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The trophic structure of *Spongosorites coralliophaga*-coral rubble communities at two northeast Atlantic cold water coral reefs

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ABSTRACT

We examined the isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of fauna living in association with the sponge *Spongosorites coralliophaga* colonizing coral rubble on cold-water coral reefs in the northeast Atlantic – the shallow inshore (122–131 m collection depth) Mingulay 01 area and the deep offshore (683–800 m) Logachev 02 mound. The $\delta^{15}\text{N}$ signatures of suspended particulate organic matter and three primary consumers, i.e. *Spongosorites coralliophaga*, *Reteporella beaniana* and *Parazoanthus anguicomus* were used as trophic baselines and the resulting trophic structure was compared. In both regions four trophic levels were distinguished. However, the use of *S. coralliophaga* or *R. beaniana* as baselines resulted in a skewed trophic structure due to the enriched $\delta^{15}\text{N}$ signatures of these two species on the Logachev 02 mound. Using suspended particulate organic matter and *P. anguicomus* as baselines, the Mingulay 01 area communities were characterized by elevated relative biomass of lower trophic levels compared to the Logachev 02 mound. Relative biomass of suspension/filter feeders was also higher at the Mingulay 01 area. The two regions differed significantly with regard to the prevailing environmental conditions: apart from the difference in depth and distance from shore, the Mingulay 01 area was characterized by higher primary production in surface waters, tight pelagic–benthic coupling and higher velocity of bottom currents, and it is hypothesized that these characteristics were the main drivers of the observed differences. This study highlighted that multiple trophic baselines can provide a better interpretation of food-web structure and that the use of sponges or bryozoans as baselines across bathymetric gradients should be avoided.

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Introduction

Heterotrophic ecosystems in the deep sea (defined here as regions below 200 m water depth) ultimately depend on the flux of organic matter from the upper layers of the ocean (Gage 2003 and references therein), and the quality, quantity and timing of this flux affect community composition and biomass (e.g. Billett et al. 2001, 2010; Ruhl & Smith 2004; Wei et al. 2010; Tecchio et al. 2013). Over the last 30 years, studies on the trophic structure of deep-sea benthos have greatly benefited from the use of carbon and nitrogen isotopic signatures that can provide information on both the source(s) of organic carbon (measured through $\delta^{13}\text{C}$) and species trophic level (measured through $\delta^{15}\text{N}$) (Minagawa & Wada 1984; Peterson & Fry 1987; Post 2002). In addition, isotopic signatures present space- and time-integrated information and can constitute a reliable approach for those species where direct examination of diet via stomach-content analysis is not possible

(e.g. small-sized invertebrates, organisms recovered from great depths) (Iken et al. 2001; Reid et al. 2012). Knowledge about trophic structure is necessary in order to understand important aspects of ecosystem functioning such as competition for food resources (e.g. Carlier et al. 2009; Iken et al. 2010; Lin et al. 2014) and elemental (re)cycling (Hoffmann et al. 2009; Maldonado et al. 2012; Perea-Blázquez et al. 2012; White et al. 2012; de Goeij et al. 2013).

Cold-water coral reefs are deep-sea heterotrophic ecosystems with high ecological and economical values (van Oevelen et al. 2009; Henry et al. 2013a, 2013b), but our knowledge of their trophic structure is limited even for reefs in the northeast Atlantic (Duineveld et al. 2007; van Oevelen et al. 2009), which are comparatively well studied (Roberts et al. 2006). Reef-forming cold-water coral species do not host symbiotic dinoflagellates (Roberts et al. 2006), but rely on organic matter produced in the euphotic zone (Kiriakoulakis et al. 2005; Dodds et al. 2009; Duineveld et al. 2012;

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Mueller et al. 2014) and as a result often occur in regions where processes such as down-welling and advection increase the supply of food particles to the seafloor (Duineveld et al. 2007; Davies et al. 2009).

This supply of organic matter also benefits other suspension- and filter-feeding organisms such as sponges (Duineveld et al. 2007; van Oevelen et al. 2009), which are among the most species-rich phyla on the northeast Atlantic cold-water coral reefs (van Soest & Lavaleye 2005; van Soest et al. 2007; Roberts et al. 2009). The sponges in turn often harbour species-rich epifaunal communities (e.g. Westinga & Hoetjes 1981; Çinar et al. 2002; Neves & Omena 2003; Schejter et al. 2012; Padua et al. 2013; Kazanidis et al. 2016), but to the best of our knowledge there are no studies examining the trophic structure of sponge epifaunal communities in deep-sea or shallow-water regions.

The Mingulay reef complex (outer Hebrides Sea) and the Logachev mounds (southeast Rockall Bank) are two reef settings in the northeast Atlantic which differ significantly with regard to food supply and hydrographic conditions. The Mingulay reef complex is an inshore and shallow reef setting where bottom currents are stronger (speed up to 60 cm s⁻¹) (Davies et al. 2009) than those recorded in the offshore and deep Logachev mounds (up to 30 cm s⁻¹) (Duineveld et al. 2007; Mohn et al. 2014). Both sea-surface chl-*a* concentrations (Fehling et al. 2012) and near-seabed polyunsaturated fatty acid concentrations (Kiriakoulakis et al. 2007 for the Logachev mounds; Duineveld et al. 2012 for the Mingulay reef complex) are indicative of higher productivity at the Mingulay reef complex than the Logachev mounds. In addition, down-welling at the Mingulay reef complex can transport

food particles from the ocean surface to the benthos in less than an hour (Davies et al. 2009), whereas in the Logachev mounds such a rapid vertical transport has not been reported (Duineveld et al. 2007; Mienis et al. 2007; Mohn et al. 2014).

This paper presents an analysis of the trophic structure of the community colonizing the sponge *Spongosorites coralliophaga* (Stephens, 1915) mixed with coral rubble at the Mingulay 01 area (Mingulay reef complex) and the Logachev 02 mound (Logachev mounds) (Roberts & shipboard party 2013). *Spongosorites coralliophaga* is a massive sponge (van Soest et al. 2007; Roberts et al. 2009; Roberts & shipboard party 2013), found frequently in cold-water coral reef settings in the Logachev mounds (van Soest & Lavaleye 2005) and the Mingulay reef complex (Vad 2013). Recently it was shown that *S. coralliophaga* acts as a settlement surface for several species (Kazanidis et al. 2016). The average abundance of individuals living attached to *S. coralliophaga* in the Mingulay 01 area was ~3 individuals cm⁻³ sponge while lower values were found for the epifauna living attached on coral rubble in that region or on sponge/coral rubble on the Logachev 02 mound (Kazanidis et al. 2016).

In the present study, (a) the number of trophic levels and (b) the relative distribution of biomass across trophic levels in the Mingulay 01 area and the Logachev 02 mound were investigated using isotopic signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of epifaunal species. The relative distribution of biomass across feeding types was also studied for each of the two regions. Multiple trophic baselines (i.e. suspended particulate organic matter and three primary consumers) were used in order to examine the role of trophic baseline in the trophic structure (Chouvelon et al. 2012; Lorrain et al. 2015). It is well known that differences in food supply and hydrographic conditions can affect the trophic structure of benthic communities (e.g. Bergmann et al. 2009; Iken et al. 2010; Feder et al. 2011; Tecchio et al. 2013; Lin et al. 2014). We hypothesize that higher food supply and higher bottom-current speeds at the Mingulay reef complex result in a relatively higher biomass of suspension/filter feeders and relatively higher biomass assembled in the lower trophic levels than observed at the Logachev mounds.

Materials and methods

Description of the study areas

During the 'Changing Oceans' expedition in May/June 2012 on board the Royal Research Ship (RRS) *James Cook* (Cruise JC073) (Roberts & shipboard party 2013),

Table 1. Coordinates and depth of locations where *Spongosorites coralliophaga*-coral rubble assemblages were collected in the Mingulay 01 area (Mingulay reef complex, MRC) and the Logachev 02 mound (Logachev mounds, LM). The ratio of dry sponge (S) volume/coral rubble (CR) volume is also given; the methodology followed for measuring these volumes is given in Kazanidis et al. (2016).

Location	Depth (m)	Latitude (decimal degrees, N)	Longitude (decimal degrees, W)	S/CR
MRC	127	56.8231	7.3949	0.127
	128	56.8232	7.3949	0.148
	127	56.8231	7.3949	0.126
	131	56.8230	7.3950	0.149
	122	56.8228	7.3947	0.091
	128	56.8232	7.3950	0.036
	128	56.8232	7.3949	0.171
	131	56.8223	7.3940	0.159
	131	56.8225	7.3936	0.284
	LM	800	55.4943	15.8202
683		55.4943	15.8186	0.219
683		55.4943	15.8186	0.187
683		55.4943	15.8186	0.035

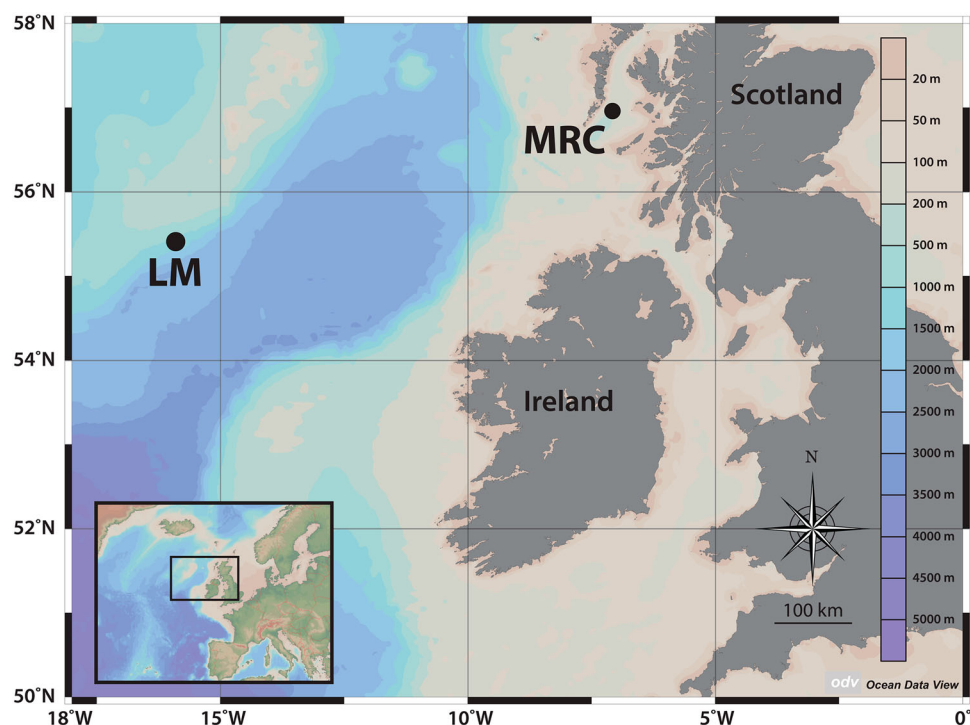


Figure 1. Sites of sample collection. Mingulay 01 area (Mingulay reef complex, MRC) and Logachev 02 mound (Logachev mounds, LM) in the northeast Atlantic.

specimens of *Spongosorites coralliophaga* that had colonized coral rubble and their associated fauna were collected from two locations in the northeast Atlantic: the Mingulay 01 area (Mingulay reef complex; 122–131 m depth of sample collection) and the Logachev 02 mound (Logachev mounds; 683–800 m depth of sample collection) (Figure 1, Table I). The Mingulay reef complex comprises live coral reef areas at 120–190 m depth in the Outer Hebrides Sea with the main coral species being the scleractinian *Lophelia pertusa* (Linnaeus, 1758) (Roberts et al. 2005, 2009). Studies on the hydrography of this area have shown a south-southwest to north-northeast direction in both surface and bottom flows as well as that rapid down-welling of surface water and advection of deep bottom water are major mechanisms supplying the reef benthos with food particles (Davies et al. 2009; Roberts et al. 2009; Duineveld et al. 2012; Findlay et al. 2014; Moreno Navas et al. 2014). The Logachev mounds are offshore carbonated mounds on the southeast Rockall Bank and they exist between 500 and 1200 m water depth (Van Weering et al. 2003; Mienis et al. 2006; Wheeler et al. 2007). They form a complex setting of mound clusters whose diameters range from hundreds of metres to a few kilometres (Wheeler et al. 2007). The Logachev 02 mound (Roberts & shipboard party 2013) is a large carbonated structure (6 km long) and it is separated from the main

clusters of Logachev mounds by up to 4 km (Roberts & shipboard party 2013).

The main coral species in the Logachev mounds are the scleractinians *L. pertusa* and *Madrepora oculata* Linnaeus, 1758 (van Weering et al. 2003; Duineveld et al. 2007). Studies on the hydrography of the region have shown the important role of advection in supplying the reef communities with food (Duineveld et al. 2007); in addition, recent modelling studies have revealed the important role that the carbonate mound structure plays in promoting local vertical mixing and the supply of organic matter to the benthic communities (Mohn et al. 2014).

Collection of samples

Being large in size and yellow in colour (see figure 2 in Kazanidis et al. 2016), the specimens of *Spongosorites coralliophaga* were easily spotted during surveys using the remotely operated vehicle (ROV) *Holland I*. The collection of samples took place randomly and was carried out using the ROV manipulator arm. The scale of spacing between samples within each region ranged from a few metres up to a few hundreds of metres. Nine sponge–coral rubble assemblages were collected from the Mingulay 01 area and four from the Logachev 02 mound. After their collection, the *S. coralliophaga*–coral rubble assemblages and their epifauna were carefully

transferred to the ROV biobox – a storage box that closes once withdrawn beneath the ROV – where they were kept until the return to the surface.

Sample storage and assignment of feeding types

The tight sampling schedule did not allow for immediate taxonomic identification and the collected fauna was therefore preserved in 10% seawater formalin as in previous studies (Demopoulos et al. 2007; Mayor et al. 2012; Jeffreys et al. 2013). Formalin preservation was chosen because freezing often results in the break-off of specimens, thus preventing the classification at the lowest-possible taxonomic level required in this study (Fanelli et al. 2010). While we acknowledge the potential effect of formalin preservation on isotopic signatures, the outcome of systematic studies addressing this issue across various marine organisms is rather inconsistent (e.g. Sarakinos et al. 2002; Fanelli et al. 2010; Syvaranta et al. 2011). In addition, effects on faunal isotopic signatures have been reported even for freezing, i.e. the commonest sample preservation method before stable isotope analysis (Feuchtmayr & Grey 2003; Syvaranta et al. 2011; Liu et al. 2013). Clearly, species-specific studies are necessary in order to evaluate the exact effects of formalin preservation on faunal isotopic signatures (Kelly et al. 2006; Bicknell et al. 2011; Xu et al. 2011a; Gonzalez-Bergonzoni et al. 2015). Information on the possible effects of formalin preservation on the isotopic signatures of fauna from deep-sea regions is even more limited (Fanelli et al. 2010). In addition, studies about taxonomic groups common both in shallow-water and deep-sea regions (e.g. sponges, cnidarians, echinoderms, ascidians) are absent. Under these circumstances, we chose to address the problem through the correction of $\delta^{13}\text{C}$ signatures (by adding 1‰ to each $\delta^{13}\text{C}$ signature) as in previous studies (Demopoulos et al. 2007; Sweetman & Witte 2008; Gontikaki et al. 2011; Hunter et al. 2012). This correction factor for $\delta^{13}\text{C}$ signatures is in agreement with previous studies mentioning a decrease up to 1‰ due to formalin preservation (Bosley & Wainright 1999; Edwards et al. 2002; Sarakinos et al. 2002; Syvaranta et al. 2008; Bicknell et al. 2011; de Lecea et al. 2011; Xu et al. 2011a; Lau et al. 2012; Rennie et al. 2012; Liu et al. 2013; Gonzalez-Bergonzoni et al. 2015). Furthermore, previous studies have shown that the effects of formalin preservation on $\delta^{15}\text{N}$ signatures were minor compared to the generally accepted trophic shift between successive trophic levels (i.e. 3.4‰, Post 2002), enabling the accurate allocation of species preserved in formalin to

trophic levels (Bosley & Wainright 1999; Sarakinos et al. 2002; Fanelli et al. 2010; Ruiz-Cooley et al. 2011; Rennie et al. 2012; Lau et al. 2012; Liu et al. 2013).

Following taxonomic identification, each species was categorized as belonging to a feeding type (i.e. suspension/filter feeders, omnivores, predators, deposit feeders/grazers) based mainly on information available in Henry et al. (2013b). Additional information was collected from Tyler et al. (1995), Boos et al. (2010) (ophiurids), Ericsson & Hansson (1973) (asteroids), Carlier et al. (2009) (echinoids), Vader (1983) (amphipods), Fauchald & Jumars (1979), Carrasco & Oyarzun (1988), Nash & Keegan (2003), Neves & Omena (2003) (polychaetes), Hayward et al. (1995) (gastropods), Nielsen & Riisgard (1998) and Bader & Schafer (2005) (bryozoans). For 15 specimens the characterization of their feeding type was not possible due to the lack of sufficient taxonomic resolution and/or the lack of information on their diet.

Processing of samples and stable isotope analysis

Fauna samples were dried at 60°C for 48 h and measurements of their dry weight were carried out (± 0.01 mg) (Kazanidis et al. 2016). After drying, samples were ground and subjected to a preliminary acidification test (using a few drops of 1 M hydrochloric acid) (Jaschinski et al. 2008; Vafeiadou et al. 2013) in order to identify the species with carbonate structures. In order to account for the optimum amount of dry matter (mg) to be placed in the silver/tin capsules for dual isotopic signatures analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), acidified and non-acidified species were analysed for organic carbon (OC) and organic nitrogen (ON) content (as % of dry mass). Species with carbonate structures were subsequently divided into two groups of subsamples. The first group was not acidified and the second was acidified through the sequential addition of 15 μl of 1 M hydrochloric acid inside the silver capsules. The cessation of the effervescence was used as the criterion that carbonates had been removed (Vafeiadou et al. 2013 and references therein). All samples were then dried at 60°C overnight. No washing with distilled water was carried out (Mateo et al. 2008).

Samples were analysed for carbon and nitrogen isotopes at the University of California Davis Stable Isotopes Facility using an Elementar Micro Cube Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK). Samples were combusted at 1000°C in a reactor packed with tungsten oxide. During analysis, samples

were interspersed with several replicates of at least five laboratory standards that had been previously calibrated against international isotope standards. The long-term standard deviation is 0.2‰ for carbon and 0.3‰ for nitrogen. In the present study $\delta^{13}\text{C}$ signatures of acidified samples and $\delta^{15}\text{N}$ signatures of non-acidified samples were used; this was done in order to avoid the possible effects of acidification on $\delta^{15}\text{N}$ signatures and thus on the trophic structure of the epifaunal community.

Total organic carbon and total organic nitrogen was calculated for each species, as well as across feeding types and trophic levels in the Mingulay 01 area and the Logachev 02 mound. Whenever possible (e.g. for molluscs, brachiopods, the sea urchin *Cidaris cidaris* (Linnaeus, 1758)), the soft tissues were separated from the calcareous structure and dry mass weight was used in the calculation of organic matter.

Trophic baselines

The calculation of the trophic level of secondary consumers was carried out using multiple trophic baselines aiming to gain a better understanding of the trophic structure (Chouvelon et al. 2012; Lorrain et al. 2015). The calculation of trophic level (TL) was carried out using the average $\delta^{15}\text{N}$ signatures of suspended particulate organic matter and three primary consumers (following Iken et al. 2010). The following equations were used:

$$\text{TL}_{(\text{SPOM})} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{SPOM}})/3.4 + 1$$

and

$$\text{TL}_{(\text{PC})} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{primary consumer}})/3.4 + 2,$$

where 3.4‰ is the generally accepted trophic shift factor for aquatic consumers (Post 2002). $\text{TL}_{(\text{PC})}$ was calculated using as baseline the average $\delta^{15}\text{N}$ signatures of the primary consumers *Spongosorites coralliophaga* (Porifera), *Reteporella beaniana* (King, 1846) (Bryozoa) and *Parazoanthus anguicomus* (Norman, 1868) (Anthozoa) as each of these three primary consumers was collected both from the Mingulay 01 area and the Logachev 02 mound. $\text{TL}_{(\text{SPOM})}$ was calculated using as a trophic baseline the average $\delta^{15}\text{N}$ signature of suspended particulate organic matter collected close to the sea surface and/or a few metres above the seafloor. The average $\delta^{15}\text{N}$ signatures of suspended particulate organic matter used in the present study (5.9‰ for surface and 6.6‰ for bottom suspended particulate organic matter from Mingulay; 4.5‰ for bottom suspended particulate

organic matter on the southeast Rockall Bank) were found in table 5 in Duineveld et al. (2012) and table 2 in Duineveld et al. (2007).

Statistical analysis

Isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of four species common in the Mingulay 01 area and the Logachev 02 mound, i.e. *Spongosorites coralliophaga*, *Parazoanthus anguicomus*, *Eunice dubitata* Fauchald, 1974 and Syllidae sp., were compared between the two regions. The normality of the distributions was checked with the Shapiro–Wilk test. In the case of normal distributions and equal variances, the existence of significant differences was tested with the two-sample *t* test; in the case of normal distributions and unequal variances the Welch's two-sample *t* test was used, while in the case of non-normal distributions a Wilcoxon rank sum test was carried out (following Reid et al. 2012; Kazanidis et al. 2016). Examination of differences was carried out in the statistical analysis environment R (R Core Team 2013).

Results

Stable isotopes

In the Mingulay 01 area the isotopic signatures of 45 species were examined. The $\delta^{13}\text{C}$ signatures ranged from -22.27‰ in the sponge *Haliclona (Haliclona) urceolus* (Rathke & Vahl, 1806) up to -11.65‰ in the asteroid *Porania (Porania) pulvillus* (O.F. Müller, 1776). Most $\delta^{13}\text{C}$ signatures were between -20 and -18‰ (Table II, Figure 2(a)). The $\delta^{15}\text{N}$ signatures ranged from 6.35‰ in the bivalve *Heteranomia squamula* (Linnaeus, 1758) up to 14.49‰ in the polychaete *Eunice pennata* (Müller, 1776) (Table II, Figure 2(a)).

On the Logachev 02 mound the isotopic signatures of 36 species were investigated. The minimum $\delta^{13}\text{C}$ signature (-23.04‰) was found in the bryozoan *Reteporella beaniana* and the maximum (-15.64‰) in the anthozoan *Paraedwardsia sarsii* (Dueben & Koren, 1847). Most of the $\delta^{13}\text{C}$ signatures were between -20 and -18‰ (Table II, Figure 2(b)). The $\delta^{15}\text{N}$ signatures ranged from 7.60‰ in the hydrozoan *Zygophylax pinnata* (Sars, 1874) up to 14.33‰ in the gastropod *Diodora graeca* (Linnaeus, 1758) (Table II, Figure 2(b)).

Intraspecific comparison of $\delta^{13}\text{C}$ signatures between the Mingulay 01 area and the Logachev 02 mound revealed significant differences for *Spongosorites coralliophaga* (Wilcoxon rank sum test = 32, $P = 0.033$) and Syllidae sp. (two-sample *t* test = -3.3818 , $P = 0.019$). In terms of $\delta^{15}\text{N}$

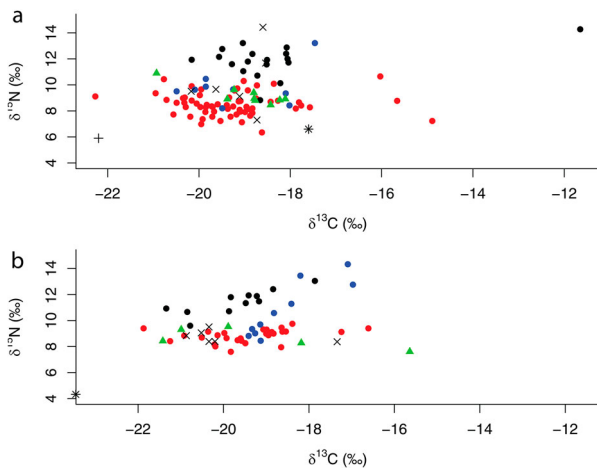


Figure 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of suspension/filter feeders (•, red circles), deposit feeders/grazers (•, blue circles), predators (•, black circles), omnivores (▲, green triangles) and unknown feeding type specimens (×) in the Mingulay 01 area (a) and the Logachev 02 mound (b) in the northeast Atlantic. Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of surface (+) and bottom (*) suspended particulate organic matter in the Mingulay were found in table 5 in Duineveld et al. (2012) while average $\delta^{15}\text{N}$ value of bottom suspended particulate organic matter in southeast Rockall Bank was found in table 2 in Duineveld et al. (2007). Please note that the $\delta^{13}\text{C}$ signatures of either surface or bottom suspended particulate organic matter at the southeast Rockall Bank are not available.

signatures, *S. coralliophaga* was the only species that showed significant differences between the Mingulay 01 area and the Logachev 02 mound (two-sample t test = 5.4453, $P < 0.001$).

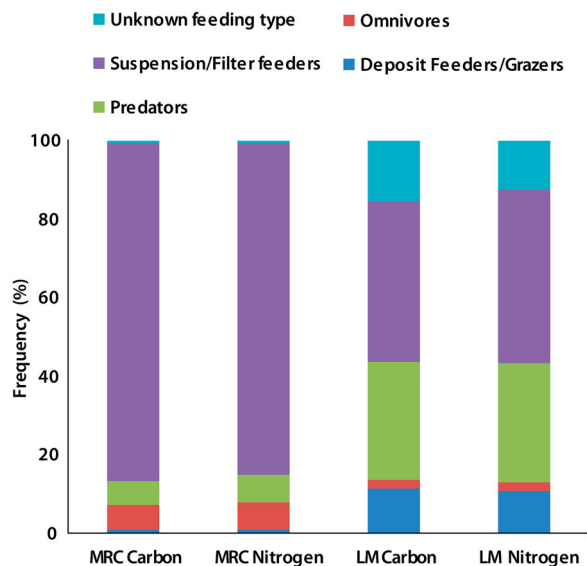


Figure 3. Distribution of epifaunal biomass (organic carbon, organic nitrogen) across feeding types at the Mingulay 01 area (Mingulay reef complex, MRC) and the Logachev 02 mound (Logachev mounds, LM) in the northeast Atlantic.

Relative distribution of biomass across feeding types

The relative distribution of biomass across feeding types differed between the two reef complexes, with the proportion of biomass of suspension/filter feeders at the Mingulay 01 area being almost double that at the Logachev 02 mound (Figure 3). At the Mingulay 01 area, the relative biomass of predators and omnivores was similar, whereas predators were more important at the Logachev 02 mound (Figure 3).

Relative distribution of species numbers and biomass across trophic levels

In both regions, four trophic levels were identified. However, as can be seen in Figure 4, the distribution of species numbers and biomass across those levels (2, 3, 4) greatly depended on the baseline used. In the Mingulay 01 area two different patterns emerged, related to the use of suspended particulate organic matter vs. any of the three primary consumers. Interestingly, for the Logachev 02 mound there was a clear distinction between the use of either *Reteporella beaniana* or *Spongosorites coralliophaga* vs. *Parazoanthus anguicomus* or suspended particulate organic matter.

Discussion

The matter of the trophic baseline

The $\delta^{15}\text{N}$ signatures of suspended or sedimented particulate organic matter have traditionally been used as a baseline for the calculation of species trophic level (e.g. Grall et al. 2006; Iken et al. 2010; Divine et al. 2015); however, the high nitrogen turnover rates of primary producers have led to high spatial and temporal variability in their $\delta^{15}\text{N}$ signatures, which has complicated trophic level calculations and comparisons between regions; as a response to this, the use of long-lived primary consumers as trophic baselines has been suggested due to the smaller spatial/temporal variability in their $\delta^{15}\text{N}$ signatures compared to those of primary producers (Cabana & Rasmussen 1996; Vander Zanden & Rasmussen 1999; Post 2002; Vander Zanden & Fetzer 2007). However, studies published more recently than those mentioning the usefulness of primary consumers as trophic baselines revealed substantial variability in $\delta^{15}\text{N}$ signatures of primary consumers both at intraspecific (Howard et al. 2005; McIntyre & Flecker 2006; Guzzo et al. 2011; Magni et al. 2013) and interspecific levels (Kohzu et al. 2009; Xu et al. 2011b). As a way forward, the simultaneous use of multiple trophic baselines

Table II. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures of fauna living in association with *Spongosorites coralliophaga* and underlying coral rubble in the Mingulay 01 area and the Logachev 02 mound in northeast Atlantic.

Taxonomic groups	FT	TL		$\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	<i>n</i>	$\delta^{15}\text{N} \pm \text{SD} (\text{‰})$	<i>n</i>
		S/R/P/SSP/BSP					
Mingulay 01 area (Mingulay reef complex)							
Porifera							
<i>Spongosorites coralliophaga</i> (Stephens, 1915)	S/F	2.0/1.8/1.8/1.7/1.4		-18.93 ± 1.27	9	8.12 ± 0.44	9
<i>Haliclona (Haliclona) urceolus</i> (Rathke & Vahl, 1806)	S/F	2.4/2.2/2.2/2.0/1.8		-21.13 ± 1.07	3	9.46 ± 0.40	3
<i>Poecillastra compressa</i> (Bowerbank, 1866)	S/F	2.5/2.3/2.3/2.1/1.9		-20.54 ± 0.32	2	9.73 ± 0.99	2
Porifera indet.	U	3.0/2.9/2.9/2.7/2.5		-18.54	1	11.68	1
Hydrozoa							
<i>Halecium</i> sp.	S/F	1.8/1.7/1.7/1.5/1.3		-19.29 ± 0.94	6	7.57 ± 0.39	6
<i>Rosalinda williami</i> Totton, 1949	S/F	1.7/1.5/1.5/1.3/1.1		-19.95	1	6.98	1
<i>Zanclaea sessilis</i> (Gosse, 1853)	S/F	1.9/1.7/1.7/1.5/1.3		-20.56	1	7.73	1
<i>Halecium muricatum</i> (Ellis & Solander, 1786)	S/F	2.3/2.1/2.1/1.9/1.7		-20.35	1	8.97	1
<i>Halecium labrosum</i> Alder, 1859	S/F	1.9/1.7/1.7/1.5/1.3		-19.18	1	7.73	1
Anthozoa							
<i>Parazoanthus anguicomus</i> (Norman, 1868)	S/F	2.2/2.0/2.0/1.8/1.6		-19.99 ± 0.23	9	8.64 ± 0.50	6
<i>Edwardsiella carnea</i> (Gosse, 1856)	O	2.8/2.6/2.7/2.5/2.3		-20.93	1	10.90	1
Anthozoa indet.	U	2.3/2.1/2.1/1.9/1.7		-19.11	1	9.12	1
Nematoda							
Nematoda indet.	U	1.7/1.5/1.5/1.3/1.1		-18.73	1	6.95 ± 0.50	2
Polychaeta							
<i>Eunice dubitata</i> Fauchald, 1974	P	3.1/2.9/2.9/2.8/2.5		-19.14 ± 0.85	4	11.86 ± 0.77	4
<i>Haplosyllis spongicola</i> (Grube, 1855)	P	2.8/2.7/2.7/2.5/2.3		-18.88 ± 0.07	2	10.95 ± 1.99	3
<i>Trypanosyllis zebra</i> (Grube, 1860)	P	3.3/3.1/3.1/2.9/2.7		-18.09	1	12.40	1
<i>Euphrosine borealis</i> Örsted, 1843	P	3.4/3.2/3.2/3.0/2.8		-19.49	1	12.76	1
cf <i>Fimbriosthenelais zetlandica</i> (McIntosh, 1876)	P	3.2/3.0/3.0/2.8/2.6		-18.81 ± 1.06	2	12.08 ± 0.10	2
Sigalionidae sp.	P	2.7/2.5/2.6/2.4/2.2		-18.43 ± 0.29	5	10.59 ± 1.18	5
<i>Serpula vermicularis</i> Linnaeus, 1767	S/F	2.3/2.1/2.2/2.0/1.8		-18.50 ± 1.40	5	9.21 ± 0.95	5
<i>Lepidonotus</i> sp.	P	3.1/2.9/3.0/2.8/2.6		-18.51	1	11.92	1
<i>Branchiomma bombyx</i> (Dalyell, 1853)	S/F	2.1/1.9/1.9/1.7/1.5		-19.36 ± 0.51	3	8.31 ± 0.13	3
<i>Bispira volutacornis</i> (Montagu, 1804)	S/F	2.2/2.0/2.0/1.9/1.6		-19.95 ± 0.47	4	8.79 ± 0.41	4
<i>Eunice pennata</i> (Müller, 1776)	P	3.5/3.3/3.3/3.2/2.9		-19.04	1	13.22	1
<i>Nereimyra punctata</i> (Müller, 1788)	O	2.4/2.2/2.2/2.0/1.8		-19.14 ± 0.30	3	9.31 ± 0.37	3
cf Sabellidae sp.	U	3.9/3.7/3.7/3.5/3.3		-18.60	1	14.43	1
Terebellidae sp.	U	2.5/2.3/2.3/2.1/1.9		-19.63	1	9.66	1
Crustacea							
<i>Aristias neglectus</i> Hansen, 1888	D	2.5/2.3/2.4/2.2/2.0		-20.25 ± 0.54	8	9.87 ± 0.52	3
<i>Janira maculosa</i> Leach, 1814	D	2.5/2.3/2.3/2.1/1.9		-19.82 ± 0.04	2	9.78 ± 0.13	2
<i>Galathea strigosa</i> (Linnaeus, 1761)	D	2.2/2.0/2.1/1.9/1.7		-18.93 ± 1.03	4	8.90 ± 0.70	4
<i>Scalpellum scalpellum</i> (Linnaeus, 1767)	S/F	2.2/2.0/2.1/1.9/1.7		-20.43 ± 0.39	2	8.83 ± 0.03	2
Mollusca							
<i>Hiatella arctica</i> (Linnaeus, 1767)	S/F	2.1/1.9/1.9/1.7/1.5		-17.82 ± 0.06	3	8.41 ± 0.24	3
<i>Modiolula phaseolina</i> (Philippi, 1844)	S/F	1.7/1.5/1.6/1.4/1.2		-14.89	1	7.21 ± 0.26	3
<i>Heteranomia squamula</i> (Linnaeus, 1758)	S/F	1.5/1.3/1.3/1.1/0.9		-18.62	1	6.35	1
<i>Palliolum striatum</i> (O.F. Müller, 1776)	S/F	1.9/1.8/1.8/1.6/1.4		-19.09	1	7.95	1
<i>Emarginula fissura</i> (Linnaeus, 1758)	D/G	3.5/3.3/3.3/3.2/2.9		-17.46	1	13.22	1
Nudibranchia indet.	U	2.4/2.2/2.3/2.1/1.9		-20.17	1	9.51	1
Bryozoa							
Candidae sp.	S/F	1.9/1.7/1.7/1.5/1.3		-18.94 ± 0.15	3	7.64 ± 0.62	5
<i>Chartella barleei</i> (Busk, 1860)	S/F	2.1/1.9/1.9/1.8/1.5		-19.39 ± 0.62	4	8.45 ± 0.44	3
<i>Reteporella beaniana</i> (King, 1846)	S/F	2.2/2.0/2.0/1.8/1.6		N/A		8.74	1
<i>Disporella hispida</i> (Fleming, 1828)	S/F	1.7/1.6/1.6/1.4/1.2		N/A		7.24	1
Brachiopoda							
<i>Terebratulina retusa</i> (Linnaeus, 1758)	S/F	3.3/3.1/3.1/2.9/2.7		N/A		12.38	1
Echinodermata							
<i>Ophiura ophiura</i> (Linnaeus, 1758)	O	2.2/2.0/2.0/1.9/1.6		-18.57 ± 0.36	11	8.79 ± 0.20	5
<i>Ophiothrix fragilis</i> (Abildgaard, in O.F. Müller, 1798)	S/F	2.3/2.1/2.2/2.0/1.8		-18.64 ± 0.85	7	9.19 ± 0.78	3
<i>Porania pulvillus</i> (O.F. Müller, 1776)	P	3.8/3.6/3.7/3.5/3.3		-11.65	1	14.28	1
Ascidiacea							
<i>Polycarpa pomaria</i>	S/F	2.4/2.2/2.3/2.1/1.9		-19.10 ± 0.33	6	9.58 ± 0.76	5
Logachev 02 mound (Logachev mounds)							
Porifera							
<i>Spongosorites coralliophaga</i> (Stephens, 1915)	S/F	2.0/2.1/2.3/2.4		-17.72 ± 0.96	4	9.43 ± 0.26	4
Hydrozoa							
<i>Zygophylax pinnata</i> (Sars, 1874)	S/F	1.5/1.6/1.8/1.9		-19.83	1	7.60	1
<i>Acryptolaria conferta</i> (Allman, 1877)	S/F	1.8/1.9/2.1/2.3		-20.92	1	8.84	1
Anthozoa							
<i>Parazoanthus anguicomus</i> (Norman, 1868)	S/F	1.7/1.8/2.0/2.2		-20.21 ± 0.29	3	8.45 ± 0.38	3
<i>Paraedwardsia sarsii</i> (Dueben & Koren, 1847)	O	1.5/1.6/1.8/1.9		-15.64	1	7.61	1
<i>Corynactis viridis</i> Allman, 1846	U	1.8/1.9/2.1/2.3		-20.87	1	8.84	1

(Continued)

Table II. Continued.

Taxonomic groups	FT	TL		$\delta^{13}\text{C} \pm \text{SD} (\text{‰})$	n	$\delta^{15}\text{N} \pm \text{SD} (\text{‰})$	n
		S/R/P/SSP/BSP					
<i>cf Edwardsiella loveni</i> (Calgren, 1892)	O	1.7/1.8/2.0/2.2		-21.42	1	8.43	1
<i>Telestula</i> sp.	U	1.8/1.9/2.1/2.2		N/A		8.74	1
Polychaeta							
<i>Eunice dubitata</i> Fauchald, 1974	P	2.7/2.8/3.0/3.1		-19.69 \pm 1.12	4	11.69 \pm 0.63	4
<i>Haplosyllis spongicola</i> (Grube, 1855)	P	2.4/2.5/2.7/2.8		-20.85	1	10.66	1
<i>Trypanosyllis zebra</i> (Grube, 1860)	P	2.7/2.8/3.0/3.1		-19.83	1	11.79	1
<i>Myrianida</i> sp.	O	2.0/2.1/2.3/2.4		-20.99	1	9.31	1
Syllidae sp.	U	2.6/2.7/2.9/3.0		-19.48	1	11.34	1
<i>Euphrosine cf borealis</i> Örsted, 1843	P	3.1/3.2/3.4/3.5		-17.86	1	13.05	1
Sigalionidae sp.	O	2.0/2.1/2.3/2.5		-19.89	1	9.53	1
<i>cf Leocrates atlanticus</i> (McIntosh, 1885)	U	1.8/1.9/2.1/2.2		-20.43 \pm 0.13	2	8.72 \pm 0.47	2
<i>cf Notophyllum foliosum</i> (Sars, 1835)	P	2.5/2.6/2.8/3.0		-19.55 \pm 0.46	2	11.29 \pm 0.83	2
<i>cf Aphroditidae</i> sp.	U	2.0/2.1/2.3/2.5		-20.34	1	9.51	1
<i>Lumbrineris tetraura</i> (Schmarda, 1861)	P	2.1/2.1/2.3/2.5		-20.78	1	9.60	1
Crustacea							
<i>Janira maculosa</i> Leach, 1814	D/G	1.9/2.0/2.2/2.4		N/A		9.25	1
Mollusca							
<i>Asperarca nodulosa</i> juveniles	S/F	1.6/1.7/1.9/2.0		-18.65	1	7.95 \pm 0.13	2
<i>Asperarca nodulosa</i> (O.F. Müller, 1776)	S/F	1.9/2.0/2.2/2.3		-18.85 \pm 0.18	8	9.06 \pm 0.14	8
<i>Karnekampia sulcata</i> (Müller, 1776)	S/F	1.8/1.8/2.0/2.2		-19.43 \pm 0.31	4	8.58 \pm 0.41	5
<i>Delectopecten vitreus</i> (Gmelin, 1791)	S/F	1.8/1.9/2.0/2.2		-19.93 \pm 0.31	3	8.61 \pm 0.44	3
<i>Lima marioni</i> Fischer, 1882	S/F	1.9/2.0/2.2/2.4		-20.36	1	9.15	1
<i>Puncturella noachina</i> (Linnaeus, 1771)	D/G	2.5/2.6/2.8/2.9		-18.34 \pm 0.96	4	11.08 \pm 1.29	4
<i>Berthella</i> sp.	U	2.4/2.4/2.6/2.8		N/A		10.63	1
<i>cf Diodora graeca</i> (Linnaeus, 1758)	D/G	3.4/3.5/3.7/3.9		-17.09	1	14.33	1
<i>Solenogastres</i> sp.	U	1.7/1.8/2.0/2.1		-18.77 \pm 2.03	2	8.38 \pm 0.02	2
<i>cf Tonicella marmorea</i> (O. Fabricius, 1780)	D/G	3.2/3.3/3.5/3.6		-18.20	1	13.45	1
Bryozoa							
<i>Reteporella beaniana</i> (King, 1846)	S/F	1.9/2.0/2.2/2.4		-22.15 \pm 1.26	2	9.11 \pm 0.99	2
Brachiopoda							
<i>Terebratulina septentrionalis</i> (Couthouy, 1838)	S/F	2.4/2.5/2.7/2.8		N/A		10.74 \pm 0.98	2
Echinodermata							
<i>Ophiura ophiura</i> (Linnaeus, 1758)	O	1.7/1.8/2.0/2.1		-18.18	1	8.28	1
<i>Ophioctenella acies</i> juveniles	D/G	1.9/2.0/2.2/2.3		-19.26	1	9.02	1
<i>Ophioctenella acies</i> Tyler, Sibuet, Guille, Murton & Segonzac, 1995	D/G	1.9/2.0/2.2/2.4		-19.06 \pm 0.34	5	9.15 \pm 0.47	6
<i>cf Goniasteridae</i> sp.	U	2.5/2.6/2.7/2.9		N/A		10.98	1
<i>Cidaris cidaris</i> (Linnaeus, 1758)	D/G	3.0/3.1/3.3/3.4		N/A		12.82	1
Holothuroidea indet.	U	1.6/1.7/1.9/2.1		N/A		8.18	1
Asciacea							
<i>Ascidia mentula</i> Müller, 1776	S/F	1.9/2.0/2.2/2.4		-21.01 \pm 1.23	2	9.13 \pm 0.37	2

Notes: FT, feeding type; S/F, suspension/filter feeder; D/G, deposit feeder/grazer; O, omnivore; P, predator; U, unknown feeding type; TL, trophic level using *Spongosorites coralliophaga*/*Reteporella beaniana*/*Parazoanthus anguicomus*/surface suspended particulate organic matter/bottom suspended particulate organic matter as a trophic baseline. Average $\delta^{15}\text{N}$ signatures of surface and bottom suspended particulate organic matter in the Mingulay reef complex were found in table 5 in Duineveld et al. (2012) while the average $\delta^{15}\text{N}$ signature of bottom suspended particulate organic matter in the southeast Rockall Bank was found in table 2 in Duineveld et al. (2007). Calculation of trophic levels using the $\delta^{15}\text{N}$ signature of surface suspended particulate organic matter was carried out only for the Mingulay 01 area because $\delta^{15}\text{N}$ for surface suspended particulate organic matter at the southeast Rockall Bank is not available. n , number of replicates for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. Mean values and standard deviations are given.

(i.e. the use of more than one primary consumer, primary consumers and suspended or sedimented particulate organic matter) has been suggested as an approach to facilitate a better assessment of species trophic level (Iken et al. 2010; Chouvelon et al. 2012; Mancinelli et al. 2013; Lorrain et al. 2015).

In both reef complexes investigated here, the indicated trophic structure was dependent on the baseline used. In the Mingulay 01 area the use of primary consumers resulted in most of the species/biomass being allocated to the third trophic level while the use of surface or bottom suspended particulate organic matter resulted in most of them being found in the second trophic level. This was probably a response to trophic-shift factor(s) lower than 3.4‰ (McCutchan

et al. 2003; Alp et al. 2013; Dodds et al. 2014; Hussey et al. 2014) or relatively enriched (i.e. higher) $\delta^{15}\text{N}$ signatures of suspended particulate organic matter due to regional patterns of nitrogen biogeochemistry (Peipoch et al. 2012; Wang et al. 2013) and/or terrestrial run-offs (Kohzu et al. 2009; Magni et al. 2013). In contrast to the Mingulay 01 area, species/biomass found in the second trophic level of the Logachev 02 mound when primary consumers were used as a baseline were higher than those measured using suspended particulate organic matter. This finding was probably due to the relatively low $\delta^{15}\text{N}$ signature of suspended particulate organic matter for the Logachev 02 mound (Duineveld et al. 2007), trophic-shift factor(s) (see above) and/or enriched $\delta^{15}\text{N}$ signatures of

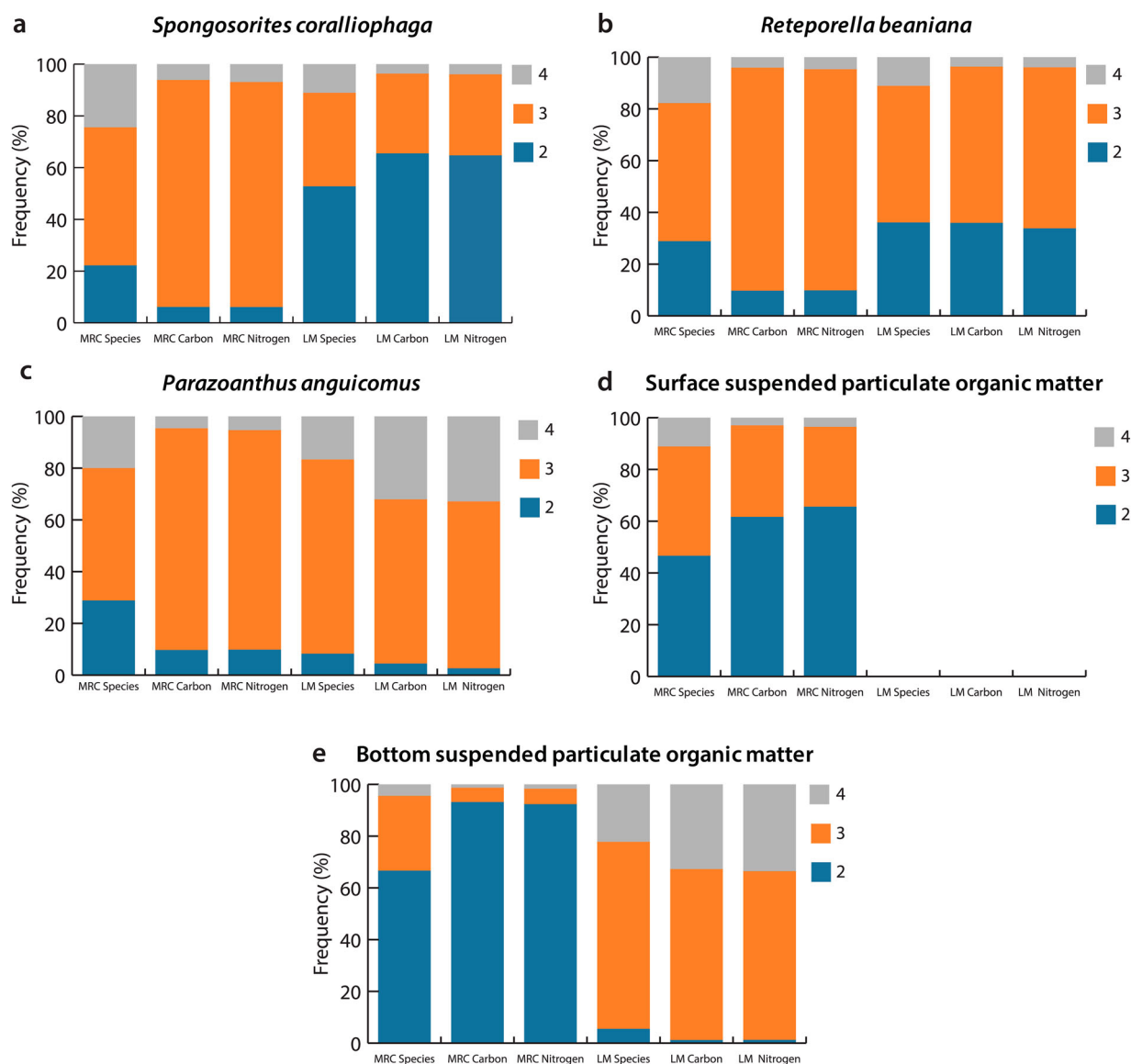


Figure 4. Distribution of epifaunal species and biomass across the second, third and fourth trophic level in the Mingulay 01 area (Mingulay reef complex, MRC) and the Logachev 02 mound (Logachev mounds, LM) in the northeast Atlantic using the average $\delta^{15}\text{N}$ signatures of primary consumers and surface/bottom suspended particulate organic matter as trophic baselines. The average $\delta^{15}\text{N}$ signatures of surface and bottom suspended particulate organic matter in the Mingulay were found in table 5 in Duineveld et al. (2012) and the average $\delta^{15}\text{N}$ signature of bottom suspended particulate organic matter in southeast Rockall Bank was found in table 2 in Duineveld et al. (2007). Please note that the $\delta^{13}\text{C}$ signatures of either surface or bottom suspended particulate organic matter at the southeast Rockall Bank are not available.

Spongosorites coralliophaga and *Reteporella beaniana*. Furthermore, the use of *S. coralliophaga* or *R. beaniana* as baselines did not show any differences between the Mingulay 01 area and the Logachev 02 mound. On the contrary, when using suspended particulate organic matter or *Parazoanthus anguicomus* as a baseline, a clear difference was recorded, i.e. more biomass was found on the fourth trophic level of the Logachev 02 mound than at the Mingulay 01 area. This difference was attributed to the transfer of the predator *Eunice dubitata* from the fourth (using

suspended particulate organic matter or *P. anguicomus* as a trophic baseline) to the third trophic level (using *S. coralliophaga* or *R. beaniana* as a baseline). This transfer from the fourth to the third trophic level was a response to the higher $\delta^{15}\text{N}$ signatures of *S. coralliophaga* and *R. beaniana* at the Logachev 02 mound than at the Mingulay 01 area. The enriched $\delta^{15}\text{N}$ signatures of these two species were probably the result of a combination of (a) enriched $\delta^{15}\text{N}$ signatures of small-sized food particles (i.e. pico- to nanoplankton) in deeper regions due to extended

resuspension and microbial degradation (Saino & Hattori 1980; Altabet 1988; Mintenbeck et al. 2007; Bergmann et al. 2009), and (b) selective feeding of *S. coralliophaga* and *R. beaniana* on small-sized particles (Winston 1977; Witte et al. 1997). The findings on nitrogen stable isotope values ($\delta^{15}\text{N}$) of suspension/filter feeders across a bathymetric gradient presented here were in good agreement with previous studies (Mintenbeck et al. 2007; Bergmann et al. 2009). In contrast to selective suspension feeders, deposit feeders have not shown a bathymetric enrichment in their $\delta^{15}\text{N}$ values, probably because they relied on a wide spectrum of food particles settled on the seabed (Mintenbeck et al. 2007; Bergmann et al. 2009). A depth-stratified approach should be followed in food-web studies across a wide bathymetric range in order to avoid the misinterpretation of findings arising from the enrichment of $\delta^{15}\text{N}$ values (Mintenbeck et al. 2007; Bergmann et al. 2009). Using suspended particulate organic matter or *P. anguicomus* as a baseline, a clear difference between the Mingulay 01 area and the Logachev 02 mound was found with regard to the distribution of biomass across the trophic levels. A different pattern was also found with regard to the distribution of biomass across feeding types. Specifically, the relative biomass (a) of suspension/filter feeders and (b) representatives of the lower trophic levels was indicated to be higher at the Mingulay 01 area than the Logachev 02 mound. These results support the hypothesis that environmental conditions would play an important role in the trophic structure of benthic communities. However, it should be mentioned that the use of suspended particulate organic matter as a baseline revealed more species and higher biomass at the second trophic level for the Mingulay 01 area than the second trophic level at the Logachev 02 mound. This finding was likely due to the higher $\delta^{15}\text{N}$ signatures of suspended particulate organic matter at the Mingulay 01 area than the Logachev 02 mound and reinforced previous suggestions that spatial/temporal variability in the $\delta^{15}\text{N}$ signatures of primary producers can complicate the comparison of trophic structure between regions (Iken et al. 2010; see also above). Based on present findings we recommend that multiple trophic baselines should be used in studies focusing on the trophic structure of ecosystems (Iken et al. 2010; Chouvelon et al. 2012; Mancinelli et al. 2013; Lorrain et al. 2015) and that sponges, bryozoans and suspended particulate organic matter as baselines across bathymetric gradients should be avoided. On the other hand, we suggest that cnidarians can probably serve as a more reliable trophic baseline compared

to sponges and bryozoans. Present findings have also shown that equal food chain length between two regions may be accompanied by differences in the distribution of biomass across the trophic levels. Based on this observation we recommend that studies on food-web structure should incorporate both the length of the food chain (e.g. Vander Zanden & Fetzer 2007) and the distribution of biomass across the trophic levels (Grall et al. 2006; Iken et al. 2010).

Environmental factors and the trophic structure of benthos

The present findings highlighted the important role of differences in the input of organic matter in the ecology of cold-water coral reefs in the northeast Atlantic. Previous studies have shown that the quantity of organic matter supplied to deep-sea ecosystems may have an influence on aspects such as the abundance, biomass, community structure (Ruhl 2008; Wolff et al. 2011), species nutritional status (Cummings et al. 2013) and community trophic structure (Iken et al. 2010). In this study, higher levels of surface primary production over the Mingulay reef complex (Fehling et al. 2012), in combination with the rapid down-welling (Davies et al. 2009), indicated that more and fresher organic matter was supplied to the shallow inshore Mingulay reef complex than the deep offshore Logachev mounds. This in turn probably fuelled higher biomass of suspension/filter feeders at the Mingulay reef complex.

The quality of organic matter settling on the deep-sea floor is an important parameter for ecosystem functionality. Changes in the biochemical composition of the organic matter input have been hypothesized as the main driving force behind radical shifts in benthic community composition, structure and functionality in the Porcupine Abyssal Plain in the northeast Atlantic (Billett et al. 2001, 2010). In the Mingulay 01 area and the Logachev 02 mound the $\delta^{13}\text{C}$ signatures in most suspension/filter feeders and grazers were depleted (i.e. smaller) compared to the $\delta^{13}\text{C}$ values of bottom suspended particulate organic matter in the Mingulay reef complex. In contrast, the $\delta^{13}\text{C}$ signatures of suspension/filter feeders and grazers were in good agreement with the $\delta^{13}\text{C}$ values of surface suspended particulate organic matter. Thus, it may be suggested that the Mingulay 01 area and the Logachev 02 mound benthos relied mainly on surface suspended particulate organic matter as a carbon source, at least for the time period of our study. Previous studies on the biochemical composition of suspended particulate organic matter in these two regions have revealed a

higher concentration of polyunsaturated fatty acids in the Mingulay reef complex (Duineveld et al. 2012) than the Logachev mounds (Kiriakoulakis et al. 2007). Polyunsaturated fatty acids are essential components for species maintenance, growth and reproduction in a number of species (Brett & Müller-Navarra 1997; Hudson et al. 2003; Barras et al. 2009) and thus their assimilation may have supported higher fecundity and successful recruitment in the Mingulay reef complex (Fuiman & Ojanguren 2011; Callan et al. 2012; Toupoint et al. 2012). The composition of polyunsaturated fatty acids in *Spongosorites coralliophaga*-coral rubble epifauna at the Mingulay 01 area and the Logachev 02 mound was not available; however, taking into account the close relationship between diet and reproduction (e.g. Wigham et al. 2003a, 2003b; Fitz-George Balfour et al. 2010; Kazanidis et al. 2014), it seems that the assimilation of polyunsaturated fatty acids by Mingulay 01 area suspension/filter feeders has facilitated their proliferation. This was most likely for the species *Parazoanthus anguicomus*, which was dominant at the Mingulay 01 area in terms of abundance and biomass but had low abundance and biomass at the Logachev 02 mound (Kazanidis et al. 2016).

Bottom currents can play an important role in the distribution of suspension feeders in the deep sea, since they suspend food particles, enhancing particle-encounter rates (Gage 2003 and references therein; Carlier et al. 2009; Purser et al. 2010; Duineveld et al. 2012), and they prevent detrimental effects arising from the accumulation of non-edible particles on organisms (Purser & Thomsen 2012; Larsson et al. 2013). The higher velocity of bottom currents at the Mingulay reef complex than those at the Logachev mounds has likely contributed to these aspects. The suspension of food particles at the Mingulay reef complex and the Logachev mounds reef settings probably inhibit the presence of deposit-feeding megafauna (e.g. holothurians) that thrive in deeper regions with lower suspension and a higher accumulation of particulate organic matter on the sediments (e.g. abyssal plains, Billett et al. 1983, 2001; Wolff et al. 2011).

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