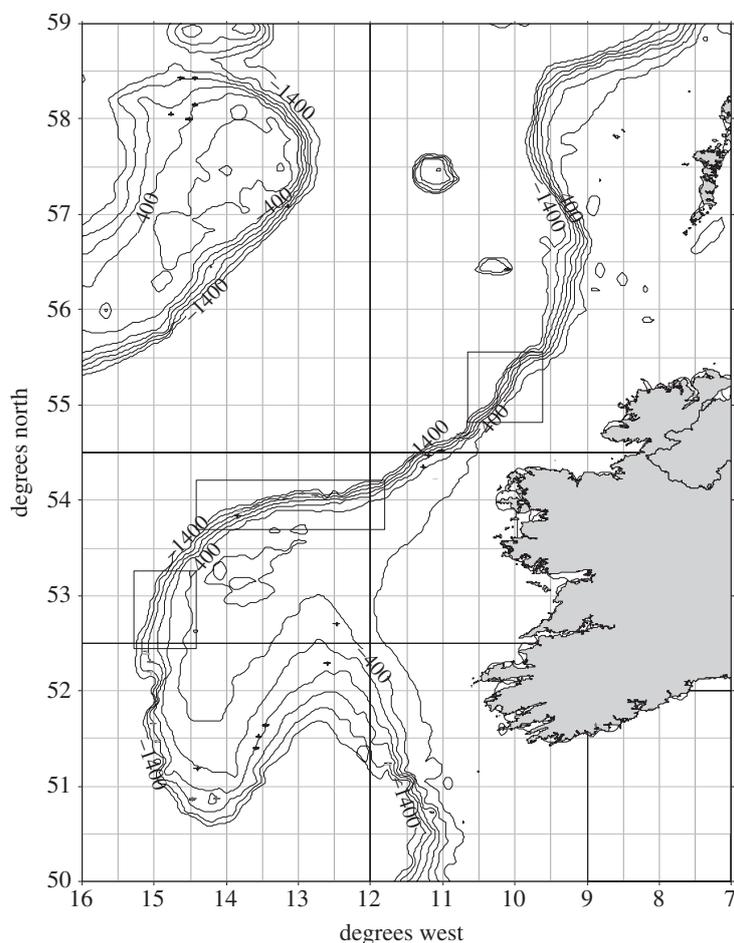


Figure 1. Areas of fish collection during this study. Other Irish deepwater survey areas not illustrated.

(c) Statistical analyses

Marine food webs are commonly strongly size-based, with most predators larger than their prey [37,38]. Here, trends in tissue isotopic compositions were explored as a function of body size rather than taxonomic affiliation, but species identity was retained and used to partition samples into functional groups. The influence of body mass (recorded as \log_2 mass (g) directly measured for the sampled fish), feeding type and depth on fish muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was explored using linear multiple regression models. Models were selected based on residual structure, p -values and proportion of explained variance. To explore community averaged metrics, stable isotope values for all species were pooled by \log_5 mass class and weighted to reflect the proportional abundance of each species within each mass class as determined from the 4 years of survey data.

3. Results

Summary isotope data are provided in the electronic supplementary material, and the full dataset is available via Dryad (doi:10.5061/dryad.n576n).

(a) Biomass trends

Fished biomass of benthic-feeding fishes declined steady over the full survey range from 500–1800 m, whereas the biomass of benthic-pelagic-feeding fishes increased to a peak at 1500 m (figure 2a). The proportion of total biomass comprised benthic-pelagic-feeding fishes also varied systematically with depth, from 40% at 500 m, to a peak of 80% at 1500 m (figure 2b).

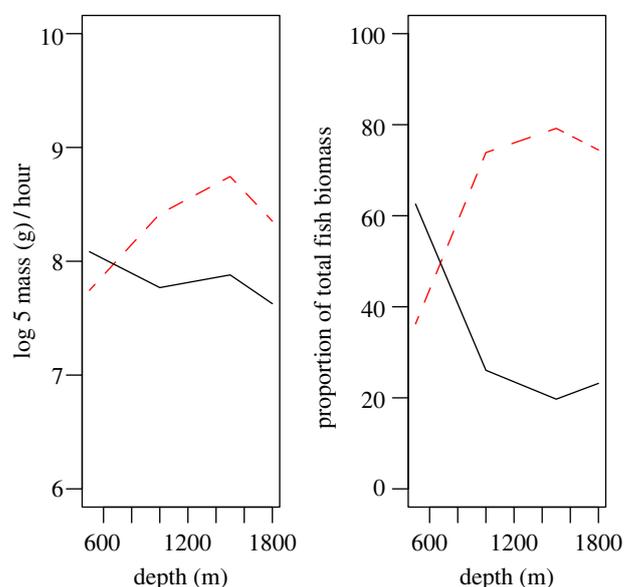


Figure 2. (a) Mean abundance (\log_5 trawled biomass g h^{-1}) in benthic (black) and benthic-pelagic (red/dashed)-feeding fishes. (b) Proportional biomass of benthic (black) and benthic-pelagic (red/dashed)-feeding fishes in the demersal trawled community. (Online version in colour.)

(b) Comparison of *a priori* functional group assignments and isotope values

The isotopic composition of fish muscle tissue supports the trophic functional groups assigned from stomach content analyses: species whose stomach contents indicate a large

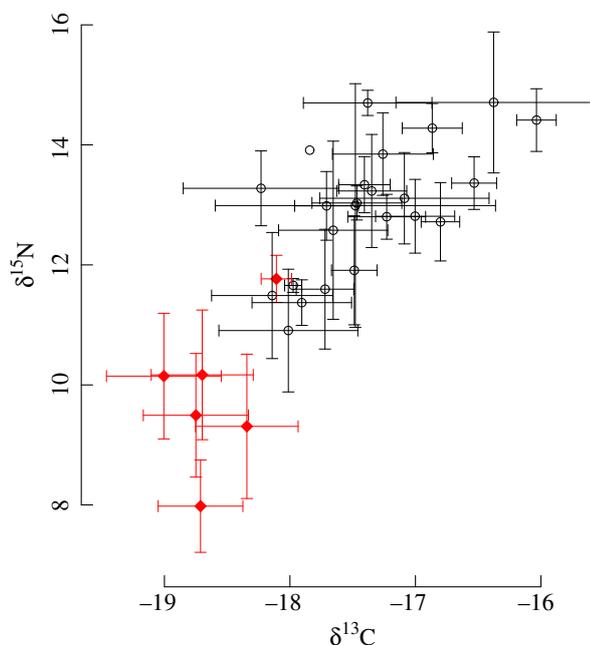


Figure 3. Stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) values of all species analysed. Data points represent species means, error bars represent ± 1 s.d. Benthopelagic-feeding fishes, filled diamond symbols; benthic-feeding fishes, open circle symbols. (Online version in colour.)

pelagic component in their diet yield relatively depleted (more negative) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (figure 3).

(c) Depth influences on trophic biology

Depth influenced the measured isotopic difference between benthopelagic- and benthic-feeding fishes with isotopic separation increasing between 500 and 1500 m (figures 4 and 5). Fish mass also influences stable isotope composition (figure 4), particularly $\delta^{15}\text{N}$ values, which increase with mass. Thus for any given mass, benthopelagic-feeding fishes have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than benthic-feeding fishes, and this distinction is greatest at low mass in deeper water (figure 4). Mass, depth and feeding type were consequently included in separate linear regression models estimating either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values. The regression model for $\delta^{15}\text{N}$ values is visualized in figure 5, and a full description of both models is provided in the electronic supplementary material. The regression model explained 78% of the variance in $\delta^{15}\text{N}$ values, and model residuals were normally distributed and evenly dispersed. In both benthic and benthopelagic-feeding species, $\delta^{15}\text{N}$ values increase with mass, but in benthic-feeding species, $\delta^{15}\text{N}$ values also increase with depth at all sizes (figure 5*a,b*). Feeding type alone did not influence $\delta^{15}\text{N}$ values, indicating overlap between the nitrogen isotope compositions of prey, but all interactions between mass, depth and feeding type significantly influenced tissue $\delta^{15}\text{N}$ values (figure 5*a,b*; electronic supplementary material). When species was included as an explanatory variable, feeding type (benthic or benthopelagic feeding) had a stronger influence on $\delta^{15}\text{N}$ values than depth or body mass, but uneven sampling resulted in poor model residual structure at this level.

Regression modelling explained 69% of the variation in $\delta^{13}\text{C}$ values, with mass the main explanatory factor. A full model description is given in the electronic supplementary material. Model residuals were normally distributed and evenly dispersed. The total explained variance increased to 80% when species was included as a predictor variable, but

uneven sampling at this level resulted in non-normally distributed residual structure.

To provide a more accurate picture of nutrient flow within the sampled community, mean $\delta^{15}\text{N}$ values for each species within each log 5 mass class were scaled according to their relative abundance within that mass class. Linear regression models were then fitted to explore the relationship between mean abundance-weighted stable isotope values and log 5 mass (figure 5*c,d*; electronic supplementary material). At 1000 m, the relationship between $\delta^{15}\text{N}$ values and body mass in benthic-feeding species is surprisingly flat, but the high and low mass classes in this sample are constrained by only one and two species respectively, and the model should be treated with caution.

In benthic-feeding species, depth influences both the absolute $\delta^{15}\text{N}$ value, and the rate of increase in $\delta^{15}\text{N}$ values with body size. The $\delta^{15}\text{N}$ value at a nominal zero mass, increases from $8.4 \pm 0.4\text{‰}$ at 500 m to $11.5 \pm 0.7\text{‰}$ at 1500 m. Trophic fractionation of $\delta^{15}\text{N}$ values (the degree of preferential enrichment of ^{15}N in a predator's tissues relative to its prey) varies between taxa, but is usually assumed to lie between two and four in marine ecosystems [39–41]. Over the small lateral distances separating depth samples, primary production can be considered isotopically homogeneous [42]. The $3.1 \pm 1.1\text{‰}$ difference in $\delta^{15}\text{N}$ values between 500 and 1500 m is therefore equivalent to an additional trophic level between demersal production and primary production. The rate at which $\delta^{15}\text{N}$ values increase with body mass, i.e. the community predator:prey mass ratio [43], also increases between 500 and 1500 m (figure 5*c*).

In benthopelagic-feeding species, absolute $\delta^{15}\text{N}$ values do not vary significantly with depth, consistent with the expectation of isotopically homogeneous primary production. The rate of increase in $\delta^{15}\text{N}$ values with body mass is apparently higher at 500 m, but this is relatively poorly constrained (figure 5*d*; electronic supplementary material).

4. Discussion

(a) Assumptions and possible influences

The isotopic composition of muscle tissue is potentially influenced by several variables, particularly relating to isotopic fractionation between body tissues and diet, and we make three explicit assumptions in the interpretation of our data.

- (1) *Isotopic fractionation between tissue and diet is not systematically different between the two defined functional groups.*

Isotopic fractionation between tissues and diet reflects the dynamic mass balance between rates of ingestion, excretion and protein synthesis, and in theory could vary systematically between functional groups if group membership correlated with differences in physiology or potentially growth rate [43]. However, in the deep water data, isotopic separation is maintained in fishes that are closely related phylogenetically and morphologically but occupy different functional groups (e.g. between the benthopelagic-feeding *Coryphaenoides rupestris* and other benthic-feeding macrourids; electronic supplementary material, table S1), whereas phylogenetically and morphologically distinct fishes within the same functional group are isotopically similar (figure 2; electronic supplementary material, table S1). It is therefore unlikely that the isotopic

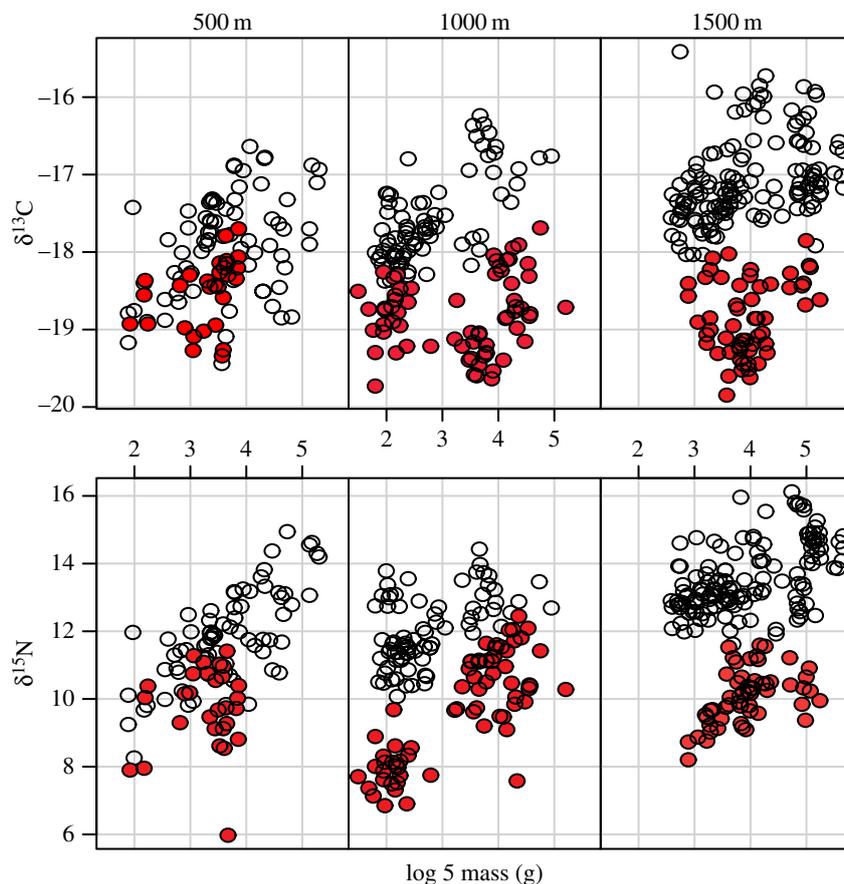


Figure 4. Relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and log 5 mass (g) in benthic-pelagic (filled symbols) and benthic (open symbols) fishes. Each data point represents an individual, all species combined. (Online version in colour.)

separation seen between fishes with benthic and benthic-pelagic diets is caused by physiological differences.

- (2) *Isotopic fractionation between tissue and diet does not vary systematically with depth (e.g. through physiological changes or increased catabolism).*

Similar to point (1) above, depth-related influences on physiology (e.g. slower growth, pressure and temperature influences on enzyme reaction rates) could theoretically influence tissue-diet fractionation. However, depth-dependent increases in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are seen in benthic but not benthic-pelagic-feeding demersal fishes (figure 4), and there is no support for consistent depth-related effects in multi-species tissue-diet fractionation factors.

- (3) *Functional groups have not changed significantly between the 1980s (when stomach content analyses were conducted) and present.*

Diversity and community composition of demersal fish faunas of the northeast Atlantic continental slope have been observed over a decade of scientific surveys, and no temporal trends or major community shifts have been found [6]. We therefore see no evidence for major changes in the functional groups to which fish species should be assigned between the stomach content analyses in the late 1980s and the present. This is supported by the agreement between *a priori* assignments of benthic and benthic-pelagic-feeding types based on stomach content surveys and stable isotope values (figure 2).

The isotopic separation seen between functional groups of fishes therefore reflects differences in the isotopic composition of their diets and provides information on the

processes by which nutrients are supplied to benthic and benthic-pelagic-feeding demersal fish communities.

(b) Benthic-pelagic production and biological nutrient supply

The proportion of demersal fish biomass with a benthic-pelagic diet increases sharply from less than 50% at depths below 1000 m to over 75% at depths in excess of 1000 m (figure 2). Three species of benthic-pelagic-feeding fishes account for more than 45% of the total trawled demersal fish biomass between 1000 and 1800 m depth. These results are consistent with global patterns where biomass of benthic-pelagic fishes increases below 1000 m, peaking at around 1500 m [4,6,14,18,44].

The mass-specific trophic level of benthic-pelagic-feeding fishes does not change with depth of capture (figure 5), implying that the degree of coupling to primary production in the benthic-pelagic-feeding fish community is unchanged between 500 and 1500 m. At water depths of less than 500 m, the entire daytime thickness of the vertically migrating community is compressed into a shallow layer and is potentially available as prey to both benthic demersal predators, and deeper diving shallow-water predators. The total vertical thickness of the DVM community, and associated non-migrating mesopelagic organisms is uncertain. At 1800 m (the maximum depth sampled in this study), the absolute and relative biomass of benthic-pelagic-feeding fishes begins to decline, implying that the maximum daytime depth of the DVM community is becoming less accessible to demersal fishes. At depths between *ca* 1000 and 1800 m, a proportion of the

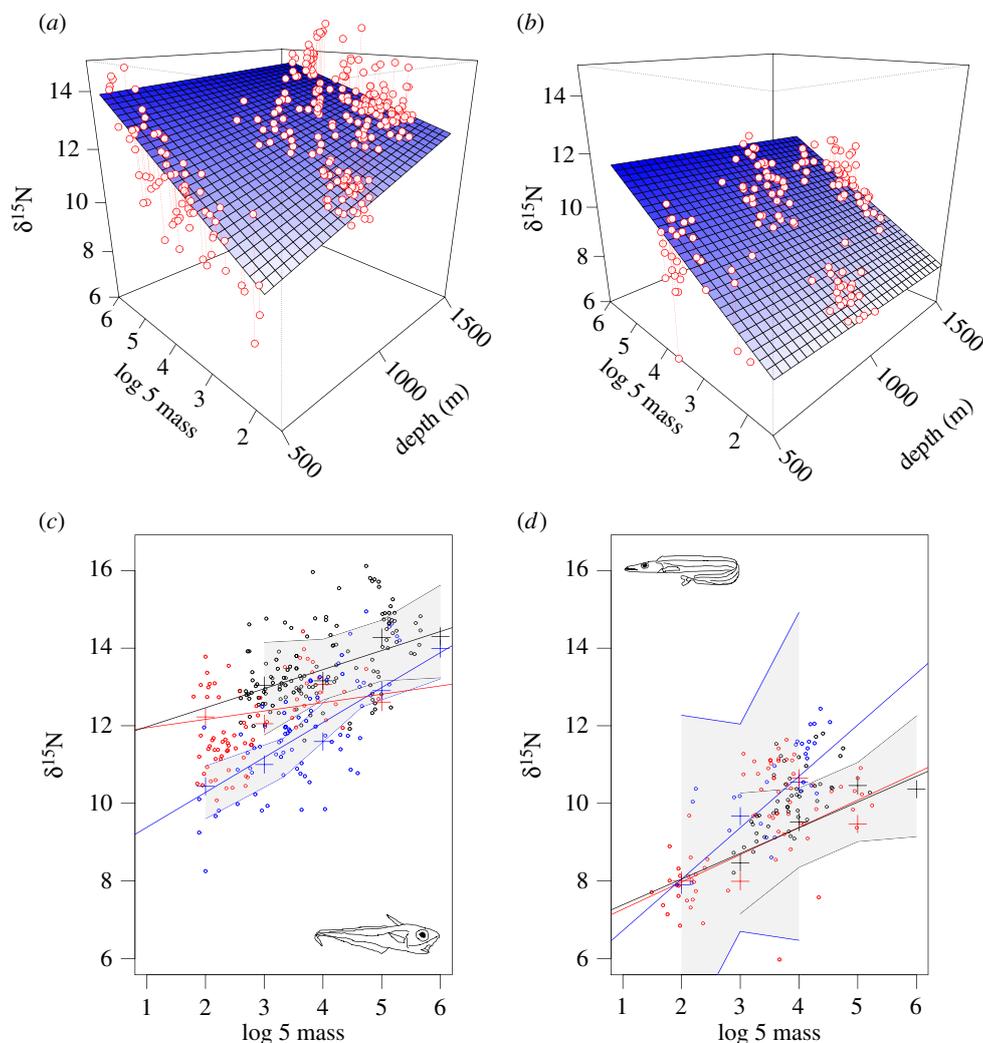


Figure 5. Relationships between $\delta^{15}\text{N}$ values, body size and depth in benthic- (*a,c*) and benthic-pelagic (*b,d*)-feeding species based on individual data (*a,b*) and community weighted data (*c,d*). In (*a,b*), planes represent the best-fit regression model containing interactions between mass and depth. In community weighted plots (*c,d*), circular symbols are individual data points, crosses are weighted average $\delta^{15}\text{N}$ values for each log 5 mass class, with individual data points weighted to reflect the proportional abundance of each species in each mass class. Blue symbols, 500 m; red symbols, 1000 m; black symbols, 1500 m. Solid lines display the best-fit regression models between body mass and weighted average $\delta^{15}\text{N}$ values, and shaded grey areas represent 95% confidence intervals around the regression models.

biomass of the mesopelagic community will therefore be inaccessible to both benthic feeders and deep diving epi-pelagic fishes and mammals during the day, but will be available for consumption by benthic-pelagic-feeding demersal fishes, through downward extension of the mesopelagic community and/or upward migration of benthic-pelagic-feeding demersal fishes. Benthic-pelagic-feeding demersal fishes therefore benefit from competitive release, and dominate demersal fish biomass between *ca* 1000 and 1800 m (figure 2). Benthic-pelagic demersal fishes thus play an important role in cross-ecosystem benthic–pelagic coupling, transporting nutrients from the deeper reaches of the DVM to the benthic community at mid-slope depths, bypassing the detrital-benthic food pathway and potentially enhancing benthic production.

At all depths, benthic-pelagic-feeding demersal fishes are distinguished through relatively light carbon and nitrogen isotopes (figures 3–5), indicating a closer trophic connection to isotopically light primary production than benthic-feeding fishes. Nutrients recycled through benthic systems are therefore not volumetrically important to the benthic-pelagic-feeding fish fauna, and once entrained in sediments or demersal organisms, nutrients are effectively retained within the benthos. These results are similar to isotopic

data from the Porcupine Abyssal Plain site showing separation between benthic and benthic-pelagic food chains [22] and are inconsistent with the suggestion or implication that the detrital particle flux of POM is the ultimate source of energy for deep water demersal (fish) production [16,17,45].

(c) Benthic production and biological nutrient supply

The isotopic distinction between benthic and benthic-pelagic-feeding deepwater demersal fishes is small at 500 m, but increases with depth owing to the increasingly heavy isotopic composition of benthic-feeding fishes (figure 4). As all secondary benthic production is fuelled by a single primary production source, these data suggest that benthic and benthic-pelagic-feeding fishes are similarly coupled to surface production at 500 m. In the North Atlantic, vertically migrating fishes, calanoid copepods and other zooplankton are concentrated at depths between 300–500 m during daylight hours, particularly during the spring phytoplankton bloom [46–48]. It is thus likely that the diurnal vertically migrating fauna impinge wholly on the benthos during the day at 500 m and are available and consumed directly by both benthic and benthic-pelagic feeders, resulting in relatively strong coupling

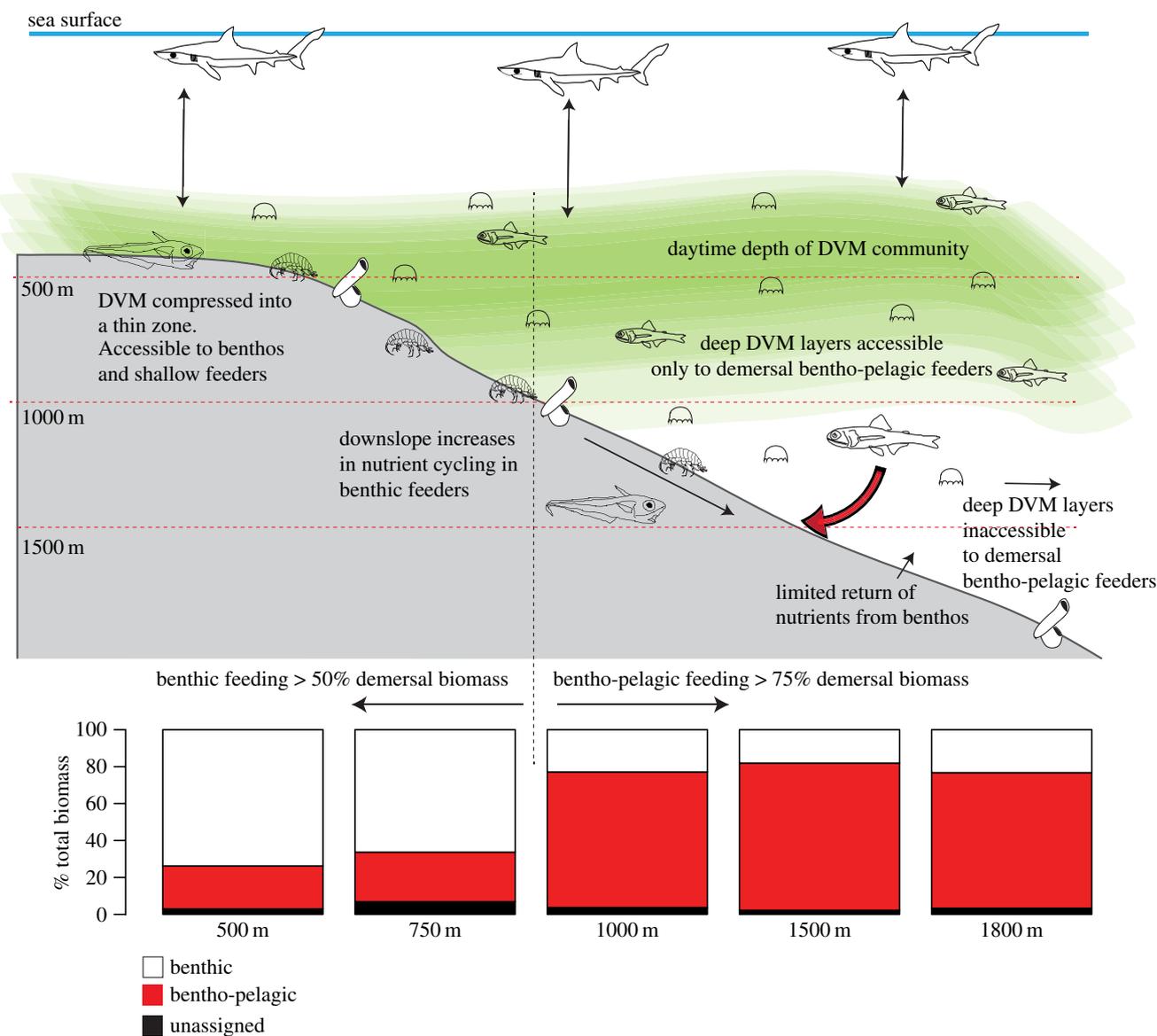


Figure 6. Schematic diagram of important nutrient flow pathways operating on the continental slope and overlying water column as inferred from stable isotope and biomass data. Shaded area represents the daytime depth of organisms within the DVM community. Lower barplot shows the relative biomass of the trawled community assigned to either a benthic or benthic-pelagic diet based on stomach content data.

between benthic and pelagic production. These data are consistent with previous observations noting no variation in carbon source between benthic and pelagic feeders at *ca* 100–200 m water depth on the Seine Seamount [49].

Between 500 and 1500 m depth, $\delta^{15}\text{N}$ values in the smallest size classes of the benthic-feeding fishes community increase from $8.4 \pm 0.6\text{‰}$ to $11.1 \pm 1.2\text{‰}$, approximately equivalent to an additional trophic level. The trophic transfer efficiency associated with marine communities is estimated at around 10–20% [37,38], thus if the depth-dependent increase in observed $\delta^{15}\text{N}$ values is explained by an additional trophic step, the biomass of benthic production should decline between fivefold and 10-fold between 500 and 1500 m. The average biomass of benthic-feeding species of all size classes in trawl samples in fact falls only slightly between 500 and 1500 m (figure 2), and *ca* 50% more biomass is observed than is predicted based on changes in trophic level. Additional nutrient sources are needed to support this ‘surplus’ benthic biomass. As discussed above, the absolute and relative biomass of benthic-pelagic fishes peaks at 1500 m, apparently supported by increased availability of the DVM below 1000 m. The high biomass of benthic-pelagic-

feeding demersal fishes thus provides an additional export flux of carbon and energy from the DVM community, supporting up to 50% of the production of benthic-feeding demersal fishes. Benthic and pelagic ecosystems are therefore relatively tightly coupled at upper and mid continental slope depths.

(d) Conceptual model of nutrient transfer within the northwest Atlantic continental slope ecosystem

A conceptual model based on stable isotope and abundance data is shown in figure 6. The daytime depth of the diurnally migrating community extends from above 500 m to at least 1000 m, and when compressed onto the seafloor on the upper slope, both benthic and benthic-pelagic feeders have access to DVM organisms. At *ca* 1000 m the proportion of organisms with a distinct benthic-pelagic diet increases dramatically, indicating separation between the benthic and benthic-pelagic trophic pathways. We propose 1000 m as the likely maximum daytime depth of the DVM. Above 1000 m, all demersal fishes capture carbon from the DVM and lock carbon into the deep biomass. Below 1000 m, benthic-pelagic-feeding fishes are

instrumental in capturing carbon from the migrating community and transferring this carbon to the demersal and benthic community. Once locked in the benthic community, there is no volumetrically-significant return transfer of carbon or other nutrients into the benthic-pelagic community.

(e) Implications for observed fishery effects

Time series of fisheries survey data show reductions in abundance and biomass of both target and bycatch species at depths that exceed the maximum depth of the fishery, and this depth-propagation of fishery effects has been explained by interception of species by the fishery at the upper end of their depth ranges [4,6]. Most commercially targeted deepwater fisheries operate at depths of highest demersal fish production, where the main commercial and bycatch species are pelagic-feeding demersal fishes (e.g. *C. rupestris*, *Aphanopus carbo*, *Alepocephalus bairdii*). If benthic-pelagic-feeding fishes are instrumental in capturing nutrients from the DVM community and transferring these to the benthos, then removal of the pelagic-feeding component could provide an additional mechanism for the enhanced depth effect of fishing activity [8]. Theoretical models suggest that strong coupling between benthic and pelagic communities enhances ecosystem resilience to disturbances [50]. Nutrient transport and capture by vertically migrating communities and benthic-pelagic fishes may therefore stabilize benthic communities and improve ecological resilience. Expansion of directed fisheries for krill and other diurnally migrating zooplankton species may also disrupt delivery of cross-ecosystem nutrient flux, and monitoring of fisheries impacts should include downstream effects of removal of biological nutrient vectors.

(f) Implications for carbon storage

Benthic-pelagic-feeding demersal fishes perform an important ecological role capturing carbon from the DVM community and retaining that carbon below the remineralization zone. To estimate the volumetric carbon sink associated with benthic-pelagic demersal fishes on the UK and Irish continental slope, we first estimate the total biomass of demersal fishes. At depths between 500 and 1800 m across the North Atlantic, demersal fish biomass estimates vary between 10^2 and 10^3 mg C m⁻² [14]. We therefore take a value of 0.5×10^3 mg C m⁻² (5×10^3 mg wet weight m⁻²) as a first estimate of the biomass of benthic-pelagic fishes. Based on our isotopic results, we take 50% as a conservative estimate of the proportion of fish biomass with a benthic-pelagic diet (figures 2 and 6). The total area of continental slope between 500 and 1800 m water depth in the UK–Irish region was calculated from National Oceanographic and Atmospheric Administration bathymetry data as 4.51×10^5 km², giving a total estimated wet weight biomass of benthic-pelagic-feeding fishes of 1.13×10^6 tonnes.

The consumption rate of benthic-pelagic fishes is poorly known, and few measurements of metabolic rates are available. We therefore infer consumption rates in benthic-pelagic fishes

from two published estimates. Heymans *et al.* [51] compiled estimates of annual consumption/biomass ratios for demersal fishes on the Rockall slope, giving a median value of 2.1 (interquartile range: 1.25). Greenstreet *et al.* [52] estimate daily ingestion rates of the demersal community of the North Sea (mean temperature 7°C) between 1 and 1.6% of total standing body mass. We take the lower estimate of 1% total standing biomass to represent daily consumption at water temperatures between 7 and 4°C, resulting in an annual consumption/biomass ratio of 3.6. The estimated biomass of carbon consumed by the benthic-pelagic community and prevented from recycling to the atmosphere therefore ranges between 3.5×10^5 T yr⁻¹ and 6.2×10^5 T yr⁻¹. Long-term sequestration of carbon is valued according to the concentration of CO₂ removed from the atmosphere [53], and under the current European Union Emissions Trading Scheme, in 2014 to date, the right to emit 1 tonne of CO₂ has a tradable value of ca €6 [54]. The estimated value of the carbon sequestration service provided by the benthic-pelagic fish community of the UK continental slope is therefore between €8 and 14 million annually, between 10 and 50% of the estimated market value of deep water fishes landed from the UK and Irish slope fisheries [55].

5. Summary conclusion

Global peaks in biomass and diversity of fishes at mid-slope depths are explained by competitive release of the demersal fish predators of mid-water organisms, which in turn supports benthic fish production. Over 50% of the biomass of the demersal fish community at depths between 500 and 2000 m is supported by biological rather than detrital nutrient flux processes, resulting in a net carbon sink to long-term storage in excess of 1×10^6 T CO₂ yr⁻¹. Alterations in the mesopelagic and benthic-pelagic communities responsible for nutrient transfer may have widespread ecosystem effects, including changes in long-term carbon storage, depletion of nutrients available to the benthic community and reduction of total benthic biomass. There is an urgent need for coordinated, global scale research into the basic biology and monitoring of mesopelagic and benthic-pelagic communities [4,5,8,9,13,14,50,52], and assessment of the broad ecological effects of anthropogenic activities on the upper and mid-slope.

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References

1. Haedrich RL. 1996 Deep-water fishes: evolution and adaptation in the Earth's largest living spaces. *J. Fish. Biol.* **49**(Suppl. A), 40–53. (doi:10.1111/j.1095-8649.1996.tb06066.x)
2. Drazen JC, Haedrich RL. 2012 A continuum of life histories in deep-sea demersal fishes. *Deep-Sea Res. Pt I* **61**, 34–42. (doi:10.1016/j.dsr.2011.11.002)
3. Devine JA, Baker KD, Haedrich RL. 2006 Deep-sea fishes qualify as endangered. *Nature* **439**, 29. (doi:10.1038/439029a)

4. Priede IG *et al.* 2011 A review of the spatial extent of fishery effects and species vulnerability of the deep-sea demersal fish assemblage of the Porcupine Seabight, Northeast Atlantic Ocean (ICES Subarea VII). *ICES J. Mar. Sci.* **68**, 281–289. (doi:10.1093/icesjms/fsq045)
5. Van Dover CL. 2011 Tighten regulations on deep-sea mining. *Nature* **470**, 31–33. (doi:10.1038/470031a)
6. Campbell N, Neat F, Burns F, Kunzlik P. 2011 Species richness, taxonomic diversity, and taxonomic distinctness of the deep water demersal fish community on the northeast Atlantic continental slope (ICES Subdivision VIa). *ICES J. Mar. Sci.* **68**, 365–376. (doi:10.1093/icesjms/fsq070)
7. Benn AR *et al.* 2010 Human activities on the deep seafloor in the north east Atlantic: an assessment of spatial extent. *PLoS ONE* **5**, e12730. (doi:10.1371/journal.pone.0012730)
8. Bailey DM, Collins MA, Gordon JDM, Zuur AF, Priede IG. 2009 Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proc. R. Soc. B* **276**, 1965–1969. (doi:10.1098/rspb.2009.0098)
9. Davison PC, Checkley Jr DM, Koslow JA, Barlow J. 2013 Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progr. Oceanogr.* **116**, 14–30. (doi:10.1016/j.pocean.2013.05.013)
10. Gage JD, Tyler PA. 1991 *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge, UK: Cambridge University Press.
11. Gaard E *et al.* 2008 Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic Ridge in June 2004. *Deep-Sea Res. Pt II* **55**, 59–71. (doi:10.1016/j.dsr2.2007.09.012)
12. Gehlen M, Bopp L, Emprin N, Aumont O, Heinze C, Ragueneau O. 2006 Reconciling surface ocean productivity, export fluxes and sediment composition in a global biogeochemical model. *Biogeoscience* **3**, 521–537. (doi:10.5194/bg-3-521-2006)
13. Lehody P, Murtugudde R, Senina I. 2010 Bridging the gap from ocean models to population dynamics of large marine predators: a model of mid-trophic functional groups. *Progr. Oceanogr.* **84**, 69–84. (doi:10.1016/j.pocean.2009.09.008)
14. Priede IG *et al.* 2013 Does presence of a mid-ocean ridge enhance biomass and biodiversity? *PLoS ONE* **8**, e61550. (doi:10.1371/journal.pone.0061550)
15. Herring P. 2002 *The biology of the deep ocean*, p. 314. Oxford, UK: Oxford University Press.
16. Kaiser MJ *et al.* 2005 *Marine ecology: process systems, and impacts*, p. 557. Oxford, UK: Oxford University Press.
17. Mintenbeck K, Jacob U, Knust R, Armtz WE, Brey T. 2007 Depth-dependence in stable isotope ratio $\delta^{15}\text{N}$ of benthic POM consumers: the role of particle dynamics and organism trophic guild. *Deep-Sea Res. Pt I* **54**, 1015–1023. (doi:10.1016/j.dsr.2007.03.005)
18. Mauchline J, Gordon JDM. 1991 Oceanic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Mar. Ecol. Prog. Ser.* **74**, 109–115. (doi:10.3354/meps074109)
19. Haedrich RL. 1997 Distribution and population ecology. In *Deep sea fishes* (eds DJ Randall, AP Farrell), pp. 79–114. San Diego, CA: Academic Press.
20. Hobson KA, Schell DM. 1998 Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). *Can. J. Fish. Aquat. Sci.* **55**, 2601–2607. (doi:10.1139/f98-142)
21. Ramos R, Gonzalez-Solis J. 2012 Trace me if you can: the use of intrinsic biogeochemical markers in marine top predators. *Front. Evol. Environ.* **10**, 258–266. (doi:10.1890/110140)
22. Iken K, Brey T, Wand U, Voigt J, Junghans P. 2001 Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progr. Oceanogr.* **50**, 383–405. (doi:10.1016/S0079-6611(01)00062-3)
23. Rau GH, Sullivan CW, Gordon LI. 1991 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations in Weddell Sea particulate organic matter. *Mar. Chem.* **35**, 355–369. (doi:10.1016/S0304-4203(09)90028-7)
24. Holmes ME, Eichner C, Struck U, Wefer G. 1999 Reconstruction of surface ocean nutrient utilization using stable nitrogen isotopes in sinking particles and sediment. In *The use of proxies in paleoceanography: examples from the South Atlantic* (eds G Fischer, G Wefer), pp. 447–468. Berlin, Germany: Springer.
25. Bergmann M, Dannheim J, Bauerfield E, Klages M. 2009 Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. *Deep-Sea Res. Pt I* **156**, 408–424. (doi:10.1016/j.dsr.2008.10.004)
26. Altabet MA. 1988 Variations in nitrogen isotopic composition between sinking and suspended particles: implications for nitrogen cycling and particle transformation in the ocean. *Deep-Sea Res. Pt A* **35**, 535–554. (doi:10.1016/0198-0149(88)90130-6)
27. Haedrich RL, Merrett NR. 1988 Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *J. Nat. Hist.* **22**, 1325–1362. (doi:10.1080/00222938800770811)
28. Collins MA, Bailey DM, Ruxton GD, Priede IG. 2005 Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish. *Proc. R. Soc. B* **272**, 2051–2057. (doi:10.1098/rspb.2005.3189)
29. Hareide N-R *et al.* 2012 Irish multidisciplinary deepwater survey report 2006, 38pp. *Irish Fisheries Bulletin* 35. Marine Institute.
30. Johnston G *et al.* 2012 Irish multidisciplinary deepwater survey report 2007, 62pp. *Irish Fisheries Bulletin* 36. Marine Institute.
31. O'Hea B *et al.* 2012 Irish multidisciplinary deepwater survey report 2008, 66pp. *Irish Fisheries Bulletin* 37. Marine Institute.
32. O'Hea B *et al.* 2012 Irish multidisciplinary deepwater survey report 2009, 49pp. *Irish Fisheries Bulletin* 38. Marine Institute.
33. Mauchline J, Gordon JDM. 1986 Foraging strategies of deep-sea fish. *Mar. Ecol. Prog. Ser.* **27**, 227–238. (doi:10.3354/meps027227)
34. Froese R, Pauly D. (eds) 2013 FishBase. World Wide Web electronic publication. See <http://www.fishbase.org>, version (02/2013).
35. Neat F, Campbell N. 2013 Proliferation of elongate fishes in the deep sea. *J. Fish Biol.* **83**, 1576–1592. (doi:10.1111/jfb.12266)
36. Hoffmann J, Sutton TT. 2010 Lipid correction for carbon stable isotope analysis of deep-sea fishes. *Deep-Sea Res. Pt I* **57**, 956–964. (doi:10.1016/j.dsr.2010.05.003)
37. Jennings S, Warr KJ, Mackinson S. 2002 Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Mar. Ecol. Prog. Ser.* **240**, 11–20. (doi:10.3354/meps240011)
38. Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet M-J, Benoit E. 2009 How does abundance scale with body size in size-structured food webs? *J. Anim. Ecol.* **78**, 270–280. (doi:10.1111/j.1365-2656.2008.01466.x)
39. Minegawa M, Wada E. 1984 Stepwise enrichment ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta* **48**, 1135–1140. (doi:10.1016/0016-7037(84)90204-7)
40. McCutchan JH, Lewis Jr WM, Kendall C, McGrath CC. 2003 Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**, 378–390. (doi:10.1034/j.1600-0706.2003.12098.x)
41. Newsome SD, Clementz MT, Koch PL. 2010 Using stable isotope biogeography to study marine mammal ecology. *Mar. Mamm. Sci.* **26**, 509–572.
42. McMahon KW, Hamady LL, Thorrold SR. 2013 A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnol. Oceanogr.* **58**, 697–714. (doi:10.4319/lo.2013.58.2.0697)
43. Trueman CN, McGill RAR, Guyard PH. 2005 The effect of growth rate on tissue-diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (*Salmo salar*). *Rapid. Commun. Mass Spectrom.* **19**, 3239–3247. (doi:10.1002/rcm.2199)
44. Sutton TT *et al.* 2008 Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Res. Pt II* **55**, 161–184. (doi:10.1016/j.dsr2.2007.09.013)
45. Jones DOB, Yool A, Wei C-L, Henson S, Ruhl HA, Watson RA, Gehlen M. 2013 Global reductions in seafloor biomass in response to climate change. *Glob. Change Biol.* **20**, 1861–1872. (doi:10.11111/gcb.12480)
46. Stemmann L, Hosiá A, Youngbluth MJ, Søiland H, Picheral M, Gorsky G. 2008 Vertical distribution (0–1000 m) of macrozooplankton, estimated using the Underwater Video Profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. *Deep-Sea Res. Pt II* **55**, 94–105. (doi:10.1016/j.dsr2.2007.09.019)

47. Bathmann U, Noji TT, von Bodungen B. 1990 Copepod grazing potential in late winter in the Norwegian Sea: a factor in the control of spring phytoplankton growth? *Mar. Ecol. Prog. Ser.* **60**, 225–233. (doi:10.3354/meps060225)
48. Sameoto DD, Herman AW. 1990 Life cycle and distribution of *Calanus finmarchicus* in deep basins on the Nova Scotia shelf and seasonal changes in *Calanus* spp. *Mar. Ecol. Prog. Ser.* **66**, 225–237. (doi:10.3354/meps066225)
49. Hirsch S, Christiansen B. 2010 The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. *Mar. Ecol.* **31**, 107–120. (doi:10.1111/j.1439-0485.2010.00366.x)
50. Blanchard JL, Law R, Castle MD, Jennings S. 2010 Coupled energy pathways and the resilience of size-structured food webs. *Theor. Ecol.* **4**, 289–300. (doi:10.1007/s12080-010-0078-9)
51. Heymans JJ, Howell KL, Ayers M, Burrows MT, Gordon JDM, Jones EG, Neat F. 2010 Do we have enough information to apply the ecosystem approach to management of deep-sea fisheries? An example from the West of Scotland. *ICES J. Mar. Sci.* **68**, 265–280. (doi:10.1093/icesjms/fsq065)
52. Greenstreet SPR, Bryant AD, Broekhuizen N, Hall SJ, Heath MR. 1997 Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES J. Mar. Sci.* **54**, 243–266. (doi:10.1006/jmsc.1996.0183)
53. Ellerman AD, Convery FJ, de Perthuis C. 2010 *Pricing carbon. The European Union Emissions Trading Scheme*, p. 368. Cambridge, UK: Cambridge University Press.
54. Intercontinental Exchange. 2014 ICE Report Center, data. See <http://www.theice.com/marketdata/reports/ReportCenter.shtml#report/148>.
55. ICES. 2013 Report of the Working Group on Biology and Assessment of Deep-sea Fisheries Resources (WGDEEP), 963 pp, 14–20 March 2013, Copenhagen, Denmark. ICES CM 2013/ACOM:17.