Tackling the jelly web: Trophic ecology of gelatinous zooplankton in oceanic food webs of the eastern tropical Atlantic assessed by stable isotope analysis

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Abstract

Gelatinous zooplankton can be present in high biomass and taxonomic diversity in planktonic oceanic food webs, yet the trophic structuring and importance of this "jelly web" remain incompletely understood. To address this knowledge gap, we provide a holistic trophic characterization of a jelly web in the eastern tropical Atlantic, based on $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis of a unique gelatinous zooplankton sample set. The jelly web covered most of the isotopic niche space of the entire planktonic oceanic food web, spanning > 3 trophic levels, ranging from herbivores (e.g., pyrosomes) to higher predators (e.g., ctenophores), highlighting the diverse functional roles and broad possible food web relevance of gelatinous zooplankton. Among gelatinous zooplankton taxa, comparisons of isotopic niches pointed to the presence of differentiation and resource partitioning, but also highlighted the potential for competition, e.g., between hydromedusae and siphonophores. Significant differences in spatial (seamount vs. open ocean) and depth-resolved patterns (0–400 m vs. 400–1000-m) pointed to additional complexity, and raise questions about the extent of connectivity between locations and differential patterns in vertical coupling between gelatinous zooplankton groups. Added complexity also resulted from inconsistent patterns in trophic ontogenetic shifts among groups. We conclude that the broad trophic niche covered by the jelly web, patterns in niche differentiation within this web, and substantial complexity at the spatial, depth, and taxon level call for a more careful consideration of gelatinous zooplankton in oceanic food web models. In light of climate change and fishing pressure, the data presented here also provide a valuable baseline against which to measure future trophic observations of gelatinous zooplankton communities in the eastern tropical Atlantic.

The open ocean constitutes the largest living habitat on earth, but it is also the least known environment (Robison 2004). The basic understanding of oceanic food webs is that primary production via photosynthesis takes place by phytoplankton in the sunlit surface layer. The resulting phytoplankton-based organic matter is then utilized by microbial communities and by herbivorous zooplankton, which are in turn consumed by carnivores such as gelatinous zooplankton, chitinous zooplankton, ichthyoplankton, planktivorous fishes, and juvenile squids (Robison 2009). Energy and matter can further be transferred to higher trophic levels, e.g., large predatory fishes, sea turtles, and seabirds (Carman et al. 2014; Thiebot et al. 2016). Degrading matter from all trophic levels can link to the microbial loop (Caron 1994) and sink to fuel deeper living communities (Chelsky et al. 2016).

Within oceanic food webs, gelatinous zooplankton constitute one of the most diverse, abundant, and widely distributed organismal groups (Robison 2004; Condon et al. 2012),

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Associate editor: Kelly Benoit-Bird

occupying habitats ranging from the epipelagic zone to the deep sea and from polar to tropical areas (Madin et al. 1997; Mapstone 2014). Taxonomic groups of gelatinous zooplankton include, e.g., hydromedusae, scyphomedusae, siphonophores, ctenophores, pelagic tunicates (hereafter named tunicates), and chaetognaths (Hamner et al. 1975; Nogueira Júnior et al. 2019). In recent decades, the ecology of gelatinous zooplankton has received increased scientific attention because some species in this group may have experienced regional increases in population size (Dong et al. 2010; Brotz et al. 2012; Tiller et al. 2017), including events of mass occurrence, so-called jellyfish blooms. The massive biomass associated with these blooms can result in shifts of ecological community structure and energy transfer (D'Ambra et al. 2013). It is important to note that assessments of trends in gelatinous zooplankton abundances have been greatly restricted by the fragile nature of gelatinous zooplankton, which has complicated quantitative sampling (Hosia et al. 2017).

Understanding the trophic niches of different gelatinous zooplankton groups is critical for the interpretation of their trophic roles in food webs. Evidence is accumulating that gelatinous zooplankton occupy key positions in food webs as both predators and prey. For example, a database consisting of 27 years of annotated remotely operated vehicle underwater observations showed that gelatinous zooplankton such as narcomedusae, siphonophores, and ctenophores were key predators in the central California deep pelagic food web (Choy et al. 2017). The same study also observed that tunicates, siphonophores, hydromedusae, and ctenophores could serve as prey items for other predators such as narcomedusae. In their function as both predator and prey, feeding interactions between gelatinous zooplankton groups, and between gelatinous and non-gelatinous zooplankton groups were relevant. The collective ecological importance and trophic roles of a large and complex gelatinous fauna have been referred to as the "jelly web" (Robison 2004; Choy et al. 2017).

Trophodynamics of many individual gelatinous zooplankton taxa have been revealed via experimental studies and field observations. These studies have highlighted the range of diets, possible functional roles, and trophic positions covered by different specific gelatinous zooplankton groups. For example, tunicates are deemed to be filter feeders, with pyrosomes feeding mainly on phytoplankton (Perissinotto et al. 2007), whereas salps can feed on bacteria, phytoplankton, and detritus (Ahmad Ishak et al. 2017). A ctenophore relevant to our study, *Beroe* spp., mainly consumes other ctenophores (Finenko et al. 2001). In contrast, copepods and ostracods can account for up to 87% of prey in chaetognaths (Froneman et al. 1998), and scyphomedusae, hydromedusae, and siphonophores have a wide range of diets, including copepods, fish larvae, pteropods, heteropods, and other gelatinous zooplankton (Purcell 2018). Additionally, the trophic position within a species might shift with ontogeny and life stages (Fleming et al. 2015).

A combined view of trophic niches of a large range of gelatinous zooplankton taxa would in turn reflect the overall trophic niche space covered by the jelly web within planktonic oceanic communities and reveal patterns in resource partitioning and competition (Boecklen et al. 2011), in line with community ecology studies on other systems. However, while a number of studies have addressed the composition and trophic structure of planktonic oceanic communities, including individual gelatinous zooplankton groups (Denda et al. 2017), dedicated studies remain rare. One major problem has been the difficulty to obtain suitable sample sets. Due to their watery and fragile body structure as well as their patchy distributions, gelatinous zooplankton taxa in oceanic regions are difficult to sample and preserve (Fleming et al. 2011). Moreover, degraded samples are often not suitable for stomach or gut content analyses, which are the traditional methods to characterize dietary niches (Pitt et al. 2009). Consequently, a holistic view reflecting the range of roles and interactions involving gelatinous zooplankton in oceanic food webs is mostly lacking, which is reflected in an often oversimplified or inaccurate representation of gelatinous zooplankton in food web models as illustrated and acknowledged by Pauly et al. (2009).

Recently, stable isotope analysis has been utilized in studies of gelatinous zooplankton feeding ecology (Pitt et al. 2009; Javidpour et al. 2016). The ratios of nitrogen and carbon isotopes of an organism provide time-integrated signals within the turnover rate of its tissues which reflect its average diet and trophic level (Fry 2006). In this context, carbon isotopes are suitable tracers of material at the base of food webs and possible food sources (Fry and Sherr 1989), whereas nitrogen isotopes can indicate the trophic positions of organisms in food webs (Post 2002). Consequently, stable isotope studies of many species within the same community can help to elucidate the structure of the food web and ultimately energy flow (McClain-Counts et al. 2017). Moreover, stable isotope analysis is a useful tool to reveal the trophic niche characteristics of organisms (Newsome et al. 2007). Isotopic differences between species or taxonomic groups point to different trophic niches, and isotopic variation reflects their respective niche width.

The eastern tropical Atlantic is one of the most biologically active regions of the world ocean because of its shallow thermocline and strong upwelling (Picaut 1985). In recent years, there has been an increase in research activities to improve biological and oceanographic understanding of this oceanic region (Devey 2014). This includes, for example, studies of oxygen minimum zones (Teuber et al. 2013), the role of seamounts as biodiversity hotspots (Hanel et al. 2010), the influence of zooplankton on organic matter flux in mesoscale eddies (Christiansen et al. 2018), the trophic ecology of pelagic and benthopelagic organisms (Merten et al. 2017), and the trophic structure of communities, including individual gelatinous zooplankton groups (Denda et al. 2017). A previous study has shown that gelatinous zooplankton in the eastern

tropical Atlantic are highly abundant and diverse (Hoving et al. 2019), but dedicated studies providing a more holistic view of characteristics of the trophic structure of gelatinous zooplankton communities in this area are lacking.

The goal of this study was to advance the understanding of the trophic structure, ecological role and possible importance of the jelly web within the planktonic oceanic food webs of the eastern tropical Atlantic using stable isotope analysis. To do so, our specific objectives were (1) to assess how isotopic niches and trophic levels compare between gelatinous and non-gelatinous zooplankton taxa, (2) to compare trophic niches for the different taxa within the gelatinous zooplankton, and (3) to assess factors (space, depth, and ontogeny) affecting isotopic variability. An additional overarching goal based on these analyses was to provide a stable isotope baseline data set against which to compare future observations, of particular relevance in the light of climate change, overfishing and potential resulting changes in gelatinous zooplankton communities.

Methods

Sampling

Sampling was conducted during November and December 2015 on board R/V "MARIA S. MERIAN" (cruise MSM49) at eight stations (latitude 12°00′N to 18°05′N, longitude 20°00′W to 24°00′W) in Cape Verdean waters in the eastern tropical Atlantic, including a shallow seamount (Senghor Seamount, 100–3300 m) and its northwestern and southeastern slopes, a cyclonic eddy, and four oceanic stations (Fig. 1). At all stations, we first deployed a CTD rosette (SBE 19 plus) carrying sensors to collect hydrographic data, including depth
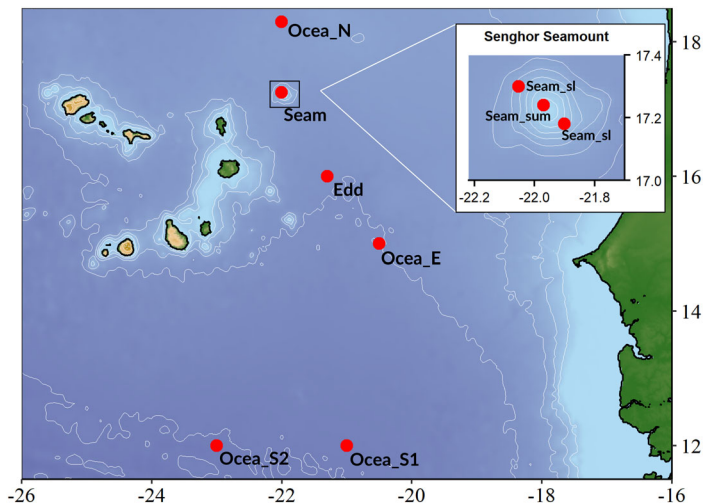

Fig. 1. Sample collection sites in the eastern tropical Atlantic (cruise: MSM49). The stations included summit (Seam_sum) and two slopes (Seam_sl1 and Seam_sl2) of a seamount, a cyclonic eddy (Edd), and four oceanic stations from the north (Ocea_N), the east (Ocea_E), and the south (Ocea_S1, Ocea_S2). Inset: Senghor seamount stations.

(m), temperature (°C), salinity (PSU), fluorescence (mg/m^3), and dissolved oxygen (μmol kg^{-1}). Biological sampling focused on the collection of gelatinous organisms from the epi- and mesopelagic zones (0–1000 m). In addition, other planktonic food web components from different trophic levels were sampled. Seston (as proxy for mixed microplankton food sources including phytoplankton, microzooplankton, degrading organic matter and inorganic particles) was collected as the baseline of the food web. Moreover, different meso- and macrozooplankton groups including crustaceans, fish larvae, polychaetes, and squids were sampled (Table 1; Table S1).

Seston sampling

Water samples were taken at four depths (25, 200, 400, and 1000 m) at each station using a CTD rosette (SBE 19 plus) equipped with 24 Niskin sampling bottles (Table 1). Seston samples were obtained by filtering 3 liters of seawater through GF/F (Whatman; pore size: 0.7 μm; diameter: 25 mm). For each depth, three replicates were prepared.

Meso- and macrozooplankton sampling

Net sampling was conducted using two types of multiple opening/closing nets and environmental sampling systems, one with 1 m^2 (three nets, mesh size: 2 mm; and six nets, mesh size: 335 μm) and one with 10 m^2 opening (five nets, mesh size: 1.5 mm), towed at a speed of 2 kn. Sampling depth intervals were targeted at 0–50, 50–100, 100–200, 200–400, 400–600, and 600–1000 m. Samples from replicate tows at the same depth and station were pooled for analyses. Despite the targeted effort to sample gelatinous zooplankton, it is important to stress that total gelatinous zooplankton diversity was likely higher than observed in our study, due to the difficulties to capture these fragile organisms in net catches. This was confirmed by underwater video transects on the same cruise showing higher gelatinous zooplankton diversity than in net catches (Hoving et al., 2019).

Zooplankton identification and storage

All specimens from net catches were identified immediately after the tow by experienced specialists to the lowest possible taxonomic levels and classified in taxonomic groups using taxon designations from the World Register of Marine Species. Samples included six taxonomic groups of gelatinous zooplankton, i.e., chaetognaths, hydromedusae, siphonophores, ctenophores (mainly *Beroe* sp.), scyphomedusae (two species of coronates), and tunicates (Table 1, Table S1, Fig. 2). All samples were then measured and rinsed with artificial seawater. The size of individuals was determined using a caliper rule, measuring the bell diameter in the case of hydromedusae and scyphomedusae, and body length in the case of chaetognaths, ctenophores, tunicates, and non-gelatinous zooplankton organisms. For siphonophores, we measured the length across nectophores (individual body units) of each specimen. Gelatinous zooplankton samples and other zooplankton organisms with a body size > 5 mm were stored individually, whereas

Table 1. Overview of sampling stations and sample sizes used in analyses. The stations included summit (Seam_sum) and two slopes (Seam_sl) of a seamount, a cyclonic eddy (Edd), and four oceanic stations from the north (Ocea_N), the east (Ocea_E), and the south (Ocea_S1, Ocea_S2). The numbers after taxonomic groups denote number of species were analyzed, with some groups were not identified to species level. Detail sample list refers to Table S1.

	Taxa (n)	Ocea_N	Seam_sl1	Seam_sum	Seam_sl2	Edd	Ocea_E	Ocea_S1	Ocea_S2	Total
Bottom depth (m)		3300	1000	100	1000	4000	4200	4700	4900	
Longitude (N)		18°05.00′	17°14.24′	17°09.99′	17°09.14′	16°08.81′	15°00.00′	12°00.00′	12°00.00′	
Latitude (W)		22°00.00′	22°00.71′	21°57.59′	21°54.68′	21°20.52′	20°30.00′	21°00.00′	23°00.00′	
Gelatinous zoopl.		85	48	16	47	43	54	92	66	451
Chaetognaths			2	4	5	2	4	8	9	34
0–400			1	4	5	2	4	2		18
400–1000			1					6	9	16
Ctenophores	1	13	14	2	9	9	11	16	9	83
0–400		9	7	2	3	7	9	2	3	42
400–1000		4	7		6	2	2	14	6	41
Hydromedusae	4	24	5	1	11	6	14	14	7	82
0–400		13	4	1	6	2	6	4	2	38
400–1000		11	1		5	4	8	10	5	44
Scyphomedusae	2	23	7		9	11	2	7	1	60
0–400		4	2							6
400–1000		19	5		9	11	2	7	1	54
Siphonophores	6	15	10	2	4	3	19	35	28	116
0–400		13	10	2	4	3	15	30	25	102
400–1000		2					4	5	3	14
Tunicates	2	10	10	7	9	12	4	12	12	76
0–400		9	10	7	8	12	3	12	12	73
400–1000		1			1		1			3
Seston		12	12	3	9	12		12		60
Seston_25 m		3	3	3	3	3		3		18
Seston_deep		9	9		6	9		9		42
Zooplankton		9	18	19	16	16	28	15	27	148
Amphipod	7	9	3	3	3	8	14	11	13	64
0–400		7	3	3	3	7	11	7	10	51
400–1000		2				1	3	4	3	13
Copepod			12	1	6	6	3	2	4	34
0–400			12	1	6	4	2	2	4	31
400–1000						2	1			3
Decapod larvae				2	3					5
0–400				2	3					5
Shrimp			3							3
0–400			2							2
400–1000			1							1
Gastropod	6				1	1	3		6	11
0–400					1	1	3		5	10
400–1000									1	1
Krill	2		2	6	3		6		1	18
0–400				6	2				1	9
400–1000			2		1		6			9
Ostracoda	2					1	1	1	3	6
0–400								1		1

(Continues)

Table 1. Continued

	Taxa (*n*)	Ocea_N	Seam_sl1	Seam_sum	Seam_sl2	Edd	Ocea_E	Ocea_S1	Ocea_S2	Total
400–1000						1	1		3	5
Polychaeta			1	7			1	1		10
0–400			1	7				1		9
400–1000							1			1
Squid		3	3	4	3	5	2	5		29
Squid		3	3	4	3	5	2	5		29
Squid larvae				1		1	1	1		4
Fish larvae	5		6	2	6	2	3	2	2	23
0–400			3	2	3	2	2	2	1	15
400–1000			3		3		1		1	8
Total		109	90	45	81	79	88	127	95	714
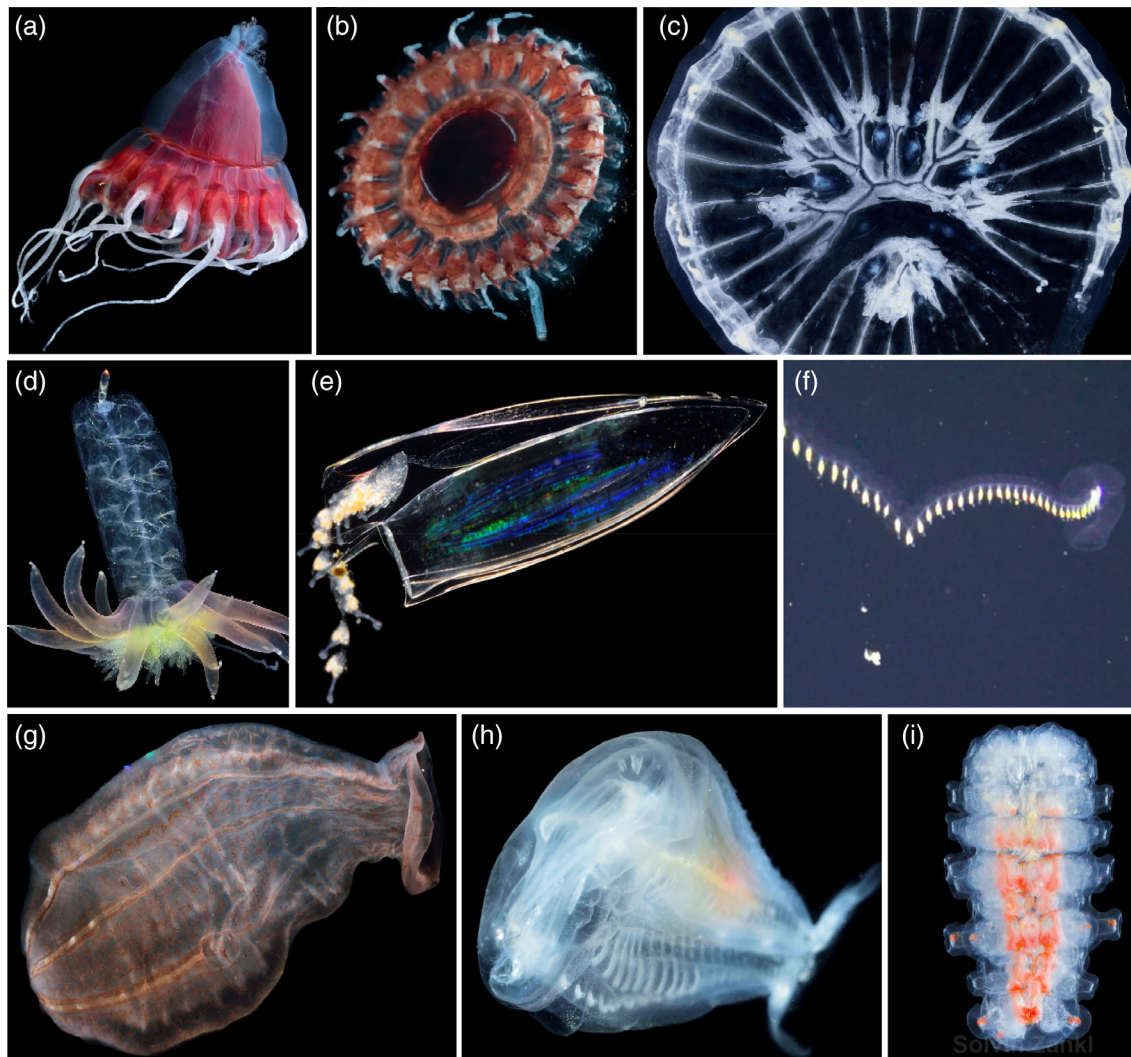
Fig. 2. Representative gelatinous specimens from net catches used for stable isotope analysis in this study. Scyphomedusae: (**a**) *Periphylla periphylla*, (**b**) *Atolla wyvillei*; Hydromedusa: (**c**) *Zygocanna vagans*; Siphonophores: (**d**) *Physophora hydrostatica*, (**e**) *Diphyes* sp., (**f**) *Praya dubia*; Ctenophore: (**g**) *Beroe* sp.; Pelagic tunicates: (**h**) *Thetys vagina*, (**i**) *Pyrostremma* sp. (photos by: Solvin Zankl [a, b, c, d, e, g, h, i]; Henk-Jan Hoving [f]).

chaetognaths and organisms with a body size < 5 mm were pooled (five individuals per Eppendorf tube). Samples were then immediately frozen and kept at −80°C until further analysis.

Stable isotope analysis
Sample preparation

Seston samples on GF/F filters were freeze-dried. A subsample of each filter was cut out and wrapped in tin foil prior to analysis. All animal samples were freeze-dried and ground to a fine powder. Subsamples of 250 ± 75 µg were then weighed into tin capsules (HEKAtech; diameter × height: 3.2×4 mm) for stable isotope analysis, which provided sufficient amounts for the low-biomass analysis pipeline described below.

Sample analysis

Samples were analyzed by a high-sensitivity elemental analyzer connected to an isotope ratio mass spectrometer (DeltaPlus Advantage, Thermo Fisher Scientific) as described by Hansen and Sommer (2007). $\delta^{15}N$ and $\delta^{13}C$ isotope values were expressed as δ values per mil deviation (‰) from the standard reference material Vienna Pee Dee Belemnite and atmospheric nitrogen as follows:

$$\delta X\,(‰) = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000$$

where X refers to ^{15}N and ^{13}C and R represents the ratio of the heavy to light isotope (Fry 2006).

System calibration was implemented by the combustion of International Atomic Energy Agency (N1-, N2-, N3-) and National Institute of Standards and Technology (NBS-22 and NBS-600) compounds. Acetanilide p.a. was used as an internal standard after every sixth sample within each sample run. The overall standard deviation for the low measurement range 2.5–8 µg N and 5–80 µg C was ± 0.25‰ and ± 0.2‰, respectively, and for the higher measurement range 3–15 µg N and 10–140 µg C was ± 0.2‰ and ± 0.15‰, respectively.

Lipid correction of $\delta^{13}C$ isotope values

Prior to the data analysis, a lipid correction was carried out according to Post et al. (2007) for specimens with high C : N (> 3.5) ratios, using the formula:

$$\delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \times C\!:\!N$$

where $\delta^{13}C_{\text{normalized}}$ was used for further analysis in this study, $\delta^{13}C_{\text{untreated}}$ are the raw data, and C : N ratio is the bulk carbon to nitrogen ratio.

Stable isotope data grouping

For further statistical analyses, we grouped samples in this study into two discrete depths, i.e., epi- and upper mesopelagic zone (0–400 m, hereafter named shallow layer) and lower mesopelagic zone (400–1000 m, hereafter named deep layer).

The foundation for this grouping was a minimum in dissolved oxygen around 400 m at all stations (Fig. 3). This was confirmed to affect organisms' vertical distributions (Lüskow et al. under review), and was reflected in available sample sizes in our studies, with samples exclusively available above (e.g., tunicates) or below (e.g., scyphomedusae) 400 m depth for several groups.

Moreover, because of the high vertical and horizontal patchiness of the occurrence of taxa and resulting imbalances in sample sizes across stations and depths in the overall data set, to compare the isotopic niche widths of taxa in the jelly web between locations and depths, the two locations with the best available sample sizes, seamount slope (pooled stations Seam_sl1 and Seam_sl2) and open ocean (station Ocea_S1), were selected.

Statistical analysis

The isotope space covered by the jelly web within the overall planktonic food web was described based on the comparison of convex hull areas. To assess and compare the relative position and overlap of isotopic niches of gelatinous zooplankton groups within this web, the standard ellipse area (Jackson et al. 2011; Syväranta et al. 2013) and the percent of overlap between groups was calculated for each group. For these purposes the "SIBER" package in R software was used (Jackson et al. 2011). To explore possible causes of variability within each gelatinous zooplankton group, we then performed general linear models (GLMs), with $\delta^{13}C$ and $\delta^{15}N$ as response variables, and sampling location, depth, and body size as potential explanatory variables. General linear models were fitted to "Gaussian" error structure and the optimum models were selected via the Akaike information criteria. The models with the lowest Akaike information criteria values were judged to be the best fitting ones.

Secondly, to assess differences between gelatinous zooplankton groups among locations and with depth, we assessed trophic differences (same group between locations or depths; groups in the same location) at the two locations with the best available sample sizes, seamount slope and open ocean (see above), by calculating and comparing isotope standard ellipse areas, and assessing the spatial and depth-related differences for different gelatinous zooplankton groups within the GLM described above. We acknowledge that an overarching GLM including all factors including gelatinous zooplankton taxon in one model would have been preferable, but highly imbalanced sample sizes between factors did not allow this approach.

All data visualizations were performed with the "ggplot2" R package (Wickham 2016) and statistical modeling was conducted with base commands in R software, version 3.4.3 (R Core Team 2017). All data is available from the PANGAEA database (https://doi.org/10.1594/PANGAEA.911939).
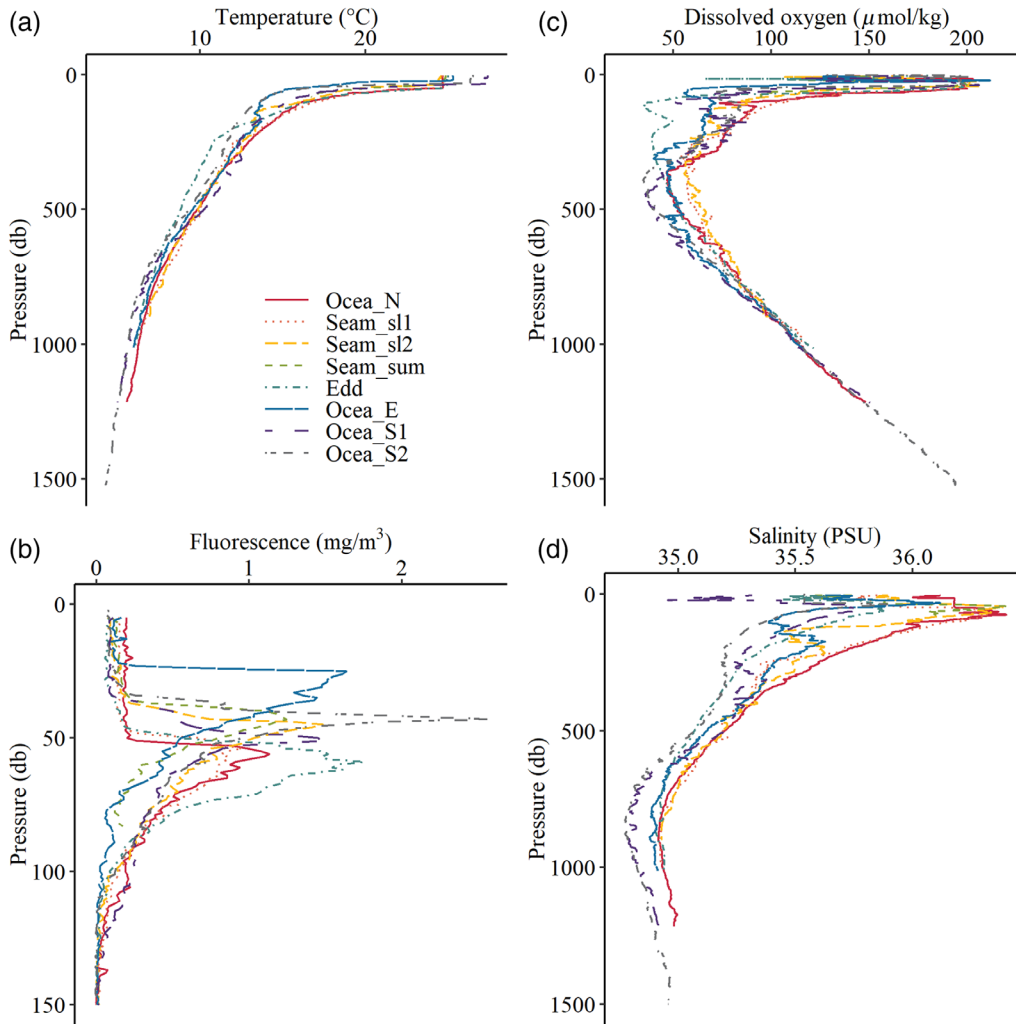
Fig. 3. Vertical profiles of (**a**) temperature, (**b**) fluorescence, (**c**) dissolved oxygen, and (**d**) salinity in the stations of the eastern tropical Atlantic.

Results

General hydrography patterns

Below a thin surface mixed layer, temperature at all stations decreased from ca. 25°C at the surface down to less than 5°C around 1500 m (Fig. 3a). The depth of maximum fluorescence values varied from ca. 25 m at station Ocea_E to ca. 60 m at station Edd, and averaged ca. 50 m at most other stations (Fig. 3b). Dissolved oxygen values were highest in the surface layer and below 1500 m depth (Fig. 3c). They reached an oxygen minimum at ca. 400 m with values lower than 50 μmol kg^{-1}. A shallow oxygen minimum layer at ca. 100 m was observed at stations Edd, Ocea_E, and Ocea_S1. Salinity decreased from the surface (36) to around 800 m (34.5) and was rather constant below (Fig. 3d).

Overview of planktonic stable isotope values of the eastern tropical Atlantic

Stable isotope values of the entire planktonic food web in the eastern tropical Atlantic ranged from 0.45‰ to 12.66‰ in δ^{15}N, and −23.66‰ to −14.58‰ in δ^{13}C (Fig. 4). Within this food web, non-gelatinous zooplankton taxa covered the range from 3.78‰ to 12.66‰ in δ^{15}N and −22.33‰ to −14.61‰ for δ^{13}C (Fig. 4b,d,f; Table S2). The δ^{15}N values of seston presented two distinct clusters, with lower values at shallow (25 m) and higher values at all other depths. Similar to seston, copepods in the shallow and deep layer displayed distinctly different stable isotopic values. Overall, copepods in the deep layer and large squids had the highest δ^{15}N values, and small calanoid copepods from the surface, krill, and decapod larvae had the lowest δ^{15}N values on average. Miscellaneous fish larvae, gastropod and amphipods varied greatly in δ^{15}N values. As for δ^{13}C, copepods from the deep layer, large squids, and krill presented similar patterns, while copepods in surface waters, amphipods and gastropods covered the largest ranges and decapod larvae had the largest values.

The jelly web within the planktonic food web of the eastern tropical Atlantic

Overall, the gelatinous zooplankton community occupied a large proportion of the isotopic niche space of the planktonic
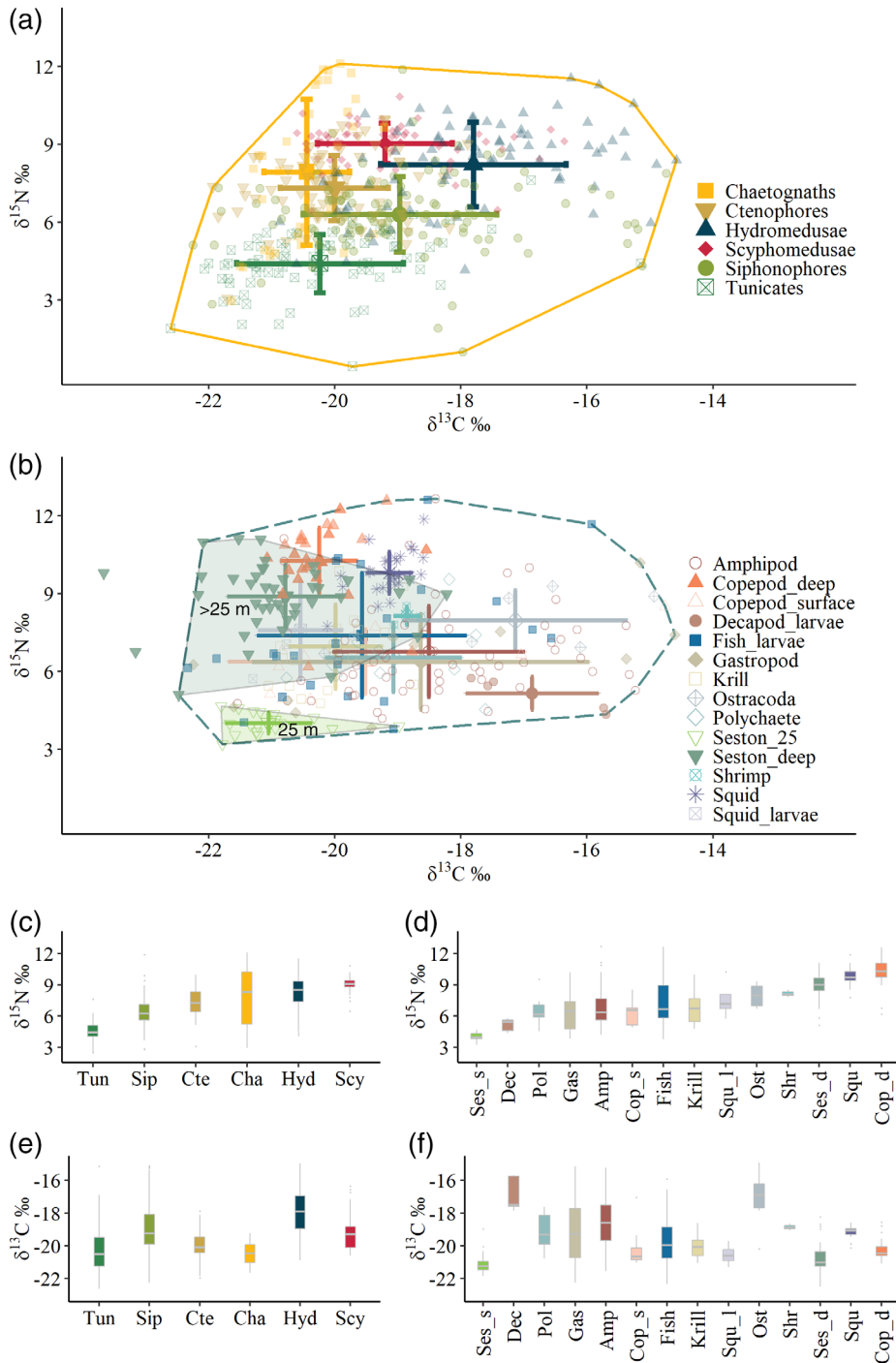
Fig. 4. (**a** and **b**) Stable isotope values and isotopic convex hull of (**a**) gelatinous zooplankton and (**b**) non-gelatinous zooplankton taxa in the planktonic food webs of the eastern tropical Atlantic (mean ± SD). The filled convex hulls denote seston in deep (> 25 m) and in surface (25 m) waters (two outliers in deep seston shown but not included in the hull area due to their disproportionate weights); (**c** and **d**) stable isotope values in $\delta^{15}N$ for (**c**) gelatinous and (**d**) non-gelatinous zooplankton taxa, (**e** and **f**) stable isotope values in $\delta^{13}C$ for (**e**) gelatinous and (**f**) non-gelatinous zooplankton taxa in the planktonic food web. Gelatinous zooplankton: Cha = Chaetognaths, Cte = Ctenophores, Hyd = Hydromedusae, Scy = Scyphomedusae, Sip = Siphonophores, Tun = Tunicates; Non-gelatinous zooplankton: Amp = Amphipod, Fish = Fish larvae, Gas = Gastropod, Ost = Ostracoda, Cop_s = Copepod in surface, Cop_d = Copepod in deep, Dec = Decapod larvae, Krill = Krill, Pol = Polychaete, Shr = Shrimp, Squ_l = Squid larvae, Squ = Squid, Ses_s = Seston in surface, Ses_d = Seston in deep.
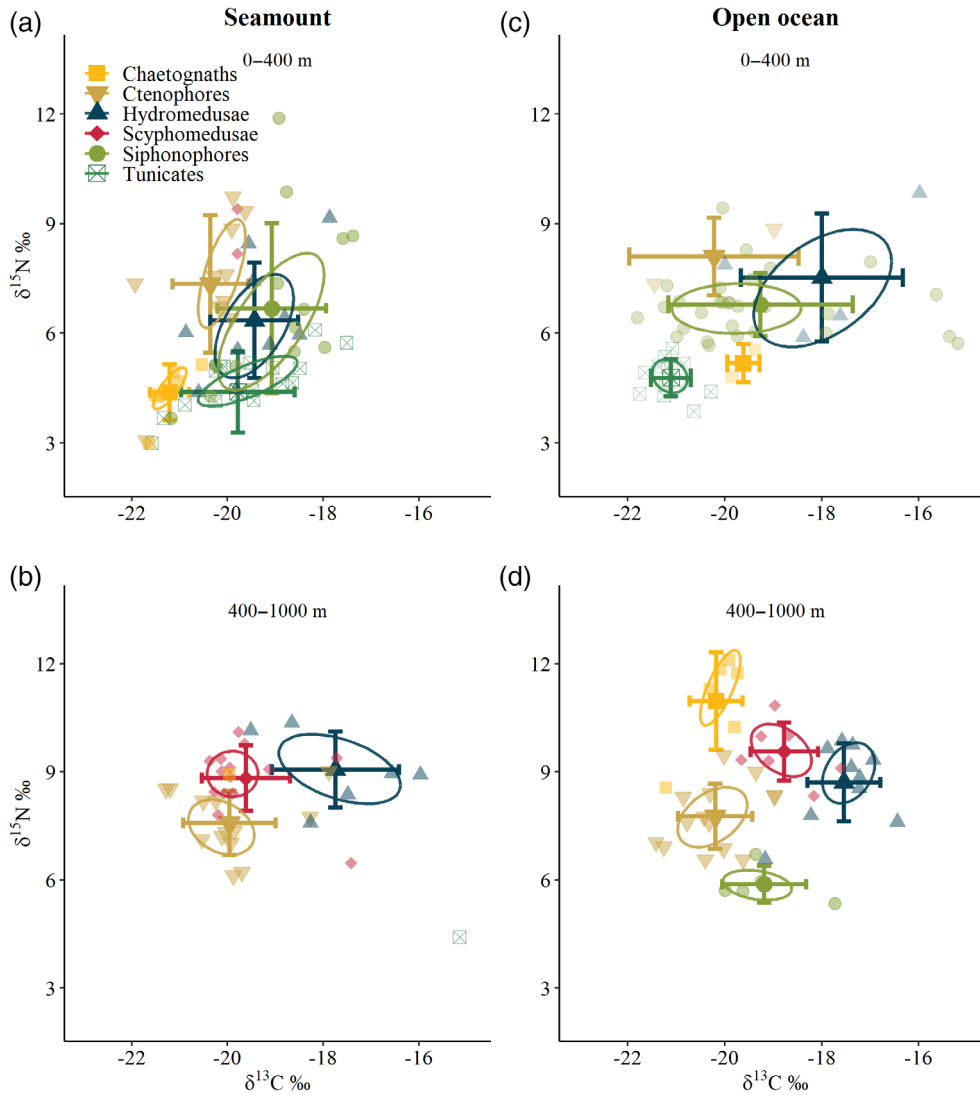
Fig. 5. Overview of the jelly web by illustrating stable isotopic bi-plots ($\delta^{13}C$ and $\delta^{15}N$, ‰, mean ± SD) and standard ellipse areas of six gelatinous taxonomic groups in shallow (**a**, **c**; 0–400 m) and deep (**b**, **d**; 400–1000 m) layers in seamount and open ocean habitats.

food web of the eastern tropical Atlantic, with stable isotope values ranging from 0.45‰ to 12.10‰ in $\delta^{15}N$, and from −22.60‰ to −14.58‰ in $\delta^{13}C$ (Fig. 4a,c,e). The strong overlap of gelatinous zooplankton and overall food web isotopic niche spaces was also indicated by the largely overlapping convex hull areas.

The lowest $\delta^{15}N$ values were displayed by tunicates with values ranging from 0.45 ‰ to 7.6 ‰, and the highest $\delta^{15}N$ values ranging from 6.44‰ to 10.84‰ were measured in scyphomedusae. Chaetognaths displayed a large range in $\delta^{15}N$ of 9.13‰ (from 2.97‰ to 12.10‰), while other groups covered smaller ranges, e.g., scyphomedusae with 4.4‰. For $\delta^{13}C$, chaetognaths (from −21.64‰ to −19.21‰) and tunicates (from −22.60‰ to −15.15‰) showed the lowest values, whereas hydromedusae displayed the highest $\delta^{13}C$ values (−20.87‰ to −14.58‰).

Isotopic niche partitioning and overlap within the jelly web

Independent of the analyzed location (seamount slope vs. open ocean) and depth (shallow vs. deep layer), the jelly web was always characterized by a large range in $\delta^{15}N$ and $\delta^{13}C$, spanning large proportions of the respective overall planktonic food webs (Fig. 5). Within these large isotopic spaces, patterns in the position and differentiation of standard ellipse areas of individual gelatinous zooplankton groups indicated the presence of both isotopic niche partitioning and overlap. In the shallow layer, standard ellipse areas of tunicates and chaetognaths were positioned lowest, ctenophores highest, and hydromedusae and siphonophores intermediate along the $\delta^{15}N$ axis for both locations (Fig. 5a,c), whereas the patterns along the $\delta^{13}C$ axis were more variable. In the deep layer, the relative positioning of standard ellipse areas showed similar patterns for both locations along both axes (Fig. 5b,d).

Table 2. Outputs of general linear models of stable isotopes of different species of gelatinous zooplankton collected from different depths and stations.

| Organisms/ seston	Response variables	Models	Variables	df	χ^2	p-value
Seston (in general)	$\delta^{15}N$	$\delta^{15}N \sim$ station + depth	Station	5	57.19	**0.02**
			Depth	1	86.4	**<0.001**
	$\delta^{13}C$	$\delta^{13}C \sim$ station + depth	Station	5	9.41	0.05
			Depth	1	0.62	0.4
Seston (surface)	$\delta^{15}N$	$\delta^{15}N \sim$ station	Station	5	22.81	0.65
	$\delta^{13}C$	$\delta^{13}C \sim$ station	Station	5	9.39	**0.003**
Chaetognaths	$\delta^{15}N$	$\delta^{15}N \sim$ station + depth	Station	6	148.01	**<0.001**
			Depth	1	56.03	**<0.001**
	$\delta^{13}C$	$\delta^{13}C \sim$ station + depth	Station	6	10.22	**<0.001**
			Depth	1	0.15	0.36
Ctenophores	$\delta^{15}N$	$\delta^{15}N \sim$ station + depth + size + station × depth + station × size + depth × size	Station	7	21.65	**0.007**
			Depth	1	0.01	0.92
			Size	1	4.59	**0.04**
			Station × depth	6	11.54	0.11
			Station × size	7	30.24	**<0.001**
			Depth × size	1	0.04	0.85
	$\delta^{13}C$	$\delta^{13}C \sim$ station + depth + size + station × depth + station × size + depth × size	Station	7	4.66	0.38
			Depth	1	0.02	0.85
			Size	1	2.5	**0.04**
			Station × depth	6	10.66	**0.01**
			Depth × size	1	1.6	0.11
Hydromedusae	$\delta^{15}N$	$\delta^{15}N \sim$ station + size + depth + depth × size	Station	7	31.8	**0.01**
			Depth	1	34.12	**<0.001**
			Size	1	4.27	0.11
			Depth × size	1	23.44	**<0.001**
	$\delta^{13}C$	$\delta^{13}C \sim$ station + depth + size	Station	7	29.22	**0.02**
			Depth	1	20.36	**<0.001**
			Size	1	4.99	0.09
Scyphomedusae	$\delta^{15}N$	$\delta^{15}N \sim$ station + size	Station	6	12.46	**<0.001**
			Size	1	3.37	**0.003**
	$\delta^{13}C$	$\delta^{13}C \sim$ station + size	Station	6	13.86	**<0.001**
			Size	1	25.68	**<0.001**
Siphonophores	$\delta^{15}N$	$\delta^{15}N \sim$ station + group + size	Station	7	56.9	**<0.001**
			Group	5	14.25	0.16
			Size	1	0.28	0.69
			Group × size	5	3.68	0.84
	$\delta^{13}C$	$\delta^{13}C \sim$ station + group + size	Station	7	37.77	**0.002**
			Group	5	67.02	**<0.001**
			Size	1	5.96	0.06
			Group × size	5	4.59	0.73
Tunicates	$\delta^{15}N$	$\delta^{15}N \sim$ station + group + size	Station	7	2.87	0.95
			Group	1	6.56	0.2
			Size	1	2.22	**0.03**
			Group × size	1	7.91	**0.01**
	$\delta^{13}C$	$\delta^{13}C \sim$ station + group + size	Station	7	28.63	**<0.001**
			Group	1	7.31	**0.005**
			Size	1	22.37	**<0.001**
			Group × size	1	13.64	**<0.001**

Significant results ($p < 0.05$) are written in bold face.
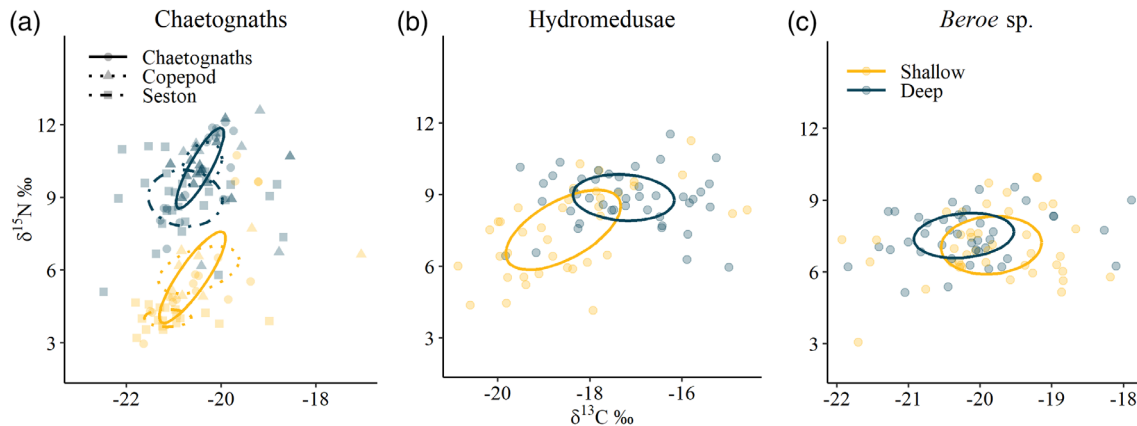
Fig. 6. Interpretation of stable isotope ($\delta^{13}C$ and $\delta^{15}N$) variations and standard ellipse areas caused by depth difference in (**a**) chaetognaths, (**b**) hydromedusae, and (**c**) ctenophore (*Beroe* sp.). Point colors denote different depth layers (deep = 400–1000 m; for chaetognaths and copepod, shallow = 0–400 m, for seston, shallow = 25 m), ellipses are calculated by standard ellipse areas.

Niche partitioning was evident in all locations and depth combinations, as indicated by non-overlapping standard ellipse areas along both the $\delta^{15}N$ and $\delta^{13}C$ axis for several gelatinous zooplankton groups. One illustrative example is provided by the standard ellipse areas of chaetognaths and tunicates, which were positioned distinctly lower along the $\delta^{15}N$ axis than ctenophores (no overlap) and separated along the $\delta^{13}C$ axis from each other in the shallow layer in both locations (Fig. 5a,c). At the same time, standard ellipse area overlap pointing to competition was frequent in the shallow layer, as illustrated, e.g., by the standard ellipse areas of hydromedusae and siphonophores (68.5% and 44.7% in the seamount and open ocean, respectively). The specific isotopic niche widths of different gelatinous zooplankton taxonomic groups varied, and standard ellipse areas appeared to show more overlap in the shallow layer and at the seamount, vs. stronger differentiation in the deep layer and open ocean. For example, in the shallow layer at the seamount, the standard ellipse area of siphonophores was large and displayed strong overlap with hydromedusae (68.5%) and tunicates (22.3%) illustrated in Fig. 5a, whereas standard ellipse areas were more contracted and showed no overlap in the deep layer of open ocean location (Fig. 5d).

Location and depth differences
Differences in baselines

Seston isotope values, used here as a measure of the isotopic baseline, showed significant differences between stations and depths. In particular, both $\delta^{15}N$ and $\delta^{13}C$ values differed significantly between stations, and $\delta^{15}N$ values were significantly lower in the surface layer (25 m) than in deeper layers (> 25 m) (GLM statistics, Table 2).

Vertical and horizontal isotopic patterns

On the level of individual gelatinous zooplankton groups, the broad majority of taxa showed significant spatial differences between stations in both $\delta^{15}N$ and $\delta^{13}C$ values (GLM statistics, Table 2). Regarding depth, the pattern was more complex: notable depth-related patterns were present, but with clear differences between gelatinous zooplankton groups (GLM statistics, Table 2). Specifically, chaetognaths displayed significantly higher $\delta^{15}N$ values but comparable $\delta^{13}C$ values in the deep layer (Fig. 5c,d). This closely mirrors the pattern observed for seston and copepods, and corresponds to consistent shifts in the positioning of standard ellipse areas for all three groups (Fig. 6a). Hydromedusae on average also showed significantly higher $\delta^{15}N$ and $\delta^{13}C$ values in the deep layer and a resulting shift in standard ellipse areas (Fig. 6b). In contrast, ctenophores did not show significant shifts with depth (Fig. 6c).

Size-related isotopic shifts within gelatinous zooplankton groups

Significant size-related shifts in stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) were present in ctenophores, scyphomedusae, and tunicates. In contrast, no shifts were detected in $\delta^{15}N$ of hydromedusae and siphonophores (Fig. 7, GLM statistics, Table 2). Chaetognaths were not assessed due to the small size range available in our sample (mean ± SD: 3.57 ± 0.67 cm). Notably, while $\delta^{13}C$ values increased with size in all analyzed groups (Fig. 7b,d,f), $\delta^{15}N$ patterns diverged strongly between groups. This was illustrated by siphonophores (no size-related shift in $\delta^{15}N$), scyphomedusae (decrease with size), and tunicates (increase with size) (Fig. 7a,c,e). Adding to this complexity, substantial differences in size-related shifts were present even within gelatinous zooplankton groups, as illustrated by the tunicates, with strongly divergent shifts in both $\delta^{13}C$ and $\delta^{15}N$ with size between pyrosomes and salps (Fig. 7e,f).
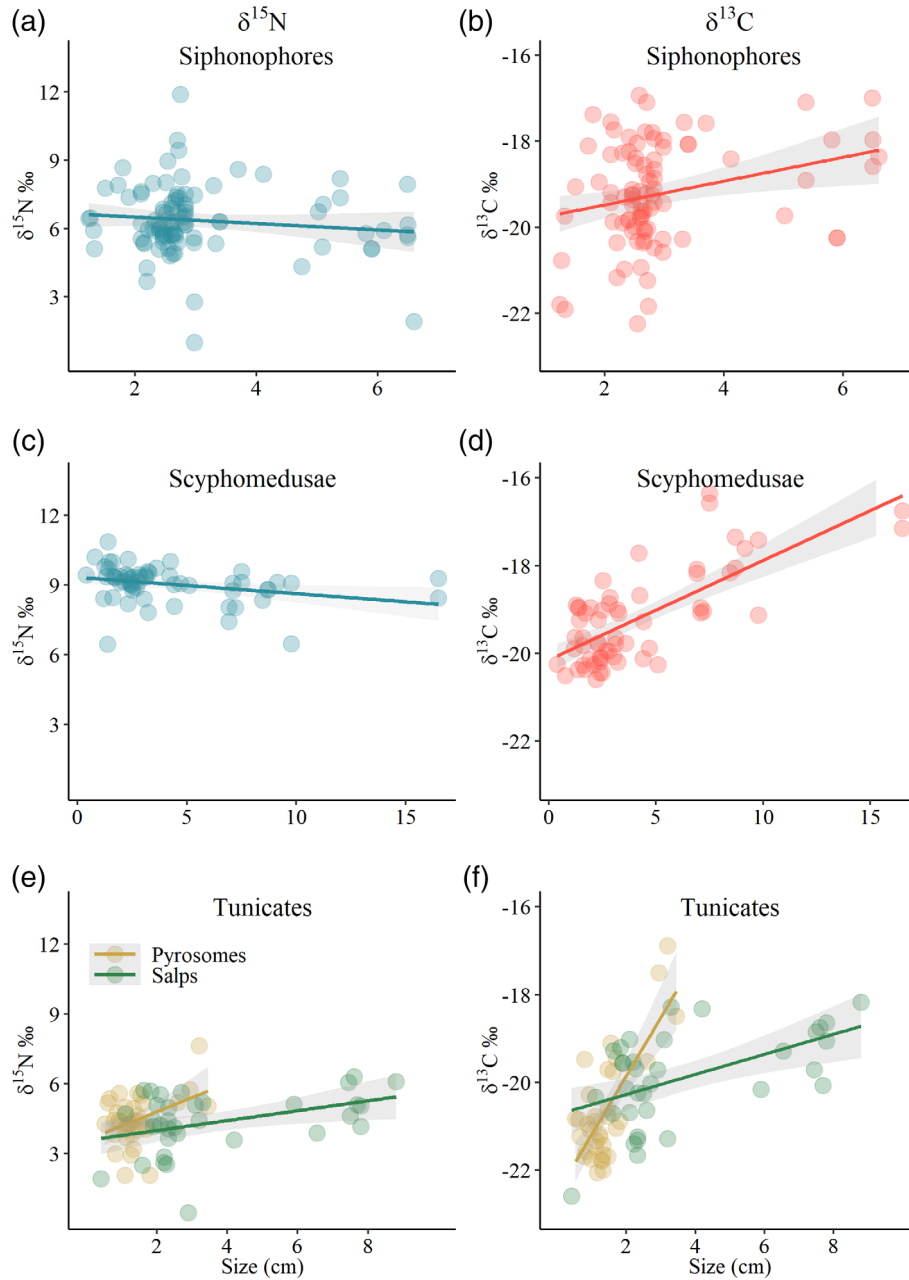
Fig. 7. Size dependency of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) values in (**a, b**) siphonophores, (**c, d**) scyphomedusae, and (**e, f**) tunicates.

Discussion

In this study, we provided the first dedicated trophic assessment of the jelly web within the planktonic food web of the eastern tropical Atlantic based on stable isotope analysis. Overall, our findings confirmed the large isotopic ranges in both $\delta^{15}N$ and $\delta^{13}C$ reported previously for the planktonic food webs (including seston, zooplankton, and micronekton) of the eastern tropical Atlantic (Denda et al. 2017). Expanding on this foundation, our findings highlighted the large proportion of this overall isotopic space covered by the jelly web, and illustrated substantial complexity resulting from patterns in trophic niche differentiation and overlap among gelatinous zooplankton groups and from variation on the spatial, depth, and taxon-specific level. In the following, we discuss the possible causes and underlying implications of these patterns.

Characterization of the jelly web trophic structure

The large range in $\delta^{15}N$ and $\delta^{13}C$ of gelatinous zooplankton indicates that this group plays different ecological roles

throughout the entire planktonic food web. In particular, there was a span of almost 12 ‰ in $\delta^{15}N$ values of the jelly web, which would represent ca. 3–4 trophic levels assuming a fractionation rate of 2.3‰ to 3.4‰ (Post 2002). This points to gelatinous zooplankton resource acquisition on all trophic levels of the food web (except top predators) and confirms the putative role as both predators and prey (West et al. 2009; Choy et al. 2017). At the same time, the large range of $\delta^{13}C$ values indicates that the jelly web integrated a high diversity of food sources and points to complex food web linkages (Hentschel 1998). The low trophic position of tunicates (here pyrosomes and salps) was consistent with their trophic function as herbi- and bacterivorous filter-feeders (Madin and Purcell 1992; Conley et al. 2018) and the high position of scyphomedusae, hydromedusae, and ctenophores was consistent with their role as predators (Haddock 2004; Stowasser et al. 2012). It is important to acknowledge that generalizations about the higher taxonomic groups should be treated with caution, because several of them were represented in our study by just a few taxa. For example, this was the case for *Beroe* sp. within the ctenophores, as well as two species of coronates representing the scyphomedusae. With a larger breadth of taxa within groups, the spectrum of isotopic and trophic niches covered even within individual groups of gelatinous zooplankton and potentially for the jelly web as a whole would therefore likely be even larger than presented in this study.

Trophic niche differentiation and overlap in the jelly web

Characterizing trophic niche differentiation and links between *resource utilization* and competition have *long* been of central interest to ecologists (Abrams 1980) and can provide insights into the mechanisms allowing the coexistence of competing species (Hutchinson 1959). Both gut content and stable isotope analysis of individual coastal gelatinous zooplankton taxa already reflected their exploitation of different diets (Décima et al. 2019). In spite of this, trophic niche differentiation of entire oceanic gelatinous zooplankton communities has rarely been characterized. The strong niche differentiation and its consistent presence in the shallow and deep layers and at seamount and open ocean stations observed here underscore that different gelatinous zooplankton groups can play distinctly different but spatially stable roles in oceanic planktonic food webs. This confirms previous reports of diverse trophic roles of gelatinous zooplankton, as for example shown in a study summarizing 27 years of visual observations in the central California deep pelagic food web (Choy et al. 2017), but extends previous information by providing a more quantitative view of trophic differentiation within the jelly web at one point in time, including first insights to spatial and depth-related structuring.

Overall, the relative trophic positions of gelatinous zooplankton groups in the jelly web in our study in most cases support conclusions of previous studies on the feeding ecology of individual gelatinous zooplankton species or groups. For example, salps are highly effective filter-feeders that can retain particles from 4 μm to 1 mm (Alldredge and Madin 1982; Conley et al. 2018). Their reported food sources include, e.g., dinoflagellates, diatoms, radiolarians, foraminiferans, coccolithophorids, and detritus (Alldredge and Madin 1982; Vargas and Madin 2004). The low trophic level indicated for salps and pyrosomes in our study, with values matching those of surface seston, agrees well with this prior classification as primary consumers. Similarly, the intermediate trophic level and overlapping standard ellipse areas of siphonophores and hydromedusae agree with the prior classification as carnivorous predators sharing a similar dietary composition (Colin et al. 2003). Moreover, scyphomedusae with the two dominant species *Atolla wyvillei* and *Periphylla periphylla* occupied the highest trophic level in the jelly web in our study, and these species have been classified as prominent predators in the mesopelagic community (Hunt and Lindsay 1998) occurring in coastal fjord ecosystems and meso- and bathypelagic depths. Finally, the isotopic niche space of chaetognaths was remarkably segregated between depth layers, which also confirm previous results in the same area (Denda et al. 2017).

Despite the strong trophic differentiation among taxonomic groups, there were also niche overlaps between specific groups of gelatinous zooplankton. These included, e.g., overlapping standard ellipse areas of tunicates and hydrozoans (siphonophores and hydromedusae) in shallow layers of the seamount station, and is consistent with in situ observations showing that hydrozoans compete with tunicates for food resources or directly prey on salps (Larson et al. 2009). This highlights that both competition and correspondingly, functional redundancy (Pianka 1974; Hérault et al. 2008), are additional features that need to be added to the complexity and functioning of the jelly web. Other phenomena such as intraguild predation of gelatinous zooplankton on other gelatinous zooplankton (Purcell 1991), which is likely to increase the number of functional links in the food web further, are difficult to elucidate with our dataset. In summary, these findings underscore that the role of gelatinous zooplankton in oceanic, or more general, marine food webs is diverse and more substantial than is currently considered in many oceanic food web models.

Vertical and horizontal isotopic patterns in the jelly web

Niche differentiation within the jelly web helped to understand substantial proportions of variability in the stable isotope dataset in this study. The analysis of differences related to geographic location (including seamount and open ocean habitat), depth differences, and the presence of size related trophic shifts within taxonomic groups offered additional opportunities to shed light on factors affecting isotopic variation among and within taxonomic groups in the jelly web.

The consistent presence of spatial differences in stable isotope values within gelatinous zooplankton groups highlighted the presence of horizontal structuring. Considering the substantial spatial differences in $\delta^{13}C$ values of seston as measure of the base of the food web, stable isotope baseline variation is likely to play a role in these patterns. Overall, these findings stress the potential for horizontal structuring of food webs and the occurrence of spatially discrete population of planktonic organisms (Harvey and Kitchell 2000), including the gelatinous zooplankton taxa in our study, in oceanic locations.

The divergent vertical patterns in isotopic values among gelatinous zooplankton groups in turn suggested group-specific differences in the extent of coupling of deep and shallow layers. This is consistent with vertical gradients in species distributions and differences in the extent of vertical migrations that are frequently observed in planktonic systems (Lampert 2005). Mesoscale ocean features such as fronts and eddies may induce or strengthen vertical ecological zonation in the eastern tropical Atlantic (Hauss et al. 2016; Christiansen et al. 2018). This phenomenon is commonly driven by food sources. For example, tunicates consume phytoplankton-based seston (Alldredge and Madin 1982; Décima et al. 2019) and thus occupy the lower trophic level in the shallow layer. Moreover, the consistent offsets in isotope standard ellipse areas for seston, copepods, and chaetognaths in our study, with a higher trophic position in the deep compared to the shallow layers, may be a prime example illustrating this pattern. While phytoplankton is consumed by grazers or decomposed with increasing depth, seston in deeper layers accumulates more macroscopic aggregates produced by zooplankton ("marine snow") (Shanks and Trent 1980), consistent with enriched $\delta^{15}N$ values and thus a higher trophic level of seston in deeper layers. This vertical difference is likely to propagate to copepods, which partly feed on seston (Kleppel 1993), and in turn, chaetognaths which prey primarily on copepods (Froneman et al. 1998). The contrasting lack of isotopic differences between shallow and deep layers for the ctenophore species *Beroe* sp. in our study point to factors preventing vertical differentiation, such as lack of vertical connectivity via migrations, for other taxa of gelatinous zooplankton. In combination, these findings underscore that due to the complexity of trophic niche differentiation in the gelatinous zooplankton community, increasing the knowledge of taxon-specific distributions of gelatinous zooplankton and the respective roles in food webs at different depths hold strong potential to further improve understanding of the jelly web.

Size-related trophic shifts

A common pattern observed in the field of feeding ecology is that organisms of larger size are able to prey on larger and more diverse prey, resulting in diet shifts and an increasing trophic level with size, e.g., in squids (Merten et al. 2017) and fishes (Sánchez-Hernández et al. 2019). While size-related trophic shifts in individual gelatinous zooplankton taxa have also been assessed (Fleming et al. 2015), systematic understanding across different gelatinous zooplankton taxa is lacking. The strongly divergent size-related patterns among different gelatinous zooplankton taxa in our study, ranging from an increase via no change (siphonophores) to a decrease in trophic level with size as indicated by $\delta^{15}N$ values with a concurrent change prey composition in all three taxa as indicated by $\delta^{13}C$ values, show the complexity of patterns within gelatinous zooplankton. This was stressed even more by the additional differences in size-related shifts on finer taxonomic scales with in gelatinous zooplankton groups, as indicated by pyrosomes and salps in the tunicates. This expands on findings by Décima et al. (2019) identifying differences in feeding and trophic levels for these two groups. While this study did not evaluate specific diet shifts and mechanisms behind the diverse patterns in size-related trophic shifts, the use of multi-stanza groups in food web reconstruction studies (small vs. big ctenophore, young vs. adult medusa, sexual vs. asexual tunicate stage) would have the potential to do so. One interesting point here is that the shifts of isotopic values with size in pyrosomes and siphonophores is unlikely to be related to a classical ontogenic shift, i.e., changes in dietary spectrum with growth in body (and gape) size of individuals (Hyndes et al. 1997). In contrast, for these taxa, most of the growth is by addition of same-sized units and not by growth of individual units (Mapstone 2009, 2014), which raises the question which mechanism is driving the observed shift.

Conclusions

This study provides a dedicated trophic characterization of a large range of gelatinous zooplankton taxa in the eastern tropical Atlantic. The large proportion of the isotopic niche space of the entire planktonic oceanic food web covered by the jelly web, in combination with the large trophic range of > 3 trophic levels ranging from herbivores to higher predators and niche partitioning within the web, highlighted the diverse functional roles and broad possible food web relevance of gelatinous zooplankton. We conclude that the broad trophic niche covered by the jelly web, patterns in niche differentiation within this web, and the substantial trophic complexity on the spatial, depth, and taxon level observed in this study call for a more careful consideration of gelatinous zooplankton in oceanic food web models. The data set presented here also holds value as baseline against which to measure future observations of gelatinous zooplankton communities in the eastern tropical Atlantic.

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Conflict of Interest

None declared.