



# Distribution and abundance of net-captured calyphorophoran siphonophores and other gelatinous zooplankton in the Sargasso Sea European eel spawning area

Florian Lüsckow<sup>1,2</sup> · Philipp Neitzel<sup>3</sup> · Michael J. Miller<sup>4</sup> · Lasse Marohn<sup>5</sup> · Klaus Wysujack<sup>5</sup> · Marko Freese<sup>5</sup> · Jan-Dag Pohlmann<sup>5</sup> · Reinhold Hanel<sup>5</sup>

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## Abstract

Gelatinous zooplankton (GZ) such as medusae, ctenophores, siphonophores, pyrosomes and salps are important components of oceanic pelagic communities and small calyphorophoran siphonophores (CS) are typically abundant at shallow depths. The Sargasso Sea spawning area of the Atlantic catadromous freshwater eels has a regular pattern of shallow autumn to spring temperature fronts. There is limited information about the southern Sargasso Sea GZ fauna, and it is not known which species are distributed across these frontal zones. Plankton samples from a survey of larval European eel (*Anguilla anguilla*) abundance in March and April 2017 using an Isaacs-Kidd Midwater Trawl (0–300 m, 35 stations, three transects) were used to examine the distribution and abundance of net-captured CS and other GZ species in relation to oceanographic characteristics. More than 2200 specimens of 15 taxa were sub-sampled, with five CS (*Abylopsis tetragona*, *A. eschscholtzii*, *Chelophyes appendiculata*, *Eudoxoides spiralis* and *E. mitra*) dominating catches at every station. GZ were most abundant around the 22 and 24 °C isotherms, and higher abundances of CS in the north were correlated with lower water temperature. The widespread presence of CS across the European eel spawning area is consistent with a recent study detecting their DNA sequences in the gut contents of young eel larvae collected in the Sargasso Sea, suggesting CS material was either eaten directly or as part of ingested marine snow particles. The present study shows that both types of organisms occupy the southern Sargasso Sea during the European eel spawning season.

**Keywords** Western North Atlantic Ocean · Co-occurrence · Leptocephalus diet · *Anguilla* · Net sampling

## Introduction

The Sargasso Sea in the western North Atlantic Ocean is part of an oligotrophic subtropical gyre with the powerful Gulf

Stream current system along its western and northern boundary. It is well known as the spawning area of the American and European eels (*Anguilla rostrata* and *A. anguilla*), which spawn south of temperature fronts that are formed in the

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✉ Florian Lüsckow  
florian.luesckow@web.de

<sup>1</sup> Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, 2039-2207 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

<sup>2</sup> Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada

<sup>3</sup> GEOMAR, Helmholtz Centre for Ocean Research Kiel, Research division: Marine Ecology, Evolutionary Ecology of Marine Fishes, Düsternbrooker Weg 20, 24105 Kiel, Germany

<sup>4</sup> Department of Marine Science and Resources, College of Bioresource Sciences, Nihon University, 1866 Kameino, Fujisawa-shi, Kanagawa 252-0880, Japan

<sup>5</sup> Institute of Fisheries Ecology, Johann Heinrich von Thünen Institute (TI), Federal Research Institute for Rural Areas, Forestry and Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

subtropical convergence zone during their winter and spring spawning season (Schmidt 1922; McCleave et al. 1987; Miller et al. 2015). The fronts can contribute to faunal discontinuities in distribution patterns, as shown for mesopelagic fish (Backus et al. 1969), juvenile cephalopods (Lischka et al. 2017) and eel *leptocephalus* larvae (Miller and McCleave 1994) in the Sargasso Sea. The rapid temperature/density changes create frontal jet currents (Eriksen et al. 1991; Weller 1991) that transport water and organisms, including eel larvae, eastward (Miller and McCleave 1994). With seasonal warming, these fronts then move in northern direction (Ullman et al. 2007). The biogeochemistry of the northern Sargasso Sea has been extensively studied at the Bermuda Atlantic Time Series station (BATS), where physical forcing has been linked to decadal-scale climate fluctuations such as the North Atlantic Oscillation (NAO) (Saba et al. 2010; Álvarez-García et al. 2011; Wu et al. 2011). There has been a wide range of studies on particulate organic carbon (POC), primary producers and zooplankton at the BATS station (Lomas et al. 2010; Steinberg et al. 2012; Stone and Steinberg 2014), and some studies have focused on GZ such as salps (Madin et al. 1996) and siphonophores (Lo and Biggs 1996).

Fewer biological oceanography related studies have been conducted farther south in the Sargasso Sea, with some extensive net sampling for eel larvae in the southern spawning area of the two species of anguillid eels (e.g., Miller et al. 2015; Westerberg et al. 2018). Recent surveys have also resulted in new insights into the biological oceanography of the Sargasso Sea frontal zone region (Andersen et al. 2011; Riemann et al. 2011; Richardson et al. 2014).

One group that has not been extensively studied from a distributional perspective in the Sargasso Sea are gelatinous organisms. A variety of studies in the Sargasso Sea region has examined several different aspects of some gelatinous species using different methodological approaches. Calycophoran siphonophores (CS) were found to be abundant in net samples near Bermuda (Lo and Biggs 1996) and also to the northwest in the northern Sargasso Sea (Grice and Hart 1962). Moore (1949) investigated the zooplankton community in the upper 300 m around Bermuda between 1938 and 1940. That work contributes to the understanding of vertical and horizontal distribution patterns as well as seasonal abundance variations of medusae, siphonophores and pelagic tunicates in this area. Harbison et al. (1978) and Purcell (1981) studied oceanic ctenophores and siphonophores and their in situ feeding biology in the northern and southern Sargasso Sea, based on specimens collected by SCUBA divers. Similarly, Biggs et al. (1981) estimated population densities of gelatinous fauna during SCUBA dives on a transect through the North Atlantic Ocean. Long-term time series analyses focusing on changes in mesozooplankton biomass based on net collections (mainly focusing on salps) were performed at the

BATS site (Steinberg et al. 2012; Stone and Steinberg 2014). Latz et al. (1988) investigated bioluminescence of the epipelagic fauna in the eastern Sargasso Sea, including gelatinous zooplankton (GZ). Other studies to the southeast of Bermuda used oblique net tows to examine annual cycles of zooplankton composition (Deevey 1971). Eden et al. (2009) investigated the zooplankton community structure in eddies around Bermuda, including gelatinous plankton taxa, but only referred to higher taxonomic levels (doliolids, salps and siphonophores). Bucklin et al. (2010) used DNA barcode analyses to estimate the zooplankton species diversity throughout the Sargasso Sea.

Gelatinous organisms are important components of marine communities such as in the Sargasso Sea because they are often key predators or grazers on zooplankton, phytoplankton or fish larvae and can efficiently reduce prey populations in coastal regions (Zeldis et al. 1995; Hansson et al. 2005). Some species are known to undertake extensive diurnal vertical migrations (DVM) (Mills 1983; Andersen et al. 1992; Júnior et al. 2015; Munk et al. 2018). There is an ongoing debate about globally increasing frequencies of GZ mass occurrences that may severely affect marine food web structures (Richardson et al. 2009; Condon et al. 2012, 2013). Further, they can be competitors of larval fish for common prey (Purcell 2003). For offshore areas of the Atlantic Ocean, it is much less documented how GZ organisms interact with other species in pelagic communities. For example, Pagès and Madin (2010) documented the ingestion of an eel *leptocephalus* larva by the siphonophore *Halistemma cupulifera*, which was even larger than the gastrozooids of the predator. It is known that GZ contribute to the diets of birds, sea turtles, marine mammals and adult fish (Cardona et al. 2012; Thiebot et al. 2017; Brodeur et al. 2018), cephalopods (Hoving and Haddock 2017) and to other gelatinous organisms (Titelman et al. 2007; Choy et al. 2017). As frequently abundant pelagic species, ctenophores, medusae, siphonophores and pelagic tunicates can have strong predatory/grazing impacts on lower trophic levels (e.g., Drits et al. 1992; Tilves et al. 2016). However, we find no evidence of studies being conducted in the frontal zone region of the Sargasso Sea farther south of Bermuda within the European eel spawning area. A detailed analysis of the species composition, spatial distribution and abundance of epipelagic GZ from a distributional perspective in the Sargasso Sea is lacking.

Understanding the distribution and ecology of hydrozoan GZ, and in particular CS, has recently become an important issue for evaluating the diet of young European eel *leptocephali* (<20 mm) within their Sargasso Sea spawning area because their DNA sequences have been detected in the gut contents of the eel larvae (Riemann et al. 2010; Ayala et al. 2018). The DNA barcoding study of Riemann et al. (2010) detected hydrozoan DNA sequences in some of the larval gut

contents, while the study by Ayala et al. (2018) used next generation sequencing (NGS) and found hydrozoan sequences in the gut contents of all of the 75 larvae they examined. In the recent NGS study, the majority of the hydrozoan sequences originated from CS (Ayala et al. 2018). However, DNA sequencing techniques are inconclusive when attempting to discriminate between active feeding on small GZ life history stages and stochastic ingestion of tissue fragments as part of particulate organic matter (POM) and marine snow, which is an apparent food of leptocephali in general (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011). In addition, the DNA studies of gut contents (Riemann et al. 2010; Ayala et al. 2018) also detected a wide range of marine taxa, including bacteria, fungi, radiolarians and crustaceans that are not likely to be directly ingested, which is only consistent with larvae that had been feeding on POM and marine snow (Miller et al. 2013a; Feunteun et al. 2015; Liénart et al. 2016). Direct observations of gut contents indicate that marine snow material is likely ingested by all types of leptocephali (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011, 2019), but in the Sargasso Sea, the important question is how CS tissue is entering the diets of European eel larvae. Many types of materials and marine organisms contribute to the aggregation and colonisation of marine snow (Alldredge and Silver 1988; Shanks and Walters 1997; Kiørboe 2000), but how GZ contribute to these materials has only been sporadically studied (e.g., Robison et al. 2005; Katija et al. 2017), and it is not known if small leptocephali can feed directly on particles originating from these species.

The aim of the present study was to (i) identify CS and other GZ species and to depict their numerical horizontal epipelagic distributions using large fine-mesh plankton trawl tows and to confirm them as widespread food web components. Further, we aim to (ii) evaluate if there are any correlations of their distributions with sea surface temperature (SST) and chlorophyll *a* concentrations and to (iii) analyse day/night abundance patterns of dominant species in the upper 300 m. This information is used to evaluate the species composition, distributions and abundances of the CS and other taxa that can be effectively identified from net samples. Finally, we discuss how siphonophores may be contributing materials that can be ingested by the larvae of the European eel. Data obtained from the present study could help to improve our understanding of the larval eel feeding ecology in relation to the biological community structure of the Sargasso Sea. This is especially critical because along with other Northern Hemisphere anguillid species, the European eel is now listed as critically endangered by the IUCN due to their population declines (Jacoby et al. 2015) that may also be linked to processes in the ocean such as larval survival (Miller et al. 2009, 2016; Westerberg et al. 2018).

## Materials and methods

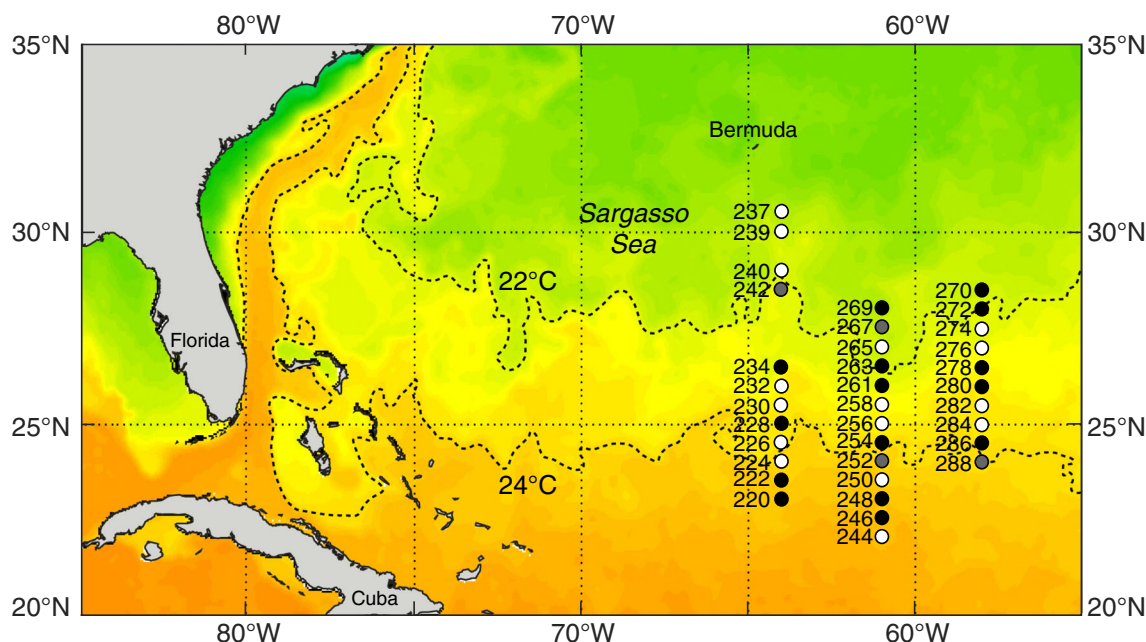
### Study area and hydrography

The present study was carried out southeast of Bermuda in the southern Sargasso Sea (western North Atlantic Ocean), along three north-south orientated transects in March and April 2017, (Fig. 1) using the *FR/V Walther Herwig III* (cruise WH404; 19 March–10 April 2017). The subtropical convergence zone in this highly oligotrophic area is known as the spawning area of European and American eels, with their small leptocephali (< 20 mm). The eel spawning area has been suggested to be located between or south of the surface expressions of the 22 and 24 °C isotherms that are linked to the two fronts that form each year from autumn to spring as shown in Fig. 1 (Kleckner and McCleave 1988; Miller and McCleave 1994; Munk et al. 2010; Miller et al. 2015). Thirty-five stations were sampled in 3 transects that crossed the predicted eel spawning area (see Table S1 for station coordinates). Along with net sampling at each station, vertical profiles of temperature, salinity and fluorescence (as proxy for chlorophyll *a* concentration) were measured down to a depth of 500 m using a conductivity, temperature and depth (CTD) profiler (Seabird SBE 911). Rough sea conditions prevented the planned sampling grid from being entirely completed (three stations on 64°W transect were dropped), but both fronts (associated with the 22 and 24 °C isotherms; Miller and McCleave 1994) were crossed during all three transects (Fig. 1). The SST image used in Fig. 1 was obtained from NOAA/NESDIS 5 km analysis (<https://www.ospo.noaa.gov/Products/ocean/sst/contour/>); however, respective CTD data might deviate slightly due to the continuous movements of the fronts.

### Specimen collection and processing

Gelatinous zooplankton (GZ) were obtained from plankton samples collected using an IKMT (Isaacs-Kidd Midwater Trawl, mesh size 500 µm, mouth opening 6.2 m<sup>2</sup>, equipped with a flowmeter). The IKMT was fished with a double oblique towing design (average ship speed was 2.3 kn). The net was deployed to 300 m at a speed of 0.5 m s<sup>-1</sup>, retrieved to near the surface at a speed of 0.3 m s<sup>-1</sup>, and this was repeated a second time (depth measured with SCANMAR sensor; tow duration range 2:04–3:12 h, mean duration 2:30 h). The sampling design was established to collect European eel larvae (Hanel et al. 2014), but the fine mesh also retains GZ species that live in the upper 300 m. A similar number of day and night IKMT-tows were made throughout the transects (16 day, 15 night and four twilight tows). On average, 55,785 ± 8910 m<sup>3</sup> of seawater was filtered per IKMT tow (range 34,816–76,833 m<sup>3</sup>).

The plankton samples were sorted for eel larvae immediately after coming onboard, with some larger GZ specimens



**Fig. 1** Sampling stations in the Sargasso Sea southeast of Bermuda plotted over the sea surface temperature (SST) from 25 March 2017, with the 22 and 24 °C contours (associated with the two fronts) shown as dotted lines. Green colours indicate lower temperatures, while orange

tones indicate higher temperatures. Symbols show stations made during the day (white circles), twilight (grey circles), and night time (black circles). Station data are listed in Table S1. The SST image was obtained from the NOAA/NESDIS 5 km analysis

(i.e. coronate medusae) being immediately removed from the samples and preserved afterwards. Umbrella diameters of small medusae were measured onboard before preservation. Gelatinous specimens (together with the bulk zooplankton) were stored in 96% ethanol in a refrigerator. No data were obtained from Stns. 228 and 278 (gear malfunction) (Fig. 1). Two months after collection, IKMT samples fixed in ethanol were sorted. Specimens removed onboard did not bias the semi-quantitative analysis because only rare, larger or conspicuous species (i.e. coronate medusae) were selected, while the semi-quantitative approach mainly focused on small-sized transparent calycophoran siphonophores.

### Species identification and abundance estimation

Specimens were identified using several identification keys (Pagès et al. 1992; Mianzan and Cornelius 1999; Pugh 1999). Specimens preserved in ethanol had a firm although bleached consistency, so working with the less dangerous (compared with formalin) fixative was suitable for our objectives. For the enumeration of specimens per species and station, samples were divided into two halves by carefully shaking them 32 times in a modified Folsom plankton splitter (McEwen et al. 1954), and sub-samples ( $1/8$  and  $1/16$ ) were analysed depending on the amount of plankton in the sample. Siphonophores are fragile and are easily damaged or destroyed using net tows (Purcell 1981). Therefore, siphonophores were enumerated by counting nectophores (primarily used for swimming). Anterior nectophores were counted for

abundance estimates (posterior nectophores were, if present, not enumerated). Based on flowmeter revolutions (used to calculate filtered water volume) and specimen count data, species- or group-specific abundances ( $A$ , ind.  $10,000\text{ m}^{-3}$ ) per station were calculated. Abundance estimates and estimated numbers of specimens collected (Table S2) were based on scaled-up values from the sub-samples.

### Statistical analyses

The intensity of a deep chlorophyll *a* maximum, or peak, will affect the composition and quantity of lower trophic level groups (phytoplankton and some zooplankton) and acts as indicator for productivity conditions. These groups serve as prey for GZ, so the relationship between sea surface temperature or peak fluorescence (as a proxy for chlorophyll *a* concentration) and group abundances were tested for significance using linear models (LMs). Therefore, abundance data were log transformed. Analysis of variance (one-way ANOVA) was performed for dominant species abundance in relation to time of day with a significance level of 0.05, followed by a Tukey-HSD post hoc test in order to differentiate between times. Three-time categories were differentiated for analysis: day, night and twilight (dawn and dusk). We have considered stations as independent replicates. Relative abundance data were log transformed to generate normally distributed data and homogenise variances. All statistical analyses were performed in R (R Core Team 2017) version 3.2.3.

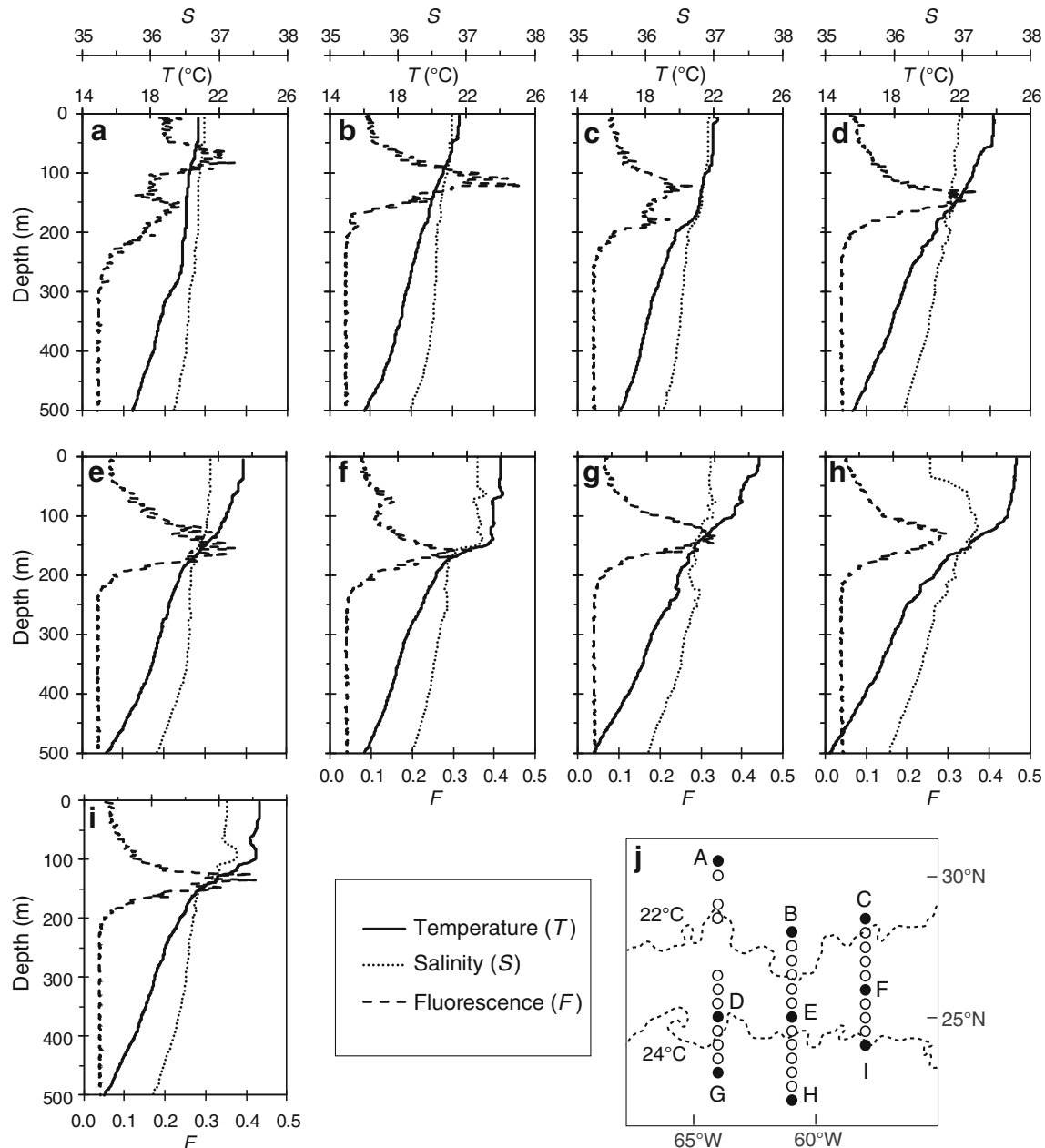


## Results

### Oceanographic conditions

The sea surface temperature (SST) north and south of the 22 and 24 °C isotherms typically ranged from 20.8–21.6 °C to 24.4–25.2 °C, respectively (Fig. 1), while gradually increasing to the south. The vertical structure of temperature, salinity and fluorescence (as a marker for chlorophyll *a* concentration) at several stations at the margins and central parts of the study area are shown in Fig. 2. The temperature profiles in the upper

300 m varied among stations (as shown in Fig. 2), with no distinct thermocline at some stations and a tendency towards more stratification at the southern stations. Temperatures decreased to about 14–16 °C at 500 m at all stations. Salinity (*S*) also varied in the upper 300 m within a narrow range of values, with surface salinities being between 36.5–37.1 and 35.9–36.4 at 500 m depth. We observed weak haloclines only at some southern stations (Fig. 2f, h, i), while at all other stations a continuous decrease in salinity over depth was recorded. Distinct fluorescence peaks were identified at all stations, as well as secondary peaks at some stations. There was a



**Fig. 2** Vertical profiles of temperature (*T*, °C, solid lines), salinity (*S*, dotted lines) and fluorescence (*F*, dashed lines) in the upper 500 m of the water column for Stns; **a** 237; **b** 269; **c** 270; **d** 228; **e** 256; **f** 280; **g** 220;

**h** 244; and **i** 288. Selected stations are distributed across the ends and central parts of the sampling grid as shown in **j** the insert panel with the station labels corresponding to the other panel labels

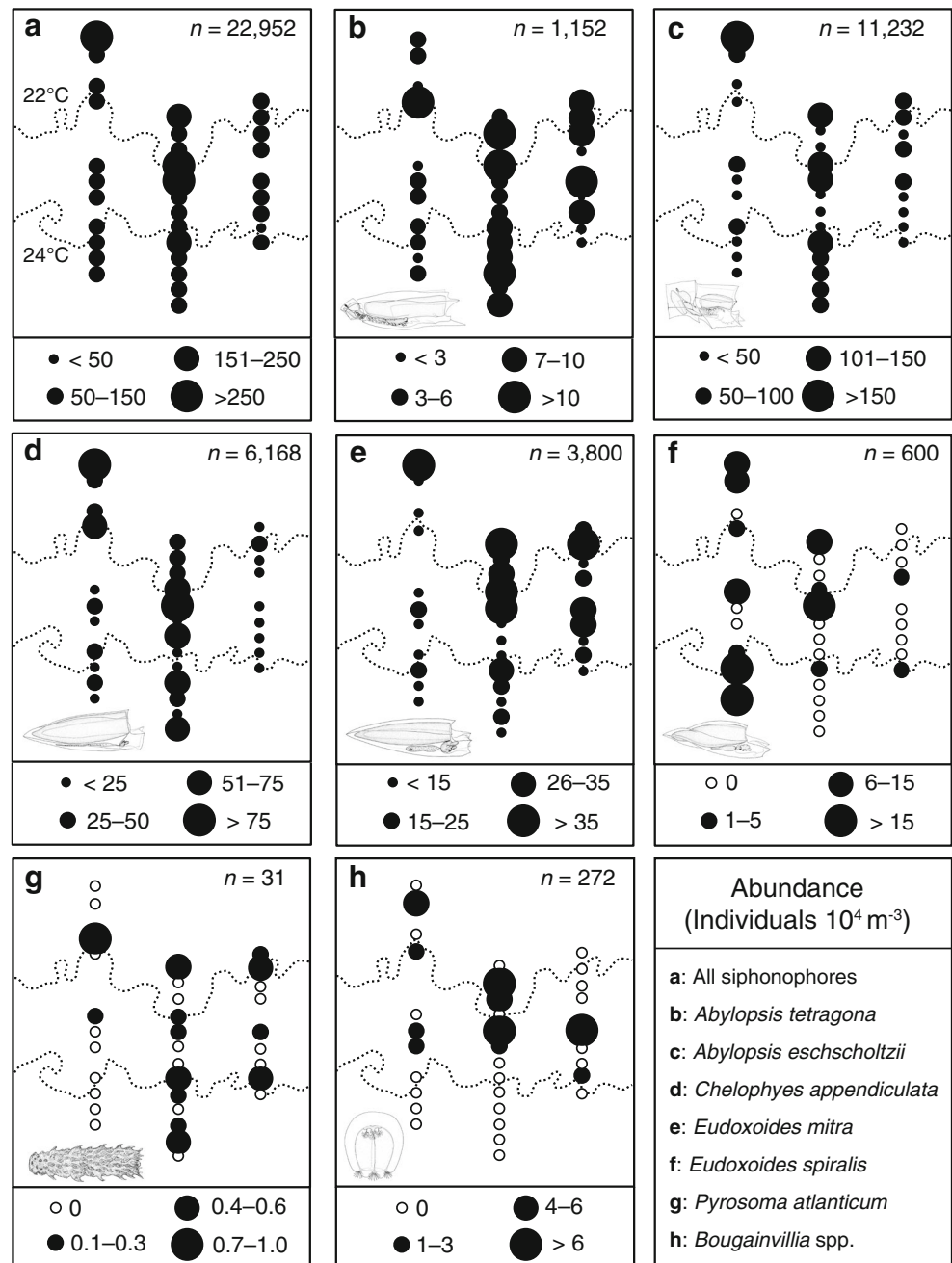
general trend of slightly shallower peaks in the north compared with in the south (Figs. 2a–c: 83–122 m, Figs. 2g–i: 132–136 m).

### Species composition of epipelagic gelatinous zooplankton

The gelatinous zooplankton (GZ) collected in the upper 300 m of the water column were comprised of at least 15 taxa (ranging from species to order levels; Table S2). More than 2200 specimens were identified, counted and their total

abundances were calculated using sub-sample factors, suggesting that about 23,500 specimens may have been collected during the survey (Table S3). A few species (listed below) showed widespread distributions with high abundances at some stations. Small-sized calycophoran siphonophores (CS; Figs. 3a–f) dominated the plankton catches ( $n = 22,952$ , Fig. 3a), with five predominant species (*Abylopsis tetragona*, *A. eschscholtzii*, *Chelophyes appendiculata*, *Eudoxoides mitra* and *E. spiralis*) constituting the majority of collected specimens. Their nectophore lengths rarely exceeded 15 mm. Two hydromedusan species (*Bougainvillia*

**Fig. 3** Horizontal distribution of abundances (A, ind.  $10,000\text{ m}^{-3}$ ) of **a** all siphonophores; **b** *Abylopsis tetragona*; **c** *A. eschscholtzii*; **d** *Chelophyes appendiculata*; **e** *Eudoxoides mitra*; **f** *E. spiralis*; **g** *Pyrosoma atlanticum*; and **h** *Bougainvillia* spp. in the upper 300 m in the study area. Circle sizes are relative to species abundances, but the abundance scales vary among panels.  $n$  = scaled-up number of specimens. Species images are taken from Pagès and Gili (1992); Pagès et al. (1992) and <https://scripps.ucsd.edu> and are partly reversed. A list of the number of taxa collected at each station is shown in Table S2, and abundance data are derived in Table S3



*platygaster* and *B. niobe*) were frequently collected in the study area. Their umbrella diameter typically ranged between 5 and 8 mm.

Besides these dominant and abundant species, a number of rare GZ taxa were collected (Table S2). The large coronate scyphozoan jellyfish species *Periphylla periphylla* was only sporadically collected ( $n = 2$  at Stn. 269). Similarly, only two specimens of *Liriope tetraphylla* were caught at Stns. 224 and 237 (diameter of 4 mm). Three specimens of the pleustonic *Velella velella* were collected at Stn. 237, while at Stn. 269 nectophores of the CS, *Hippopodius hippopus* were collected. The towing time was likely too long (min 2:04 h, max 3:12 h, mean 2:30 h) to successfully collect fragile organisms, such as ctenophores (rarely caught in good shape). Only two damaged specimens of the comparatively robust *Beroe* sp. were found in the samples. It was not possible to make a more detailed species identification of those two specimens based on morphological features or size estimates. Doliolid and salp specimens (Table S2) were usually damaged and were not identified to a lower taxonomic level, but might have included as many as ten species.

### Abundance and distribution of gelatinous zooplankton

The distributions and abundance estimates shown in Fig. 3 indicate that abundances were highly variable among stations (maximum overall siphonophore abundance of 419 per 10,000 m<sup>3</sup>, Stn. 237), but they also indicate that GZ species are widespread components of the pelagic community in the studied area. All the common calyccophoran taxa showed high abundances near the northern front (Fig. 1) in the middle transect (Fig. 3), as well as at a few other stations. All common siphonophore species (*Abylopsis tetragona*, *A. eschscholtzii*, *Eudoxoides spiralis*, *E. mitra* and *Chelophyes appendiculata*) tended to occur in the northern part of the study area in higher numbers and especially around the 22 and 24 °C isotherms of the 61°W transect. These species, except for *E. mitra*, were collected at every station, and *A. eschscholtzii*, followed by *C. appendiculata* were clearly more abundant than the other species. *Eudoxoides spiralis* was also abundant at two stations in the southwest area (Fig. 3f), and big catches of *A. eschscholtzii*, *C. appendiculata* and *E. mitra* were made at the northwesternmost station that was closest to Bermuda (Figs. 1 and 3c–e). *Chelophyes appendiculata* was rare in the eastern transect compared with the other transects (Fig. 3d) and *Eudoxoides spiralis* was rare in the east and southeast (Fig. 3f). The two *Bougainvillia* species were absent from the subsamples from all stations south of the 24 °C isotherm (Fig. 3h). The pelagic tunicate, *Pyrosoma atlanticum*, was sometimes caught, but was patchily distributed except in the southern part of the western transect, where it was absent (Fig. 3g).

Abundance correlations for the various taxa with sea surface temperature (SST, °C) and peak fluorescence (*F*) shown in Fig. 4 indicate that most siphonophore species (overall, *A. eschscholtzii*, *E. mitra* and *C. appendiculata*) tended to be more abundant in cooler than in warmer waters (range: 20.7–25.2 °C,  $p < 0.001$ , Table 1 and Fig. 4). *Abylopsis tetragona* and *E. spiralis* showed no correlation with temperature ( $R^2 = 0.001$  and 0.04, respectively). There were correlations between peak fluorescence and abundance of all siphonophores, *A. tetragona*, *A. eschscholtzii*, *E. mitra* and *Chelophyes appendiculata* (LM,  $p < 0.001$ –0.03, Table 1).

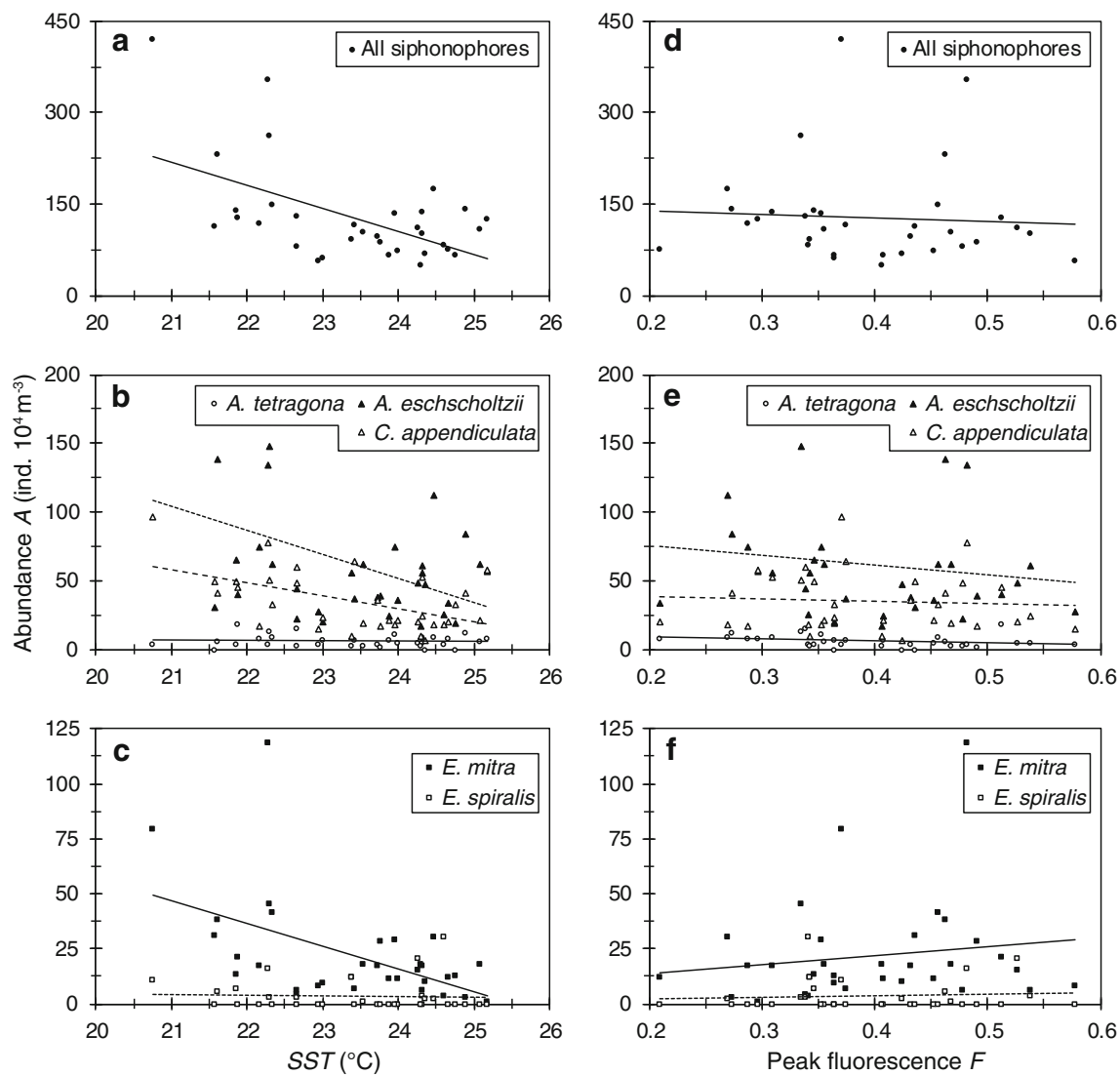
### Diurnal abundance patterns

Abundances of frequently collected species (*Abylopsis tetragona*, *A. eschscholtzii*, *Eudoxoides spiralis*, *E. mitra*, and *Chelophyes appendiculata*, *Pyrosoma atlanticum* and *Bougainvillia* spp.) were compared among day, night and twilight tows (Fig. 5), but too few specimens of other taxa were collected to be tested. Significant differences in time of day abundances were only detected for *P. atlanticum* ( $p < 0.001$ ), with abundances at day ( $6 \pm 25$  ind.  $10^6$  m<sup>-3</sup>, mean  $\pm$  SD) and twilight ( $8 \pm 15$  ind.  $10^6$  m<sup>-3</sup>) stations being significantly lower than during night ( $32 \pm 20$  ind.  $10^6$  m<sup>-3</sup>) stations ( $p < 0.001$ –0.04). No significant differences were found for all siphonophore abundance ( $p = 0.65$ ), *Chelophyes appendiculata* ( $p = 0.45$ ), *Abylopsis tetragona* ( $p = 0.41$ ), *A. eschscholtzii* ( $p = 0.47$ ), *Eudoxoides mitra* ( $p = 0.51$ ), *E. spiralis* ( $p = 0.72$ ) and *Bougainvillia* spp. ( $p = 0.37$ ) (Table 2), even though there were trends towards more GZ specimens in the upper 300 m during night. There was a tendency for *A. eschscholtzii*, *E. mitra* and *E. spiralis* (Fig. 5) to be more abundant in the upper 300 m during night. The high abundances of some species at the two northwesternmost day stations (Stns. 237 and 239) might have biased the results, with further abundance differences between times of day not being detected (*A. eschscholtzii*, *E. mitra* and *E. spiralis*, data not shown).

## Discussion

### Species composition of southern Sargasso Sea gelatinous zooplankton

The collection of gelatinous zooplankton (GZ) in the southern Sargasso Sea using the IKMT provided the first geographic information about the distribution and relative abundances of the calyccophoran siphonophore species (CS) and about a few other species. The semi-quantitative catches were dominated by five CS species that were *Abylopsis tetragona*, *A. eschscholtzii*, *Eudoxoides spiralis*, *E. mitra* and *Chelophyes appendiculata* (families Abylidae and



**Fig. 4** Correlation analysis between sea surface temperature (SST, °C) and the abundance (A, ind. 10,000 m<sup>-3</sup>) of **a** all siphonophores; **b** *Abylopsis tetragona*, *A. eschscholtzii* and *Chelophyes appendiculata*; **c** *Eudoxoides mitra* and *E. spiralis*, and between fluorescence (F) as proxy

for chlorophyll *a* concentration and the abundance (A, ind. 10,000 m<sup>-3</sup>) of **d** all siphonophores; **e** *A. tetragona*, *A. eschscholtzii* and *C. appendiculata* and **f** *E. mitra* and *E. spiralis*. Linear regressions are shown to indicate trends

Diphyidae). These are cosmopolitan species (Mapstone 2014) that are present in tropical and temperate regions, including the Mediterranean Sea (Pagès and Gili 1992; Pagès et al.

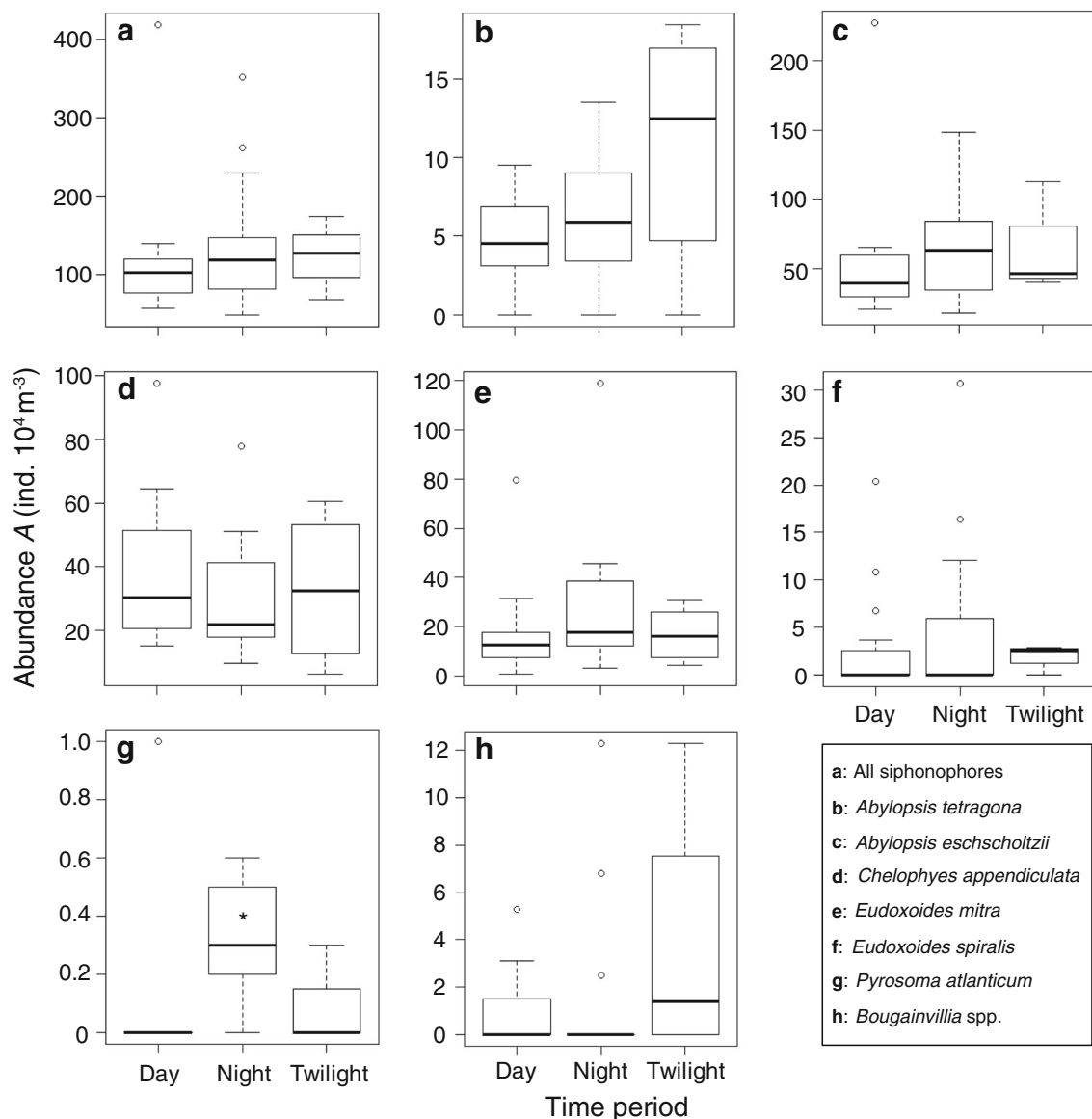
1992), and they have been collected northeast of Bermuda (Grice and Hart 1962), near Bermuda (Moore 1949; Lo and Biggs 1996) and east of Bermuda and across the Atlantic to

**Table 1** Linear models (LMs) for correlation between sea surface temperature (SST, °C), peak fluorescence (F) and log transformed abundance estimates (A, ind. 10,000 m<sup>-3</sup>) of various gelatinous fauna taxa shown in Fig. 4

Taxon	SST (°C)			F		
	<i>p</i> value	<i>t</i> -value	<i>R</i> <sup>2</sup>	<i>p</i> value	<i>t</i> -value	<i>R</i> <sup>2</sup>
All siphonophores	< 0.001	6.38	0.26	< 0.001	12.15	0.01
<i>Abylopsis tetragona</i>	0.45	0.76	0.01	< 0.001	4.33	0.09
<i>Abylopsis eschscholtzii</i>	< 0.001	3.98	0.12	< 0.001	8.56	0.03
<i>Chelophyes appendiculata</i>	< 0.001	4.60	0.21	< 0.001	6.76	0.01
<i>Eudoxoides mitra</i>	< 0.001	4.49	0.29	0.031	2.26	0.05
<i>Eudoxoides spiralis</i>	0.19	1.32	0.04	0.76	0.31	0.01

Significant correlations (*p* < 0.05) are indicated in *italics*





**Fig. 5** Abundances (A, ind.  $10,000\text{ m}^{-3}$ ) of various gelatinous fauna taxa in the upper 300 m in the study area separated by time of the day: day ( $n = 16$  IKMT tows), night ( $n = 13$ ) and twilight ( $n = 4$ ). Significant correlations ( $p < 0.05$ ) are indicated with an asterisk (see Table 2)

the east (Pugh 1975). All zooplankton (including CS and other GZ) were preserved in 96% ethanol, which is primarily used as a fixative for genetic and stable isotope analyses (Hobson et al. 1997). Known to cause significant tissue shrinkage and weight loss (which was not of interest here), ethanol has been shown to be an equally good preservative as formalin (Wetzel et al. 2005) and allowed satisfactory morphological investigation of specimens prior to enumeration. Probably only the more robust species, such as CS and medusae with thick mesoglea (e.g., *Bougainvillia*, *Liriope*, *Veleva* and *Periphylla*) tolerated this fixation.

CS feed on copepods and other small zooplankton organisms captured with their numerous small gastrozooids that have tentacles with stinging batteries, or tentilla, on numerous side branches (Purcell 1981; Mapstone 2014). The CS species

that were widespread in our sampling area are common in many regions, but they appear to vary in relative abundance both spatially and seasonally (Moore 1949). A similar set of CS (*Abylopsis eschscholtzii*, *A. tetragona*, *Bassia bassensis*, *Chelophyes appendiculata*, *Diphyes bojani*, *Eudoxoides spiralis*, *E. mitra*, *Hippopodius hippopus* and *Lensia fowleri*) was reported to be common in the northeastern Sargasso Sea in the upper 200 m (Grice and Hart 1962). A transect of stations from east of Bermuda to the other side of the North Atlantic across  $32^{\circ}\text{N}$  found that *E. mitra* was the most abundant species in the catches to the west of the transect (Pugh 1975); however, it was only the third most abundant species in our sampling. It was also either the first or second most abundant species south of Bermuda (Lo and Biggs 1996). Regular sampling by Moore (1949) around Bermuda between 1938 and 1940 revealed that

**Table 2** Analysis of variance (ANOVA) and Tukey-HSD post hoc test for correlation between day time (day, night and twilight) and log transformed abundance estimates (A, ind. 10,000 m<sup>-3</sup>) of various gelatinous fauna taxa shown in Fig. 5

All siphonophores ( $df=30$ , $p=0.65$ , $F=0.43$ )				<i>Eudoxoides mitra</i> ( $df=30$ , $p=0.51$ , $F=0.69$ )			
	Day	Night	Twilight		Day	Night	Twilight
Day	1			Day	1		
Night	0.64	1		Night	0.49	1	
Twilight	0.88	0.99	1	Twilight	0.99	0.81	1
<i>Abylopsis tetragona</i> ( $df=30$ , $p=0.41$ , $F=3.59$ )				<i>Eudoxoides spiralis</i> ( $df=30$ , $p=0.72$ , $F=0.33$ )			
	Day	Night	Twilight		Day	Night	Twilight
Day	1			Day	1		
Night	0.67	1		Night	0.70	1	
Twilight	0.42	0.77	1	Twilight	0.96	0.96	1
<i>Abylopsis eschscholtzii</i> ( $df=30$ , $p=0.47$ , $F=0.78$ )				<i>Pyrosoma atlanticum</i> ( $df=30$ , $p<0.001$ , $F=18.46$ )			
	Day	Night	Twilight		Day	Night	Twilight
Day	1			Day	1		
Night	0.46	1		Night	< 0.001	1	
Twilight	0.78	0.99	1	Twilight	0.36	0.04	1
<i>Chelophyes appendiculata</i> ( $df=30$ , $p=0.45$ , $F=0.87$ )				<i>Bougainvillia</i> spp. ( $df=30$ , $p=0.37$ , $F=1.03$ )			
	Day	Night	Twilight		Day	Night	Twilight
Day	1			Day	1		
Night	0.51	1		Night	0.90	1	
Twilight	0.63	0.98	1	Twilight	0.34	0.52	1

Significant correlations ( $p<0.05$ ) are indicated in italics

as many as 24 CS species inhabit the upper 300 m of the water column. Monthly sampling during several years near Bermuda found there were six dominant CS species in the upper 100 m (Lo and Biggs 1996), including *A. eschscholtzii*, *E. spiralis*, *E. mitra* and *C. appendiculata*. Their abundances were two orders of magnitude higher (sampling with a 1 m diameter open net, 333  $\mu$ m mesh size) than reported in the present study, possibly because these species might be more abundant in the upper 100 m than between 200 and 300 m, which was also sampled in our study. However, their abundances mostly peaked during other months than March and April, so it is possible that our sampling occurred when all of these species are at low or decreasing abundance levels if they have similar seasonal cycles in the southern Sargasso Sea compared to just south of Bermuda (Lo and Biggs 1996). A similar set of dominant siphonophore species was reported by Moore and Sander (1979) from Jamaican waters. Eden et al. (2009) also mentioned that most CS sampled near Bermuda belonged to the families Abylidae and Diphyidae, which is in agreement with our data. However, *Lensia* species have been reported from the northern Sargasso Sea (Grice and Hart 1962; Lo and Biggs 1996), but we did not collect them in our survey. Furthermore, we detected low numbers of other cosmopolitan species including the large scyphomedusa *Periphylla periphylla* and the more fragile hydromedusae *Bougainvillia niobe*, *B. platygaster*, *Velella velella* and *Liriope tetraphylla*, the CS *Hippopodius hippopus* as well as the ctenophore

*Beroe* sp., which have been described previously from the Sargasso Sea (e.g., Grice and Hart 1962; Latz et al. 1988; Pagès et al. 1992). *Periphylla periphylla* and *Beroe* sp. have been also reported from the waters north of Bermuda (Leavitt 1938). *Periphylla periphylla* typically occurs at greater depths due to its pronounced light sensitivity (Piatkowski et al. 1994; Youngbluth and Båmstedt 2001) and may have been collected by the IKMT at the deeper sampling depths or as a result of vertical migration was caught at shallower depth during night sampling. Stone and Steinberg (2014) studied long-term population dynamics of 21 salp species in the Sargasso Sea and assessed their respective frequency in the net catches. Earlier, Moore (1949) listed eight salp species as being present in Bermuda waters and depicted the seasonal abundance changes for the most common one. Pyrosomes were not specified. Salps and doliolids were recorded at some stations in the present study, but pelagic tunicates can experience localized blooms (Zeldis et al. 1995). It appears that either our collection/preservation techniques were not adequate to sample them or we did not encounter any pelagic tunicate blooms. However, the relatively few specimens we collected were heavily damaged by the IKMT and could not be identified to species level. Nonetheless, identifiable morphological differences suggest the presence of as many as ten different species.

Overall species diversity data obtained by net tows might considerably underestimate the GZ species richness present in

an area, by only including robust species, such as pyrosomes and CS. However, most of the larger siphonophore species might have been (if encountered and caught) destroyed during the long IKMT towing duration. It is likely that the number of GZ species is lower in the warmer lower productivity waters of the southern Sargasso Sea, compared with the northern Sargasso Sea, where previous studies have been conducted (Grice and Hart 1962; Pugh 1975; Lo and Biggs 1996). The present approach of enumerating GZ directly from the IKMT that was deployed specifically to catch anguillid leptocephali needs to be considered as semi-quantitative. It still allows for new insights into the horizontal distribution and relative abundances of particularly CS in the southern Sargasso Sea. Similarly, Legand (1969) used an IKMT to obtain macroplankton/micronekton biomass and abundance data in the Indian Ocean (mainly focusing on larger GZ), while Nishikawa et al. (2001) deployed a rectangular midwater trawl (RMT 1 + 8) focusing on micronekton and large GZ in the North Pacific and Bering Sea. Insights from IKMT tow samples highlight the need for using visual techniques, such as remotely operated vehicles (ROVs) and underwater video profilers (UVPs) (Corgnati et al. 2016) in combination with net tows (Choy et al. 2017; Hosia et al. 2017) to obtain a comprehensive view of the GZ biodiversity in data-poor areas such as the southern Sargasso Sea. Luo et al. (2014) and Greer et al. (2015) accurately quantified siphonophore and other species abundances across mesoscale fronts using an in situ ichthyoplankton imaging system (ISIIS) and compared that with Bongo net hauls. Remsen et al. (2004) pointed out based on a comparison of zooplankton abundances, species compositions and size distributions using net tows and recordings from zooplankton imaging system (SIPPER) that plankton net tows can heavily underestimate zooplankton biomass and species diversity. The number of species in this IKMT-based study in a relatively narrow region of the western North Atlantic is considerably lower than more extensive investigations using a variety of different sampling gears (Multinets, UVPs and ROVs were used for vertical plankton catches) at the Mid-Atlantic Ridge (Hosia et al. 2008, 2017). However, it can be expected to encounter higher GZ abundances and species diversity in close vicinity to Bermuda and the Gulf Stream region where upwelling and coastal offshore transport can occur (Leavitt 1938; Grice and Hart 1962; Lo and Biggs 1996).

### Distribution of gelatinous zooplankton across the frontal zone

This study demonstrates the widespread distribution of some GZ species such as the CS, while others (*Pyrosoma* and *Bougainvillia*) were characterised by a high degree of patchiness, which seems to reflect a general pattern for GZ in offshore areas (Hamner et al. 1975; Graham et al. 2001). Part of

this may be seasonal cycles of abundance (Lo and Biggs 1996), but other factors also may have some influence. In our study, the overall GZ abundance (Fig. 3a) peaked around the 22 and 24 °C isotherms and north of the 22 °C isotherm, while *Bougainvillia* spp. were completely absent south of the 24 °C SST isotherm. GZ are well-known to aggregate along oceanographic isoclines (thermoclines, haloclines, oxyclines) (e.g., Graham et al. 2001; Purcell et al. 2001; Huwer et al. 2008), and in this region water likely converges into the temperature fronts (Mied et al. 1986; Eriksen et al. 1991), which may be one reason for the higher frequency of larger catches in the areas near the 22 and 24 °C isotherms that represent where the fronts form.

High abundances of predatory GZ species may be expected in areas (and depths) where zooplanktonic prey is present in sufficient concentrations. There was a tendency of higher abundances in colder waters such as in the northern part of the study area, where there is more prey (Andersen et al. 2011). Riemann et al. (2011) measured chlorophyll *a* concentrations in a similar latitudinal range and season in the Sargasso Sea and found higher levels in waters with lower temperature. GZ abundances were found in the present study to be higher in precisely these waters, suggesting a connection to primary and secondary production. Siphonophore relative abundance therefore is likely closely linked to the production of zooplankton (indicated by overall increased primary production). There were also higher biomasses of ciliates, dinoflagellates and copepods north of 24°N compared with more southern stations (south of 24°N) in Andersen et al. (2011) who sampled across the frontal zone in March and April 2007. Similarly, more species and higher abundances of mesopelagic fishes were reported in the northern waters (Backus et al. 1969). The detailed data about the pelagic community across the frontal zone (Andersen et al. 2011; Riemann et al. 2011; Richardson et al. 2014) suggest that the observed distribution pattern of net-collected GZ is in agreement with the horizontal epipelagic distribution of organisms from lower trophic levels.

Some CS species are known to show diurnal vertical migrations (DVM), including *Chelophyes appendiculata* and *Abylopsis tetragona* in the Mediterranean Sea (Andersen et al. 1992, 1998, 2004) and in the South Brazilian Bight (Júnior et al. 2015). Diurnal vertical abundance differences of *A. tetragona* have, however, not been found in the present study, even though DVM have been observed at Bermuda (Moore 1949) and Fuerteventura, Canary Islands (Pugh 1974). Earlier studies found that some species of siphonophores moved up shallower at night and did not completely leave the upper 300 m during the day (Mackie et al. 1987), such as *C. appendiculata* (Pugh 1974). However, during the present cruise, no DVM were observed for *C. appendiculata*. Contrarily, Moore (1949) did not find (or only marginally found) DVM of *A. eschscholtzii*, which is consistent with the results of the present study. So similar fishing effort could

have occurred in layers they occupied during our study in both day and night, resulting in no clear differences in abundance, despite their DVM behaviour. Abundance differences at different day times have been previously observed for GZ that follow their planktonic prey (Mills 1983; Pugh 1984; Júnior et al. 2015). Yet, the present water column-integrated approach would not detect DVMs that are mostly within the upper 300 m. Munk et al. (2018) showed vertical abundance profiles from the Sargasso Sea for the hydrozoan *Bougainvillia niobe* and the CS *Amphicaryon acaule* with increased surface (50 m depth) values during night compared with day time. *Pyrosoma atlanticum* was shown to migrate across several 100 m of depth in the Mediterranean Sea (Andersen et al. 1992; Andersen and Sardou 1994). Similarly, *P. atlanticum* was detected at higher abundances during night than day and twilight in the southern Sargasso Sea, suggesting they were using DVM behaviour; however, we could not determine their vertical distribution patterns.

### Hydrozoans in Sargasso Sea food webs and leptocephalus diets

The overall abundance of GZ organisms in the studied area in spring 2017 indicates that the distributions of CS directly overlapped with the leptocephali of anguillids and other species (e.g., Miller et al. 2013b). Other recent surveys we conducted in March and April (2011, 2014, 2015) in the same area that did not explicitly focus on GZ species also observed the same widespread presence. The small larvae of the two anguillid species (*Anguilla anguilla* and *A. rostrata*) are primarily present south of the northern front at 22 °C (Kleckner and McCleave 1988; Munk et al. 2010), but are widely distributed longitudinally at those latitudes (Schoth and Tesch 1982; Hanel et al. 2014; Miller et al. 2015).

Therefore, the GZ species recorded in the present study are part of the epipelagic Sargasso Sea food web (Ayala et al. 2018) that includes about 50 species of anguillid and other leptocephali (Miller and McCleave 1994). Observations of gut contents (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011, 2019) and other types of information (Miller et al. 2013a; Tomoda et al. 2015; Chow et al. 2017) indicate that leptocephali feed on marine snow type of particulate organic matter rather than on zooplankton like most other fish larvae, but it remains unclear which components of items they consume are actually digested and assimilated (Feunteun et al. 2015; Liénart et al. 2016). Therefore, GZ species with possibly breakable tentacles (i.e. siphonophores, medusae and tentaculate ctenophores) (Larson 1976; Purcell et al. 1987; Madin 1988) may contribute tissue to marine snow that could be consumed by leptocephali. Calycophoran and other siphonophores have extensive tentacle arrays that are used to capture prey (Mapstone 2014), so it seems likely that parts of these tentacles break off when extensively agitated.

Interestingly, possible cnidarian tentacles were observed within Sargasso Sea marine eel leptocephalus gut contents (Miller et al. 2019).

This is one explanation for why the DNA sequencing studies (Riemann et al. 2010; Ayala et al. 2018) detected high proportions of hydrozoan 18S rRNA gene sequences in the European eel larva gut contents. Feeding on marine snow would also explain the presence of DNA sequences of many other marine species in those gut contents (Riemann et al. 2010; Ayala et al. 2018). Neither study reported on the species-level correspondences of the sequences they detected, although Ayala et al. (2018) mentioned that CS accounted for 75% of the hydrozoan sequences. However, two of the 14 types of hydrozoan sequences detected by Riemann et al. (2010) matched with 98 and 100% species similarity with the CS *Vogtia glabra* and *Sphaeronectes gracilis* (not found in the present study). Another species (*Liriope tetraphylla*) was detected (99% similarity; identified in the present study), so the barcoding study may have detected more/different species (14) of hydrozoans compared with the net-caught ten species we identified. Therefore, direct DNA barcoding of damaged GZ species is another possibility for understanding the species present in the Sargasso Sea if enough sequences are available in GenBank (Bucklin et al. 2010; Ortman et al. 2010; Lindsay et al. 2015).

Although the present study documented the widespread presence of GZ species, and the DNA sequencing studies showed that hydrozoan tissues are frequently ingested, neither type of study provides a clear indication of how these tissues are entering the larval gut contents. Riemann et al. (2010) only found one to two sequences (usually one) representing different species in each individual leptocephalus intestine, which suggests the larvae were not targeting GZ material. Ayala et al. (2018) presented abundance data for leptocephali and GZ, but did not find a significant positive correlation between both group densities (their Supplementary Figs. 2 and 3) providing obvious predator-prey linkage between the groups. It is difficult to explain the extreme range of all types of taxa detected in the gut contents (Riemann et al. 2010; Ayala et al. 2018) except by the leptocephali feeding on marine snow. Hence, the consistent presence of GZ sequences in the gut contents may be suggesting they are widespread contributors to the material consumed by leptocephali. In fact, Ayala et al. (2018) also found hydrozoan DNA sequences in about 60% of the marine snow particles they analysed.

Marine snow aggregates contain many types of materials such as discarded appendicularian houses (Katija et al. 2017), zooplankton faecal pellets (frequently seen in leptocephali gut contents; Miller et al. 2011, 2019), pteropod webs, gelatinous phytoplankton sheaths and phytoplankton and their exudates. These particles are also colonised by microorganisms and some zooplankton (Alldredge and Silver 1988; Shanks and



Walters 1997; Kiørboe 2000). Therefore, barcoding of leptocephalus gut contents would be expected to detect a wide range of sequences if they had consumed marine snow. GZ tissue fragments might also trigger the aggregate formation, resulting in GZ material being frequently ingested.

An alternative hypothesis for the GZ DNA-rich gut contents of leptocephali might be direct feeding on larval stages of GZ and small life history stages (eudoxids) of CS that reproduce by producing eggs (some about 0.3–0.5 mm in diameter; Mackie et al. 1987; Carré and Carré 1991). Oceanic ctenophores and medusae that most often reproduce without benthic life cycle stages (e.g., Alldredge and Madin 1982; Lucas and Reed 2010) also have small eggs and early larval stages (about < 0.5–1.3 mm; Buecher et al. 1996; Jarms et al. 1999). Appropriately sized GZ early life history stages might be suitable food for leptocephali, because studies with first-feeding eel larvae have indicated that they will ingest rotifers in the laboratory (Tanaka et al. 1995; Wullur et al. 2013). Ciliates, dinoflagellates and particulate material found in some marine eel leptocephalus intestines (Govoni 2010), and GZ early life history stages may also aggregate into marine snow.

Irrespective of how they are ingested, it is not known if tissues of these GZ stages are digested and assimilated by leptocephali. The digestion times for chitinous and gelatinous prey items have been studied (Purcell 2003; Jaspers et al. 2018), but this may not be applicable to leptocephali feeding on marine snow.

## Conclusion

The present study provides detailed information about the distribution patterns of abundant GZ species (mainly CS) and also of rarer species in the spawning area of the European eel, where the early development of the larvae occurs. Their wide distributions in the spawning area of two catadromous freshwater eel species indicate that some GZ species have the potential to contribute tissue material to the marine snow that is ingested by leptocephali. For example, the trophic position of small Japanese eel larvae in their spawning area is too low for predatory GZ having contributed much nutrition to their growth however (Miller et al. 2013a), and there is clearly a majority of materials in the stomachs of leptocephali that is not of GZ origin (Otake et al. 1993; Mochioka and Iwamizu 1996; Miller et al. 2011, 2019). Therefore, it may be unlikely that directly consumed adult GZ organisms or tissue fragments are an important food source for eel larvae, but GZ material is clearly a component of what leptocephali eat in the Sargasso Sea. Further research using more appropriate sampling and preservation techniques and combined methodological approaches (Choy et al. 2017; Hosia et al. 2017) is needed to be able to evaluate the complete GZ fauna in the Sargasso Sea spawning area of the European

eel and to identify pathways for how material from some GZ species ends up in leptocephali gut contents and if it can be digested and assimilated.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no competing interests.

**Ethical approval** All applicable international, national and institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

**Data availability** All data used to create Figures and Tables in this paper can be accessed from the Supplementary Material.

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