Role of Astrophorina sponges (Demospongiae) in food-web interactions at the Flemish Cap (NW Atlantic)

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ABSTRACT: Deep-sea sponges are important contributors to carbon and nitrogen cycling due to their large filtration capacity. Species of the suborder Astrophorina form dense sponge grounds in the North Atlantic, where they serve as prey for spongivores, but also have non-trophic interactions with commensal epi- and endobionts. At the Flemish Cap (NW Atlantic), Astrophorina sponges are present in 4 previously described deep-sea epifaunal assemblages: the deep-sea coral assemblage, lower slope assemblages 1 and 2, and the deep-sea sponge assemblage. To investigate their role in trophic and non-trophic interactions at the Flemish Cap, we developed trophic and non-trophic interaction web models for each of the 4 faunal assemblages using the published literature. By excluding the sponges from the models, we estimated how many trophic, and facultative and obligatory non-trophic, interactions would be lost, and how this removal affected food-web properties (number of compartments, links, link density, and connectance). Astrophorina sponges were mostly linked via facultative non-trophic interactions to 59, 58, 84, and 90 compartments in the deep-sea coral, the lower slope 1 and 2, and the deep-sea sponge assemblages, respectively. Direct trophic interactions only existed with Syllidae, Echinasteridae, and Pterasteridae. Astrophorina sponges were considered highest impact taxa in all faunal assemblages and, together with sea pens, they were identified as structural species/habitat formers and foundation species in the deep-sea coral and deep-sea sponge habitat. Hence, even less abundant, or non-representative (indicator), species can be important for food-web integrity via trophic and non-trophic interactions.

KEY WORDS: Presence—absence · Data modeling · *Geodia* sp. · Deep-sea benthos · Food-web · Connectance

1. INTRODUCTION

Sponges (Porifera) are important filter feeders that efficiently filter large amounts of bacterioplankton, dissolved organic matter (DOM), and particulate organic matter (POM) out of the water column (Maier et al. 2020, Bart et al. 2021a,b). Clear examples of the magnitude of this function are sponge grounds on the continental shelf of northern Norway, where they were estimated to pump 250 million m[3] of water every day, consuming 50 t C d^{−1} (Kutti et al. 2013), and the sponge grounds of the Karasik Seamount (Langseth

Ridge, central Arctic Ocean). There, 1 m^2 sponge ground was estimated to process all of the water in the overlying 600 m of water column per year (Morganti et al. 2022). Sponge grounds consisting of the demosponge *Geodia* Lamarck, 1815 are also very important for nitrogen cycling. Hoffmann et al. (2009) estimated that sponge-mediated nitrification rates transform up to 16 mmol N m^{-2} d^{-1} and remove 2.7 mmol N m^{-2} d^{-1} as N$_2$, which implies that nitrogen removal rates could be 2 to 10 times higher than nitrogen removal rates on continental slopes (Middelburg et al. 1996, Seitzinger & Giblin 1996, Hoffmann et al. 2009).

The biomass in sponge grounds consisting of the demosponge suborder Astrophorina (primarily species of *Geodia*, *Thenea* Gray, 1867, and *Stryphnus* Sollas, 1886) is not only controlled by the availability of food sources in the water column (i.e. bottom-up control), but also by the presence of spongivores/predators (i.e. top-down control). Bart et al. (2021a) described a deep-sea sponge loop in which Ophiuroidea either consume detritus produced by *Geodia barretti* Bowerbank, 1858 (i.e. the deep-sea detrital sponge loop) or in which they directly prey upon *G. barretti* (i.e. the deep-sea predatory sponge loop). In both cases, sponges recycle DOM and make it available as a food source to higher trophic levels.

In addition to these trophic interactions (TIs), sponges are also involved in non-trophic interactions (NTIs) by providing 3-dimensional habitats for commensal epi- and endobionts. For example, a study of 7 sponge species collected at the US Atlantic continental shelf and slope revealed a mean ± SD density of 1976 ± 3267 individual associated fauna per liter sponge volume (Fiore & Cox Jutte 2010). For comparison, tunicates had a mean density of associated fauna of 642 ± 619 individual associated fauna per liter tunicate volume (Fiore & Cox Jutte 2010). Most of the fauna associated with sponges were polychaetes (93%), whereas tunicates hosted polychaetes (28%), decapods (28%), and amphipods (32%) (Fiore & Cox Jutte 2010). Even when only larger invertebrate megabenthos, which is visible on photos, is considered, sponge grounds host a higher diversity and density of benthos than adjacent areas without sponges (Beazley et al. 2013). In the Flemish Cap on the Canadian continental margin of the Atlantic Ocean, non-sponge grounds had a mean ± SE megabenthos density of 33 ± 3 ind. m^{-2} and a mean Shannon diversity *H'* index of 1.3 ± 0.04, whereas sponge grounds had a mean megabenthos density of 65 ± 5 ind. m^{-2} and mean *H'* index of 2.1 ± 0.02 (Beazley et al. 2013).

Statistical analyses of invertebrate epibenthos data from the Flemish Cap identified 12 significantly different epibenthic assemblages (Murillo et al. 2016), including a deep-sea coral assemblage, 2 lower slope assemblages (lower slope 1, lower slope 2), and a deep-sea sponge assemblage (Fig. 1). The deep-sea coral assemblage occurs between 500 and 900 m water depth in sandy-silty sediments and is characterized by various coral species, i.e. *Stauropathes arctica* (Lütken, 1871), *Flabellum* (*Ulocyathus*) *alabastrum* Moseley, 1876, *Funiculina quadrangularis* (Pallas, 1766), *Heteropolypus sol* Molodtsova, 2013, and *Acanella arbuscula* (Johnson, 1862) (Murillo et al. 2016). Lower slope assemblage 1 is present on sandy and clayed-silt sediments between 800 and 1200 m depth and includes the characteristic species *Phormosoma placenta* Thomson, 1872, *Bathybiaster vexillifer* (Wyville Thomson, 1873), *Zoroaster fulgens* Wyville Thomson, 1873, *F. quadrangularis*, *Anthoptilum grandiflorum* (Verrill, 1879), *Balticina finmarchica* (Sars, 1851), and *Pennatula aculeata* Danielssen, 1860 (Murillo et al. 2016). Lower slope assemblage 2 (620–1400 m water depth) has the same representative species as lower slope assemblage 1, but it experiences more bottom trawling than the other assemblage (Murillo et al. 2016). The deep-sea sponge assemblage is present from 700 to 1400 m depth on clayed-silt, silty-sand, and sandy-silt sediments and is represented by a large biomass of Astrophorina sponges (Murillo et al. 2016).

Traditionally, the study of TIs is based on topological food webs (e.g. Morato et al. 2016, Hanz et al. 2022) and energy flow webs (e.g. Soetaert & van Oevelen 2009, van Oevelen et al. 2009, Stratmann et al. 2018, de Jonge et al. 2020, Stratmann 2023), whereas NTIs have been studied via interaction webs (e.g. Salinas et al. 2023). In 2015, van der Zee et al. (2016) introduced a modeling approach to combine the assessment of TIs and NTIs in interaction webs. In these webs, NTIs may be commensal relationships, i.e. relationships in which one species benefits while the other species is not affected. These NTIs may be obligatory or facultative. An example of an obligatory NTI includes the dependence of deep-sea incirrate octopods on stalked sponges in the abyssal central Pacific where these octopods lay their eggs around the stalks of sponges and brood them (Purser et al. 2016). In comparison, a facultative NTI exists, for example, when anthozoans of the family Hormathiidae grow physically attached to Astrophorina sponges at the Langseth Ridge (Stratmann et al. 2022), where the sponges serve as hard substrate. However, these

Fig. 1. Fauna characteristic of the 4 benthic community types. (A) Deep-sea coral assemblage showing typical species (left to right): *Stauropathes arctica*, *Flabellum* (*Ulocyathus*) *alabastrum*, *Funiculina quadrangularis*, *Heteropolypus* cf. *sol*, and *Acanella arbuscula*. (B) Typical species of lower slope assemblages (left to right): *Phormosoma placenta*, *Anthoptilum grandiflorum*, *Balticina finmarchica*, *Pennatula aculeata*, and *Bathybiaster vexillifer*. (C) Deep-sea sponge assemblage typified by high biomass of large sponges mainly from the suborder Astrophorina (left to right): *Stryphnus* cf. *fortis* encrusted with the yellow *Hexadella dedritifera*, *Geodia* cf. *barretti*, *Geodia parva/G. phlegraei*, *Thenea* sp., and *Stelletta* cf. *normani*. Scale bars are approximately 5 cm. Note that identification of sponges from photographs is not definitive, but photos are illustrative of the general size and appearance of each species

anthozoans also grow on rocks or larger gravel (T. Stratmann pers. obs.).

Stratmann et al. (2021) further developed the approach of van der Zee et al. (2016) to assess the role of polymetallic nodules for food-web integrity in abyssal plains of the SE and central Pacific. However, the approach is not limited to abiotic hard substrate (i.e. the polymetallic nodules in Stratmann et al. 2021); it can also be applied to assess the importance of specific taxonomic groups and to identify the so-called 'highest impact taxa', i.e. taxa whose removal results in the largest changes in food-web properties, such as number of species or interaction-web links. In brief, this approach allows removal of a selected compartment from 2 matrices with TIs and NTIs to identify all TIs, facultative NTIs, and obligatory NTIs that will be lost, when the selected compartment is removed. This so-called 'level 1 loss' happens as follows: a compartment A has a single TI and/or one or more NTIs with Compartment B, so that removing Compartment B will cause the immediate loss of Compartment A. However, if Compartment A has TIs with several other compartments, then removing Compartment B will not affect Compartment A on a trophic level, and only on a non-trophic level if NTIs exist. A so-called 'maximum secondary loss' is the loss of any compartment that will be lost because it has a (single) TI, and/or a facultative/obligatory NTI with a compartment that has been lost during the level 1 loss. In a 'maximum tertiary loss' (or in other higher-order losses), a compartment will also be lost when it has TIs with several compartments that are lost in a level 1 loss and/or as maximum secondary losses.

In this study, we investigated (1) the importance of the representative species of the 4 deeper faunal assemblages characterized by Murillo et al. (2016) for TIs and NTIs at the Flemish Cap. For this, we studied the effects of removing these species on a suite of network indices (Pimm et al. 1991). We further identified (2) the species with most TIs and NTIs in the different assemblages, and (3) the highest impact taxa. Our results are discussed in the context of impacts of bottom-contact fishing gears and protection of vulnerable marine ecosystems (FAO 2009).

2. MATERIALS AND METHODS

2.1. Study site

The Flemish Cap is a bank in the high seas of the continental margin off Newfoundland, Canada, with a radius of ~200 km at the 500 m isobath and minimum depth of approximately 122 m (Fig. 2). It is considered both a bioregion and an ecosystem production unit, based on analyses of a suite of physiographic, oceanographic, and biotic variables (NAFO 2014). It is treated as a discrete unit, North-west Atlantic Fisheries Organization (NAFO) Division 3M, for the management of commercial fisheries executed on the bank, and for ecosystem summaries informing fisheries management. There are steep slopes to the east and south, below 1000 m depth, but more gradual gradients to the north and west. It is separated from the Grand Banks by the Flemish Pass, a 1200 m deep, mid-slope channel. Two major ocean currents influence this area: the Labrador Current, flowing from the north, and the North Atlantic Current, which represents an extension of the warm Gulf Stream. When the Labrador Current reaches the Flemish Pass, it bifurcates, with the major branch flowing southwards to the south-eastern slope of the Grand Bank, while the side branch circulates clockwise around the Flemish Cap.
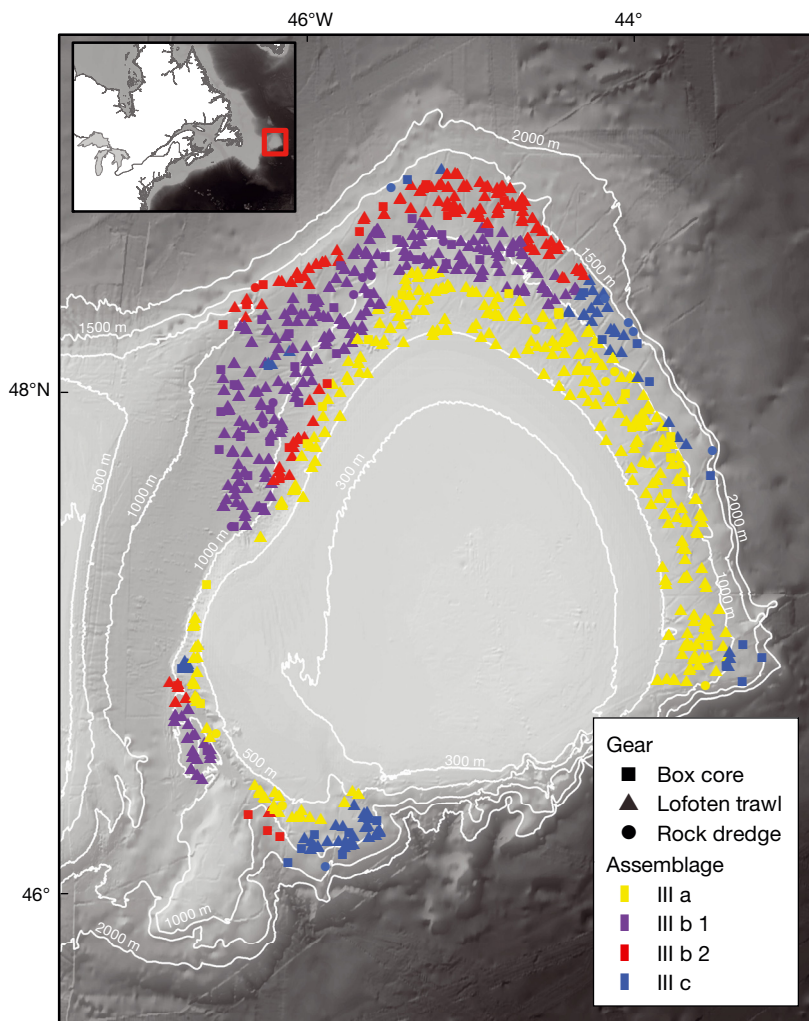

Fig. 2. Study area on the Flemish Cap, northwest Atlantic (inset), showing the distribution of samples by collection gear type and color-coded by the benthic assemblages delineated by Murillo et al. (2016): III a = deep-sea coral assemblage; III b 1 = lower slope assemblage 1; III b 2 = lower slope assemblage 2; III c = deep-sea sponge assemblage. Triangles represent research vessel survey trawl start positions, squares represent box core locations, and circles represent rock/scallop dredge locations. The positions of the 300, 500, 1000, 1500, and 2000 m isobaths are shown. The depth ranges of the samples are provided in Table 1

2.2. Sample collection

For this study, we combined published fish and invertebrate epifauna data collected by bottom trawls, with published (meiobenthos and macrobenthos) infauna data collected by mega box cores (soft sediment) and additional epifauna collected by rock dredge/scallop gear (hard seabed bottom: compacted sands, gravel, and rock) (Fig. 2, Table 1).

Bottom-trawls were conducted with standardized sets of a Lofoten bottom trawl (mean swept area of ≈39 000 m^2 each) between 2011 and 2019 as part of the EU Flemish Cap bottom-trawl research surveys (Vázquez et al. 2014, Murillo et al. 2016). They were conducted by the Instituto Español de Oceanografía together with the Instituto de Investigaciones Marinas and the Instituto Português do Mar e da Atmosfera aboard the Spanish RV 'Vizconde de Eza'. The surveys sampled the Flemish cap and the eastern side of the Flemish Pass between 470 and 1440 m depth, following a depth-stratified random sampling design. Samples were processed as described by Vázquez et al. (2014). In brief, all invertebrates and fish captured were sorted, identified to the lowest tax-

Table 1. Summary of data collected with each of the 3 sampling gears in each of the 4 benthic community types described by Murillo et al. (2016)

Benthic community	Lofoten trawl			Rock dredge			Box core		
	Number of deployments	Depth range (m)	Sampling years	Number of deployments	Depth range (m)	Sampling years	Number of deployments	Depth range (m)	Sampling years
Deep-sea coral assemblage	376	470−974	2011−2019	7	605−956	2009−2010	18	688−1125	2010
Lower slope 1 assemblage	301	775−1202	2011−2019	8	935−1132	2009	31	800−1181	2010
Lower slope 2 assemblage	151	855−1440	2011−2019	1	1264−1294	2009	17	981−1391	2009
Deep-sea sponge assemblage	62	653−1355	2011−2019	6	1316−1589	2009−2010	19	750−1537	2009

onomic level possible, and weighed on board (wet mass).

Infauna and additional unpublished epifauna data were obtained from the NEREIDA program (Durán Muñoz et al. 2012, NAFO 2013). The NEREIDA surveys were undertaken aboard the Spanish RV 'Miguel Oliver' in the Flemish Pass and Flemish Cap during spring and summer of 2009 and 2010 at depths between 605 and 1589 m. For infauna collection with mega box cores, a United States Naval Electronics Laboratory (USNEL)-type box core (0.25 m^2 sampling area) was deployed. All macrofauna samples were processed as detailed in Barrio Froján et al. (2016). Briefly, organisms were sieved on 0.5 mm mesh sieves, stored in buffered 4% formaldehyde solution, and identified to morphotaxa, i.e. identified to the 'identity of the organism most evident to a marine invertebrate taxonomist without having to refer to the formal taxonomic literature' (Barrio Froján et al. 2016, p. 407). Afterwards, each specimen was weighed (wet mass) and transferred to 70% ethanol.

The rock dredge/scallop gear deployed for infauna collection on hard bottom consisted of a rectangular metal collar, coupled with a coarse mesh net protected by a rubber mat. This device was towed for approximately 1 km along the seabed allowing the rectangular metal mouth of the dredge to dig into the substrate, parts of which are then retained in the sample net. The towing speed was between 2 and 3 knots (NAFO 2013). All invertebrates retained were sorted, photographed, identified to the lowest taxonomic level possible, weighed on board (wet mass), and preserved in 70% ethanol.

All fish, invertebrate epifauna, and infauna data sets included geographical information about the position and the biomass (and abundance for some) of each species identified in every sample.

2.3. Data compilation

The sampling location of each collected sample was used to partition the data in the 4 faunal assemblages 'deep-sea coral assemblage', 'lower slope assemblage 1', 'lower slope assemblage 2', and 'deep-sea sponge assemblage' based on the benthic assemblage boundaries qualitatively mapped by Murillo et al. (2016), applying the 'spatial join' function in ArcMap version 10.7 (ESRI 2019). Biomass data were converted to presence−absence data, as the model is based on binary, i.e. presence−absence, data. For each specimen record, taxonomic ranking was assigned following the World Register of Marine Species (Horton et al. 2018). The species list for each of the 4 faunal assemblages was compiled from the 3 gear types (trawl, corer, and rock dredge). Representative species were those identified as diagnostic species with a high fidelity to the assemblage as analyzed through ISOPAM by Murillo et al. (2016).

Afterwards, literature searches were conducted for each taxon to support (1) designation of dominant adult feeding strategy, and diet items for elucidation of TIs, (2) adult size class (meiobenthos > 32 μm; macrobenthos > 250 μm/> 500 μm; invertebrate megabenthos > 1 cm), (3) facultative/ obligatory NTIs with other taxa, and/or (4) facultative/obligatory NTIs with Astrophorina sponges. Commensal relations with Astrophorina sponges were assessed separately because we wanted to investigate the role of NTIs of sponges of this suborder across all faunal assemblages, independent of the actual species present, while still obtaining information about TIs per Astrophorina sponge species. The evidence base for the species associations was therefore varied and included stomach content analyses, *in situ* observations with remotely oper-

ated vehicle (ROV) or drop camera, and isotope analyses, amongst others.

All data were compiled for analysis per faunal assemblage, including information about sampling gear, trophic ranking from phylum to the lowest possible taxonomic resolution per taxon, name of the faunal compartment, size class, information about facultative/obligatory NTIs with other fauna and/or the Astrophorina sponge compartment, feeding type, and diet/prey items.

2.4. Trophic/non-trophic interaction web modeling

We used R (version 4.3.0) (R Core Team 2022) to construct TI and NTI web matrices of the following form:

NTI or TI =

$$\begin{bmatrix} \text{Food compartment}_{1,2,n} & \text{Astrophorina sponge} & \text{Faunal compartment}_{1,2,n} \\ \text{Astrophorina sponge} & \cdots & \cdots \\ \text{Faunal compartment}_{1,2,n} & \cdots & \cdots \end{bmatrix}$$

The 'Food compartment' included additional diet items, such as bacteria or detritus (Table 2), for taxa that were not predators, and the 'Astrophorina sponges' compartment allowed us to assess NTIs of taxa with members of the sponge suborder Astrophorina. By default, there were no TIs with this compartment, as TIs with specific Astrophorina sponge species were assessed separately. For instance, when 2 species of the suborder Astrophorina were present in a faunal assemblage, TIs between these 2 species were listed individually as TIs between sponge species A and its predators and sponge species B and its predators. A more detailed description of the implementation of the interaction web model is presented in Text S1 in the Supplement at www.int-res.com/articles/suppl/m729p099_supp.pdf.

By iteratively removing each faunal compartment and the Astrophorina compartment from the TI and NTI matrices, we identified which compartments would be lost, and calculated changes in network indices for each individual iteration. These indices included S (i.e. number of interaction web compartments), L (number of network links), D (link density), and C (connectance). D is calculated as $D = L/S$, and C, which is the fraction of all realized links in comparison to all links that are possible (Pimm et al. 1991), is calculated as $C = L/S^2$.

The taxon whose removal caused the highest absolute change in one or more of the network indices S, L, D, and C was considered the highest impact taxon. Furthermore, we assessed the importance of representative taxa of the individual faunal assemblages on each assemblage by removing them from the TI and NTI matrices and by calculating changes in network indices. We also determined how the removal of faunal compartments with the most TIs as prey (i.e. which taxa had most predators) or predators (i.e. which taxa preyed upon most prey) and faunal compartments with the most NTIs altered network indices and whether they triggered the loss of any further compartments.

3. RESULTS

3.1. Food webs of the different faunal assemblages at the Flemish Cap

3.1.1. Intact deep-sea coral assemblage

The deep-sea coral assemblage consisted of 252 faunal interaction-web compartments including protozoan and metazoan meiobenthos (0.79%), macrobenthos (8.33%), invertebrate megabenthos (57.1%), and fish (33.7%). Most of the taxa were carnivores (62.7%) and filter/suspension feeders (19.0%) (Fig. 3A), and the dominant phyla were Arthropoda (15.1% of all faunal compartments), Chordata (34.1%), Cnidaria (15.1%), Echinodermata (13.9%),

Table 2. List of extra food sources that were included in the trophic interaction matrices of the 4 benthic assemblages

| Benthic assemblage	Extra food sources
Deep-sea coral assemblage, lower slope assemblages 1 and 2	(Endosymbiotic chemosynthetic) bacteria, carrion, dissolved organic matter, fish eggs and larvae, macrobenthic/megabenthic Foraminifera, microbial mats, (labile) sedimentary detritus, sedimentary and suspended diatoms, suspended particulate organic matter
Deep-sea sponge assemblage	Bacteria, carrion, dissolved organic matter, fish eggs, macrobenthic/megabenthic Foraminifera, (labile) sedimentary detritus, phytodetritus, suspended particulate organic matter, sedimentary diatoms
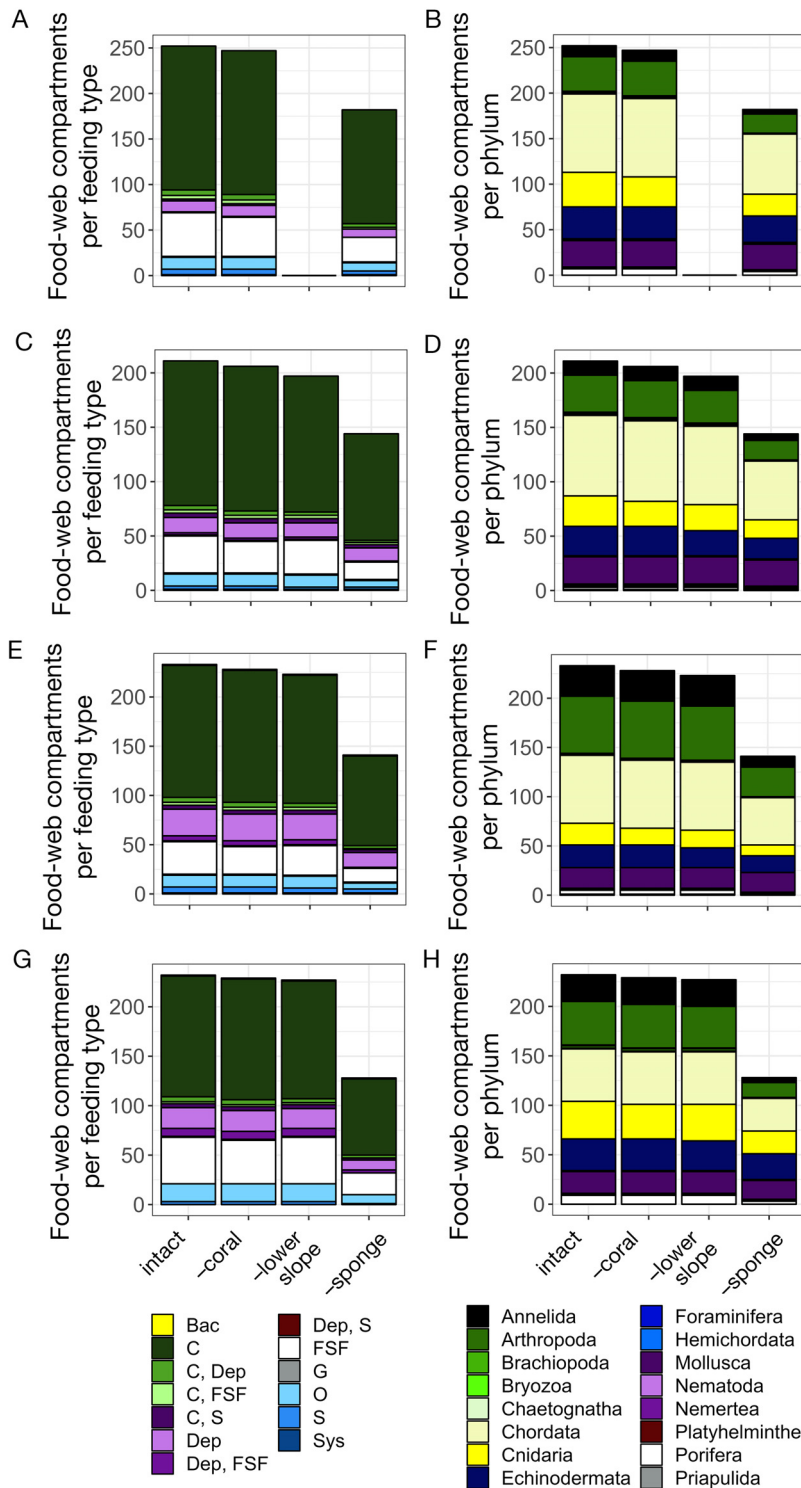
Fig. 3. Comparison of the number of feeding types (left column) and phyla (right column) between the intact assemblage (intact) and the assemblages without representatives of the deep-sea coral assemblage (−coral), of the lower slope assemblages (−lower slope), and of demosponges of the suborder Astrophorina (−sponge) for the (A,B) deep-sea coral assemblage, (C,D) lower slope assemblage 1, (E,F) lower slope assemblage 2, and (G,H) deep-sea sponge assemblage. Bac: bacterivore; C: carnivore; Dep: deposit feeder; FSF: filter/suspension feeder; S: scavenger; G: grazer; O: omnivore; Sys: symbiosis

and Mollusca (11.5%) (Fig. 3B). In the interaction-web model, all compartments were linked via 9939 TIs with their respective food sources (Table 3; Fig. S1A), and the NTI web comprised 246 interactions. D was 37 and C was 0.14. The predator with the most TIs in the deep-sea coral assemblage was *Amblyraja radiata* (Donovan, 1808), and the prey with the most TIs was krill of the order Euphausiacea. The taxon with the most (commensal) NTIs was the polychaete family Polynoidae.

3.1.2. Intact lower slope assemblage 1

Lower slope assemblage 1 contained 211 faunal interaction web compartments, of which 0.47% belonged to protozoan and metazoan meiobenthos, 10.9% to macrobenthos, 54.0% to invertebrate megabenthos, and 34.6% to fish. Most of the taxa were carnivores (63.0%) and filter/suspension feeders (16.1%) (Fig. 3C) and the dominant phyla were Chordata (35.1% of all taxa), Arthropoda (16.1%), Cnidaria (13.3%), Echinodermata (12.8%), and Mollusca (11.8%) (Fig. 3D). In total, 4488 TIs connected all compartments with their respective food sources (Table 3; Fig. S1B). D was 20 and C was 0.089. Additionally, the compartments were connected with 225 interactions in the NTI web. *Anarhichas denticulatus* Krøyer, 1845 was the predator with the most TIs; the prey with most TIs were macrobenthic Copepoda, and polychaetes of the family Polynoidae had the most NTIs.

3.1.3. Intact lower slope assemblage 2

Lower slope assemblage 2 consisted of 233 faunal interaction-web compartments, of which 0.86% were protozoan and metazoan meiobenthos,

Table 3. Changes in network properties dependent on the presence (intact assemblage) or absence of specific taxa. The network properties were calculated for the trophic interaction webs of the deep-sea coral assemblage, lower slope assemblages 1 and 2, and deep-sea sponge assemblage, and when the highest and second highest impact taxa were absent. The network properties were also calculated for the trophic interaction webs without the taxa with the most trophic and non-trophic links. The changes in percent with respect to the default webs are shown in brackets. *Significant change, i.e. a change in network properties that was caused by the loss of more than only the actively removed taxa

	Number of interaction web compartments S	Number of network links L	Link density D	Connectance C
Deep-sea coral assemblage				
Intact assemblage	266[a]	9939	37	0.14
Without representative taxa of the deep-sea coral assemblage (*Stauropathes arctica*, *Flabellum alabastrum*, *Funiculina quadrangularis*, *Heteropolypus sol*, and *Acanella arbuscula*)	261 (−1.88%)	9694 (−2.47%)	37 (0%)	0.14 (0%)
Without representative taxa of the deep-sea sponge assemblage (Astrophorina sponges)*	195 (−26.7%)	5464 (−45.0%)	28 (−24.3%)	0.14 (0%)
Without the second highest impact taxon (*Anthoptilum* sp.)	261 (−1.89%)	9286 (−6.57%)	36 (−2.70%)	0.14 (0%)
Without the third highest impact taxon (Copepoda)	261 (−1.88%)	9641 (−3.00%)	37 (0%)	0.14 (0%)
Without the predator with most trophic links (*Amblyraja radiata*)	265 (−0.38%)	9784 (−1.56%)	37 (0%)	0.14 (0%)
Without the prey with most trophic links (Euphausiacea)	265 (−0.38%)	9833 (−1.07%)	37 (0%)	0.14 (0%)
Without the taxon with most non-trophic links (Polynoidae)	265 (−0.38%)	9902 (−0.37%)	37 (0%)	0.14 (0%)
Lower slope assemblage 1				
Intact assemblage	225[b]	4488	20	0.089
Without representative taxa of the deep-sea coral assemblage (*Stauropathes arctica*, *Flabellum alabastrum*, *Funiculina quadrangularis*, *Heteropolypus sol*, and *Acanella arbuscula*)	220 (−2.22%)	4438 (−1.11%)	20 (0%)	0.092 (+3.37%)
Without representative taxa of the lower slope assemblages (*Phormosoma placenta*, *Bathybiaster vexillifer*, *Zoroaster fulgens*, *Funiculina quadrangularis*, *Anthoptilum grandiflorum*, *Balticina finmarchica*, and *Pennatula aculeata*)*	211 (−6.22%)	3982 (−11.3%)	19 (−5.00%)	0.089 (0%)
Without representative taxa of the deep-sea sponge assemblage (Astrophorina sponges)*	157 (−30.2%)	2187 (−51.3%)	14 (−30.0%)	0.089 (0%)
Without the second highest impact taxon (*Anthoptilum* sp.)	222 (−0.13%)	4294 (−4.32%)	19 (−5.00%)	0.087 (−2.25)
Without the third highest impact taxon (*Rouleina attrite*)	224 (−0.44%)	4364 (−2.76%)	19 (−5.00%)	0.087 (−2.25)
Without the predator with most trophic links (*Anarhichas denticulatus*)	224 (−0.44%)	4371 (−2.61%)	20 (0%)	0.087 (−2.25)
Without the prey with most trophic links/ the third highest impact taxon (Copepoda)	221 (−1.78%)	4316 (−3.83%)	20 (0%)	0.088 (−1.12%)
Without the taxon with most non-trophic links (Polynoidae)	224 (−0.44%)	4426 (−1.38%)	20 (0%)	0.088 (−1.12%)
Lower slope assemblage 2				
Intact assemblage	248[c]	5124	21	0.083
Without representative taxa of the deep-sea coral assemblage (*Stauropathes arctica*, *Flabellum alabastrum*, *Funiculina quadrangularis*, *Heteropolypus sol*, and *Acanella arbuscula*)	243 (−2.02%)	4994 (−2.54%)	21 (0%)	0.085 (+2.41%)
Without representative taxa of the lower slope assemblages (*Phormosoma placenta*, *Bathybiaster vexillifer*, *Zoroaster fulgens*, *Funiculina quadrangularis*, *Anthoptilum grandiflorum*, *Balticina finmarchica*, and *Pennatula aculeata*)*	238 (−4.03%)	4629 (−9.66%)	19 (−9.52%)	0.082 (−1.20%)

Table 3. (continued)

	Number of interaction web compartments S	Number of network links L	Link density D	Connectance C
Without representative taxa of the deep-sea sponge assemblage (Astrophorina sponges)★	155 (−37.5%)	2254 (−56.0%)	15 (−28.6%)	0.094 (+13.3%)
Without the second highest impact taxon (*Anthoptilum* sp.)	245 (−1.21%)	4912 (−4.14%)	20 (−4.76%)	0.082 (−1.20%)
Without the third highest impact taxon (*Calathura* sp.)	247 (−0.40%)	4973 (−2.95%)	20 (−4.76%)	0.082 (−1.20%)
Without the predator with most trophic links (*Todarodes sagittatus*)	247 (−0.40%)	5000 (−2.42%)	20 (−4.76%)	0.082 (−1.20%)
Without the prey with most trophic links (Copepoda)	247 (−0.40%)	5039 (−1.66%)	20 (−4.76%)	0.083 (0%)
Without the taxon with most non-trophic links (Polynoidae)	247 (−0.40%)	5082 (−0.82%)	21 (0%)	0.083 (0%)
Deep-sea sponge assemblage				
Intact assemblage	243[d]	9303	38	0.16
Without representative taxa of the deep-sea coral assemblage (*Stauropathes arctica*, *Flabellum alabastrum*, and *Heteropolypus sol*)	240 (−1.23%)	9150 (−0.16%)	38 (0%)	0.16 (0%)
Without representative taxa of the lower slope assemblages (*Phormosoma placenta*, *Zoroaster fulgens*, and *Anthoptilum* sp.)★	238 (−2.06%)	8746 (−5.99%)	37 (−2.63%)	0.15 (−6.25%)
Without representative taxa of the deep-sea sponge assemblage (Astrophorina sponges)★	138 (−43.2%)	3756 (−59.6%)	27 (−28.9%)	0.20 (+25.0%)
Without the second highest impact taxon (Mysida)★	230 (−5.35%)	8814 (−5.26%)	38 (0%)	0.17 (+6.25%)
Without the third highest impact taxon (*Anthoptilum* sp.)★	240 (−1.23%)	8894 (−4.40%)	37 (−2.63%)	0.15 (−6.25%)
Without the predator with most trophic links (Oedicerotidae)	242 (−0.41%)	9093 (−2.26%)	38 (0%)	0.16 (0%)
Without the prey with most trophic links (Euphausiacea)	242 (−0.41%)	9218 (−0.91%)	38 (0%)	0.16 (0%)
Without the taxon with most non-trophic links (Polynoidae)	242 (−0.41%)	9224 (−0.85%)	38 (0%)	0.16 (0%)

[a]266 interaction-web compartments = 252 faunal compartments + 13 food source compartments (Table 2) + 1 Astrophorina compartment
[b]225 interaction-web compartments = 211 faunal compartments + 13 food source compartments (Table 2) + 1 Astrophorina compartment
[c]248 interaction-web compartments = 233 faunal compartments + 14 food source compartments (Table 2) + 1 Astrophorina compartment
[d]243 interaction-web compartments = 232 faunal compartments + 10 food source compartments (Table 2) + 1 Astrophorina compartment

26.2% were macrobenthos, 43.8% were invertebrate megabenthos, and 29.2% were fish. Most of the taxa were carnivores (57.5%), filter/suspension feeders (14.2%), and deposit feeders (11.6%) (Fig. 3E), and 67.4% of all faunal compartments were Annelida (12.9% of all taxa), Arthropoda (24.9% of all taxa), and Chordata (29.6% of all taxa) (Fig. 3F). All compartments were linked with 5124 TIs with their prey and other food sources (Table 3; Fig. S1C). Furthermore, 212 NTIs existed among compartments in the NTI web. D was 21 and C was 0.083. The predator with the most TIs in this assemblage was the megabenthic *Todarodes sagittatus* (Lamarck, 1798), the prey with the most predators were Copepoda, and the taxon with the most NTIs was the polychaete family Polynoidae.

3.1.4. Intact deep-sea sponge assemblage

For the deep-sea sponge assemblage, 232 faunal interaction-web compartments were recorded, ranging in size from protozoan and metazoan meiobenthos (0.86%), to macrobenthos (20.7%), invertebrate megabenthos (56.0%), and fish (22.4%). Of all compartments, 82% were carnivores (52.6% of all taxa), filter/suspension feeders (20.3% of all taxa), and deposit feeders (9.05% of all taxa) (Fig. 3G). All faunal compartments were connected to their corresponding prey and food sources via 9303 TIs (Table 3; Fig. S1D). The NTI web consisted of 312 interactions. *D* was 38 and *C* was 0.16. Members of the megabenthic amphipod family Oedicerotidae were the predators with the most TIs, and Euphausiacea was the prey taxon with the most TIs. Polychaetes of the family Polynoidae were the taxon with the most *NTIs*.

3.2. Removing specific taxa from the different faunal assemblages

3.2.1. Removing representative taxa of the deep-sea coral assemblage

The removal of representative taxa of the deep-sea coral assemblage, i.e. *Stauropathes arctica*, *Flabellum alabastrum*, *Funiculina quadrangularis*, *Heteropolypus sol*, and *Acanella arbuscula*, from the other assemblages did not result in the knock-down of any further compartments (Table 3).

3.2.2. Removing representative taxa of the lower slope assemblages 1 and 2

Removing representative taxa of the lower slope assemblages, i.e. *Phormosoma placenta*, *Bathybiaster vexillifer*, *Zoroaster fulgens*, *F. quadrangularis*, *Anthoptilum grandiflorum*, *Balticina finmarchica*, and *Pennatula aculeata*, from the lower slope assemblage 1 did eliminate compartments (i.e. macrobenthic Copepoda, megabenthic *Acanthephyra* A. Milne-Edwards, 1881, *Pandalus montagui* Leach, 1814, and *Sebastes fasciatus* Storer, 1854) due to facultative NTIs. The compartments *Eusergestes arcticus* (Krøyer, 1855), members of the ophiuroid family Gorgonocephalidae, and *Halargyreus johnsonii* Günther, 1862 were lost subsequently because of TIs with Copepoda.

Removing representative taxa of the lower slope assemblages from lower slope assemblage 2 resulted in the loss of macrobenthic Copepoda, *Acanthephyra pelagica* (Risso, 1816), and *P. montagui* due to facultative NTIs.

The removal of lower slope assemblage taxa from the deep-sea assemblages resulted in the disappearance of *Acanthephyra* sp. and *Pandalus* Leach, 1814 due to NTIs.

3.2.3. Removing representative taxa of the deep-sea sponge assemblage

Removing the sponge suborder Astrophorina compartment from the deep-sea coral assemblage led to the loss of 26.7% of all interaction-web compartments (Table 3), indicating that Astrophorina sponges comprised the highest impact taxon. The high percentage of losses of interaction-web compartments was the result of a first-order removal of facultative NTIs with Astrophorina (Table S2), second-order removal of facultative NTIs with other fauna, and tertiary losses of TIs (Figs. 4A & 5 subpanels 1 and 2). The lost compartments included macrobenthos (17.1% of all lost compartments), invertebrate megabenthos (55.7%), and fish (27.1%). Most of the removed faunal taxa were 'carnivore, filter/suspension feeder' (50.0%) and 'filter/suspension feeder' (43.8%). Additionally, the removal of Astrophorina resulted in the complete (100%) disappearance of the feeding types 'carnivore and scavenger' and 'deposit feeder and filter/suspension feeder' (Fig. 3A). Phyla that disappeared due to the removal of Astrophorina were mostly Brachiopoda (100% loss), Bryozoa (100% loss), and Annelida (58.3% loss) (Fig. 3B).

The loss of Astrophorina sponges from the lower slope assemblage 1 caused the removal of 67 taxa. This corresponded to the removal of 30.2% of all compartments (Table 3), and therefore, Astrophorina sponges were considered the highest impact taxa. Most of the taxa removed belonged to invertebrate megabenthos (53.7%), 28.4% belonged to fish, and 17.9% belonged to macrobenthos. Except for the megabenthic sea star families Echinasteridae and Pterasteridae, *E. arcticus*, and *H. johnsonii* that disappeared from the interaction webs due to the loss of their food sources, all other lost compartments had facultative NTIs with Astrophorina or other fauna (Figs. 4B & 5 subpanel 3; Table S2). About 50% of the taxa of the feeding types 'deposit feeder, filter/suspension feeder' and 'filter/suspension feeder' disappeared, and the feeding type 'deposit feeder, scavenger' was removed completely (Fig. 3C). Furthermore, 100% of the phyla Brachiopoda, Bryozoa, and Porifera were lost (Fig. 3D).
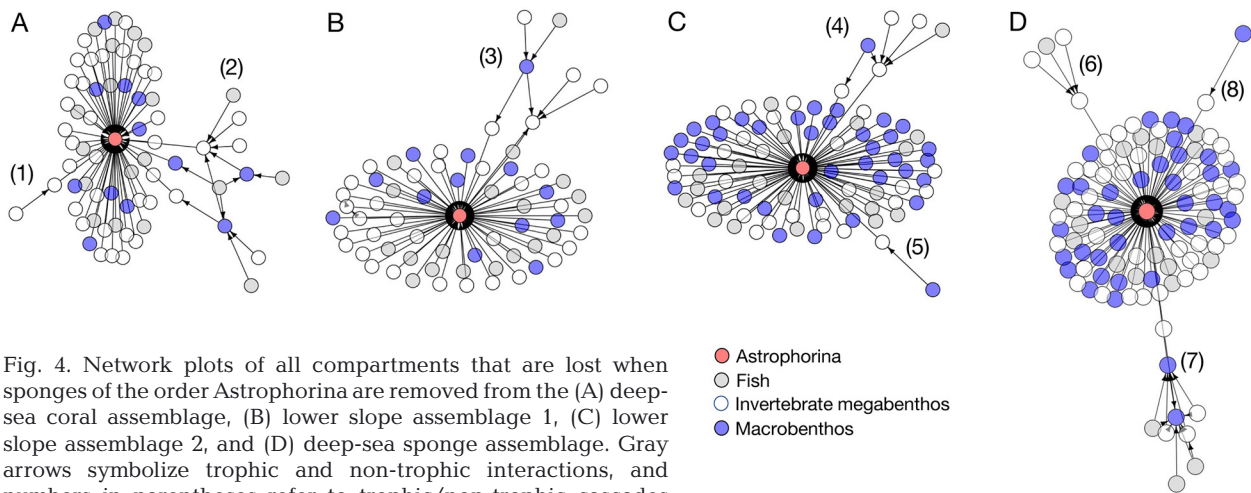
Fig. 4. Network plots of all compartments that are lost when sponges of the order Astrophorina are removed from the (A) deep-sea coral assemblage, (B) lower slope assemblage 1, (C) lower slope assemblage 2, and (D) deep-sea sponge assemblage. Gray arrows symbolize trophic and non-trophic interactions, and numbers in parentheses refer to trophic/non-trophic cascades and clusters that are shown in detail in Fig. 5

Eliminating the sponge suborder Astrophorina from the lower slope assemblage 2 resulted in the loss of 37.5% of all compartments (Table 3), implying that Astrophorina sponges were the highest impact taxa. We found that 41.3% of all macrobenthos, 37.0% of invertebrate megabenthos, and 21.7% of all fish disappeared, mainly due to the loss of facultative interactions of taxa with Astrophorina sponges. Most of these lost taxa were carnivores (32.1%), filter/suspension feeders (57.6%), and deposit feeders (44.4%) (Fig. 3E), and they belonged mainly to the phyla Annelida (66.7% loss), Arthropoda (48.3% loss), Chordata (30.4%), and Cnidaria (50.0% loss) (Fig. 3F). Only megabenthic sea stars of the family Echinasteridae and polychaetes of the family Syllidae were lost due to TIs with Astrophorina sponges, whereas macrobenthic Copepoda and amphipods of the family Unciolidae were lost indirectly (i.e. maximum secondary loss) due to facultative interactions with *Anthoptilum* Kölliker, 1880, *B. finmarchica*, and *Umbellula* Gray, 1870 (Figs. 4C & 5 subpanels 4 and 5; Table S2). *Acanthephyra pelagica*, *P. montagui*, and the fish *Benthosema* Goode & Bean, 1896 were facultatively non-trophically linked to *Anthoptilum* sp. and were therefore lost in a second-order loss.

Removal of the sponge suborder Astrophorina from the deep-sea sponge assemblage resulted in the loss of 43.2% of all interaction-web compartments (Table 3), signifying that Astrophorina sponges were again the highest impact taxa. Most of the taxa belonged to invertebrate megabenthos (46.1%), 35.6% belonged to the macrobenthic size class, and 18.3% to fish. The removal of Astrophorina led to the disappearance of 36.9% of all carnivores, 50.0% of all

omnivores, 52.4% of all deposit feeders, and 53.2% of all filter feeders (Fig. 3G). Macrobenthic Calanidae, megabenthic *Desmophyllum dianthus* (Esper, 1794), the crustaceans Euphausiacea and *Robustosergia* Vereshchaka, Olesen & Lunina, 2014, *Gorgonocephalus lamarckii* (Müller & Troschel, 1842), and the mesopelagic *Sigmops bathyphilus* (Vaillant, 1884), *Cyclothone microdon* (Günther, 1878), and *Poromitra* Goode & Bean, 1883 were lost due to the loss of TIs, i.e. due to the loss of their prey (Figs. 4D & 5 subpanels 6—8; Table S2). All other compartments were lost due to NTIs with Astrophorina (95.7%) and facultative interactions with other fauna (4.26%).

3.2.4. Removing taxa with the most TIs/NTIs and the second/third highest impact taxa

The removal of taxa with most TIs and NTIs from the deep-sea coral assemblage interaction web did not result in the knock-down of any further compartments (Table 3). In comparison, the removal of the second highest impact taxon (i.e. taxon whose removal resulted in the second largest changes in food-web properties), *Anthoptilum* sp., caused the disappearance of 1.89% of all compartments, as macrobenthic amphipods, *Acanthephyra* sp., and *P. montagui* had facultative NTIs with it. Subsequently, *Ceratoscopelus* Günther, 1864 was lost in a second-order loss due to the disappearance of its only prey, the amphipods. Removing the third highest impact taxon, Copepoda, resulted in the removal of *Leptagonus decagonus* (Bloch & Schneider, 1801), macrobenthic amphipods, and *E. arcticus* that all prey upon Copepoda, whereas
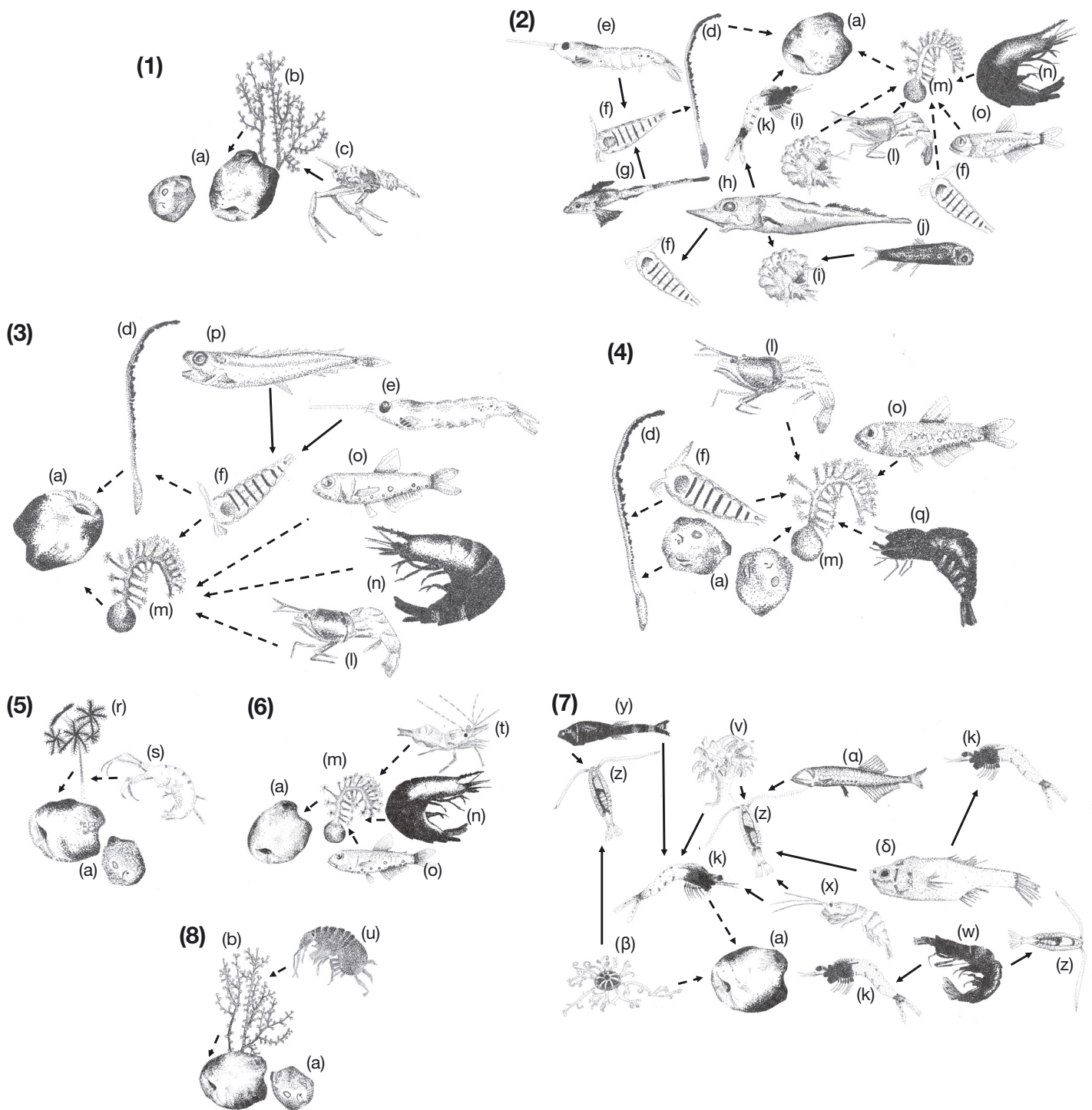
Fig. 5. Taxa that are lost in trophic/non-trophic cascades and clusters due to removal of Astrophorina sponges. The cascades/clusters presented as panels (1) − (8) correspond to the respective cascades/clusters visualized in Fig. 4. Solid arrows symbolize trophic interactions, dashed arrows show non-trophic interactions. The taxa presented in the drawings are the following: (a) Astrophorina, (b) *Acanthogorgia* sp., (c) *Munidopsis curvirostra*, (d) *Balticina finmarchica*, (e) *Eusergestes arcticus*, (f) Copepoda, (g) *Leptagonus decagonus*, (h) *Trachyrincus murrayi*, (i) Amphipoda, (j) *Ceratoscopelus* sp., (k) Mysida, (l) *Pandalus montagui*, (m) *Anthoptilum* sp., (n) *Acanthephyra* sp., (o) *Benthosema* sp., (p) *Halargyreus johnsonii*, (q) *Acanthephyra pelagica*, (r) *Umbellula* sp., (s) Unciolidae, (t) *Pandalus* sp., (u) Pleustidae, (v) *Desmophyllum dianthus*, (w) *Robustosergia* sp., (x) Euphausiacea, (y) *Poromitra* sp., (z) Calanidae, (α) *Cyclothone microdon*, (β) *Gorgonocephalus lamarckii*, (γ) *Sigmops bathyphilus*. Sizes of species in the drawings are not to scale

Ceratoscopelus sp. was lost in a second-order knock-down after the removal of its only prey, the amphipods, from the interaction web.

Losing the predator with the most prey (i.e. *A. denticulatus*) and the taxon with the most NTIs (i.e. Polynoidea) from the lower slope assemblage 1 did not result in the knock-down of any other compartments (Table 3). However, the removal of the prey taxon with the most predators (i.e. Copepoda) from the interaction web resulted in the loss of *H. johnsonii*, *E. arcticus*, and Gorgonocephalidae due to TIs. The removal of the second highest impact taxon (i.e. *Anthoptilum* sp.) implied losing *Acanthephyra* sp. and *P. montagui* due to NTIs. Removing the third highest impact taxon, in comparison, did not trigger any cascade of compartment losses.

Removing the taxa with most TIs (i.e. *T. sagittatus*, Copepoda) and NTIs (i.e. Polynoidae) from the lower slope assemblage 2 had no further effect on any other compartment (Table 3). The taxon that had the second highest impact on food-web properties was *Anthoptilum* sp., and *Calathura* Norman & Stebbing, 1886 was the third highest impact taxon, but only removing *Anthoptilum* sp. affected other interaction-web compartments, i.e. *P. montagui* and *A. pelagica*.

The removal of taxa with the most TIs (Oedicerotidae, Euphausiacea) and NTIs (Polynoidea) did not cause any knock-down of other compartments in the deep-sea sponge assemblage (Table 3). In comparison, removing the second highest impact taxon (Mysida) caused the loss of 5.35% of all compartments in a 3-level knock-down cascade (Fig. 5 subpanel 7). In this cascade, first, macrobenthic Calanidae disappeared due to the loss of their prey, Mysida, and in a second-order loss, *S. bathyphilus* and *C. microdon*, *D. dianthus*, Euphausiacea, *Robustosergia* sp., and *G. lamarckii* were lost after the loss of their prey. Subsequently, in a third-order loss, *Lampadena* Goode & Bean, 1893, *Lampanyctus* Bonaparte, 1840, *Myctophum* Rafinesque, 1810, *Notoscopelus* Günther, 1864, and *Poromitra* sp. vanished.

3.3. Changes in network properties of different faunal assemblages at the Flemish Cap

Removal of the Astrophorina compartment in the deep-sea coral assemblage, the lower slope assemblages 1 and 2, and the deep-sea sponge assemblage led to a substantial decrease in L (deep-sea coral: 45.0% decrease; lower slope 1: 51.3% decrease; lower slope 2: 56.0% decrease; deep-sea sponge: 59.6% decrease) and D (deep-sea coral: 24.3% decrease, lower slope 1: 30.0% decrease, lower slope 2: 28.6% decrease, deep-sea sponge: 28.9% decrease) (Table 3). However, C was only affected by removing Astrophorina in the lower slope assemblage 2 (+13.3%) and in the deep-sea sponge assemblage (+25.0%), whereas the C of the deep-sea coral assemblage and lower slope assemblage 1 remained unaffected. Removing any of the taxa with the most TIs and NTIs, or second highest impact taxa never changed the network indices by more than 7% (Table 3).

4. DISCUSSION

The aim of this study was to assess the relevance of representative species of the deep-sea coral assemblage, lower slope assemblage 1, lower slope assemblage 2, and the deep-sea sponge assemblage for TIs/NTIs and network indices of the corresponding faunal assemblages. We furthermore investigated the role of species with the most TIs/NTIs for network indices and identified the highest impact taxa.

Here, we will first compare the role of the representative species in TIs and NTIs with the role that the highest impact taxon, Astrophorina sponges, plays in these interactions, and afterwards, we will compare the sponge grounds at the Flemish Cap with sponge grounds in the NE Pacific and at Schulz Bank, a seamount on the Arctic Mid-Ocean Ridge.

4.1. Role of representative species in faunal assemblages at the Flemish Cap

When all representative taxa of the deep-sea coral assemblage (*Stauropathes arctica*, *Flabellum alabastrum*, *Funiculina quadrangularis*, *Heteropolypus sol*, and *Acanella arbuscula*) were removed, only 2.5% of the links were lost, whereas link density and connectance remained unaffected. This might be surprising at first glance, because corals are usually considered autogenic ecosystem engineers (i.e. organisms that 'change the environment via their own physical structure' and 'modulate the distribution and abundance of other resources'; Jones et al. 1994, p. 373−4), or foundation species sensu Dayton et al. (1974) (i.e. 'organisms that provide structure, moderate local biotic and abiotic conditions, and have a large, positive effect on other species in a community'; Angelini et al. 2011, p. 783). However, deep-sea coral assemblages on hard substrate are more species rich than assemblages on soft sediments (Baker et al. 2012). As the deep-sea coral assemblage at the Flemish Cap

occurred in sandy-silty sediments, the estimated low number of lost interactions might be related to the specific coral community inhabiting soft sediments. Additionally, the cnidarians with most interactions were not representative species of the deep-sea coral assemblage itself, but 2 sea pen species, *Anthoptilum grandiflorum* and *Balticina finmarchica* (Murillo et al. 2016). They have been suggested to act as biogenic habitat (Baillon et al. 2014) and indeed, removing *Anthoptilum* sp. from the interaction web caused a 2-order extinction cascade. In a first step, 4 additional faunal compartments were lost that had facultative NTIs with *Anthoptilum* sp., and in the subsequent step, *Ceratoscopelus* sp. disappeared as maximum secondary loss due to the loss of its prey (Table S2). In comparison, the highest impact taxon Astrophorina sponges facultatively host up to 62 species in the deep-sea coral assemblage, which can be lost in 2-order extinction cascades when these sponges are removed. Hence, the sea pens and Astrophorina sponges can both be considered foundation species, as their interactions with other taxa are mainly of non-trophic nature (Ellison 2019). They could also be called structural species or habitat formers (i.e. species that 'create physical structures, produce variability in physical conditions, provide resources, and create habitat for associated [...] species'; Ellison 2019, p. 258) since they control biodiversity in a similar way to foundation species, but their impacts on ecosystem functions are unspecific (Ellison 2019). However, due to the possible role as a nursery area for fish and crustacean larvae (Baillon et al. 2012, 2014) and the low abundance of Astrophorina sponges on the soft sediment, we hypothesize that the sea pens are more important for the deep-sea coral assemblage than the sponges.

The 2 lower slope assemblages 1 and 2 are represented by *Phormosoma placenta*, different sea stars, and sea pens. Sea stars of the families Echinasteridae and Pterasteridae prey upon Astrophorina sponges, so the removal of this sponge suborder from the interaction webs resulted in a loss of TIs with these specific families. In fact, sea stars are common spongivores: they prey upon *Geodia* sp./*Stelletta* Schmidt, 1862 at the Langseth Ridge in the central Arctic Ocean (Stratmann et al. 2021) and at the Schulz Bank (Hanz et al. 2022, Meyer et al. 2023), upon various sponge species along the continental margin of the NW Atlantic and the Gulf of Mexico (Mah 2020), or upon reef sponges in the Caribbean (Wulff 1995). However, beyond being spongivores, the role of these sea stars in the food web of the Flemish Cap appears to be rather limited, as their removal from the interaction webs of lower slope 1 and 2 did not affect any other taxon.

Sea pens, in contrast, are often seen as biogenic habitat providers in soft-sediment habitats (Tissot et al. 2006, Baillon et al. 2014, Miatta & Snelgrove 2022). At the continental margin off northern Norway (NE Atlantic), decapods of the families Caridea and Munididae were observed near 20% of the sea pens (De Clippele et al. 2015) and in the Laurentian Channel (Canada, NW Atlantic), macrobenthic diversity is higher at sites with sea pens compared to sites with bare sediment (Miatta & Snelgrove 2022). Like in the deep-sea coral assemblages, sea pens may provide nurseries for larvae of crustaceans and *Sebastes fasciatus* (Baillon et al. 2012, 2014) in the lower slope assemblages and therefore, they have facultative NTIs with fish and arthropods, that are connected via TIs to *Halargyreus johnsonii*, *Eusergestes arcticus*, and sea urchins. Astrophorina sponges also have further facultative NTIs with a diverse range of annelids, cnidarians, arthropods, echinoderms, and fish in the lower slope assemblages.

The deep-sea sponge assemblage consists mainly of sponges of the suborder Astrophorina (i.e. *Geodia* sp., *Thenea* sp.) which can be considered key species sensu Davic (2003), as they regulate energy and nutrient dynamics due to their large biomass (Murillo et al. 2012) and consequently, high rates of carbon and nitrogen cycling (Pham et al. 2019). They can also be considered ecosystem engineers because they modulate the distribution and abundance of resources (Jones et al. 1994), i.e. nutrients (Hoffmann et al. 2009). They are structural species/habitat formers and create habitat for associated fauna (Ellison 2019). Since most of the interactions between Astrophorina sponges and other members of the interaction webs are non-trophic, they are foundation species sensu Dayton (1972) (Ellison 2019). In fact, Astrophorina sponges in the deep-sea sponge assemblage have facultative NTIs with 90 different taxa, which are more TIs or NTIs than Astrophorina sponges have in any of the other investigated faunal assemblages.

4.2. Comparison of sponge grounds at the Flemish Cap with other sponge grounds

It is not only demosponges like the Astrophorina sponges that have been identified as foundation species, but also glass sponges. Archer et al. (2020) developed food-web models for 20 glass sponge reefs in British Columbia (Canada) and showed that these glass sponges are an important prey for all investigated taxa. This is very different from the role that Astrophorina sponges play at the Flemish Cap, where they are

mostly involved in NTIs. However, the diet information for the Flemish Cap is mostly taken from published literature, whereas Archer et al. (2020) based their food-web topology on stable isotope analysis and stomach content analysis from specimens collected at the sites for which they developed their models. Hence, we might underestimate the role of Astrophorina sponges in TIs at the Flemish Cap due to a lack of site-specific diet information for potential predators. Interestingly, however, Archer et al. (2020) found that the sponge cover has an influence on food-web topology. When the glass sponge cover is <10%, the food webs are less connected, and first- and second-order consumers depend on fewer food sources and are preyed upon by fewer predators. When the glass sponge coverage is >10%, the food web is more connected, and the species rely on more food sources but are also preyed upon by more predators. In comparison, the faunal assemblage with the highest sponge coverage at the Flemish Cap, the deep-sea sponge assemblage, has only a 0.02 higher connectance than the faunal assemblage with the second-highest sponge coverage (deep-sea coral assemblage), but a 0.071 and 0.077 higher connectance than the lower slope assemblages 1 and 2 with the lowest sponge coverage. Hence, sponge coverage likely does not only affect connectance on a trophic level, but also on a non-trophic level in sponge-dominated ecosystems.

Sponge grounds consisting of Astrophorina sponges also occur at the Schulz Bank (Meyer et al. 2019, 2023, Morrison et al. 2020, Hanz et al. 2022). Particularly cluster C (~579–1100 m water depth; substratum type: spicule mat) was dominated by sponges, like *Schaudinnia rosea* (Fristedt, 1887)/*Trichasterina borealis* Schulze, 1900/*Scyphidium septentrionale* Schulze, 1900, *Geodia parva* Hansen, 1885/*Stelletta rhaphidiophora* Hentschel, 1929, and *Geodia hentscheli* Cárdenas, Rapp, Schander & Tendal, 2010 (Meyer et al. 2023). NTIs with these large demosponges were regularly observed, as with *Gersemia rubiformis* (Ehrenberg, 1834) settling on the sponges or *Hexadella dedritifera* Topsent, 1913 growing on *G. parva/S. rhaphidiophora* (Meyer et al. 2023). In comparison, at the Flemish Cap, the sponges *Asconema* Kent, 1870, *Craniella* Schmidt, 1870, *Pavona* Lamarck, 1801, and *Tentorium* Vosmaer, 1887 had facultative NTIs with Astrophorina sponges. Both sites had spongivores in common. At the Schulz Bank, the asteroid *Tylaster willei* Danielssen & Koren, 1881 preyed upon *G. parva/S. rhaphidiophora* and *S. rosea/T. borealis*/S. *septentrionale* (Hanz et al. 2022, Meyer et al. 2023), whereas at the Flemish Cap, the asteroids *Benthopecten* Verrill, 1884, *Hippasteria phrygiana* (Parelius, 1768), *Pontaster*

Sladen, 1885, *Pteraster* Müller & Troschel, 1842, *Solaster* Forbes, 1839, and *Stephanasterias albula* (Stimpson, 1853) preyed upon *Geodia* sp. and *Thenea* sp.

Hence, both sponge grounds have comparable major TIs and NTIs with (Astrophorina) sponges, although the species were not the same, mainly due to differences in substratum type and species-specific substrate preferences. Therefore, it would be interesting to develop TI/NTI webs for the different clusters at the Schulz Bank to gain more information about the role of substrate and species dependence on it in TIs/NTIs. At the Flemish Cap, the 4 faunal assemblages are present on soft sediments with different grain size ranging from clayed-silt to sandy-silt (Murillo et al. 2016), whereas at the Schulz Bank, the various faunal clusters occur on spicule mats (Cluster C), mixed sediments (Clusters K and X), soft sediments (Clusters X and AB), and bed rock (Cluster S).

4.3. Data and model limitations

The highly resolved interaction webs of the 4 different faunal assemblages at the Flemish Cap were very well resolved for macrobenthos, invertebrate megabenthos, and demersal fish, but less for meiobenthos. This was related to the sampling gear deployed during previous research expeditions on which data for this study were based. Bottom trawls are commonly used to collect invertebrate megabenthos and fish (Gage & Tyler 1991), although at the Porcupine Abyssal Plain (NE Atlantic), trawls underestimated invertebrate megabenthos biomass by a factor of 40 to ~200 compared to photo surveys (Durden et al. 2017). USNEL box corers are appropriate to sample macrobenthos but are rarely used to collect meiobenthos samples (Danovaro 2010). Hence, we included only 3 different meiobenthos taxa at the order (Harpacticoida) and phylum levels (Nematoda, Foraminifera), even though sponge grounds, coldwater coral gardens, and soft-sediment communities can have a high meiobenthos diversity (Raes & Vanreusel 2006, Sandulli et al. 2015). Therefore, we likely underestimated the complexity of the food webs of the 4 faunal assemblages. However, comparable TI/NTI web models developed for abyssal plains in the central and SE Pacific included 34% meiobenthos compartments, of which none was lost when the highest impact taxa, i.e. the stalked sponges *Hyalonema* Gray, 1832 and *Caulophacus* Schulze, 1886, were removed (Stratmann et al. 2021). Therefore, it could be expected that the results of our study are reasonably robust to the poorly resolved meiobenthos in our models.

The sampling tools used in this study created the species lists associated with each of the found benthic assemblages. They were not used to establish TIs or NTIs due to the different spatial scales and catchability of the gears deployed. This is appropriate, as it is well known that trawls integrate data over kilometer scales while cameras and grabs are able to collect high-resolution data from small areas. In the Skagerrak between Norway and Denmark, and in the Norwegian trench, for example, the ophiuroid *Asteronyx* Müller & Troschel, 1842 has an NTI with *F. quadrangularis*, and Buhl-Mortensen et al. (2023) observed via ROV transects that several *Asteronyx* sp. specimens can sit on 1 *F. quadrangularis* specimen. During trawling, however, ophiuroids tend to lose their grip and *F. quadrangularis* often break, so that the information about this NTI is lost if data on associations are based on trawl observations alone. Here, we obtained species lists from each of the 4 benthic communities found to be statistically differentiated from one another in species composition. The nature of the associations among species was subsequently determined from the literature, where a wide variety of methods were used, including stomach analyses, photographic evidence, and radio isotope analyses. Hence, although we likely underestimated NTIs among species, our results were not contingent on the sampling devices deployed.

Furthermore, it should be stressed that the consequences of the removal of specific compartments on the TIs/NTIs constitute extreme cases, as we assume that the links removed are the critical ones. While this is not an issue in relative terms (i.e. to assess which removals are generally expected to have a higher risk of impact), the results do not necessarily reflect true expected impacts.

5. CONCLUSIONS

This study showed that sponges of the suborder Astrophorina are the highest impact taxa not only in the deep-sea sponge assemblage, but also in in the deep-sea coral and lower slope assemblages at the Flemish Cap. This result implies that when identifying the significant adverse impacts of fishing on vulnerable marine ecosystems (i.e. ecosystems that 'may be physically or functionally fragile' and 'experience substantial alteration from short-term or chronic disturbance'; FAO 2009, p. 4), it is important to examine TIs and NTIs which may increase the severity of the impact differentially according to, in this case, whether or not Astrophorina sponges or sea pens are

removed. The results of our study demonstrate how important even less abundant/non-representative indicator species can be for TIs and NTIs and therefore food-web integrity.

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