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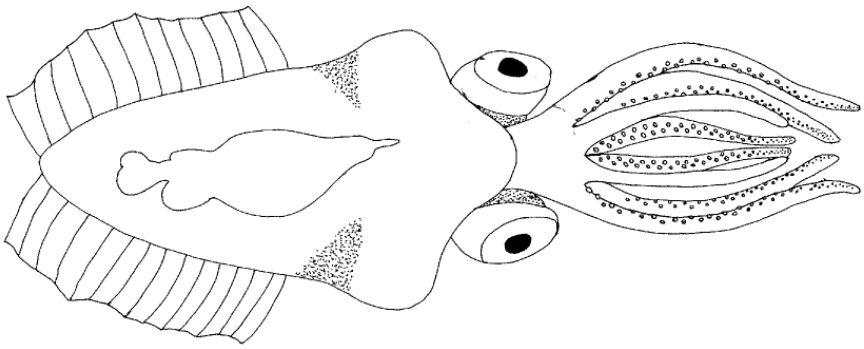
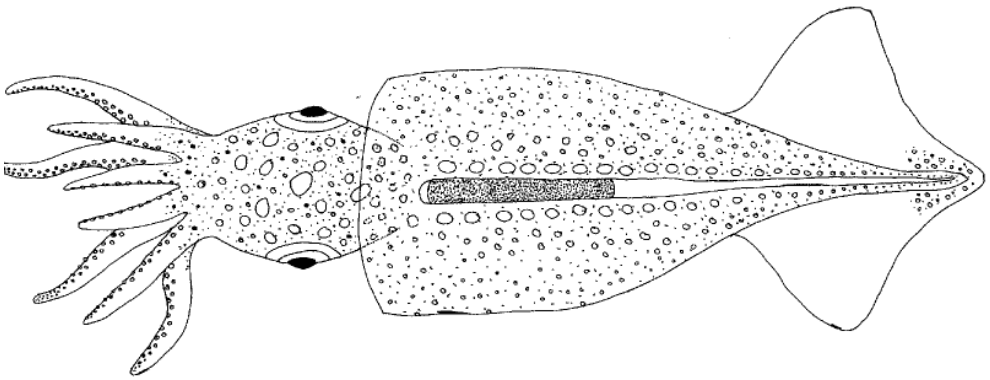


Master Thesis

Cephalopods of the Sargasso Sea
Distribution patterns in relation to hydrographic conditions



Alexandra Lischka

November 2015

Christian-Albrechts-Universität zu Kiel
Mathematisch-Naturwissenschaftliche Fakultät
Sektion Biologie

Masterarbeit

“Cephalopods of the Sargasso Sea Distribution patterns in relation to hydrographic conditions”

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25. November 2015

Eidesstattliche Erklärung

Hiermit erkläre ich, Alexandra Lischka,

dass ich die vorliegende Masterarbeit selbständig verfasst sowie alle inhaltlichen und wörtlichen Zitate als solche gekennzeichnet habe.

Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Kiel, den 25. November 2015

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Acknowledgement

Mein Dank gilt zunächst Dr. Uwe Piatkowski für die Einarbeitung in die Cephalopoden-Thematik, ohne ihn hätte ich mir nicht einen solch taxonomischen Überblick verschaffen können. Ich danke Ihm für seine Geduld, den wissenschaftlichen Beistand, die konstruktiven Vorschläge sowie die Ermöglichung der vielen wissenschaftlichen Kontakte.

Zudem danke ich PD Dr. Reinhold Hanel für die Bereitstellung des Themas und seinen wissenschaftlichen Rat. Durch seine Betreuung wurde es mir ermöglicht, Cephalopoden nicht nur aus dem Museumsregal zu bestimmen.

Professor Dr. Günther Hartl möchte ich ganz besonders für die Übernahme der Zweitkorrektur danken sowie die Unterstützung während meines Studiums, was außerstudienplanmäßige Praktika angeht.

Vielen Dank an Dr. Malte Demerau für die tolle Einarbeitung in die DNA Sequenzierung und das Erstellen phylogenetischer Stammbäume. Danke an Dr. Mike Miller für die Stationskarten und seinen Tintenfischenthusiasmus, sowie an Dr. Håkan Westerberg für sein ozeanographisches Fachwissen. Ich danke Dr. Rabea Diekmann für die tatkräftige Unterstützung bei der PCA und Claudia Klimpfinger für die Zeichnungen meines Deckblattes.

„Jede Thesis trägt die Handschrift des Erstellers, und doch ist sie niemals die Arbeit eines Einzelnen.“ In diesem Sinne danke ich allen weiteren für die wertvolle Unterstützung während meiner Masterarbeit.

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Abstract

A comprehensive collection of mainly early life cephalopods that were sampled during two research cruises to the Sargasso Sea with the FRV Walther Herwig III in April 2014, and the RV Maria S Merian in April 2015, is analysed in this work. In 2014, 714 specimens were collected by a pelagic midwater trawl, and further 1,349 specimens by an Isaacs-Kidd Midwater Trawl (IKMT). A total of 2,487 cephalopods were caught during the cruise in 2015. They belonged to 36 species (20 families). The most abundant family was represented by the Flying squids (Ommastrephidae). Identification of cephalopods was supported by DNA barcoding based on partial COI sequences. The subtropical convergence zone (STCZ) was found at approximately 27°N. This frontal system is characterised by a sharp near-surface temperature gradient and divides the Sargasso Sea into a northern and a southern area. This distinction was also reflected in the cephalopod community composition. For example, the cranchiid *Leachia lemur* prevailed in the northern part, while the cirrate octopod, *Japetella diaphana* was mainly distributed in the southern part of the study area. PCA and RDA analyses detected a significant correlation between species occurrence and sea surface temperature. Ordination analysis (MDS) showed significant differences in the cephalopod assemblages between day and night with midwater species (Enoploteuthidae, Pyroteuthidae) dominating the night catches, probably due to their upward migration into the top 200 m during the night.

Zusammenfassung

Während zweier aufeinanderfolgender Expeditionen der deutschen Forschungsschiffe Walther Herwig (WH 373) und Maria S. Merian (MSM 41) in die Sargassosee in den Jahren 2014 und 2015 wurden frühe Lebensstadien sowie subadulte Cephalopoden gesammelt. 2014 wurden insgesamt 714 Individuen mithilfe eines pelagischen Schleppnetzes (PMT) und weitere 1,349 Cephalopoden mithilfe eines engmaschigem Netzes (IKMT) gefangen. Insgesamt 2,487 Cephalopoden wurden während der Forschungsfahrt im Jahr 2015 gesammelt, welche 36 Arten (20 Familien) angehören. Die häufigste Familie stellten die Flugkalmare (Ommastrephidae) dar. Mithilfe von genetischen Barcoding Studien des COI Genlokus sollte die morphologische Identifizierung gewisser Arten unterstützt werden. Des Weiteren wurde die subtropische Konvergenzzone bei ungefähr 27°N identifiziert. Dieses Frontensystem wird über einen starken oberflächennahen Temperaturgradienten ausgezeichnet, der die Sargasso See in einen nördlichen und einen südlichen Teil trennt. Diese Unterteilung spiegelt sich ebenfalls in der Artenzusammensetzung wieder. Beispielsweise dominierte der Glaskalmar, *Leachia lemur*, im nördlichen Areal, wohingegen der cirrate Oktopode, *Japetella diaphana*, hauptsächlich im südlichen Teil des untersuchten Gebietes angetroffen wurde. PCA und RDA Analysen wiesen auf eine signifikante Korrelation zwischen Artenvorkommen und Oberflächentemperatur. Multidimensionale Skalierung (MDS) detektierte signifikante Unterschiede in der Cephalopodengemeinschaft bezüglich der Tag- und Nachtfänge von pelagischen Arten (Enoploteuthidae, Pyroteuthidae), welche überwiegend in den Nachtfängen vorkamen. Dies kann vermutlich mit nächtlichen vertikalen Migrationsmustern in die oberen 200 m der Wassersäule erklärt werden.

1. Introduction

1.1. The Sargasso Sea

The Sargasso Sea is famous for its myths around the Bermuda triangle and the presence of the pelagic brown algae *Sargassum* whose occurrence traditionally defined the boundaries of this ocean (Andersen et al., 2011). Located in the western North Atlantic Ocean, and also known as the North Atlantic Subtropical Gyre, the Sargasso Sea is bordered by several currents (Fig. 1). The Gulf Stream marks the western and the Canaries Current the eastern borders. The northern and southern frontiers are marked by the North Atlantic and the North Equatorial Current (Voorhis and Hersey, 1964). Except for the island of Bermuda, the Sargasso Sea does not contain any land masses. In its centre, between 20° and 30°N, the Subtropical Convergence Zone (STCZ) is located. This is the latitude band which separates the westerlies to the easterly (easterlies) trades where a distinct temperature front develops from fall to spring (Halliwell et al., 1994; Voorhis and Hersey, 1964) . Colder northern waters meet tropical southern water masses which affects near-surface temperature as well as the salinity gradients and results in a more productive, colder northern and a warmer, less productive southern region. During winter, a large water mass of about 18°C, which varies highly in intension and volume, located around 31°N, is ventilated to the surface which extends to the permanent thermocline (Pacariz et al., 2014). The surface waters begin to stratify during spring which affects phytoplankton bloom. The seasonal changes only occur north but not south to the STCZ, which mark the southern Sargasso Sea as an even more oligotrophic area (DuRand et al., 2001).

Thermal fronts, irregular mesoscale eddies (Eden and Dietze, 2009; McGillicuddy et al., 1998), advective transport of water masses (Palter et al., 2005) and a seasonal convective overturn (Hansell and C. A. Carlson, 2001) have strong influences on the planktonic system (Andersen et al., 2011). Bermuda Atlantic Time series Study (BATS) and the Bermuda Testbed Mooring (BTM) illustrate the physical, biogeochemical as well as biological oceanography of this area in relation to seasonal changes (Dickey et al., 1998).

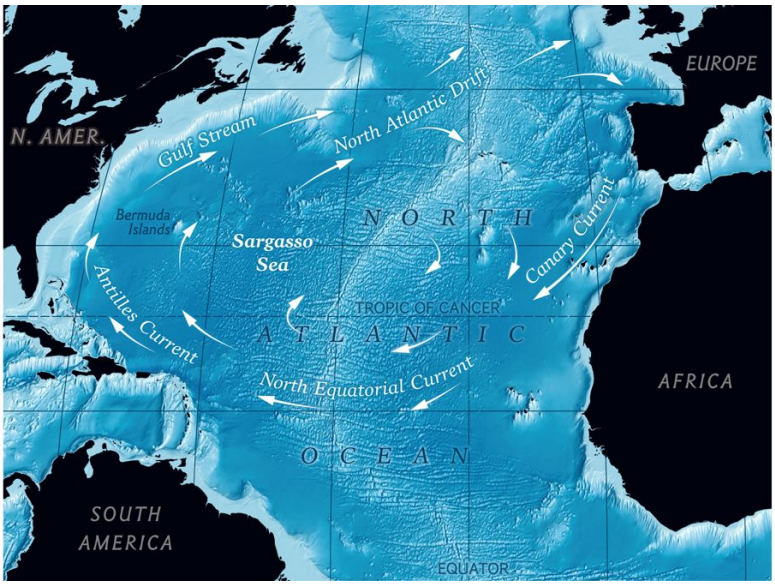


Fig. 1: Map showing the Sargasso Sea including its restricting currents (obtained from: http://www.svgoldenglow.com).

1.2. Pelagic fauna of the Sargasso Sea

It is known for long that the Sargasso Sea is referred to as an oceanic desert, an oligotrophic, low productive ocean (Menzel and Ryther, 1960). Due to the stratification of the surface waters, nutrient availability is reduced to the euphotic zone, which affects phytoplanktonic primary production and thus limits the zooplanktonic food supply (Riley, 1957). Because of the frontal temperature system that divides the Sargasso Sea into a northern and a southern part, it cannot be defined as a homogeneous ocean. This division also affects the primary productivity as represented in fig 2.
Concerning the Sargasso Sea pelagic food web, the main part of zooplankton community is represented by small copepods, estimated abundance of 75 to 87% in the upper 500 m, (Böttger, 1982). Copepods as well as other zooplankton organisms, e.g. pteropods, provide an important food resource for early life stages of many fish species. Associated with many juvenile fish species, also different eel larvae, the so called leptocephali, inhabit the Sargasso Sea (Riemann et al., 2010). Amongst them, young American and European eel larvae occur before they start their long juvenile migrations to fresh waters or coastal marine areas (Miller and J. McCleave, 1994; Schmidt, 1923; Tesch and White, 2008). Several early life stages of mesopelagic fish were found to be associated with pelagic *Sargassum*. Especially fish species like tuna, billfish or marlin play an

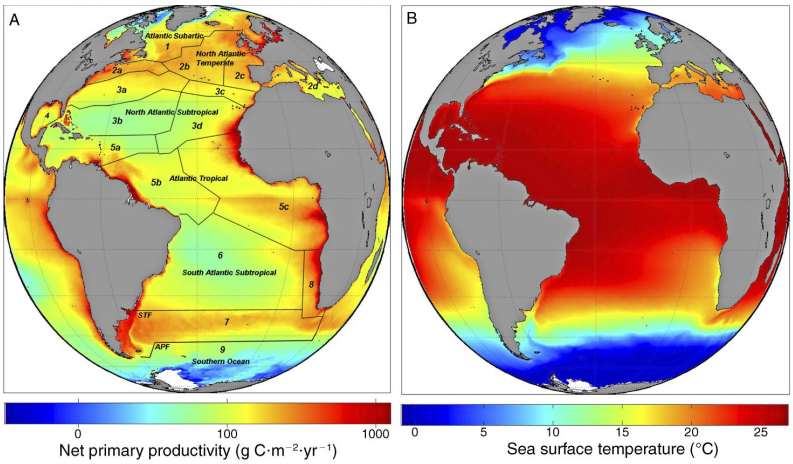


Fig. 2: (A) World Ocean means of net primary production along selected areas, including the northern Sargasso Sea (3a) and the southern Sargasso Sea (3b); (B) Mean yearly sea surface temperature (from Rosa et al., 2008, adapted from Backus et al. 1977).

important role as apex predators in pelagic marine food webs (Fig. 3). Within the food web, fish larvae and some copepods are generally planktivorous feeders (Luckhurst, 2014). Jellyfishes occur as predators but also contribute to the diet of sea turtles like the Leatherback turtle (*Dermochelys coriacea*), which occurs as a migratory species in the Sargasso Sea as well (Gray et al., 2006).

1.3. Cephalopods

Ecology

Cephalopods form one of the key components of the pelagic food web of the Sargasso Sea. Together with early life stages of marine fishes, young cephalopods constitute a major part of the macrozooplankton, which is an essential link in the marine food web. Most pelagic cephalopods are short-lived species with a general life span of less than two years (Boyle, 1987). Due to their fast growth rates, they generally spend a short time at lower trophic levels (Arkhipkin et al., 1998). Adult cephalopods are the major prey of marine top predators in high seas regions such as the Sargasso Sea (Fig. 3). For example swordfish, white marlins (Sato et al., 2004) or common dolphinfish (Oxenford and Hunte, 1999) are known to frequently feed on cephalopods. Furthermore, worldwide, approximately 4 million tonnes of cephalopods have been harvested worldwide in 2014 for human consumption (FAO, 2014), Fig. 4.

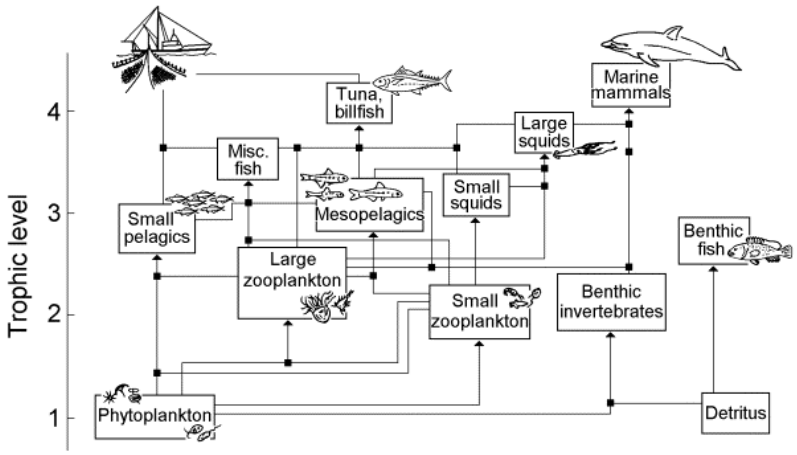


Fig. 3: Pelagic marine food web of an open-sea ecosystem (after Pauly, 1999).

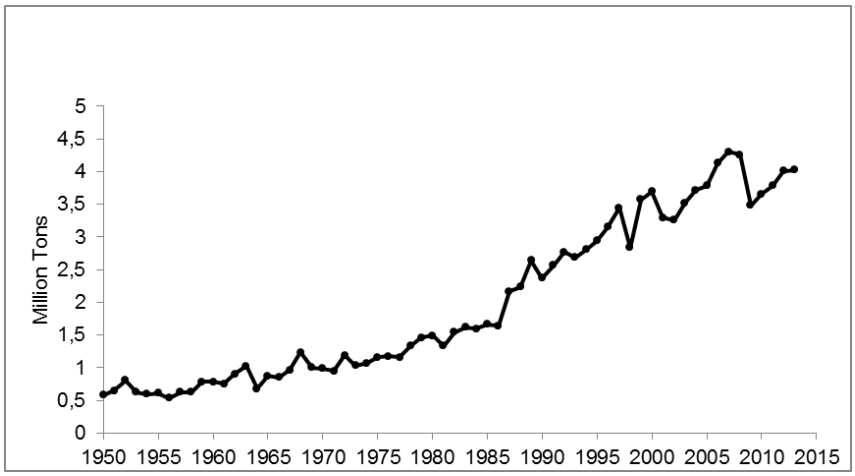


Fig. 4: World catch rate of cephalopods from 1950 to 2013 (FAO, 2015).

Concerning the cephalopod diversity in the Sargasso Sea, species richness differs along the STCZ, marking the northern part (Zone 3a, Fig. 2) with higher levels of cephalopod diversity in comparison to the less diverse southern part (Diekmann and Piatkowski, 2002). Those differences can be linked to lower sea surface temperatures as well as higher net primary production in the northern area of the Sargasso Sea (Rosa et al., 2008). The thermal front in the Sargasso Sea represents a pronounced faunal boundary concerning cephalopod abundance and diversity with restricting certain species occurrences to the southern

or northern parts (Diekmann and Piatkowski, 2002).

Taxonomy

The exclusively marine class of Cephalopoda belongs to the phylum Mollusca. It represents an ancient group with a fossil record of approximately 10,500 species. Approximately 900 recent species are described, belonging to two main groups, the Nautiloidea and the Coleoidea (Fig. 5). The Nautiloidea only comprise a few species with the pearl boat, *Nautilus pompilius* being the most prominent, characterized by a typical external shell. The majority of recent cephalopod species belongs to the Coleoidea which are divided into four orders: the Sepioidea (cuttlefishes and sepiolids), the Teuthoidea (squids), the Vampyromorpha (vampire squid), and the Octopoda (octopuses) (Jereb and Roper, 2010), Fig. 5.

The major common feature of the Sepioidea and Teuthoidea are the four arm pairs and the two tentacles. This group comprises cuttlefishes and squids. Cuttlefishes exhibit an internal shell, the cuttlebone. As they are able to rapidly change their skin colour and shape, they are often referred to as the chameleons of the ocean (Hanlon et al., 1985; Mäthger et al., 2006). Important characteristics for the identification of cephalopods are the shape and form of the arms and suckers. In cuttlefishes and squids, especially the club or armature, the distal part of the tentacles, is an important identification trait (Fig. 6). In male cephalopods one arm is specialized for the transfer of spermatophores to the female, which is called "hectocotylus". For species identification of male cephalopods, the hectocotylus represents an important feature (Robson, 1926). Squids (Teuthoidea) can be divided into two main groups, the Myopsida, which exhibit a cornea covering their eyes and the Oegopsida, which lack such a cornea (Fig. 6 b). Squids have no cuttlebone but a gladius, an internal structure primarily consisting of chitin. For identification, many features have to be considered, some important ones are the funnel- as well as the mantle locking cartilages or the funnel groove. The buccal anatomy also represents an important characteristic including the buccal connectives and crown in the middle of the arms, which lead to the chitineous beak (Jereb and Roper, 2010). The eight-armed octopods (Octopoda) can be divided into finned cirrate, and incirrate octopods. Cirrate octopods exhibit spikes, the so called cirri on their arms which they use in feeding. Most of them are typical inhabitants of the deep-sea. The incirrate octopods are mostly bottom dwelling benthic octopuses, with many still undescribed species (Fig. 6, Allcock et al., 2006).

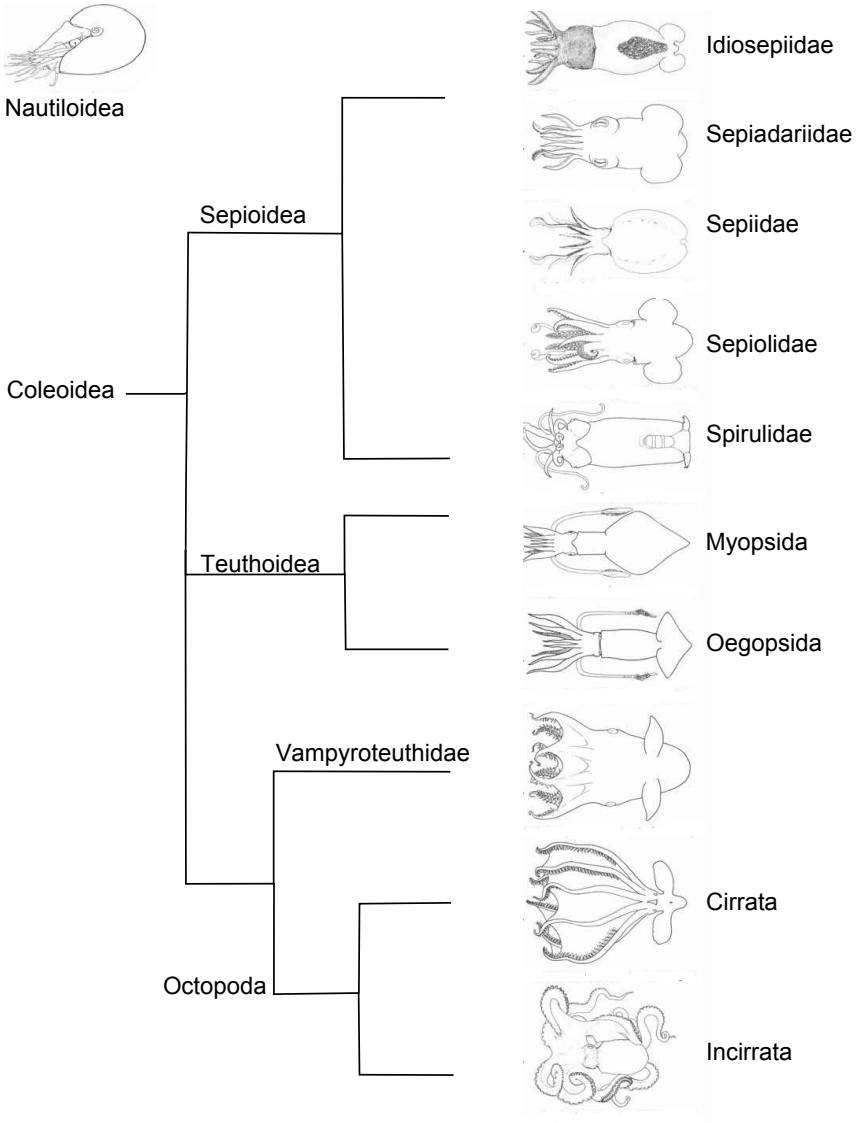


Fig. 5: Orders of living cephalopods (Jereb and Roper, 2010).

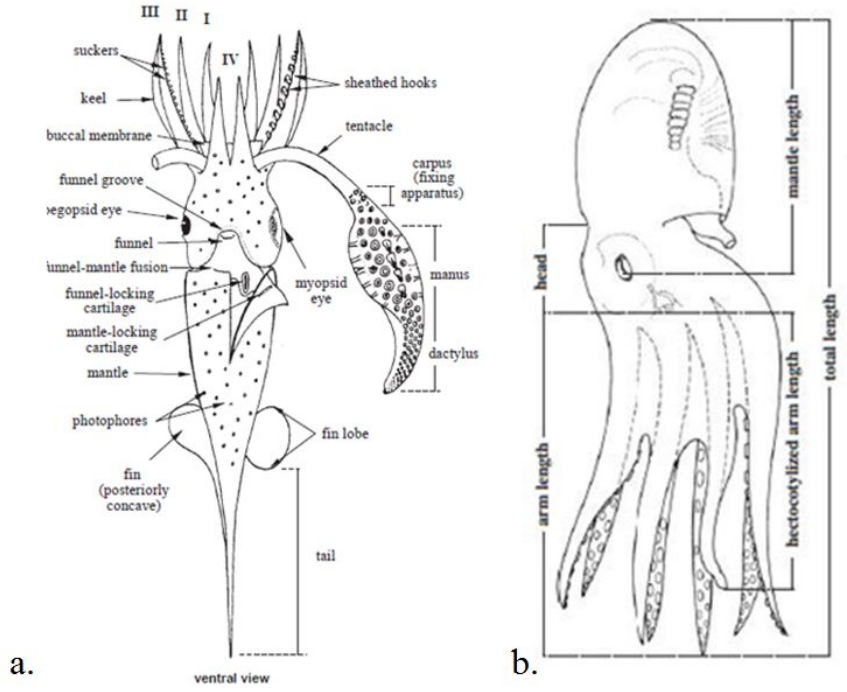


Fig. 6: (a) Teuthida specimen, important traits are the different eye types (Myopsid/Oegopsid squid), the photophore pattern, the funnel and mantle locking cartilages. (b) Incirrate Octopod cephalopod (Roper and Lu, 1979).

Cephalopod early life stages

Knowledge about cephalopod early life stages is generally sparse and often restricted to economically important species (Boletzky, 2003). Several oceanic cephalopods exhibit a warm water associated life cycle that also exploits the opportunities along shelf breaks, which includes bottom near spawning (Laptikhovsky and Nigmatullin, 1993). For example *Todarodes pacificus* (Ommastrephidae), one of the most important commercially exploited squid, spawns its egg masses at the isopycnic surface around 15°C. Early life stages then migrate vertically from the thermocline water layer to lower epipelagic waters at 100-150 m of depth. Subadults then descend to deeper water layers and supposedly mate as adults close to the bottom of slopes before they start the upward migration for spawning (Sakurai et al., 2000), Fig. 7.

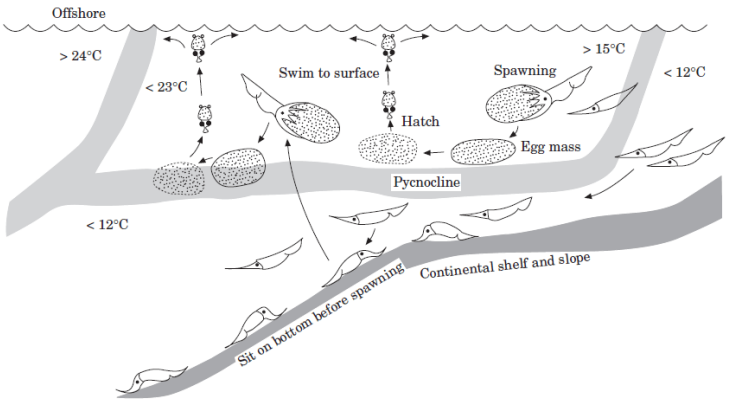


Fig. 7: Reproduction model of *Todarodes pacificus*, including spawning at the isocline, ascending hatchlings and migration of subadults to deeper waters (Sakurai et al., 2000).

All cephalopods show a direct development without a true metamorphosis. Despite the lack of a true larval stage, the early life stages of many taxa not only differ in size but also in external morphology from the adult life forms and are called "paralarval" stages (R. E. Young, 1988). One example for a striking differentiation during the paralarval development is represented by the family Ommastrephidae (Flying squids). Newly hatched ommastrephid squid tentacles are fused into a "proboscis", which starts to separate into the tentacles by a mantle length of 3-4 mm (Fig. 8). Because of this dimorphism, they were formerly mistaken for an own taxon, called *Rhynchoteuthis* (Chun, 1903). By reaching a dorsal mantle length of about 10 mm the separation is finished for most species. During the separation process, tentacles and arms gain in size whereas the growth of the mantle is reduced (Chun, 1903; Vidal, 1994). Because of these distinct morphological changes during development, the early life stages of ommastrephid squid might allow the term "larvae" (Boletzky, 1974). There is, however, no single morphological change common to all cephalopods (compared to e.g. the notochord flexion in fish), therefore the term "larvae" should be avoided (Shea and Vecchione, 2010).

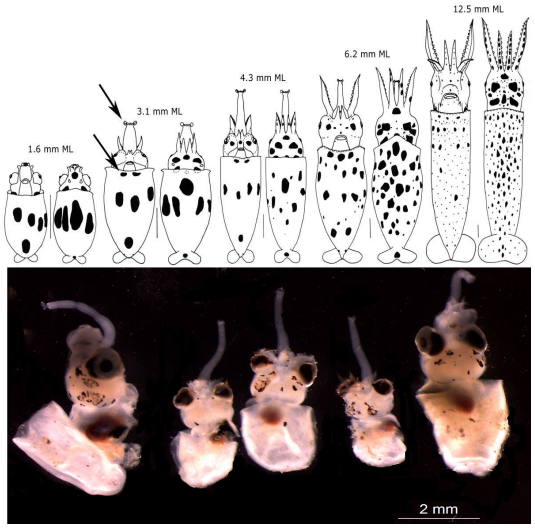


Fig. 8: Above: Growth of an ommastrephid squid illustrating the separation of the proboscis from 1.4 to 9 mm DML (R. E. Young and Hirota, 1990). Below: Paralarval ommastrephid life stages.

During the planktonic life stage, the cephalopod paralarvae predatorily feed on zooplankton and are active swimmers by using jet propulsion. However, as for other early marine life stages, their distribution strongly dependends on the oceanic circulation (Moreno et al., 2009; Shea and Vecchione, 2010) .

1.4. Barcoding

Due to the morphological differentiation during growth, identification of young cephalopods is not always clear, especially if important taxonomic traits are not yet fully developed. Another tool, besides morphological identification, represents the analysis of genetic differences between species.

The idea of facilitating species identification by comparing selected gene loci has attracted biologists on a broad range (Hebert and Gregory, 2005). The method of "DNA Barcoding" is widely applied, which means that short DNA sequences are used for species identification, similar to a supermarket scanner. The obtained sequences are then provided to a public database, like the Barcode of Life Database (BOLD) or NCBI's GenBank in order to cover a broad range of taxa (Hebert et al., 2003). A recent taxonomic tool, including marine taxonomy, has been the use of the mitochondrial cytochrome c oxidase subunit I (COI) DNA sequences for species identification and clarification of taxonomic

status (Hebert et al., 2003). Especially for fish species, a variety of projects focus on this method, which integrates with the Fish Barcode of Life Initiative (FISH-BOL; www.fishbol.org; Hanner et al., 2005). COI is a relatively fast evolving gene with a higher molecular evolutionary rate than those of 12S and 16S rDNA (Knowlton and Weigt, 1998). It is flanked by highly conserved DNA regions, enabling the use of universal primers for amplification in a wide range of taxa (Folmer et al., 1994; Zhang and Hewitt, 1997). Nonetheless, amino-acid sequence changes of COI occur more slowly compared to most other mitochondrial genes making it highly suitable to delimit taxa on the species level (Lynch and Jarrell, 1993). Since the Cephalopod International Advisory Council (CIAC) meeting in February 2006, there is an increasing interest in contributing genetic sequences of cephalopods to the Cephalopod Barcode of Life Database (Bonnaud et al., 1997; Strugnell and Lindgren, 2007). Up to now, many cephalopod barcoding projects have been approached but an extensive database, as established for e.g. fishes, is still missing. Especially for so called cryptic species or species complexes, groups that can even comprise several genera, morphological identification is not always sufficient. One example for a species complex in cephalopods represents the hooked-squid, *Onykia carriboea*. In comparing genetic sequences, morphological species identification can be supported. So far, 48.395 nucleotide sequences of cephalopods are listed in GenBank (http://www.ncbi.nlm.nih.gov/genbank), with more than 50% deriving from octopods. However, sequences from rare as well as economically negligible species are still lacking.

1.5. Aim of the study

During two oceanographic expeditions on board the German research vessels Walther Herwig (cruise number WH373) and Maria S. Merian (cruise number MSM41), intense plankton sampling in an overlapping area of the Sargasso Sea at the same season of two consecutive years (2014, 2015) was conducted. As cephalopods represented one of the major macrozooplanktonic groups in the Sargasso Sea, this study focuses on the distribution and abundance of early life stages of cephalopods in this area.

The central objective of the study was to identify if the Subtropical convergence zone (STCZ) has effects on the composition of cephalopod communities in the Sargasso Sea. Therefore, species assemblages of this area were to be described with mostly morphologically based species identification and additional molecular genetic analyses. Those were conducted especially to support the morphological identification of several hooked-squids (family Onychoteuthidae), including the potentially cryptic species complex formed by *Onychoteuthis banksii* and *Onykia carriboea*, which might include more than two species. Furthermore, three morphotypes belonging to the flying squids, Ommastrephidae, were identified and compared to the molecular data. In addition, DNA from the most abundant species of the research area was sequenced as well as from two rare morphotypes. One of them potentially representing the early life stage of the giant squid, *Architeuthis dux*, and the other resembling a cycloteuthid, referred to as "Stern".

This study represents the most comprehensive analysis on early life stages of cephalopods ever conducted in the Sargasso Sea and will be compared to other subtropical and tropical oceans.

2. Material and Methods

2.1. Sampling and study areas

FFS Walther Herwig III cruise 373

The cephalopod specimens were sampled in the Sargasso Sea from March to April 2014 during cruise 373 of the German vessel Walther Herwig. Focus of the cruise was the investigation of distribution and abundance of European eel (*Anguilla anguilla*) early development stages and its accompanying fauna. The study area covered the central Sargasso Sea with stations ranging from 36° to 24°N and 70° to 27°W. Sea surface temperatures were generated from the National Oceanic and Atmospheric Administration, NOAA/ESRL Physical Sciences Division, Boulder Colorado, http://www.esrl.noaa.gov/psd/) and illustrate the temperature front around 26° to 28°N (Fig. 9). Sampling was mainly carried out with an Isaacs-Kidd Midwater Trawl (IKMT) with a 6.2 m^2 mouth opening, a length of 10 m, and 0.5 mm mesh (Hydro-Bios Apparatebau GmbH). In total 56 IKMT tows along seven north-to-south transects as well as nine additional IKMT stations were sampled between the core study area and Ponta Delgada, Azores (Fig. 9). Double oblique IKMT tows covered the epipelagic zone, from sea surface to 300 m of depth. The seven additional IKMT tows were double oblique tows down to 150 m depth except for one single oblique tow down to 700 m. Each IKMT tow filtered between 29,652 and 113,447 m^3 water (mean: 72,825 ± 17,277 m^3). At seven sampling stations also a pelagic fisheries trawl (Multisampler, Engel Netze) was used that had a width of 45 m, a height of 30 m, a length of 145 m and mesh sizes from 180 cm down to 80, 40, 20, 10, 8, 6, 4 cm in the codend. Deployment of this midwater trawl was through the ships back with the help of trawl cables on both sides. The mean towing speed was 3.4 knots. Five tows were conducted down to 300 m, one to 700 and another one to 1,000 m. Water filtered by the pelagic trawl could not be accurately estimated because of the different mesh sizes. Therefore, cephalopod yield of each pelagic trawl sample is expressed in absolute numbers for each species occurring.

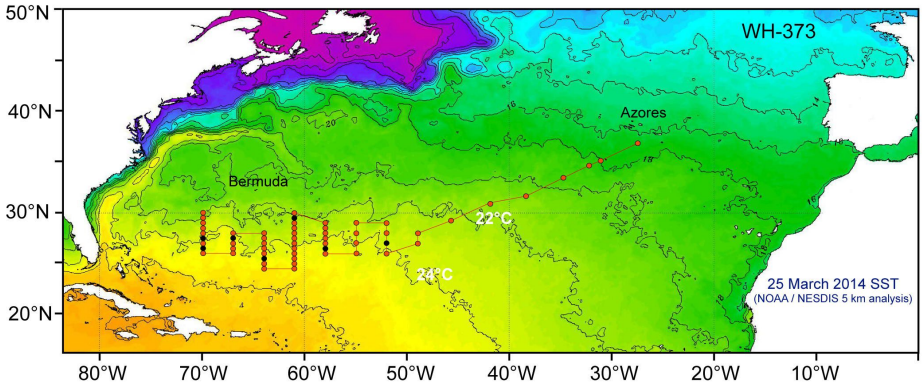


Fig. 9: Research area including the station grid of WH 373 in relation to the SST at the beginning of the cruise. Dark dots indicate PMT and orange dots IKMT stations. Map provided by M. Miller, 2015.

Maria S. Merian cruise 41

In April 2015 cephalopods were collected during the cruise MSM 41 of the German research vessel Maria S. Merian. One of the major tasks of this cruise was the investigation of abundance and biomass of macrozooplankton in the Sargasso Sea. The study area ranged from 22° to 31°N and 58° to 70°W, with a total of 49 oceanographic stations that were arranged along five north-to-south transects (Fig. 10).

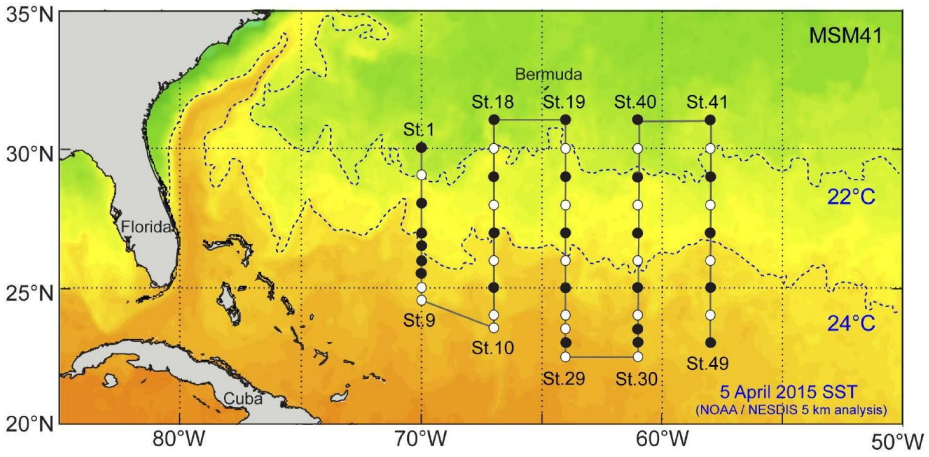
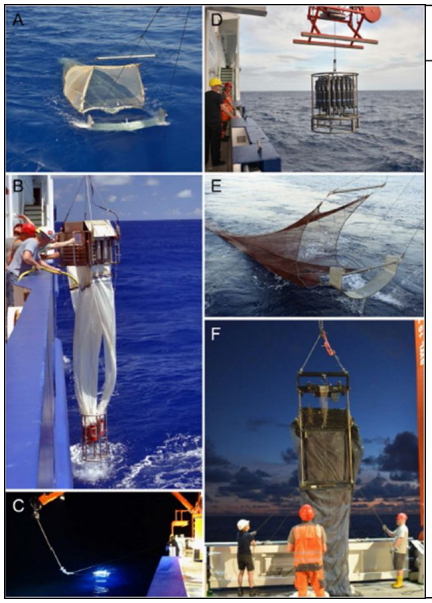


Fig. 10: MSM 41 cruise map including the station grid of the study area in relation to SST. Dark dots indicate night and white dots day hauls. Map provided by M. Miller, 2015.

Sampling Gear

Stations were sampled using six types of gear: a CTD Rosette (Sea-Bird Electronics Inc, USA) for recording hydrographical data, and taking water samples; and several nets to collect macroplankton (IKMT-0.5, IKMT-5, Manta Trawl, MOCNESS, MSNV; Fig. 11).



Gear	Abbreviation	Mesh size
(A) Isaacs-Kidd- Midwater Trawl	IKMT-0.5	0,5 mm
(B) Hydro-Bios Multinet Midi	MN	0,2 mm
(C) Manta Trawl	MT	0,33 mm
(D) Conductivity-Temperature-Depth Sonde	CTD	
(E) Isaacs-Kidd- Midwater Trawl	IKMT-5	> 5 mm
(F) Multiple Opening and Closing Environmental Sensing System	MOCNESS	0,33 – 2 mm

Fig. 11: Sampling gear used during MSM 41. Photos from cruise report MSM 41, 2015.

The CTD, short for Conductivity-Temperature-Depth, is a sonde, which records hydrographical parameters such as pressure, temperature, conductivity, and which has attached a metal rosette wheel with bottles for taking water samples at selected depths (Fig. 11D). It was always deployed in advance of the net tows at each sampling site down to 500 or 1,000 m, respectively. At each station plankton was collected by double oblique tows using the Isaacs-Kidd Midwater Trawl (IKMT) with a 6.2 m^2 mouth opening, a length of 10 m, and 0.5 mm mesh size (Hydro-Bios Apparatebau GmbH, Germany). Sampling was conducted from sea surface to 300 m of depth and lasted for about 3 hours. At towing speeds of approximately 3 knots, a depressor is responsible for the net opening and zooplankton was collected in a net bag (Fig. 11A). The filtered water volume of the nets was estimated using a flow meter (General Oceanics, USA), the size of the net mouth opening and a calibration factor (Miller and McCleave, 1994 & 2007). In total, 26 stations were sampled at night and

23 stations during daytime. At selected stations, additional hauls with an IKMT net of 5 mm mesh size (13.5 m^2 mouth opening) were conducted to catch larger leptocephali and cephalopods (Fig. 11E). 10 hauls were performed in total with this net type, usually during day or dawn, covering stations from each transect. The IKMT tows were conducted with a major focus on the distribution and abundance of the European as well as the American eel larvae (*Anguilla anguilla*, *A. rostrata*). Besides leptocephali, cephalopods were quantitatively sorted out from the plankton samples.

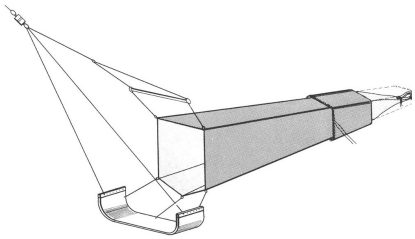


Fig. 12: Schematic drawing of an IKMT net (Hydro-Bios Apparatebau GmbH, Germany)

The Manta Trawl is a net designed for surface sampling (90 cm x 16 cm net opening) with a manta ray resembling shape (Design by Jens Harder, MPI Bremen, Germany). During the cruise it was mainly used for collecting microplastic particles and neuston organisms (Fig. 13).

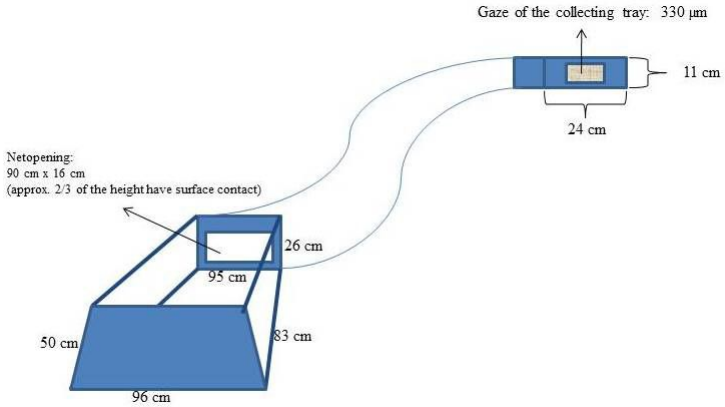


Fig. 13: Schematic drawing of the Manta Trawl, including unit sizes.

Alternating with a vertical multi net (MN), stratified vertical tows of the MOCNESS were conducted at every second station down to 500 m except for

the middle transect at 64°W where the MOCNESS was deployed down to 1,000 m. MOCNESS stands for Multiple Opening/Closing Net and Environmental Sensing System and each net can be opened and closed independently at selected depths (Wiebe, 1976; Fig. 14).

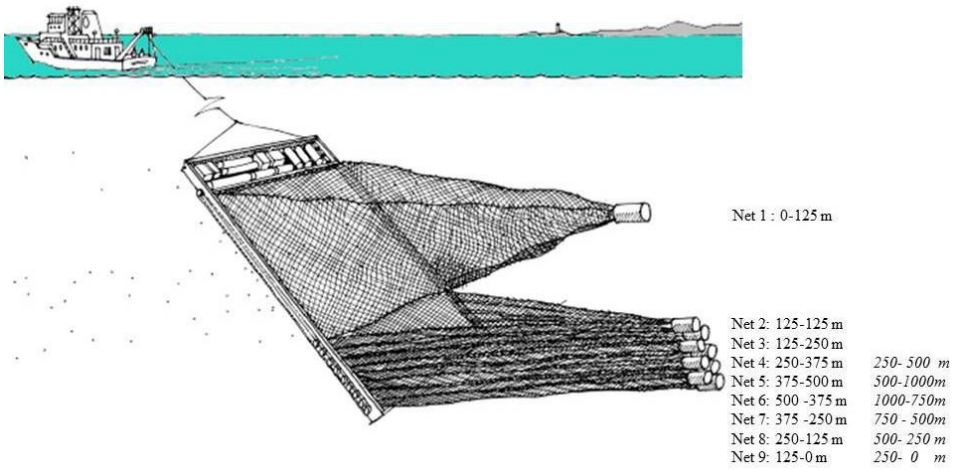


Fig. 14: MOCNESS net with net depths indicated for the 500 m tows. Depths of the nets for the 1,000 m tow are shown in italic letters (drawing after the Gulf of Maine Research Institute).

2.2. Species Identification

Early life stages of cephalopods as well as juvenile specimens were quantitatively sorted out from all sampling nets and identified to the lowest taxonomic level possible. The identification was based on published keys (Diekmann and Piatkowski, 2002; Jereb and Roper, 2010; Nesis, 1987; Sweeney et al., 1992). For the identification, specimens were examined using a stereomicroscope. The dorsal mantle length of the specimens was measured and species were photographed (Camera IC 80H, Binocular MZ8, 10-40x; Leica Microsystems GmbH, Germany). Specimens were either frozen at -20°C or conserved in 70% ethanol. Some specimens that were in good condition were fixed in 4% formalin for later detailed detailed morphological studies. Tissue samples of each species were taken from freshly caught specimens and fixed in 70% ethanol for further genetic analyses.

2.3. Data analysis

Univariate data analysis

The largest amount of cephalopods was caught with the smaller mesh size IKMT net during the MSM 41 cruise.Therefore, this comprehensive data set was used to investigate distribution and diversity patterns of cephalopods and to describe their community structure in the Sargasso Sea cephalopod densities (n/10,000 m^3) were calculated for each station and used for the spatial analysis of the community structure. In order to smoothen the dominating effect of the most abundant species, the catch numbers of each species were fourth-root transformed (Field et al., 1982). The median catch rates of cephalopod species as well as specimens were calculated for the latitudes and longitudes of the study area and visualized as boxplots. To test for normality in the transformed data, Shapiro-Wilk's W test was applied and host-hoc Tukey HSD test was used to detect significant differences between the means of the different latitudes and longitudes. For descriptive statistics, univariate indices such as the Margalef's species richness index (d) were calculated. It describes the total number of species at a sampling site, with S representing the total number of species in the sample (at a single station or transect) and N representing the number of individuals (Margalef, 1958).

$$Margalef's\ species\ richness\ index\ (d) = \frac{S-1}{ln(N)}$$

The Shannon-Wiener diversity index (H') was calculated in order not only to consider the amount of species but also the relative abundance of each species. This index assumes that individuals are randomly sampled from an infinitely large community and that every species is represented in the sample (Shannon and Weaver, 2015).

$$Shannon-Wiener\ diversity\ index\ (H') = -\sum p_\mathrm{i} \cdot ln(p_\mathrm{i})$$

with

$$p_\mathrm{i} = \frac{n_i}{N}$$

representing the amount of species (i) relatively to the total number of individuals (N).
The Pielou's evenness index (J) was applied for the different stations. Using the Shannon-Wiener diversity index (H'), this index characterises the biodiversity of a sample by describing its evenness referring to the species number (S).

The Pielou's evenness index takes up values between 0 and 1, less variation is demonstrated by high J' values (Pielou, 1966).

$$Pielou's\ evenness\ index\ (J) = \frac{H'}{ln(S)}$$

As a proxy for the biodiversity of a habitat, the probabilities that two sampled individuals belong to the same species were calculated with the Simpson's index (Begon et al., n.d.; Magurran, 1988). 0 hereby represents infinite diversity whereas 1 indicates no diversity.

$$Simpson's\ diversity\ index\ (\lambda) = \sum p_i^2$$

Multivariate data analysis

Multivariate statistical analyses were applied to describe community structure, abundance and species composition of early life cephalopod associations in the Sargasso Sea. The study area was divided into northern and southern as well as eastern and western transects and compared by different methods of the Primer-E software (Version 6, Clarke and Warwick, 2001). Analysis of similarity, ANOSIM, (Clarke and Warwick, 2001) was performed to identify differences in the community structure of the different transects (northern vs. southern as well as western-eastern areas). Additionally, the similarity percentage routine, SIMPER (Clarke and Warwick, 2001) was conducted to identify dominant species, which were responsible for community differences. If a species identification was not possible, individuals were grouped to higher taxa (usually to the family level), specimens that could only be identified as Teuthoidea indet. were excluded from the analysis.
Agglomerative, hierarchical cluster analysis and non-metric multidimensional scaling (MDS) was used for the analysis concerning species compositions of day and night catches. MDS analysis detects the best assemblage of data points based on the dissimilarity values of the data set. Thus, similar data points are visualized by proximity, dissimilar points are grouped farther apart from each other, illustrating discrete clusters. Sample classification was based on the group-average linking method (Field et al., 1982; Kruskal, 1964) and the Bray-Curtis measurement was used as the measure for distance (Bray and Curtis, 1957; Field et al., 1982). Similarities in cephalopod community compositions between stations sampled during cruise MSM41 were investigated with a Principal Component Analysis (PCA). PCA is a method which reduces the complexity of a dataset in defining linear combinations of the orginal data, the so-called principal components (PCs), and transforming them to a new

coordinate system. The greatest amount of variance of the total data set is explained by the first PC. Every successive PC explains a smaller proportion of the total variance. The individual contributions of the variables to the PCs are called loadings, the new coordinates of the objects (samples) called scores. In this study, PCA was used for the illustration of possible spatial patterns of cephalopod communities. The examination of eigenvalues led to the choice of showing only the first two PCs.
In order to examine the relationships between environmental factors and community composition, redundancy analysis (RDA) was applied. RDA is a linear eigenvector ordination technique related to PCA, which constrains the axes to be linear combinations of explanatory variables. Since not all the potential factors influencing the species composition could be quantified and included in the canonical analysis RDA was performed as an add-on to the PCA. Only daytime and SST were used as environmental variables as other variables like fluorescence were not available or were highly correlated (depth, salinity) between sample sites. RDA results were shown in triplots, an ordination diagram of samples, species, and environmental conditions. Alikeness of sites and species with respect to the environmental variables is expressed with grouping them closer together. The strengths of the relationships, or rather the informative value of the representation through the levels, are represented by the arrow lengths, and their assosciations by the acuteness of the angle. The significance of the relationship was investigated by Monte Carlo permutation tests, including the test of the null hypothesis of independence between the two data sets with the canonical eigenvalues.
PCA was conducted with the software R 3.0.2 (R Core Team 2013) for statistical computing and the related package vegan (Oksanen et al., 2013). Prior to the analysis, species abundances taxon specific densities (n/10000 m^3) were fourth root transformed and a chord distance transformation was applied (Legendre and Gallagher, 2001) to avoid the so-called double-zero problem.

2.4. Barcoding

Barcoding studies were performed with specimens from the WH373 cruise at the Thünen Institute of Fisheries Ecology in Hamburg. In total, 42 specimens were analysed from both IKMT and pelagic midwater trawls (PMT).

DNA extraction, amplification and sequencing

Mantle tissue was carefully removed with a sterile scalpel from specimens,

which had been preserved in 70% ethanol. DNA was extracted from the tissues by using the Qiagen DNEasy Kit (Valencia, CA) developed for the purification of DNA from animal tissues (Spin Column Protocol), following the manufacturer's protocol. DNA from the cytochrome c oxidase subunit I gene locus was amplified using primers LCO1490 (forward) and HCO2198 (reverse) after Folmer el al., 1994.

Primer	Sequence
LCO1490	5'-ggtcaacaaatcataaagatattgg-3'
HC02198	5'-taaacttcagggtgaccaaaaaatca-3'

The concentration of DNA was checked with the Cary 50 UV-Visible spectrophotometer (Varian Inc) and DNA concentrations of 100 ng/µl were aimed by the extractions. The ratio of absorbance at defined wavelengths can be used to estimate the purity of DNA. Samples with a ratio at 260 nm/280 nm of 1.8 were considered as "pure". For the amplification of the gene fragments 1 µl template DNA, 7.5 µl Taq-PCR Master Mix (Qiagen), 6 µl sterile water and 0.5 µl of each 10 mM primer were mixed. The polymerase chain reaction was initiated by a simplified hot start at 94°C for 7 minutes followed by 35 cycles of 60 s at 94°C (denaturation), 60 s at 45°C (annealing) and 90 s at 68°C (extension), followed by a final extension phase of 7 minutes at 68 °C. The PCR products were kept at 4°C. The PCR products were checked for successful amplification by electrophorese through a 1.4% agarose gel. Sequencing PCRs were performed using the BigDye Terminator v.3.1 Cycle Sequencing Kit, following the manufacturer's instructions. A volume of 0.76 µl PCR product was mixed with 0.4 µl of either the forward or reverse primer (Folmer et al., 1994), 1 µl 3.1 Sequencing Buffer (5X), 1 µl Mastermix 3.1. and 6.84 µl sterile water, resulting in a total volume of 10 µl. The amplification products were purified, thus, excessive fluorescent dNTPs were removed, by adding 5 µl BigDye-X-Terminator Reaction Mix, 14.5 µl sterile Water and 22.5 µl SAM solution to 8 µl of each PCR product in a total volume of 50 µl (Applied Biosystems, Inc). Sequences were read with the AB3500 Genetic Analyser (Applied Biosystems, Inc). Nucleotide sequence analysis Sequence reads from both DNA strands were verified by eye and aligned using CodonCode Aligner v5.1.1 (CodonCode Corporation). Alignments were trimmed to avoid problems with missing data in the following analyses. Nucleotide variability was scored using the software DNASP v5 (Rozas et al., 2003). The phylogenetic relationship among taxa was assessed with three different approaches. Based on genetic distances a neighbour-joining (NJ) tree was constructed using the Bioedit 7.2.5 software

(Hall, 1997-2001). In addition, one tree was inferred based on the maximum likelihood (ML) method as implemented in RaxML v.8.0.26 (Stamatakis, 2006) and another tree was constructed based on Bayesian Inference (BI) using MrBayes 3.2.4 software (Huelsenbeck and Ronquist, 2001). For the last two trees the best-fitting models of nucleotide substitution were chosen by likelihood scores obtained by jModelTest 0.1.1 (Posada, 2008). The best model for ML calculation was F81+I+G, the most appropriate model for Bayesian analyses was HKY+I+G. The basic local alignment search tool (BLAST) was used to compare the obtained sequences to available nucleotide sequences in GenBank, based on the maximum sequence identity percentage.

3. Results

3.1. Walther Herwig cruise 373

3.1.1. Hydrography

During the research cruise, transects were supposed to cross the two temperature isotherms. This was achieved for almost all seven transects of the core study area even if the front was moving northwards. Further nine stations were sampled on the way to the Azores. Hydrographic sections were detected at the 22°C and the 24°C isotherms. OSTIA 1/20° global grid (6.5 km) L4 SST analysis (UK Met Office) was used to estimate daily sea surface temperatures. A thermal front with a temperature gap between 22°C and 24°C could be observed for the western part of the core study area which was more diffuse in the eastern area (Fig. 15).

At every station of the seven transects, a hydrographic profile was generated from CTD data. In total, 107 CTD casts were made. A convergence zone, an increased SST change over a short distance, could be observed within the main study area between 26° and 28°N (Fig. 16). Salinity changes were observed in a west-eastern gradient. Changes concerning fluorescence, salinity and temperature were observed for the upper 300 m. With increasing depth, abiotic variables were comparable for the different transects.

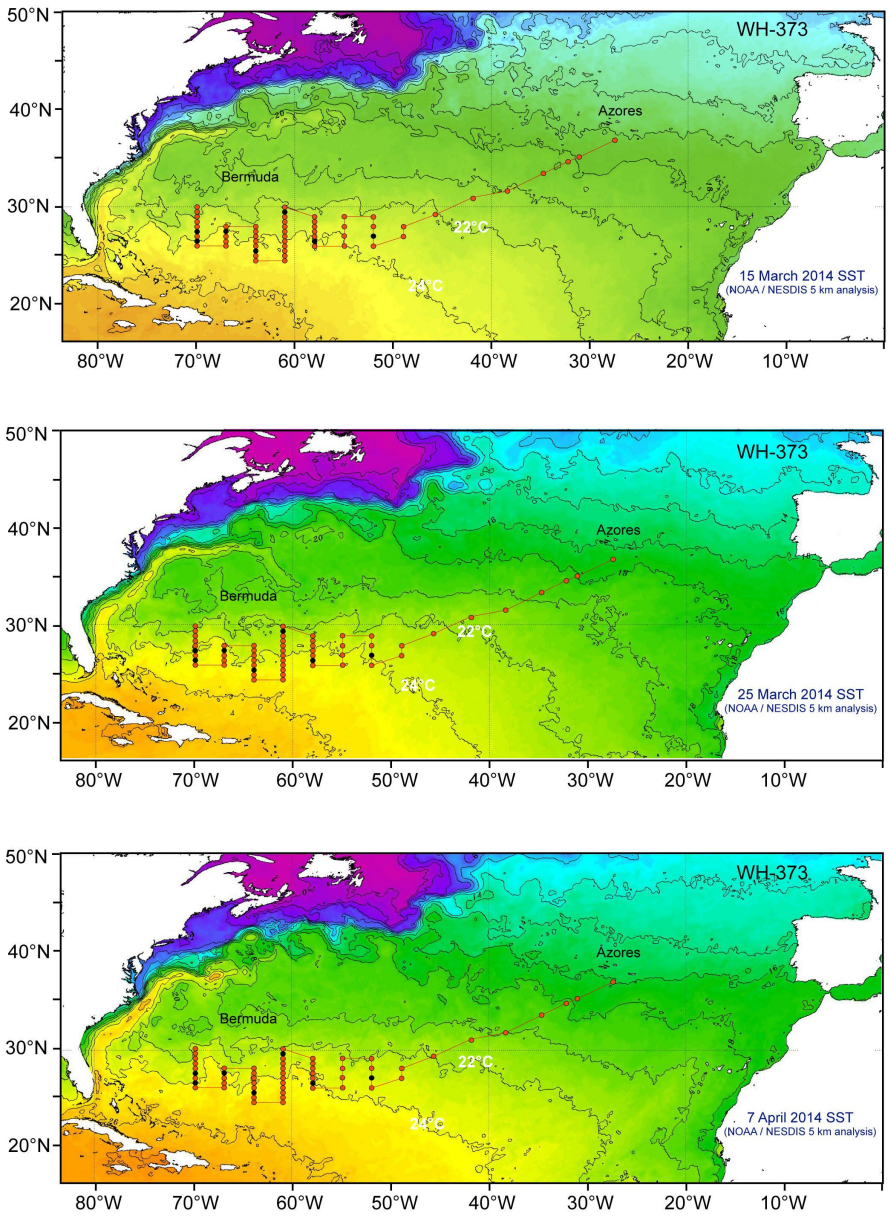


Fig. 15: Oversea surface temperature during WH 373 (generated from the National Oceanic and Atmospheric Administration (NOAA) from the beginning to the end of the survey (15th March 2014, 25th March 2014, 7th April 2014). Dark dots indicate PMT and orange dots IKMT stations. Maps provided by M. Miller, 2015.

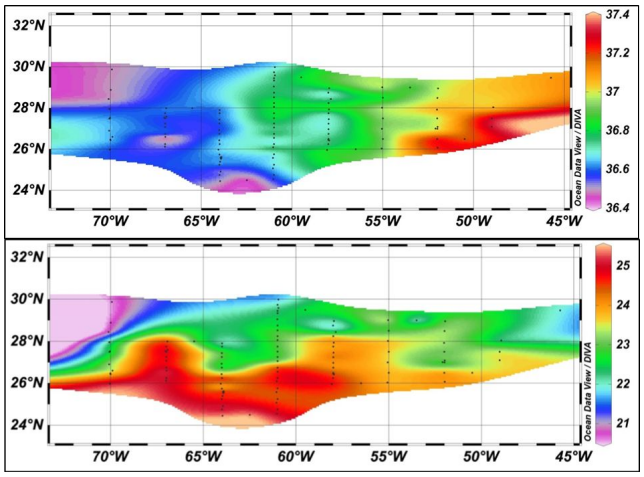


Fig. 16: Graphs interpolating sea surface temperature and salinity from 107 CTD casts of the core study area.

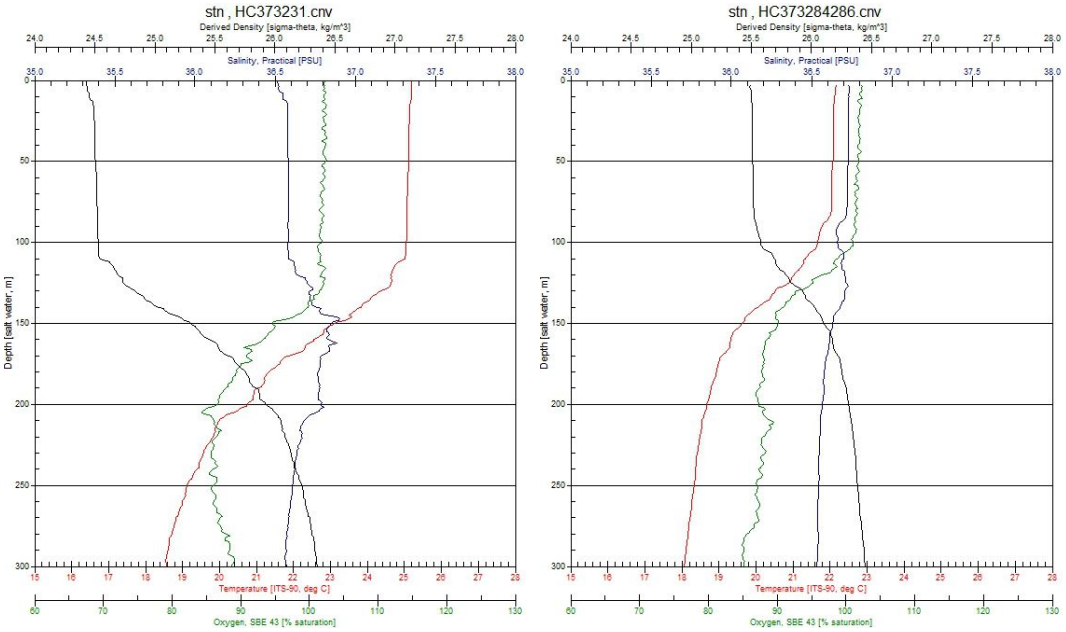


Fig. 17: Depths profiles of temperature, salinity, density and fluorescence for two stations north and south to the STCZ are shown.

3.1.2. Abundance of cephalopods and trawl comparison

During the WH373 cruise, 2,063 cephalopods belonging to 21 families were quantitatively sorted from the catches of all seven pelagic trawls and from 57

out of 65 catches of the IKMT trawls. Most specimens were caught with the IKMT.

Tab. 1: Cephalopods collected by different gear.

Gear	Absolute number of specimens	Sampling Depth	Number of Trawls
IKMT-0.5	1,349	0 - 300 m	57
PMT	714	0-1,000 m	7

3.1.3. Taxonomic composition of catches

Pelagic Midwater Trawl

In total, 714 specimens of 21 species (14 families) were caught with the pelagic midwater trawl (Fig. 18, of which 57%, belonged to the family of the flying squids, Ommastrephidae; 15% of the fire squids, pyroteuthids; 11% belonged to the hooked-squids, Onychoteuthidae; and 8% of the total catch was represented by the combed squid *Chtenopteryx sicula*. 9% of the individuals belonged to the remaining ten families. One deep-sea vampyroteuthid, *Vampyroteuthis infernalis*, was caught during the 1,000 m trawl (Fig.18.

Isaacs-Kidd-Midwater-Trawl
1,349 individuals belonging to at least 36 species (20 families) were sampled using the IKMT (Fig. 18). Mostly teuthoid cephalopods were caught (97%), 3% of the catch was composed of octopods and three sepiid specimens, which could be identified as *Heteroteuthis dispar*. The hugest amount of the collected specimens belonged to the Onychoteuthidae (28%), 15% of the samples were glass squids, Cranchiidae, and 13% of the trawls were composed of enope squids, Enoploteuthidae (Fig.18 .

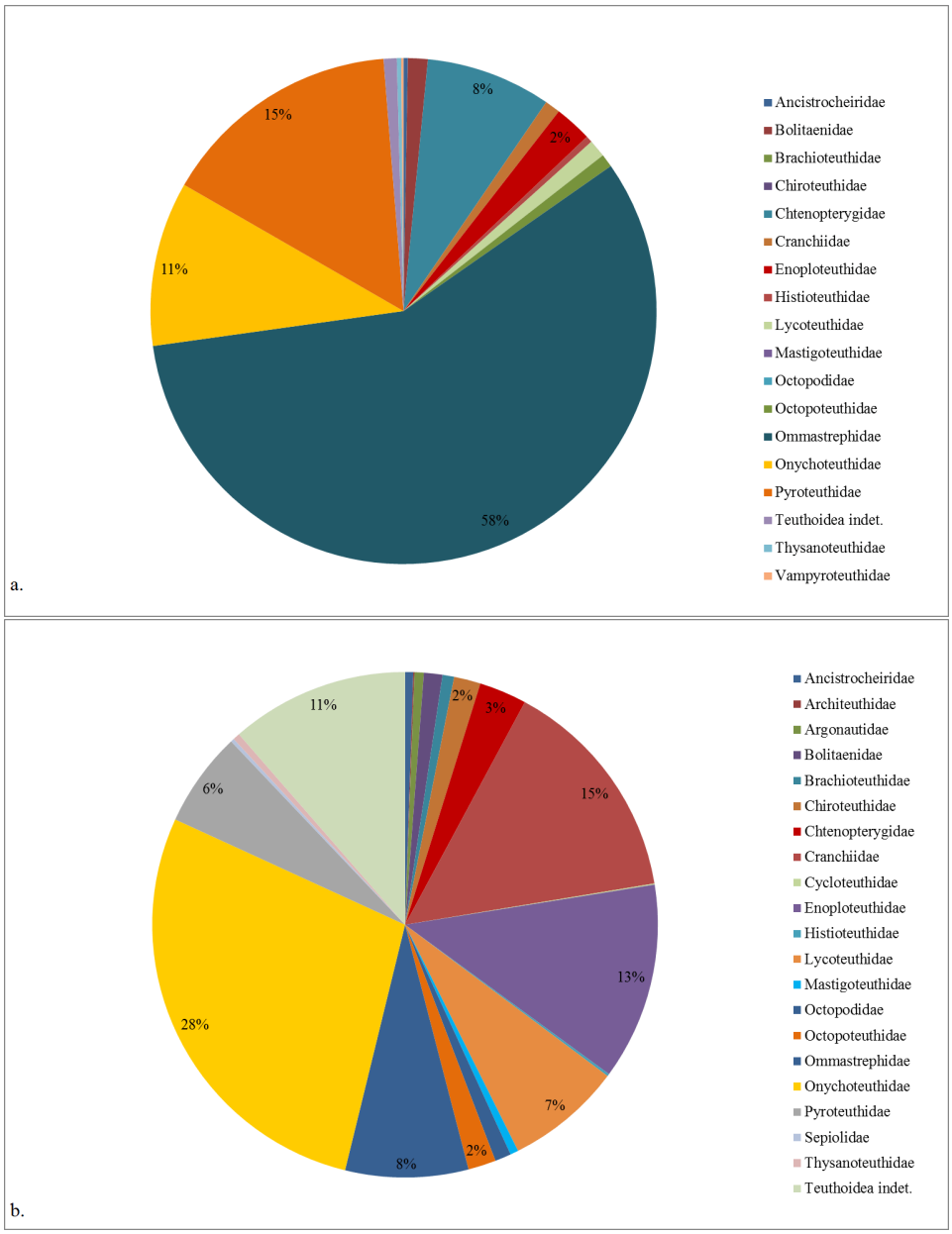


Fig. 18: General composition of cephalopod families of the total catch during WH373 using the PMT (above) and IKMT (below) nets.

Tab. 2: Abundance of collected cephalopods by PMT and IKMT hauls during WH373.

IKMT-0.5				PMT		
Taxon	n	%	size range (mm)	n	%	size range (mm)
Sepiida						
Sepiolidae						
Heteroteuthis dispar	3	0.22	2-8			
Teuthoidea Oegopsida						
Ancistrocheiridae						
Ancistrocheirus sp.	7	0.52	1-15	2	0.28	100-103
Architeuthidae						
Architeuthis dux	1	0.07	2			
Brachioteuthidae						
Brachioteuthis sp.	10	0.74	2-13			
Chiroteuthidae						
Chiroteuthis veranyii	13	0.96	5-50			
Planctoteuthis sp.	10	0.74	3.5-11			
Chtenopterygidae						
Chtenopteryx sicula	41	3.04	1-10	57	7.98	14-50
Cranchiidae						
Bathothauma lyromma	8	0.59	4-15			
Cranchiidae indet.	34	2.52	2.5-5			
Helicocranchia sp.	56	4.15	4-21			
Leachia sp.	64	4.74	4-31			
Liguriella sp.	16	1.19	2-9			
Liocranchia sp.	7	0.52	10			
Megalocranchia oceanica	6	0.44	2-28	7	0.98	24-110
Teuthowenia sp.	5	0.37	6-23			
Cycloteuthidae						
Discoteuthis sp.	1	0.07	15			
Enoploteuthidae						
Abralia veranyi				1	0.14	20
Abralia sp.	1	0.07	10			
Abraliopsis morisii				1	0.14	12
Abraliopsis sp.	67	4.97	1.5-16			
Enoploteuthidae indet.	101	7.49	1-6			
Enoploteuthis anapsis	1	0.07	20	15	2.10	18-69
Histioteuthidae						
Histioteuthis corona corona	1	0.07	17	1	0.14	22
Histioteuthis sp.	1	0.07	2.5	2	0.28	
Lycoteuthidae						
Selenoteuthis scintillans	96	7.12	1.5-13	8	1.12	9-34
Mastigoteuthidae						
Mastigoteuthis sp.	7	0.52	6.5-11			
Octopoteuthidae						
Octopoteuthidae indet.	23	1.7	1.5-4			
Octopoteuthis sicula	1	0.07	9	5	0.7	35-180
Taningia danae	1	0.07	9	1	0.14	80
Ommastrephidae						
Hyaloteuthis pelagica	4	0.3	1.5-3.5	302	42.3	11-70
Illex sp.	4	0.3	1-3			
Ommastrephes batramii				108	15.13	11-84
Ommastrephidae indet.	102	7.56	1-9			
Onychoteuthidae						
Onychoteuthis banksii	337	24.98	3-14	64	8.96	9-51
Onykia carriboea	41	3.04	1.5-13	11	1.54	14-30
Pyroteuthidae						
Pyroteuthidae indet.	3	0.22	4-13			
Pyroteuthis margaritifera	79	5.86	1.5-33	110	15.41	9-39
Thysanoteuthidae						
Thysanoteuthis rhombus	6	0.44	3-5			
Teuthoidea indet.	154	11.42	1-6	6	0.84	24-36
Octopoda						
Argonautidae						
Argonauta argo	8	0.59	2-4	2	0.3	20
Bolitaenidae						
Bolitaenidae indet.	1	0.07	8			
Bolitaena pygmaea	1	0.07	4	1	0.14	17
Japetella diaphana	14	1.04	3-23	8	1.12	18-30
Tremoctopodidae						
Tremoctopus sp.				1	0.14	24
Octopodidae indet.	8	0.59	2-4			
Octopus sp.	6	0.44	2-8			
Vampyroteuthidae						
Vampyroteuthis infernalis				1	0.14	40
Sum		1,349		714		

3.1.4. Species distributions and sizes

Cephalopods of the PMT trawls were sorted out quantitatively from the samples. The five catches to a depth of 300 m were very similar in their faunal composition which is supported by their strong grouping in the MDS plot. Differences in family composition/species assemblage appeared for stations 233 (700 m) and 316 (1,000 m), where Cranchiidae and Enoploteuthidae were more abundant.

Sepiida

Sepiolidae
Heteroteuthis dispar
Three sepiids were caught at station 328 and 329 and could be identified as *Heteroteuthis dispar*, which belong to the Sepiolidae. They were caught with the IKMT and measured 2,3 and 8 mm in DML.

Teuthoidea Oegopsida

Ancistrocheiridae
Ancistrocheirus lesueurii
Two juvenile individuals (DML 100; 103 mm) were caught by the PMT (stations 259; 284) and seven early life stages (DML 1- 15 mm) with the IKMT at transects 4, 5, 6 and at station 323 (27.5°N, 49°W; Table 2).

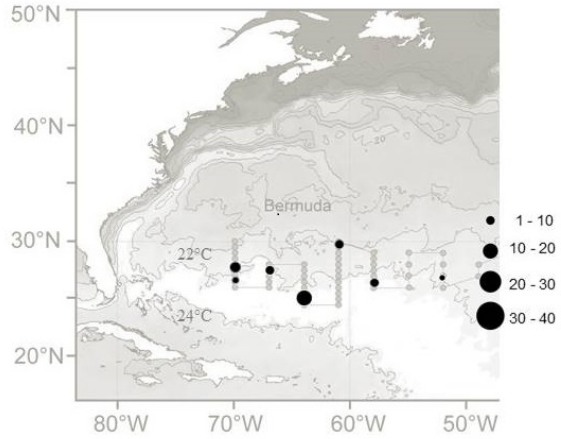
Architeuthidae
Architeuthis dux
One specimen differed significantly from all other specimens that could be allocated to families. It was sampled at station 306 (27°N, 54°W). This animal (DML 2 mm) showed extremely long arms with more than twice the length of the mantle, a pre-stretched head and tentacles which were completely armed with suckers. Provisional identification led to the paralarval stage of the giant squid, *Architeuthis dux*.

Brachioteuthidae
Brachioteuthis sp.
Identification of the Brachioteuthidae was difficult as they resemble early life stages of Mastigoteuthidae and Chiroteuthidae. Ten individuals (2 – 13 mm DML caught by the IKMT were classified as *Brachioteuthis* sp. (Table 2) and appeared at one of the most eastern IKMT stations (station 327; 33.3°N,

34.4°W). Early life stages of this poorly described genus exhibit an extendable neck, numerous proximal tentacular suckers and an elongated, slightly pointed mantle.

Chiroteuthidae
Chiroteuthis veranyi
The planktonic life stages of the chiroteuthids were formerly known as "Doratopsis" larvae and are characterized by an extremely long neck, a short arm crown and long clubs with numerous suckers. Thirteen paralarvae were caught by the IKMT (DML 5 – 50 mm) They were mostly in poor condition but fin shape, head and tentacle morphology were always distinct characteristics for species identification.
Planctoteuthis sp.
Specimens of this genus were not always clear concerning identification but could be distinguished by their fin structure and head shape. 10 individuals were sampled in total from the IKMT hauls (DML 3.5 - 11 mm).

Chtenopterygidae
Chtenopteryx sicula
This species was abundant in the PMT catches where 57 individuals were caught (DML 14 – 50 mm). Additionally, 41 individuals were collected from IKMT hauls (DML 1 - 10 mm, Fig. 19).



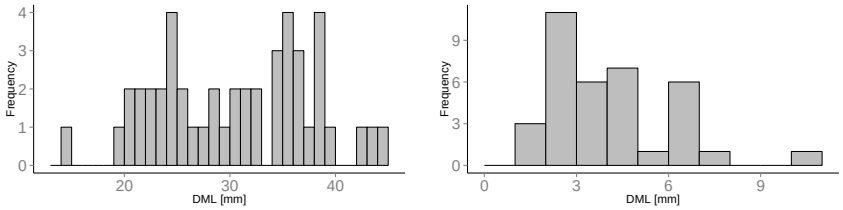


Fig. 19: *Chtenopteryx sicula*. Geographical distribution according PMT catches. Dot size represents range of absolute number of individuals collected. Size histograms according samples witch PMT (left), n= 57, and IKMT (right), n=41.

Cranchiidae
In the PMT trawls, only *Megalocranchia oceanica* specimens (n=7) occurred which were easy to identify due to the complex photophores on the digestive gland. From IKMT samples, at least 7 different species were identified (see Table 2). Thirty-four very small or damaged individuals with no distinct characteristics could only be identified as Cranchiidae indet., (DML 2.5 - 5 mm). The Cranchiidae were distributed throughout the whole study area and the following genera could be differentiated: *Bathothauma lyromma*, *Helicocranchia* sp., *Leachia* sp., *Liguriella* sp., *Liocranchia* sp., *Megalocranchia oceanica* and *Teuthowenia* sp. (Table 2). Most of the Cranchiidae belonged to the genera *Leachia* (n=64) and *Helicocranchia* (n=56).

Cycloteuthidae
Discoteuthis sp.
One possible *Discoteuthis* individual was collected at IKMT station 279 (28°N, 61°W). It exhibited large fins, 4 rows of tentacular club suckers with more than 12 suckers in total which is a distinctive feature in contrast to young life stages of Octopoteuthis . Species identification was endorsed by genetic barcoding (see chapter 3.1.6).

Enoploteuthidae
This family is characterised by their typical photophores on head, eyes?, mantle,arms and tentacles. In total, 170 specimens were sampled from the IKMT trawls with 101 individuals that could only be identified as Enoploteuthidae indet. due to their poor condition or their small size which did not allow a more precise identifications. Striking for the PMT stations was that the major share of Enoploteuthidae (n=14) was caught at station 316 (27°N, 51.5°W) which represented the only station that trawled down to a depth of 1,000 m (see also Table 2).

Abralia sp.
Two specimens of the genera *Abralia* were sorted from the samples, one adult individual (DML= 20) could be clearly identified as *Abralia veranyi* as its fins reached the posterior end of the mantle and it exhibited three club hooks alternating with two series of suckers.
Abraliopsis sp.
The genus *Abraliopsis* is characterised by three enlarged photophores on the distal tips of the fourth arms. Sixty-seven individuals of this genus, ranging between 1.5 and 16 mm DML were collected from the IKMT hauls; one larger specimen (DML 12 mm) that was identified as *Abraliopsis morisii* was caught with the PMT (27°N, 51.5°W).
Enoploteuthis sp.
This genus is recognisable by a tail that extends beyond the fins, two rows of tentacular hooks and usually nine photophores around the eyes. From the PMT trawls, 15 individuals could be identified as *Enoploteuthis anapsis* (DML 18 – 69). The biggest individual was an adult that measured 69 mm and was identified by its tentacular clubs and the continuous lines of photophores on the mantle. In total, 117 specimens contributed to the genus *Enoploteuthis*, the major share within the Enoploteuthidae (Table 2).

Histioteuthidae
These squids are also known as cock-eyed squid because of their enlarged left eye: futher they bear numerous photophores on head, mantle and arms which form characteristic patterns. All three Histioteuthidae collected by the PMT were juveniles. Two of them were in a bad condition that did not allow further species identification. One larger individual of 22 mm mantle length was identified as *H. corona corona*, an endemic species of the Atlantic Ocean that exhibits 17 photophores around the eyelids.

Lycoteuthidae
Selenoteuthis scintillans
From the IKMT trawls, 96 specimens of *Selenoteuthis scintillans* were collected, with a DML ranging from 1.5 to 13 mm. Individuals could be identified by their posterior as well as the intestinal and/or ocular photophores. Eight juvenile specimens derived from the pelagic trawl and measured between 9 and 34 mm in DML. Those specimens were all collected at PMT station 316 which trawled down to 1,000 m.

Mastigoteuthidae
Individuals were characterised by an elongated mantle, more than four rows of club suckers, heart-shaped fins and a posterior protruding spike-like tail. Few specimens of the genus *Mastigoteuthis* (n=7) were collected from the IKMT trawls with DML between 6.5 and 11 mm.

Octopoteuthidae
Octopoteuthidae are easily confused with Ancistrocheiridae at their early life stages as both families exhibit enlarged club suckers, proportionally big eyes and broad fins. Adult specimens exhibit eight arms as they lose their tentacles at the subadult stage which stands for the genus name, *Octopoteuthis*. Identification of early life stages of octopoteuthids was not always clear and genetic barcoding was used to proof correct species identification (see chapter 3.1.6). All Octopoteuthidae were caught until a maximum depth of 300 m and showed no pattern concerning the PMT stations. For 23 individuals, collected from IKMT trawls, identification to species level was not reliable. They were classified as *Octopoteuthidae indet.* (Table 2).

Octopoteuthis sicula
From the pelagic trawls, five *Octopoteuthis sicula* specimens were caught of which two were mature females (DML 140; 180 mm) and one an adult male (DML 115 mm). Arm tip photophores, the absence of tentacles, two light organs on the ventral side of mantle and the ink sac as well as the presence of hooks instead of suckers were clear characters for species identification. One Taningia danae (80 mm) was identified from the pelagic trawl due to the presence of large photophores on the tip of the second arms and the lack of photophores on the tip of the other arms. Another specimen of 9 mm DML was caught with the IKMT. It exhibited a photophore on the ink sac and an unseparated fin musculature.

Ommastrephidae
Early life stages of Ommastrephidae are characterised by fused tentacles (a proboscis) that start to separate around 3 mm of mantle length ("rhynchoteuthion larvae"). This family represented the most abundant taxon of the pelagic trawls (n= 410) and was very common in IKMT catches (n = 110). A relatively large number of early life Ommatrephidae collected with the IKMT (n=102) was not identified, because of their small size that did not show species specific characters (see Table 2).

Hyaloteuthis pelagica

The majority of the Ommastrephidae caught by the PMT were identified as *Hyaloteuthis pelagica*. Specimens exhibited the conspicuous photophore pattern on the ventral side of the mantle (Fig. 20, 21).

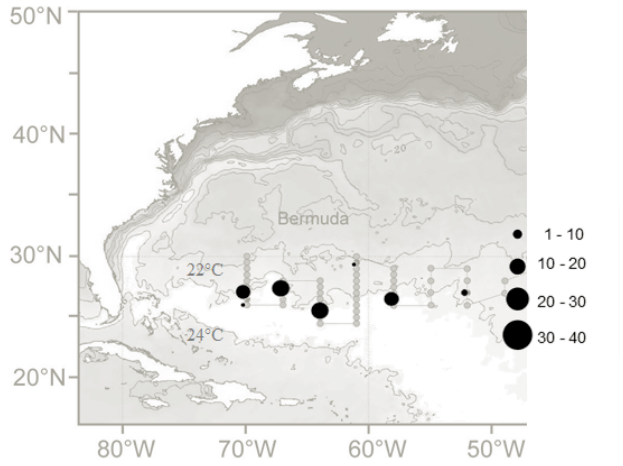


Fig. 20: *Hyaloteuthis pelagica*. Geographical distribution according PMT catches with dot size representing range of absolute number of individuals collected

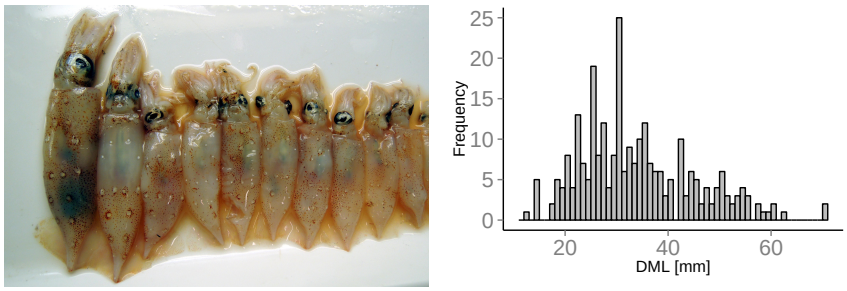


Fig. 21: *Hyaloteuthis pelagica*. Specimens sampled with the PMT at station 228 (27°N' 69.5°W) exhibiting the species characteristic photophore pattern on the ventral mantle side (left), histogram of the dorsal mantle lengths from all PMT samples (n = 302 specimens) (right).

Illex sp.

Four early life stages from IKMT stations were identified as *Illex* sp. with unenlarged lateral suckers and a relatively short proboscis. Identification should be proofed with barcoding.

Ommastrephes bartramii

For the juvenile specimens, identification of *O. bartramii* was distinct due to the absence of photophores and the presence of an opal strip along the ventral side of the mantle. Size range of specimens caught with the PMT was between 11 and 84 mm DML (Fig. 23).

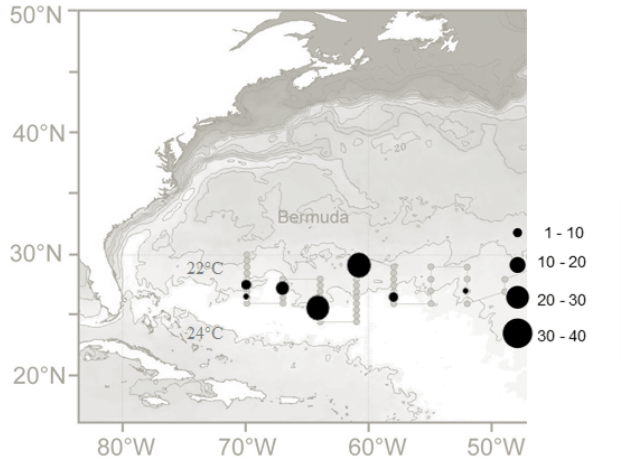


Fig. 22: *Ommastrephes bartramii*. Geographical distribution according PMT catches with dot size representing range of absolute number of individuals collected.

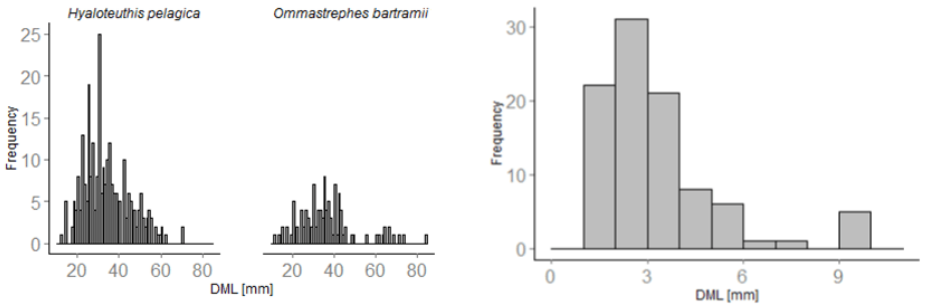


Fig. 23: Ommastrephidae. Histogram of the dorsal mantle lengths of specimens sampled with PMT (left): *Hyaloteuthis pelagica* n= 302, *O.batramii*, n= 108 and IKMT (right): Ommastrephidae total, n=102.

Onychoteuthidae

The hooked-squids represented the most abundant cephalopod group of the

IKMT hauls. Also, referring to the whole samples, they were always in the best condition. Because this family is under revision, species identification still followed the nomenclature of Jereb and Roper (2010). Accordingly, two species were found in the samples, *Onychoteuthis banksii* and *Onykia carriboea*, which were morphologically clearly distinguishable. *O. carriboea* has an unclarified taxonomic status which moreover represents a species complex. Concerning the IKMT samples, 337 individuals between 3 and 44 mm DML were identified as O. banksii as they possessed ocular and intestinal photophores. 41 specimens with a broader mantle, dark dorsal chromatophores could be classified as O. carriboea (DML 1.5 – 13 mm). Sixty-four *O. banksii* and 11 *O. carriboea* specimens were caught by the PMT; one of the *O. carriboea* was an adult female (DML 30 mm) (Table 2, Fig. 24, 25). For underlying the morphological identification, genetic barcoding experiments were performed.

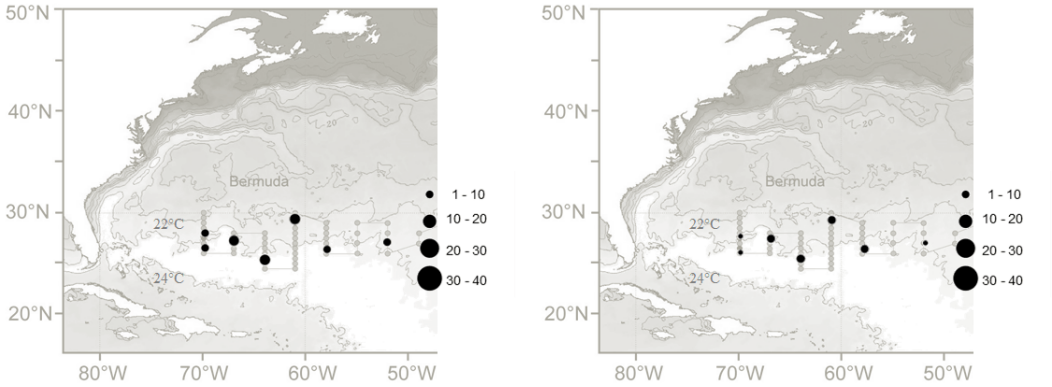


Fig. 24: *Onychoteuthis banksii* (left) and *Onykia carriboea* (right). Geographical distribution according PMT catches with dot size representing range of absolute number of individuals collected.

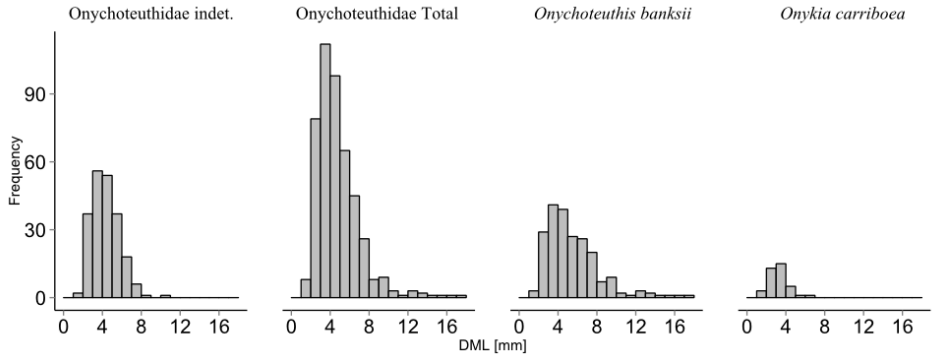


Fig. 25: Onychoteuthidae. Histogram of the dorsal mantle lengths of *Onychoteuthis banksii* and *Onykia carriboea* sampled with PMT (left), n= 337, 41, and IKMT (right), n=64, 11.

Pyroteuthidae

Individuals of the fire-squids are easy to recognize by their conspicuous photophore pattern around the eyes and on the viscera. The tentacular stalks are usually bent in young life stages and allow identification even of very small individuals. The main characteristics for species identification is the relation between the size of anal and gill photophores (smaller in *Pterygioteuthis*, larger in *Pterygioteuthis*) and the occurrence of pink patches at the tentacular base in Pyroteuthis. The Pyroteuthidae were very abundant in the PMT trawls where they made up 15.41 % of the total catch (Table 2). 110 individuals were identified as *Pyroteuthis margaritifera* due to their conspicuous pink patches. The sex of seven individuals could be identified for four adult males (maturity stage: 2-3) and three adult females (maturity stage: 4). The Pyroteuthidae also occurred in relatively high densities in the IKMT samples with 79 *P. margaritifera*and 3, possibly *Pterygioteuthis giardi* individuals which exhibited no tentacular hooks and a different fin shape.

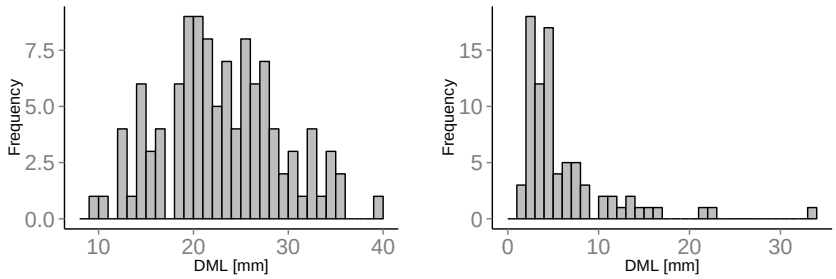


Fig. 26: Pyroteuthidae. Histogram of the dorsal mantle lengths of pyroteuhids sampled with PMT (left), n= 110 and IKMT (right), n=82.

Thysanoteuthidae
Only one species, *Thysanoteuthis rhombus*, is known for this worldwide distributed family, which early life stages exhibit broadly separated eyes, rhomboidal fins and large chromatophore patterns. 6 individuals of this not so common species were collected from the IKMT trawls; they ranged between 3 and 5 mm in dorsal mantle lengths.
Teuthoidea indet.
160 other teuthoid cephalopods were collected with the two nets but their poor condition did not allow further species identification.

Octopoda

Argonautidae
Argonauta argo
This species is also known as the "greater Argonaut", females secrete a calcareous shell and males remain in a "dwarf stage" which is easy to identify because of their hectocotylized arm three which is located in a pouch. From the PMT trawls, one female individual including the shell (DML= 20 mm) and one shell (female, 11 mm) were caught at the first transect (station 224, 228). Further eight individuals were collected from the IKMT trawls which were clearly distinguishable as argonautid males.

Bolitaenidae
Most individuals of this family were identified as *Japetella diaphana*, 14 individuals derived from IKMT and 8 individuals from pelagic trawls. One additional IKMT specimen was identified as *Bolitaena pygmaea* due to its enlarged arm suckers and one individual did not allow further species identification (Bolitaenidae indet.). Barcoding analysis should underline the morphological

differences.
Japetella diaphana
This species was the most abundant of the octopods with 14 individuals from the IKMT and 8 individuals collected from the PMT samples which covered stations from 26- 29°N and 57 to 70°W. Concerning the IKMT stations, individual were sampled from stations up to a maximum of 27.5°N.

Tremoctopodidae
One poorly conserved individual (24 mm DML) from the PMT was identified as *Tremoctopus sp.* due to its very large dorsal arms and the developing hectocotylus pouch beyond the eye.

Octopodidae
8 individuals deriving from IKMT stations could not be further identified to genus level.
Octopus sp.
Six *Octopus* sp. specimens (DML= 2 -8 mm) were collected from the IKMT samples of which further species identification was impossible.

Vampyroteuthidae
Vampyroteuthis infernalis
One individual of the so-called vampire squid was sampled at the unique PMT haul down to 1,000 m. The specimen was in a poor condition but the gelatinous body with the characteristic black pigmentation allowed the identification of the single species within this genus.

3.1.5. Species Richness and relative abundance in relation to Distribution

Cephalopods were collected quantitativly from seven stations trawled with the pelagic net. Trawls were performed down to 300 m except for station 316 (1,000 m) and 233 (700 m). Highest amount of specimens as well as highest species richness were observed at station 284 (29°N, 60.5°W). The highest Margalef's species index was observed at station 316 (27°N, 51.5°W) which was the deepest trawl of the study.
The latitudinal distribution of the family catches along the sampled stations showed a consistent occurrence of cranchiids from 25.3 to 29.3 °N, slightly more ommastrephids were caught at northern latitudes. No Tremoctopodidae individuals were collected at stations below 29.3 ° N (Fig. 27 a). The presence

Tab. 3: Diversity indices for the 7 stations of the pelagic midwater trawl during WH373. Presented are species number (S), specimen number (N), Margalef's species richness (d), Pielou's eveness (J'), Shannon-Wiener-Index (H'(log e), Simpsons Diversity Index (1-Lambda').

Sample	S	N	d	J'	H'(log e)	1-Lambda'
Stn228	7	79	1,373	0,7011	1,364	0,6985
Stn233	4	10	1,303	0,9232	1,28	0,7778
Stn240	7	87	1,344	0,5992	1,166	0,5646
Stn259	8	157	1,384	0,5745	1,195	0,6013
Stn284	11	240	1,825	0,414	0,9926	0,4289
Stn300	6	107	1,07	0,6701	1,201	0,6452
Stn316	9	34	2,269	0,7809	1,716	0,7754

of the different families along the seven transects showed highest specimen numbers of ommastrephids at 60°W, of Chtenopterygidae (*Chtenopteryx sicula*) at 63°W and pyroteuthids at 57°W (Fig. 27 b).

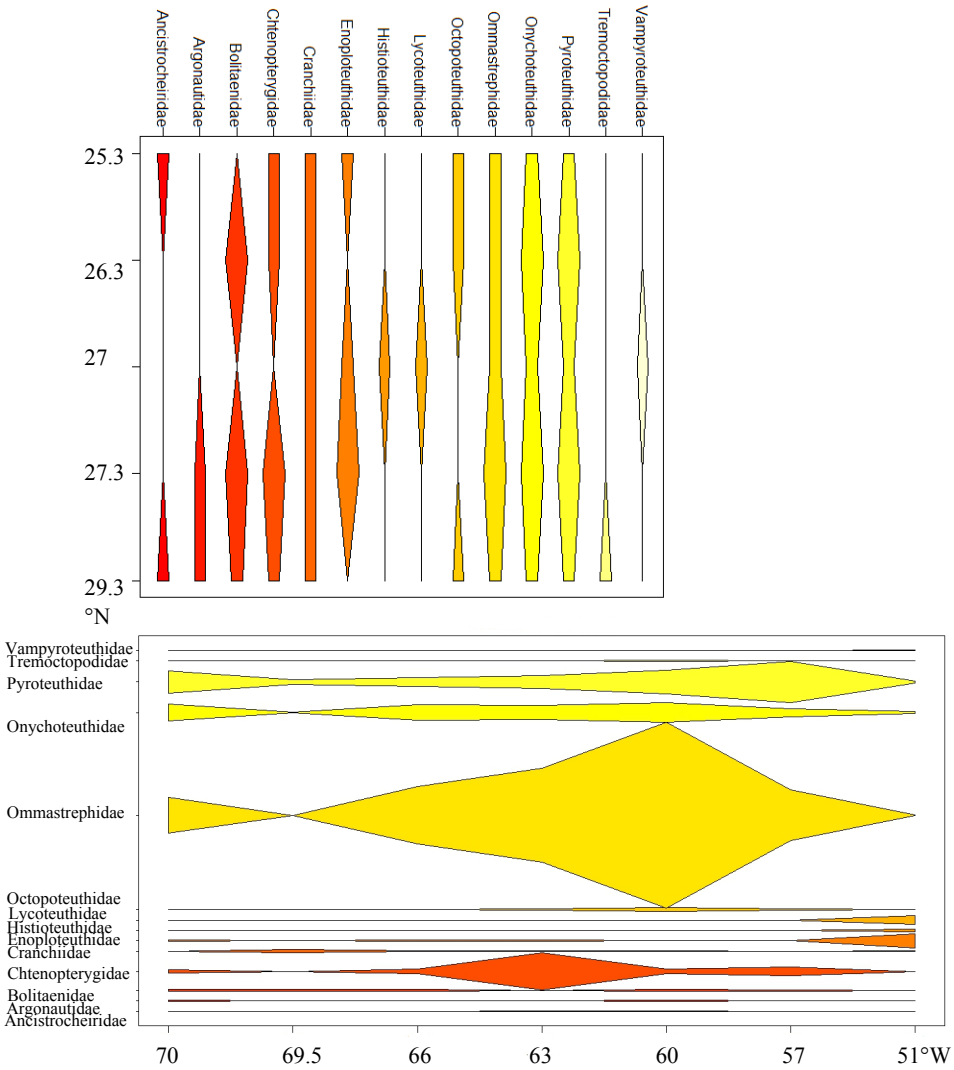


Fig. 27: Kitecharts demonstrating the catch rates of the families according to the latitudinal (top) and longitudinal (bottom) distribution of the seven stations. The width of the kites is proportional to the absolute number of sampled specimens.

3.2. Barcoding

Sequences were obtained for 33 of 42 specimens. For 17 individuals only one DNA strand could be successfully sequenced even if several attempts were performed.

Tab. 4: Summary of sequenced specimens compared to sequences available in GenBank using BLAST. "f" significates forward and "r" reverse primers.

Specimen No	Coordinates	DML	Net	Provisional species identification	(ident) Highest Consensus	Primer
31	27°N, 67°W	47	PMT	*Onychoteuthis banksii*	88% *Onychoteuthis* sp. borealijaponicus	f+r
33	27°N, 67°W	37	PMT	*Ommastrephes bartrami*	100 % *Ommastrephes batramii*	f
40	27°N, 67°W		PMT	*Japetella diaphana*	99 % *Japetella diaphana*	f
45	26°N, 58°W	60	PMT	*Hyaloteuthis pelagica*	98% *Hyaloteuthis pelagica*	f+r
50	26°N, 58°W	28	PMT	*Pyroteuthis margaritifera*	100% *Pyroteuthis margaritifera*	f+r
107	27°N, 70°W	22	PMT	*Onychoteuthis banksii*	88% Onychoteuthis borealjaponicus	f+r
197	27°N, 52°W		PMT	*Vampyroteuthis infernalis*	100% *Vampyroteuthis infernalis*	r
200	27°N, 52°W	9	PMT	*Selenoteuthis scintillans*	87% *Onychoteuthis banksii*	f
222	27°N, 52°W	45	PMT	*Megalocranchia oceanica*	88% *Onychoteuthis banksii*	f
231	29°N, 61°W	66	PMT	*Ommastrephes bartrami*	91 % *Ommastrephes bartramii*	f
262	29°N, 61°W	17	PMT	*Onykia carriboea*	99% *Pareledone* sp.	f+r
266	25°N, 64°W	30	PMT	*Ommastrephes bartrami*	91% *Ommastrephes batramii*	f+r
482	26°N, 64°W	11	PMT	*Onychoteuthis banksii*	89% *Onychoteuthis borealijaponicus*	f+r
483	26°N, 64°W	8	PMT	*Onychoteuthis banksii*	87% *Onychoteuthis* sp.	f+r
598	27°N, 55°W		PMT	*Architeuthis dux*	91% *Abraliopsis pfefferi*	f+r
601	27°N, 55°W	6	PMT	*Onykia carriboea*	88% *Onychoteuthis banksii*	f+r
846	26°N, 55°W	4	PMT	*Octopoteuthis* indet.	99% *Enoploteuthis leptura*	f
899	26°N, 61°W	4	PMT	Ommastrephidae indet.	98% *Hyaloteuthis pelagica*	f
1050	27°N, 49°W	3	IKMT	Onychoteuthidae indet.	88% *Onychoteuthis* sp.	f
1055	28°N, 61°W	15	IKMT	*Discoteuthis* sp.	90% *Octopoteuthis deletron*	f+r
1070	26°N, 70°W	11	IKMT	Onychoteuthidae indet.	98% *Hyaloteuthis pelagica*	f+r
1093	26°N, 70°W	2,5	IKMT	*Onykia carriboea*	88% *Moroteuthis* sp.	f
1169	28°N, 64°W	12	IKMT	Onychoteuthidae indet.	98% *Hyaloteuthis pelagica*	f
1192	27°N, 64°W	2	IKMT	*Ommastrephes batramii*	98% *Hyaloteuthis pelagica*	f
1275	33°N, 34°W	6	IKMT	*Japetella diaphana*	99% *Japetella diaphana*	f
1254	33° N, 34°W	4	IKMT	*Bathothauma lyromma*	97% *Helicocranchia* sp.	f+r
1267	26°N, 67°W	1,5	IKMT	*Hyaloteuthis pelagica*	98% *Hyaloteuthis pelagica*	r
1441	29°N, 61°W	3	IKMT	*Ancistrocheirus lesueuri*	99% *Enoploteuthis leptura*	f
1564	28°N, 60°W	1,5	IKMT	*Octopus* sp.	97% *Argonauta nodosa*	f
1568	28°N, 60°W	2	IKMT	Ommastrephidae indet.	97% *Hyaloteuthis pelagica*	f+r
1796	24°N, 61°W	1	IKMT	*Illex* sp.	99% *Hyaloteuthis pelagica*	r
*	29°N, 45°W	3	IKMT	Teuthoidea indet.	99% *Chiroteuthis veranyi*	f+r
Lea	29°N, 52°W		IKMT	*Leachia lemur*	100% *Leachia lemur*	f+r

The 33 aligned 536 bp fragments showed 147 variable sites and a total number of 236 mutations among sequences. The overall GC content was 0.36, 19 haplotypes were observed with a diversity of 0.922 (variance 0.001, standard deviation 0.033) and the nucleotide diversity (per site) Pi was 0.15074 (sampling variance 0.00007, standard deviation 0.00859). An average number of nucleotide differences of 55.01894 was calculated. No insertions, deletions or stop codons were observed in any sequence.

Comparison between phylogenetic trees

All three trees were consistent in grouping *Octopoteuthis* and *Ancistrocheirus*, the two *Japetella* specimens (040, 1275), *Ommastrephes* 033, 231, 266 as well as the *Onychoteuthis* 107, 1050, 482, 483 as distinct clusters. Type specimens "Stern" and "Leachia" formed a cluster in the ML whereas "Stern" built a clade with Archi598 in the NJ tree. Archi598 formed a single branch in the BI tree where Stern also built a single clade (100 % posterior probability). For all trees, *Vampyroteuhis infernalis* was chosen as the out-group, to which Octopus1564 formed the nearest clade.

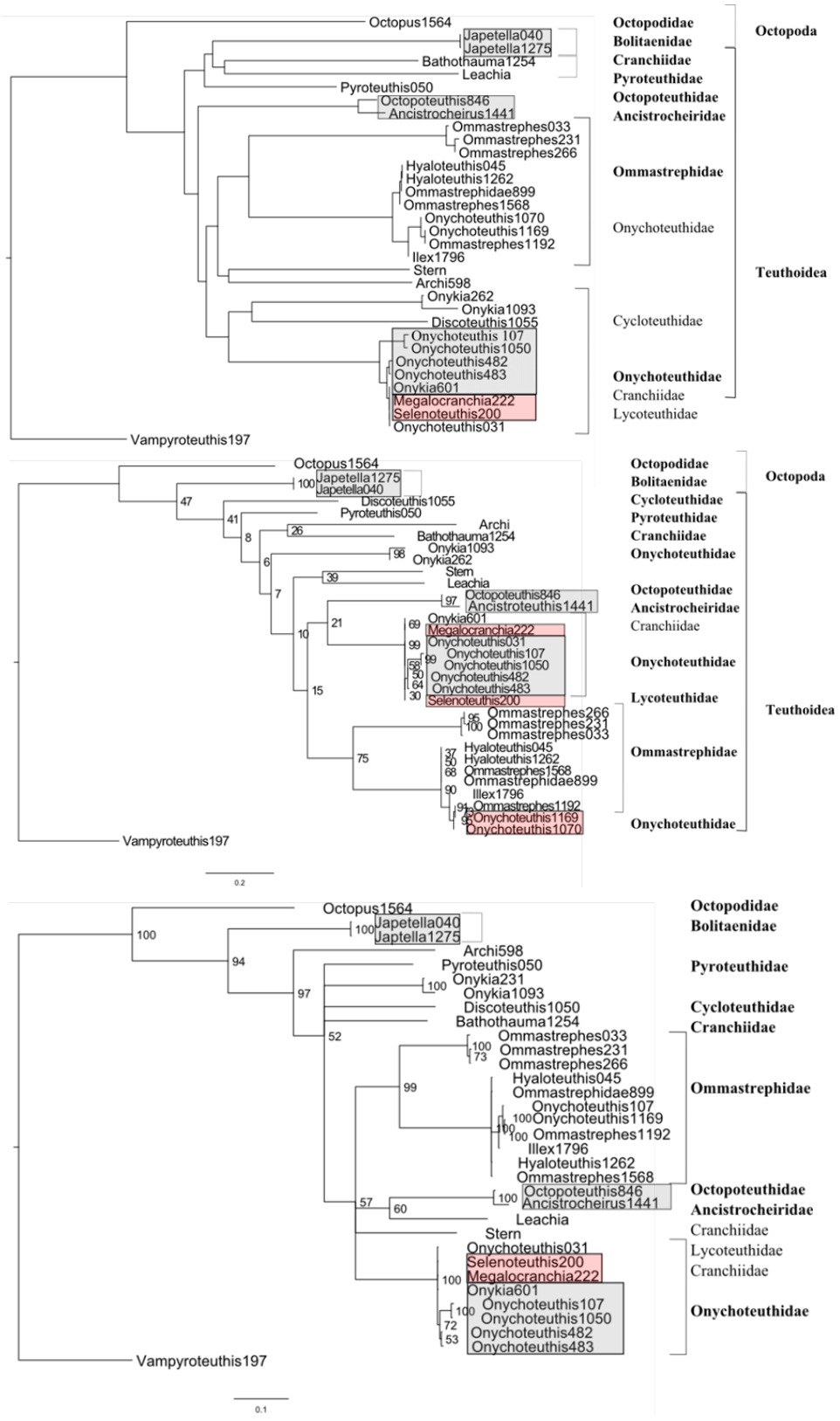


Fig. 28: Phylogenetic trees based on the COI gene locus of 33 cephalopod specimens, using neighbour-joining (NJ), maximum likelihood (ML, with bootstrap support) and Bayesian inference methods (node labels are posterior probabilities). The green areas represent congruent clades appearing in all three analyses. Red areas show specimens of different families that were grouped into another family clade. *Vampyroteuthis infernalis* was chosen as the out-group.

Vampyroteuthis infernalis was chosen as the out-group for the phylogenetic trees because it belongs to the Octopodiformes, the sister clade of the Decapodiformes, which diverged early from the remaining taxa (Lindgren, 2010; R. E. Young and Vecchione, 2002). Concerning the octopods, Octopus 1564 was closely grouped with *Vampyroteuthis* in all trees. Blast results for *Vampyroteuthis* showed 100% consensus with a *V. infernalis* sequence in GenBank (Accession: GU145059), which derived from an individual also caught in the Sargasso Sea. Blasting of Octopus 1564, identified as *Octopus* sp., resulted in 97% consensus with *Argonauta nodosus*, an octopus also known as pearl boat, but this species is only distributed in the southern hemisphere. Therefore, the compared sequence in GenBank does not represent a reliable match for the provisional identification.

The Ommastrephidae appeared in the phylogenetic trees as one branch, with high bootstrap support for the ML method (75%) and a high posterior probability for the Bayesian tree (99%). This branch included all morphologically identified ommastrephids and two further onychoteuthids (1070, 1169). As *Ommastrephes* 033, 231 and 266 always derived from one node, this strongly hints that the specimens belong to the same species, *Ommastrephes batramii*, which was also in accordance to the morphological identification. Nevertheless, as this genus is in general need for revision, it cannot be excluded that more than one species was present. It is very unlikely that the two onychoteuthids included in the branch were misidentified as they showed distinct morphological characteristics. Although the highest genetic similarity obtained by blasting against GenBank resulted in 98% identity with *Hyaloteuthis pelagica*, they did not exhibit any photophores, which should be visible at a dorsal mantle length of >=10 mm in *H. pelagica* (the individuals already measured 11 and 12 mm). Furthermore, they differed from *H. pelagica* or other ommastrephids by the whole habitus, especially by exhibiting a protruding spine between the fins.

Concerning the other onychoteuthids, for *Onykia* 494 no clean sequence was recovered. The individual identified as *Onykia* 231 formed a clade with the early life stage *Onykia* 1093, which strongly indicates that those individuals belong to the same species (complex) and are distinct from the other onychoteuthids. Nevertheless,*Onykia* 601 formed a different cluster with the other onychoteuthids, which might be due to misidentification. The result from blasting for *Onykia* 1093, matching to 99% with *Eledone sp.* (best hit), should represent a reliable match but seems rather unlikely as *Eledone sp.* is a benthic octopod genus, which, besides its distinct morphological traits, inhabits coastal waters. Only Onykia1093 corresponded to 88% with an individual that was identified as *Moroteuthis*, the former genus name for *Onykia*. Even if this match is very weak and does not proof the identification of the two *Onykia*

specimens, it might support accurate species identification. In comparing the specimen's sequence to sequences available in GenBank individual 601 best matches with *Onychoteuthis banksii*, although with a low identity of 88%, which is not a reliable percentage for species identification, but might explain the grouping of this individual with other onychoteuthids rather than building a distinct cluster with the two *Onykia* specimens. The incoherent grouping and blasting of the Onykia specimens reflect its controversial taxonomic status. Nevertheless, except for individual 601, the other two specimens formed a distinct clade compared to the other onychoteuthids, supporting the presence of two distinct lineages. Concerning the BLAST results, especially for the cranchiids, *Bathothauma lyromma*, *Megalocranchia oceanica* and *Liguriella* sp. no sequences were available for comparison in GenBank.
The possible *Architeuthis dux* individual, Archi 598, was grouped with the cranchiid *Bathothauma lyromma* in the ML analysis tree with a bootstrap support of only 26%. The Bayesian tree did not recover this clade but placed it separately from the other individuals (97% posterior probability). The different grouping of this individual within the phylogenetic trees as well as the molecular data suggests its particular lineage already indicated by its morphological identification. However, the provisional identification could not be proofed by BLAST results with an unreliable best hit of 91% sequence consensus with the enoploteuthid, *Abraliopsis pfefferi*. Inferred from its distinct morphological features and particular grouping, it cannot be excluded that the individual represents an early life stage of the giant squid.
What remains unclear is that the three cranchiids, *Leachia*, *Megalocranchia* and *Bathothauma*, do not form a consistent clade in the trees. Only in the neighbour-joining tree, *Leachia* and *Bathothauma* are sharing one branch. It could be that the COI loci are inappropriate for presenting divisions in genera within the family of the Cranchiidae. Specimen "Stern" was sampled from one of the most eastern stations (29°N, 45°W) of the WH373 expedition and appears in the phylogenetic trees rather isolated which is coherent with its morphological features, which lead to a provisional identification as a chiroteuthid squid. BLAST results showed a 99% consensus with *Chiroteuthis veranyi* (accession number: AY557529.1), which strongly hints that this specimen represents a species of the genus Chiroteuthidae. Cranchiidae and Chiroteuthidae are closely related families of the order Oegopsida, which have recently been comprised as chiroteuthid squids (Lindgren et al. 2010). Stern and *Leachia* sp. form a clade in the maximum-likelihood tree with a low bootstrap support of 39%. In the Bayesian tree, "Stern" builds a single branch with 100% posterior probability. The phylogenetic position of the "Stern" specimen remains unclear whereas the identification as *Chiroteuthis veranyii* is relatively robust. Consistent was that

all trees constructed single clades for the Bolitaenidae specimens as well as for the only pyroteuthid, *Pyroteuthis margaritifera*.

3.3. Maria Merian 41

3.3.1. Hydrography

Within the study area of the subtropical convergence zone, two temperature fronts were measured. The northern front, around 30°N, was marked with a surface temperature of 22°C, the southern front (approx. 27°N), exhibited a surface temperature of about 24°C. The maximum sea surface temperature of 26.55°C was measured at station 27 (30°N, 23.5°W). The lowest sea surface temperature, 20.82°C, was measured at station 39. Surface salinity was always around 36 PSU with little variation. The highest salinity was measured at station 42 (30°N, 30°W) with 36.86 PSU and the lowest at station 28 (30°N, 23°W) with 36.13 PSU. During the cruise the thermal front moved in a northwards direction (Fig. 29).
Data collected from CTD sampling showed that the five transects were comparable in temperature and salinity values below 300 m. Concerning the upper 300 m, different temperature and salinity gradients were observed. Fluorescence was also measured but reliable data could only be obtained from station 22 to 49. A shift in fluorescence was there observed between 100 to 200 m (Fig. 30 up from station 23).

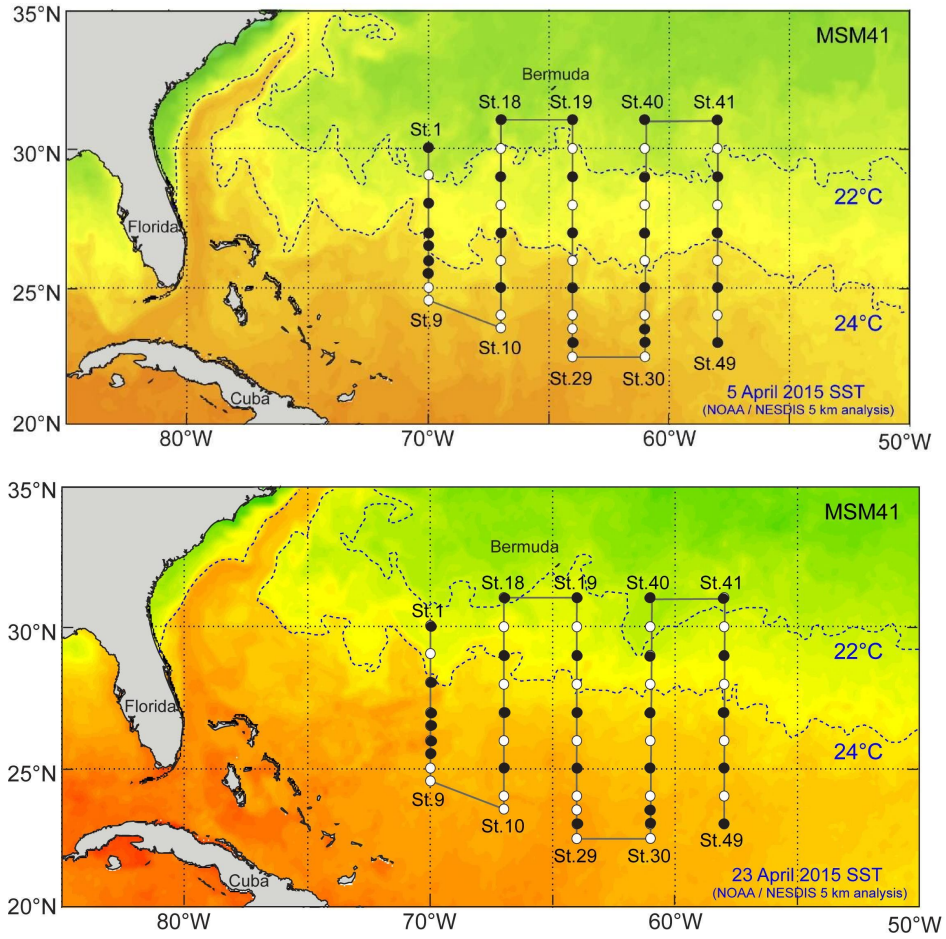


Fig. 29: The maps show the sea surface temperature (generated from the National Oceanic and Atmospheric Administration (NOAA) at the beginning, 5th April 2015, and the end, 23rd April 2015, of the cruise. Night howls are indicated by dark and day howls by white dots. Maps provided by M. Miller, 2015.

Tab. 5: Cephalopods of the MSM41 cruise, collected by different gear.

Gear	Absolute number of specimens	Sampling Depth (m)	Number of trawls	Mesh size [mm]
IKMT-0.5	2,406	0 - 300	49	0.5
IKMT-5	57	0 - 1,000	10	5
Manta trawl	10	Surface (0- 0.2)	32	0.33
MOCNESS	14	0- 1,000	23	0.33 - 2

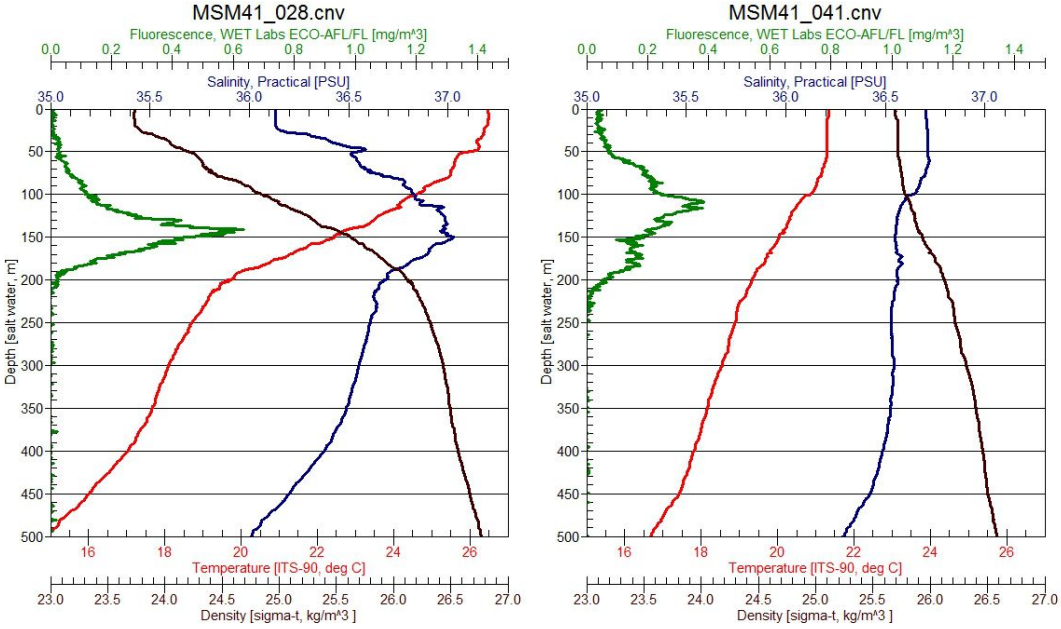


Fig. 30: Depicted are temperature, salinity, density and fluorescence measurements for one station north and one south to the SCTZ.

3.3.2. Abundance of cephalopods and Trawl comparison

During the MSM 41 cruise, 2,487 cephalopods belonging to 18 different families were collected. Specimens from all nets were sampled and allowed quantitative analysis (5).
Most of the paralarvae, 2,406 of 2,487 specimens, were caught using the IKMT with a mesh size of 0.5 mm. Larger and fewer specimens were caught using the wide-meshed IKMT (IK-5). Most possibly, because smaller specimens might have passed through the net and only fewer, larger individuals remained. Individuals from the MOCNESS trawls were always in a perfect condition but

sampling rate was quite low which might relate to the smaller water volume filtered by the nets. The poorest catching rate concerning cephalopods showed the Multi-Net (MSNV) which caught no specimens.

3.3.3. Taxonomic composition / Systematics and Distribution

Following, only paralarval cephalopods caught with the IKMT- 0.5 will be further analysed due to the small number of individuals caught by other gear. The mean density was 8.73 individuals per $10m^3$ m^3 and mean species richness $2.18/10^3$ m^3. 98.75% of the collected cephalopods belonged to the order Teuthoidea (squids), the remaining 1.25% were octopod cephalopods. The most abundant taxon was the family of the Onychoteuthidae, comprising 19.49% of the paralarvae which was followed by the Ommastrephidae (16.33%) and the Cranchiidae (16.21 %). Other abundant families were the Pyroteuthidae (10.72%), Enoploteuthidae (8.94%) and Lycoteuthidae (6.57%). Only parlarvae that allowed an appropriate identification were analysed. Therefore, 9.94% of the paralarvae could only be identified as Teuthoidea indet. because of their poor conditions. The contribution of other families to the total amount ranged between 0.25 and 2.95% Less abundant families were the Thysanoteuthidae with only six recordings of *Thysanoteuthis rhombus* and Vitreeledonellidae with a single recording of *Vitreledonella richardii*. Concerning the octopods, 22 of 30 collected individuals were identified as *Japetella diaphana* (Fig. 31).

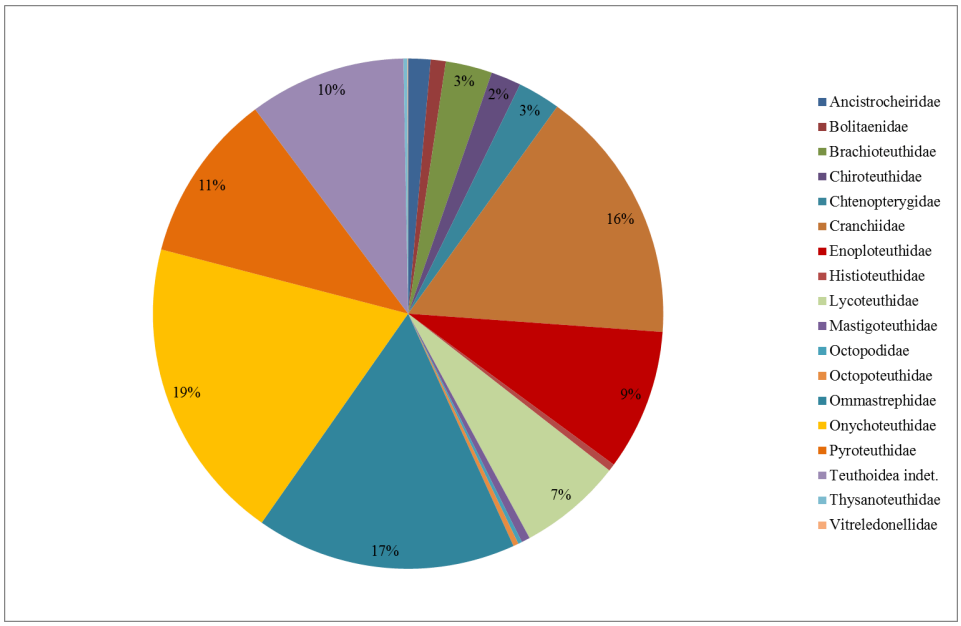


Fig. 31: General composition of cephalopod families of the total catch during MSM41.

3.3.4. Species distributions and morphometrics

Following, characters for identification of the collected species as well as their distribution along the station grid are described. Species tables are represented in the appendix, Fig. 32 gives an overview of a typical cephalopod community sample.

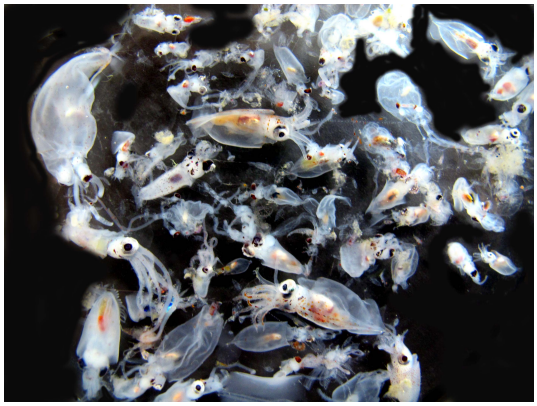


Fig. 32: Typical cephalopod community of a sampled station from petri dish.

Tab. 6: Species table of the specimens collected during MSM 41.

	IK-0.5				IK-5				MOCNESS			
Taxon	n	n/ 10^3m^3	%	size range (mm)	n	n/ 10^3m^3	%	size range (mm)	n	n/ 10^3m^3	%	size range (mm)
Teuthoidea Oegopsida												
Ancistrocheiridae												
Ancistrocheirus sp.	34	0.12	1.4	2-5								
Brachioteuthidae												
Brachioteuthis sp.	71	0.25	2.9	1-19								
Chiroteuthidae												
Chiroteuthis veranyii	32	0.11	1.33	2.5-30					1	0.1	7.14	22
Planctoteuthis sp.	14	0.05	0.58	6-17					1	0.1	7.14	12
Chtenopterygidae												
Chtenopteryx sicula	66	0.23	2.74	1-22	1	0.005	1.67	9	1	0.1	7.14	7
Cranchiidae												
Bathothauma lyromma	14	0.05	0.58	4-29								
Cranchiidae indet.	15	0.05	0.62	2-7								
Helicocranchia pfefferi	109	0.39	4.53	2-22	1	0.005	1. 67	6	3	2.99	21.43	
Helicocranchia sp.	227	0.8	9.43	1-19								
Leachia sp.	22	0.08	0.91	2-33	7	0.037	11.67	23-45				
Liguriella sp.	3	0.01	0.12	10-13								
Megalocranchia oceanica	1	0.0035	0.04	4								
Enoploteuthidae												
Abraliopsis pfefferi	46	0.16	1.9	2-28	2	0.01	3.34	7-32	2	1.99	14.28	4-6.5
Abraliopsis sp.	29	0.1	1.2	2-28								
Enoploteuthidae	125	0.4	5.19	1-6					1	0.1	7.14	4.5
Enoploteuthis sp.	15	0.05	0,62	2-8	1	0.005	1, 67					
Histioteuthidae												
Histioteuthidae indet.	11	0.04	0,46	2,5-5								
Lepidoteuthidae												
Lepidoteuthis grimaldii	0	0	0		1	0.005	1. 67	5				
Lycoteuthidae												
Lycoteuthidae indet.	121	0.43	5.03	1-7								
Selenoteuthis scintillans	37	0.13	1.54	2-13	3	0.016	5	6-17				
Mastigoteuthidae												
Mastigoteuthis sp.	13	0.05	0.54	4-25	1	0.005	1. 67	22				
Octopoteuthidae												
Octopoteuthidae indet	5	0.02	0.21	4-5	2	0.01	3.34	8-10				
Octopoteuthis sp.	3	0.01	0.12	2-8.1								
Ommastrephidae												
Hyaloteuthis pelagica	126	0.45	5.24	1-11					2	1.99	11.11	6
Ommastrephes batramii	43	0.15	1.79	1.5-11.5								
Ommastrephidae indet.	228	0.81	9.48	1-5								
Onychoteuthidae												
Onychoteuthidae indet.	212	0.75	8.81	1-10	1	0.005	1. 67	6				
Onychoteuthis banksii	214	0.71	8.89	1.5-17	7	0.04	11.67	7-20	3	2.99	16.67	5-12.5
Onykia carriboea	39	0.14	1.62	1.5-6								
Pyroteuthidae												
Pyroteuthidae indet.	153	0.54	6.36	1-6	1	0.005	1. 67	9				
Pyroteuthis margaritifera	105	0.37	4.36	1-20	25	0.13	41.67	2.5-31	4	3.99	22.23	3-7
Thysanoteuthidae												
Thysanoteuthis rhombus	6	0.02	0.25	3-8								
Teuthoidea indet.	239	0.85	9.93	1-20	3	0.016	5	1 - 11				
Octopoda												
Bolitaenidae												
Japetella diaphana	21	0.074	0.87	2.5-11	4	0.021	6.67	7-35				
Vitreledonellidae												
Vitreeledonella richardi	1	0.003	0.041	30								
Octopus sp.	6	0.02	0.25	2-5								
Sum	2,406				60				18			

Teuthoidea Oegopsida

Ancistrocheiridae
Ancistrocheirus lesueurii
Ancistrocheirus lesueurii specimens were most abundant at transects 5 and 3, only two individuals could be identified at the first two transects (Fig. 33).

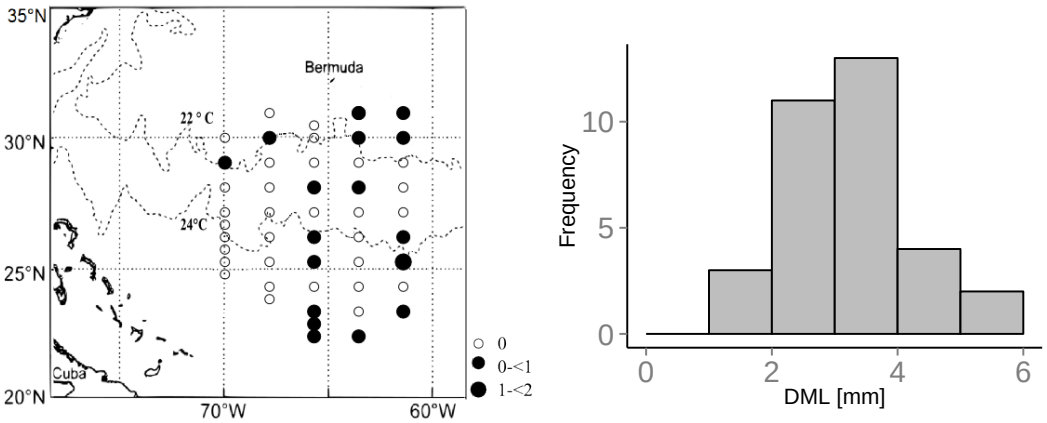


Fig. 33: *Ancistrocheirus* sp.. Distribution of individuals according to the station grid and histogram of the dorsal mantle lengths. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances are represented according to the amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Brachioteuthidae
Brachioteuthis sp. In total, 71 individuals ranging from 1-19 mm in dorsal mantle length were caught with the IKMT-0.5. Problems in identification existed due to similarity with mastigoteuthids and chiroteuthids as well as damaged posterior mantle parts of single individuals.

Chiroteuthidae
Chiroteuthis veranyii
31 specimens were caught with the IKMT-0.5 ranging from 2.5 to 30 mm in mantle length and a single individual of 32 mm DML derived from the MOCNESS (125 - 0 m depth).

Planctoteuthis sp.
Specimens of this type genus were characterized by a usually broken, longer spine than *Brachioteuthis spp.* individuals. 14 individuals were caught using

the IKMT-0.5 ranging from 6- 17 mm in DML, one additional specimen was caught by the IKMT-5 with a DML of 12 mm. Morphological differences between individuals were detected which might hint that more than one species was presented for this family. A single individual of 14 mm DML was caught with the MOCNESS (250 – 125 m depth).

Chtenopterygidae
Chtenopteryx sicula
One single species was identified for this family of which 66 specimens between 1 - 22 mm DML were caught. The rayed fins and the distinct tentacular pads simplify identification of even very small individuals. One individual (DML= 7 mm) was collected from 375-250 m depth with the MOCNESS net another individual (DML=9 mm) with the IKMT-5. Most *C. sicula* individuals were identified at transects 4 and 5, general abundance of this species was low, and most specimens exhibited mantle lengths between 2 to 4 mm (Fig. 34).

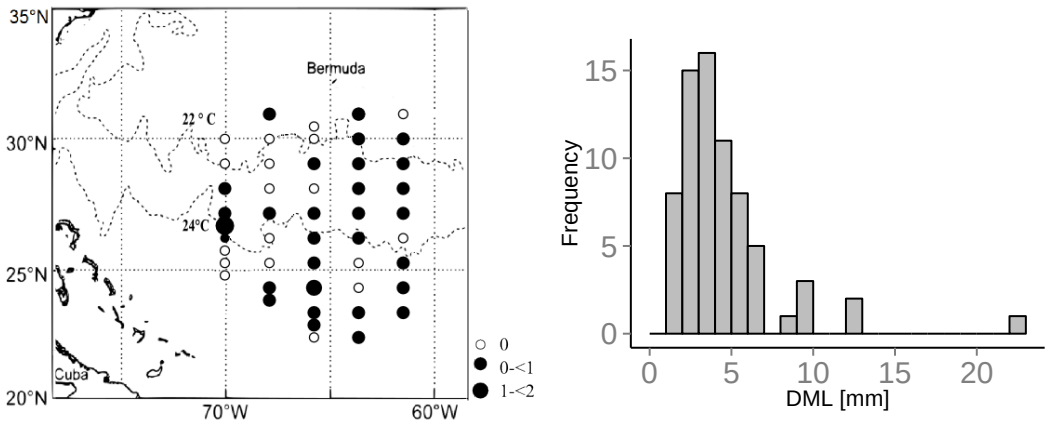


Fig. 34: *Chtenopteryx sicula*. Distribution of individuals according to the station grid and histogram of the dorsal mantle lengths. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Cranchiidae
At least 6 different species of cranchiid squids could be identified. 15 very small or damaged individuals with no distinct characteristics were only described as *Cranchiidae indet.*, occurring in a size range between 2-7 mm DML (Fig. 35).

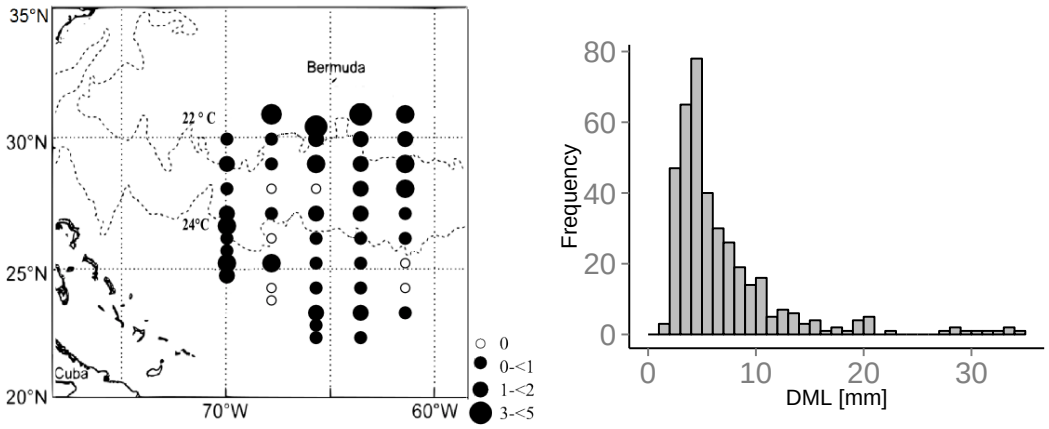


Fig. 35: Cranchiidae. Distribution according to the station grid and histogram of the dorsal mantle lengths. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Cranchiids were distributed throughout the whole sampling area and showed the highest frequencies at transects 4 and 5. The most abundant genus was represented by *Helicocranchia sp.* which was present at nearly each sampling location, whereas the genus *Leachia* only occurred at the northern stations and was absent from stations below 26°N. All cranchiid species taken together showed a higher abundance at the northern (20% of the total catch) than at the southern stations (10%). Southern stations were defined as stations below 27°N.

Bathothauma lyromma
14 specimens of this species usually ranging between 4 and 10 mm were described. The largest individual exhibited a mantle length of 29 mm and had very distinct long eye stalks, a short arm crown and paddle-shaped fins. Smaller individuals could be distinguished from other cranchiids by their gelatinous long eye stalks.

Helicocranchia sp.
This genus probably comprises more than 11 undescribed species (Voss et al., 1992). 340 individuals of this genus were caught with the IKMT-0.5 (n=336), the IKMT-5 (n=1), and the MOCNESS (n=3, 125 – 0 m depth). By a dorsal mantle length of 10 mm, except for very damaged individuals, specimens could be clearly identified as *Helicocranchia pfefferi* (n= 109, 2-22 mm DML). 227 specimens were identified as *Helicocranchia* sp. ranging between 1 and 19 mm

(Fig. 36). *Helicocranchia* individuals exhibit a very broad funnel, paddle-shaped fins. Additionally, *Helicocranchia pfefferi*'s posterior end of gladius ends in a long, narrow rostrum.

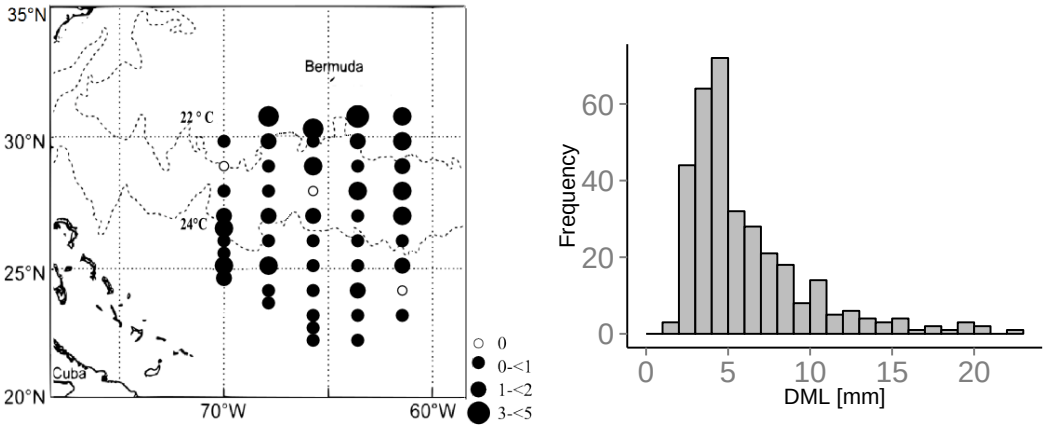


Fig. 36: *Helicocranchia* sp.. Distribution according to the station grid and histogram of the dorsal mantle lengths. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Leachia sp.

Individuals of the genus *Leachia* show very distinct elliptical fins and a solid gladial spine. Larger individuals should exhibit a cartilaginous strip on the mantle. 22 individuals were caught with the IKMT-0.5, measuring between 2 and 33 mm (Fig. 37). Larger individuals (23-45 mm DML) were caught with the IKMT-5. Because of the poorly understood systematics of *Leachia*, individuals were only identified as *Leachia* spp.. Due to the known geographical distribution, specimens of the Southern Sargasso Sea most possibly belong to *Leachia lemur*.

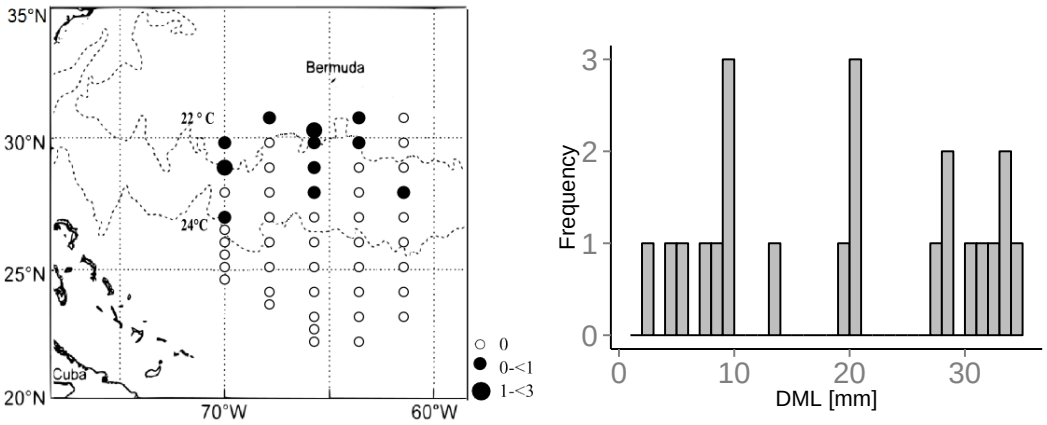


Fig. 37: *Leachia* spp.. Distribution according to the station grid and histogram of the dorsal mantle lengths. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per $10^3 m^3$ water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Liguriella sp.
This species occurred in a very low abundance, 3 individuals between 10 and 13 mm DML, which could be distinguished from the other cranchiids by their fin shape, eye and tentacle forms.

Megalocranchia oceanica
Only one individual of a mantle length of 4 mm could be identified at station 4. The four-composed photophore on the digestive gland was the main character for the morphological identification.

Enoploteuthidae
At least one species and three genera could be identified of this genus. The identification of 125 very small and poorly preserved individuals (1- 5mm DML) remained at family level (*Enoploteuthidae* indet.). Enoploteuthids occurred at each transect but highest abundance was observed at transect five. At station 5 (26.5 ° W) a high amount of enoploteuthids (without *Abraliopsis* individuals) of 4.7 individuals per 10^3 m^3 water was observed (Fig. 38).

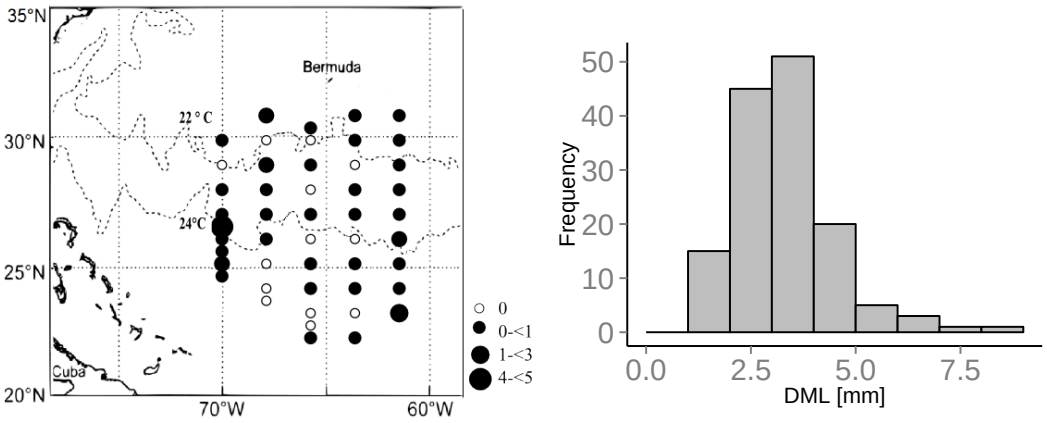


Fig. 38: Enoploteuthidae. Distribution according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Abraliopsis sp.

In total, 75 individuals, ranging between 2 and 28 mm DML were collected of which 46 could be identified as *Abraliopsis morisii*. Two *A. morisii* specimens (DML= 4 and 6.5 mm) derived from MOCNESS trawls at 125 – 0 m depth and another two from IKMT-5 (DML= 7 and 32 mm, Fig. 39). *Abraliopsis morisii* is known to be distributed from the tropical to warm-temperate eastern and western Atlantic Ocean to the Gulf of Mexico as well as the Mediterranean Sea (FAO, 2014).

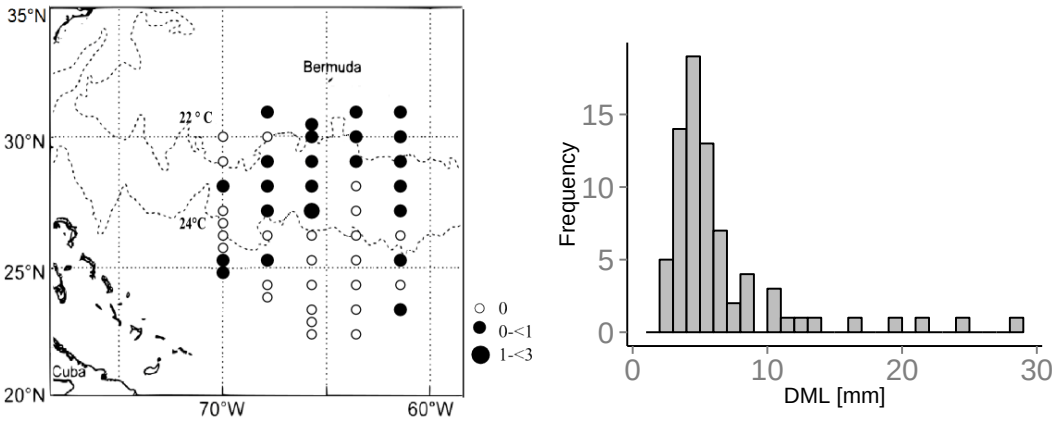


Fig. 39: *Abraliopsis morisii.* Distribution according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Enoploteuthis sp.
In total, 15 individuals (size range = 2 - 8 mm) were grouped into this genus. Another perfectly preserved specimen, 4.5 mm DML; was caught with the MOCNESS at a depth of 125 – 0 m. One juvenile, DML= 34 mm, individual was caught with the IKMT-5 but identification remained at genus level.

Histioteuthidae
11 individuals between 2.5 and 5 mm dorsal mantle length were identified as *Histioteuthis* sp.. Further species identification was impossible due to their conditions.

Lepidoteuthidae
One juvenile scaled-squid, *Lepidoteuthis grimaldii* (20 mm DML), has been collected with the big-meshed IKMT. This species is known from subtropical and tropical Atlantic regions but was rarely caught. Young Lepidoteuthids are characterized by their small papillae on the mantle which develop into scales. Adult specimens lose their tentacles whereas in young individuals, tentacles exhibit sucker like club structures.

Lycoteuthidae
Most probably, all of the lycoteuthids collected belong to the species *Selenoteuthis scintillans.* As small individuals were lacking the species specific photophore at the posterior end of the mantle, they were classified as *Lyco-*

teuthidae indet. (n=121, size range= 1 - 7 mm). Individuals with a distinct, developing photophore at the posterior part between the fins were identified as *Selenoteuthis scintillans* (n=37, size range= 2 - 13mm). Additional, 3 individuals ranging between 6 to 17 mm in DML were collected with the big-meshed IKMT. The highest abundance of Lycoteuthids was observed at transect 3, in particular at station 28 (22.5°W) with 5.7 individuals per 10^3 m^3 (Fig. 40).

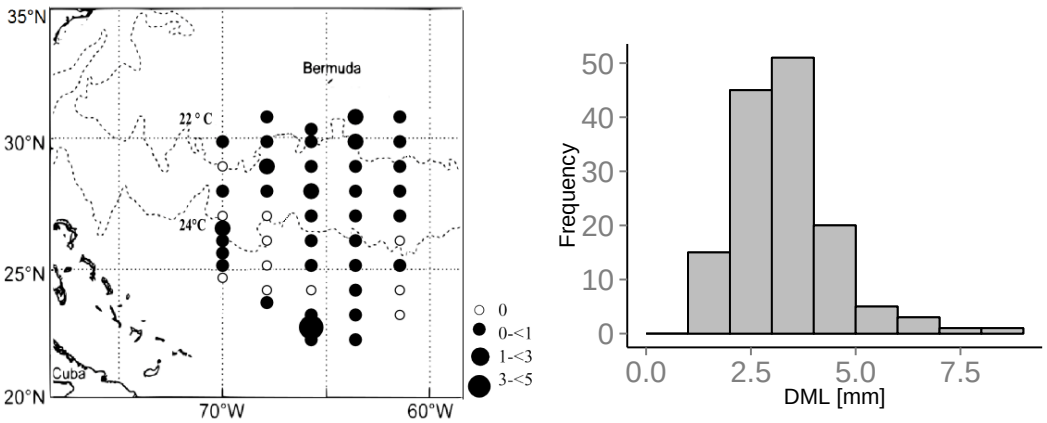


Fig. 40: *Selenoteuthis scintillans*. Distribution according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Mastigoteuthidae
As different morphological types could be distinguished of this family, individuals were identified as *Mastigoteuthis sp.*. In total, 13 individuals ranging between 3 and 25 mm in dorsal mantle length were caught with the IKMT-0.5, another specimen of 22 mm DML was caught with the IKMT-5.

Octopoteuthidae
Two morphotypes of this family were analysed, 5 indviduals were identified as *Octopoteuthis* sp. (size range= 4 – 5 mm), 5 additional individuals were described as *Octopoteuthidae* indet. (size range= 2- 10 mm) which were collected by both IKMTs. Due to their external morphology (more robust tentacular stalks, smaller suckers), they might belong to the species *Taningia danae*.

Ommastrephidae
Two species could be distinguished within the family of the so-called flying squids. The worldwide distributed species *Hyaloteuthis pelagica* (n= 126, 1 – 11

mm DML) and *Ommastrephes batramii* (n= 43, 1.5 – 11.5) were distinguished mainly due to ocular and visceral photophores in *Hyaloteuthis* individuals. For 228 individuals, ranging between 1 and 5 mm mantle length, further taxonomic identification was impossible because of unrecognisable photophores. Most specimens exhibited a mantle length below 2 mm. A general decrease in abundance with length was observed for all ommastrephids (Fig. 42). Two additional *H. pelagica* individuals were sampled at station 47 with the MOCNESS, both measuring 6 mm. Ommastrephids were present in each transect but showed higher densities in transects 3 to 5 (the eastern transects, Fig. 41). Ommastrephids represented 24 % of the total catch at the southern and 11 % at the northern stations. Thus, exhibited a higher abundance at stations below 27°N. Most *Hyaloteuthis pelagica* individuals were identified at transect two and three (Fig. 41, 42).

Additionally, one adult ommastrephid squid, 178 mm DML, was caught by fishing gear at night time. The specimen exhibited large trabecular membranes at the third arm pair. Taxonomic identification led to *O. batramii*.

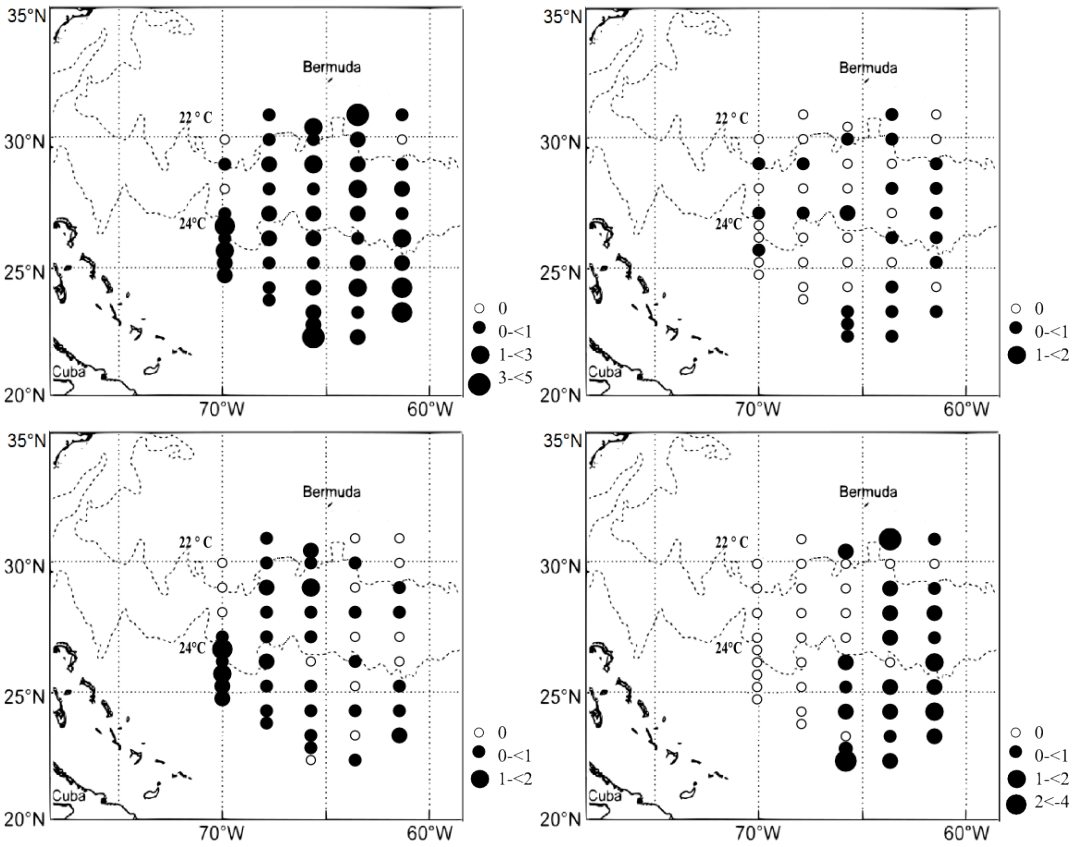


Fig. 41: From left to right: Distribution of Ommastrephidae Total, *O. batramii*, *Hyaloteuthis pelagica*, *Ommastrephidae indet.* according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances are represented according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

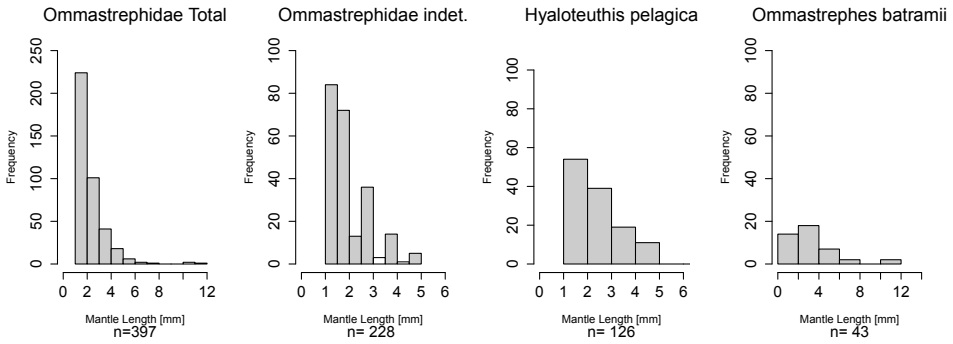


Fig. 42: Size-frequency distribution of Ommastrephidae individuals.

Onychoteuthidae

As for the WH 373 individuals, species identification was restricted to two species, *Onychoteuthis banksii* and *Onykia carriboea*. 212 individuals between 1 and 10 mm DML stuck with the family name, *Onychoteuthidae indet.* 214 individuals (1.5 – 17 mm DML) could be identified as *O. banksii* as they possessed ocular and intestinal photophores. 39 specimens with a broader mantle, dark dorsal chromatophores could be distinguished from the samples as *Onykia carriboea* (1.5 – 6 mm). The bigger meshed-IKMT caught one *Onychoteuthidae* indet. and 6 *O. banksii* specimens, 7-20 mm DML. The most abundant length was between 3 and 5 mm, the biggest individuals were identified as *Onychoteuthis banksii* (Fig. 43, 44).

Onychoteuthid cephalopods occurred at each transect but showed highest abundance at transect five with 128 individuals and lowest at transect one with 77 individuals in total. A general trend of onychoteuthids occurring in a higher abundance at western, (22 % of the total catch) compared to eastern stations (17 %), was observed. Identified *Onykia carriboea* individuals were relatively few but most were identified at transect 3 where also most *Onychoteuthis banksii* individuals occurred.

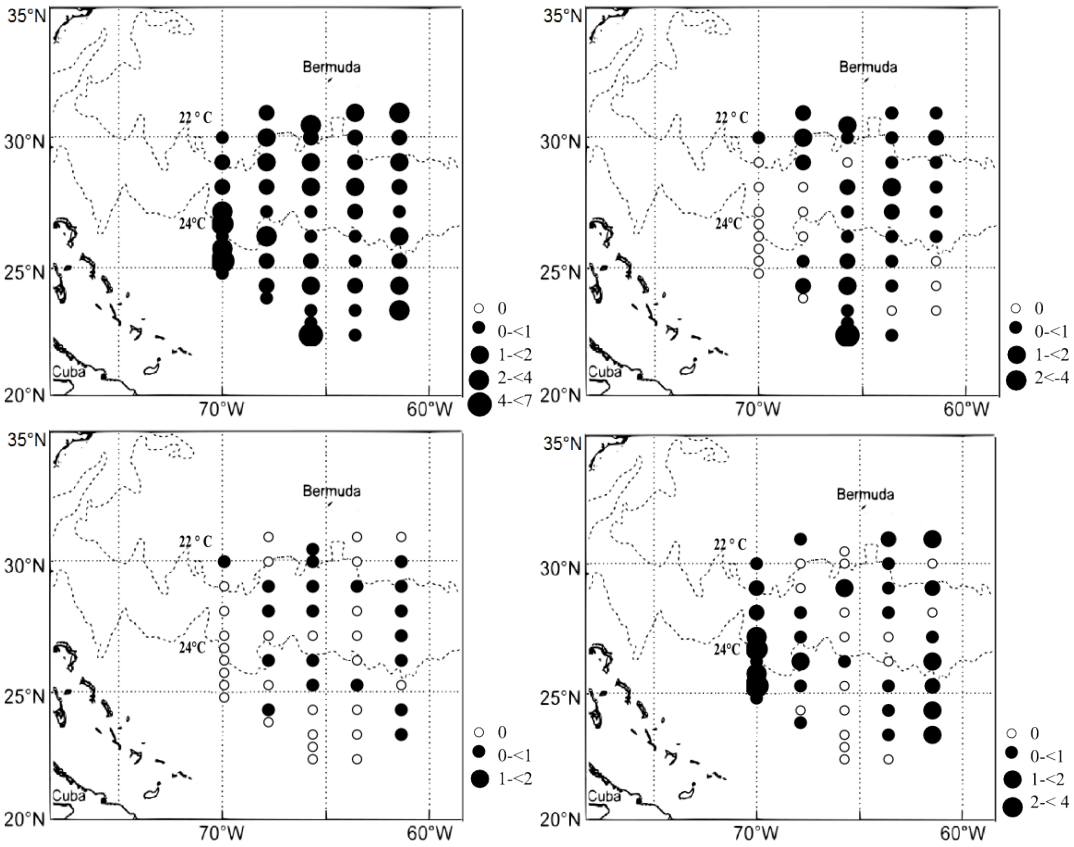


Fig. 43: Onychoteuthidae. From top left to right: Distribution of Onychoteuthidae Total, *O. banksii*, *Onykia* and *Onychoteuthidae indet.* according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances are represented according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

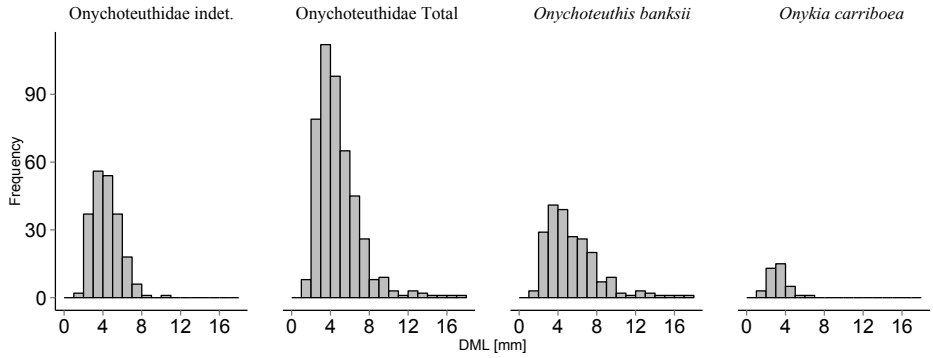


Fig. 44: Onychoteuthidae. Size-frequency distribution of individuals.

Three further *O. banksii* individuals were collected with the MOCNESS from 250- 125 and 250 - 0 m depth. Additionally, during night trawls, 10 cephalopods were collected from surface waters using the Manta Trawl. All of these specimens were identified as *Onykia carriboea*. The distribution of their dorsal mantle lengths is shown in figure 45.

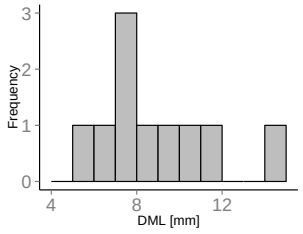


Fig. 45: *Onykia carriboea*. Size-frequency distribution of individuals collected from surface waters by the Manta Trawl.

Pyroteuthidae

In total, 105 specimens (size range: 1 – 20 mm) were clearly identified as *P. margaritifera*. 153 individuals, very small animals with a mantle length between 1 and 6 mm, remained at family level (*Pyroteuthidae* indet.). Four additional (3-7 mm DML) *P. margaritifera* individuals were caught by the MOCNESS and 26 specimens by the IKMT-5. *Pyroteuthis margaritifera* represented the family that was caught in the highest abundance with the bigger meshed IKMT. The highest abundances of pyroteuthids were observed at transects 4 and 5. Most specimens were identified at station 41 (31°N, 58°W) with 6.5 individuals per 10^3 m^3 (Fig. 46). Concerning family composition and the absolute amount of

cephalopods collected, the family Pyroteuthidae showed a higher abundance at the eastern stations (61°W and 57°W) with 15 %. In comparison, 6 % of the cephalopods collected at the western stations (70 to 64°W) belonged to the Pyroteuthidae. The northern stations, 27 to 30°N, showed a higher abundance of pyroteuthids (15 %) than the southern Stations (24 to 26°N) with 4 % of the total catch.

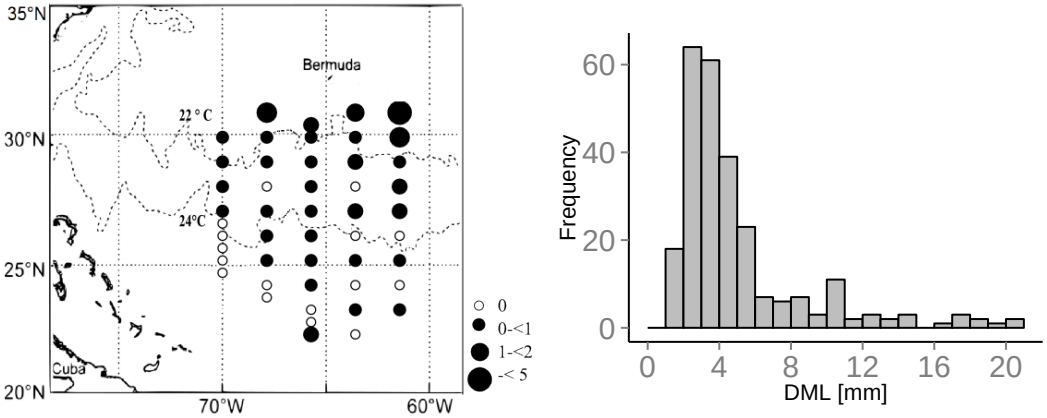


Fig. 46: *Pyroteuthis margaritifera*. Distribution according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances are represented according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Thysanoteuthidae
Thysanoteuthis rhombus
This species occurred in a very low abundance (n=6), ranging between 3 and 8 mm in dorsal mantle length.

Teuthoidea indet.
242 other teuthoid cephalopods were collected with the two IKMTs but could not be further identified due to their poor conditions. They often exhibited an inverted mantle.

Octopoda
Most of the octopod cephalopods collected belonged to the family Bolitaenidae with the species *Japetella diaphana* (n= 21, size range = 2.5- 11 mm, Fig. 47), and one single *Vitreeledonella richardii* (30 mm) individual. Additional four *Japetella diaphana* individuals were caught at station 28 with the big-meshed

IKMT.

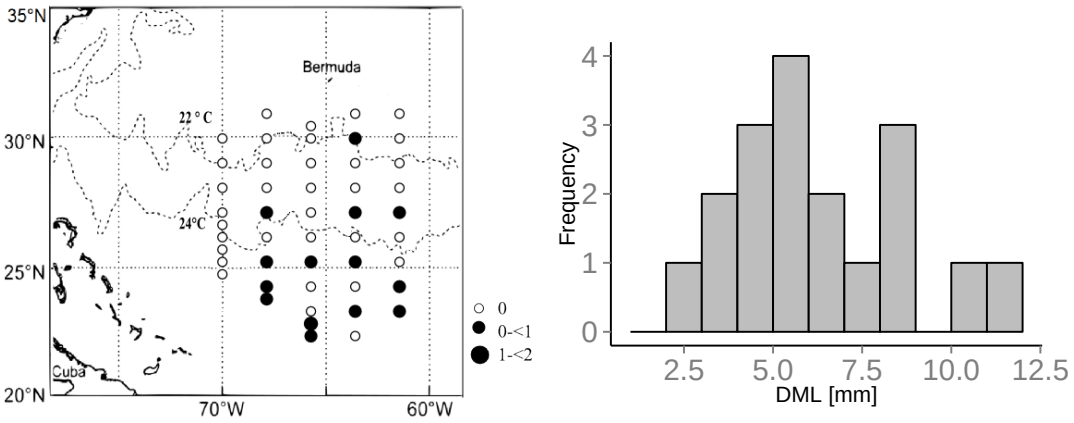


Fig. 47: *Japetella diaphana*. Distribution according to the station grid. Only specimens deriving from IKMT-0.5 Trawls have been included. Abundances are represented according to amount of specimens per 10^3 m^3 water mass. The temperature lines indicate the thermal front deriving from NOAA/ESRL data from the 5th April 2015.

Six *Octopus* sp. specimens (DML= 2 -5 mm) were collected whose external morphology did not allow further species identification.

3.3.5. Species Richness and relative abundance in relation to distribution

In table 7 the species richness at each station is represented by the species number and the relative abundance by the number of individuals per 10,000 m^3 water volume. The abundance of cephalopods was recorded at station 28 with 32.45 individuals/10 m^3, the lowest cephalopod abundance showed station 33 with 1.89 individuals/10^3 m^3 . The highest amount of species was observed at station 49 with 26 specimens belongig to 20 different species. Concerning the amount of species per water volume, the highest was observed at station 5 with 5.88 species/10^3 m^3 .

Tab. 7: Diversity indices for the 49 stations during MSM41. Presented are species number (S), specimen number (N), Margalef's species richness (d), Pielou's eveness (J'), Shannon-Wiener-Index (H'(log e), Simpsons Diversity Index (1-Lambda').

Sample	S	N	d	J'	H'(log e)	1-Lambda'
Stn1	11	22	3,235	0,9164	2,197	0,9091
Stn2	9	19	2,717	0,8708	1,913	0,8596
Stn3	9	19	2,717	0,9023	1,983	0,883
Stn4	11	41	2,693	0,789	1,892	0,7963
Stn5	10	41	2,424	0,9117	2,099	0,8829
Stn6	4	7	1,542	0,9751	1,352	0,8571
Stn7	9	43	2,127	0,822	1,806	0,804
Stn8	6	40	1,355	0,7787	1,395	0,7103
Stn9	8	27	2,124	0,9105	1,893	0,8575
Stn10	7	13	2,339	0,9686	1,885	0,9103
Stn11	8	19	2,377	0,8693	1,808	0,8363
Stn12	10	28	2,701	0,8217	1,892	0,8307
Stn13	8	33	2,002	0,7331	1,524	0,7254
Stn14	13	39	3,276	0,9406	2,413	0,9217
Stn15	11	26	3,069	0,946	2,269	0,92
Stn16	13	101	2,6	0,8238	2,113	0,8321
Stn17	6	32	1,443	0,7805	1,398	0,7218
Stn18	14	87	2,911	0,8669	2,288	0,8821
Stn19	14	83	2,942	0,8682	2,291	0,8836
Stn20	12	26	3,376	0,9425	2,342	0,9262
Stn21	15	63	3,379	0,7897	2,139	0,8607
Stn22	13	46	3,134	0,8356	2,143	0,8657
Stn23	13	35	3,375	0,8956	2,297	0,9042
Stn24	10	23	2,87	0,8102	1,866	0,8142
Stn25	12	36	3,07	0,9306	2,312	0,9127
Stn26	9	17	2,824	0,8884	1,952	0,875
Stn27	10	18	3,114	0,9208	2,12	0,9085
Stn28	14	171	2,528	0,6751	1,782	0,7646
Stn29	13	23	3,827	0,87	2,231	0,8775
Stn30	11	16	3,607	0,962	2,307	0,95
Stn31	11	31	2,912	0,8164	1,958	0,8323
Stn32	12	38	3,024	0,7842	1,949	0,8108
Stn33	9	16	2,885	0,9315	2,047	0,9083
Stn34	15	44	3,7	0,8859	2,399	0,9027
Stn35	13	36	3,349	0,8699	2,231	0,8825
Stn36	14	72	3,04	0,8736	2,305	0,8854
Stn37	19	60	4,396	0,9544	2,81	0,9492
Stn38	13	70	2,825	0,7913	2,03	0,8133
Stn39	12	61	2,676	0,86	2,137	0,8623
Stn40	18	127	3,509	0,8005	2,314	0,8543
Stn41	16	105	3,223	0,8176	2,267	0,872
Stn42	14	73	3,03	0,8255	2,179	0,8573
Stn43	17	82	3,631	0,8851	2,508	0,9118
Stn44	16	65	3,593	0,8444	2,341	0,875
Stn45	18	81	3,869	0,8588	2,482	0,9003
Stn46	13	47	3,117	0,7206	1,848	0,7734
Stn47	17	77	3,683	0,8985	2,546	0,9207
Stn48	11	47	2,597	0,8038	1,927	0,8224
Stn49	20	80	4,336	0,8459	2,534	0,9054

The mean catch rate of specimens and species (per 10^3 m^3) in relation to the longitudinal degree (transects 1-5) is represented in figure 48 a.
The mean variation of species and individuals collected in relation to the latitudinal degrees is demonstrated in figure 48 b. The highest mean abundance (15.41 specimens/10^3 m^3) was observed at 31°N. The lowest abundance was observed at 25°N with a mean of 5 individuals/10^3 m^3. Median specimen and species abundances as well as the Shannon-Wiener Index are shown in figure 48. Median abundances at 22 to 24 °N (section h) and at 28°N differ significantly from the other latitudes. The highest median abundances have been observed at 31°N (15.38 specimens/10^3 m^3) and the lowest at 25°N with 4.03 individuals/10^3 m^3.

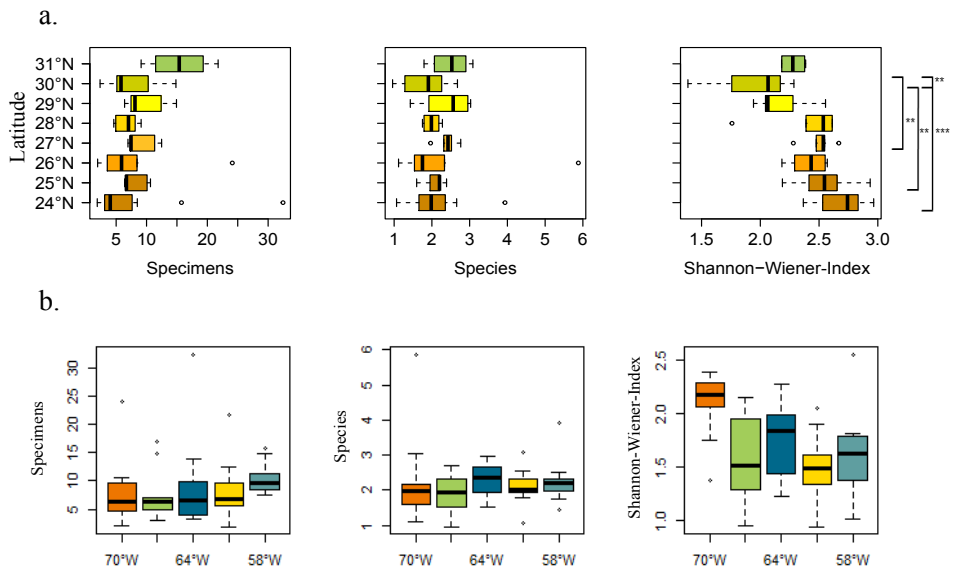


Fig. 48: Median range of specimens and species caught as well as the Shannon-Wiener Index in relation to Latitude (a.) and Longitude, Transects, (b.). Levels of significance according to Tukey's HSD post-hoc test (** p <0.05, *** p< 0.001).

Analysis of similarity showed differences concerning the family composition at stations between an area north to the convergence zone, a central and a southern area (Fig. 49). The results of the SIMPER analysis are represented in table 8. Striking is the absence of *Japetella diaphana* individuals from the northern and central area as well as the absence of *Leachia sp.* from the southern area.

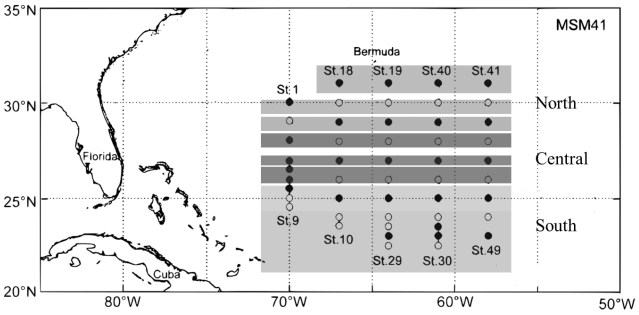


Fig. 49: Map of the study area during MSM 41 with the division of the latitudinal sections used for SIMPER analysis.

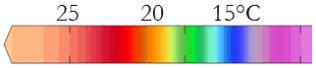
Tab. 8: SIMPER analysis discriminating species/families between northern, central and southern stations of the study area. Species are ordered with decreasing contribution (%) to the total dissimilarity.

Species/Family	Average abundance Northern Sargasso Sea	Central Sargasso Sea	Contribution (%)	Cumulative Contribution (%)
Pyroteuthidae	1.67	0.91	11.42	11.42
Lycoteuthidae	1.1	0.92	9.25	20.67
Brachioteuthidae	0.71	0.81	8.75	29.42
Chtenopteryx sicula	0.62	0.87	8.52	37.94
Ommastrephidae	1.32	1.54	8.29	46.23
Chiroteuthidae	0.6	0.62	8.07	54.3
Enoploteuthidae	1.41	1.28	7.27	61.58
Ancistrocheiridae	0.48	0.37	6.77	68.34
Cranchiidae	1.85	1.54	5.55	73.9
Onychoteuthidae	1.81	1.64	4.71	78.61
Mastigoteuthis sp.	0.34	0	4.43	83.04
Histioteuthidae	0.16	0.29	4.36	87.4
Bolitaenidae	0.13	0.3	4.25	91.65
Species/Family	Average abundance Northern Sargasso Sea	Southern Sargasso Sea	Contribution (%)	Cumulative Contribution (%)
Pyroteuthidae	1.67	0.64	13.52	13.52
Enoploteuthidae	1.41	0.91	9.81	23.33
Lycoteuthidae	1.1	0.91	8.35	31.67
Brachioteuthidae	0.71	0.67	8.16	39.83
Chtenopteryx sicula	0.62	0.71	7.38	47.22
Chiroteuthidae	0.6	0.56	7.38	54.6
Ommastrephidae	1.32	1.64	7.24	61.84
Bolitaenidae	0.13	0.6	6.74	68.58
Ancistrocheiridae	0.48	0.44	6.58	75.16
Cranchiidae	1.85	1.36	6.22	81.38
Onychoteuthidae	1.81	1.59	4.8	86.18
Mastigoteuthis sp.	0.34	0	4.07	90.25
Species/Family	Average abundance Central Sargasso Sea	Southern Sargasso Sea	Contribution (%)	Cumulative Contribution (%)
Pyroteuthidae	0.91	0.64	11.18	11.18
Lycoteuthidae	0.92	0.91	10.52	21.71
Enoploteuthidae	1.28	0.91	9.92	31.63
Chtenopteryx sicula	0.87	0.71	8.73	40.36
Brachioteuthidae	0.81	0.67	8.5	48.86
Bolitaenidae	0.3	0.6	8.33	57.19
Chiroteuthidae	0.62	0.56	7.76	64.95
Ancistrocheiridae	0.37	0.44	7.4	72.35
Ommastrephidae	1.54	1.64	6.32	78.67
Onychoteuthidae	1.64	1.59	5.38	84.05
Cranchiidae	1.54	1.36	4.94	88.99
Histioteuthidae	0.29	0.05	3.9	92.89
Onychoteuthidae	1.64	1.59	5.38	84.05
Cranchiidae	1.54	1.36	4.94	88.99
Histioteuthidae	0.29	0.05	3.9	92.89

3.3.6. Cephalopod abundance in relation to Hydrography

The most abundant families in the study area were Chtenopterygidae, Cranchiidae, Enoploteuthidae, Lycoteuthidae, Ommastrephidae, Onychoteuthidae and Pyroteuthidae. Concerning the catch rates of those families specimens were generally more abundant along stations north to the convergence zone, which exhibited colder water temperatures. Station 5 represents an exception; it showed the highest catch rate of the whole cruise with 18.08 specimens per 10^3 m^3 (concerning the most common families) and 24.11 specimens per 10^3 m^3 with respect to all identified cephalopod families.
With regard to the family composition along the transects/stations, generally more ommastrephids were caught at southern stations with water temperatures above 23°C in the upper 300 m. Onychoteuthids occurred, except for station

18, at every station. Catch rates of the most abundant families according to the sampled stations are represented in figure 50. The corresponding density sections are also represented using the following colour gradient:



Principal component analysis

The chord-distance based PCA of all sampling sites, except for station 1, produced two axes that represented 37.72% of the variance in the samples. The first axis was positively related to the species *Helicocranchia* sp. as well as to the families Enoploteuthidae, Octopoteuthidae or Onychoteuthidae and negatively related to Ancistrocheiridae or Cranchiidae. Positive loadings along the second axis were for example measured for Bolitaenidae, Brachioteuthidae, Ommastrephidae or *Chtenopteryx sicula* while negative loadings were recorded for Pyroteuthidae or *Leachia* sp.. *Mastigoteuthis sp.*, Pyroteuthidae and *Leachia* built one distinct group as well as Octopoteuthidae and Enoploteuthidae (figure 51).

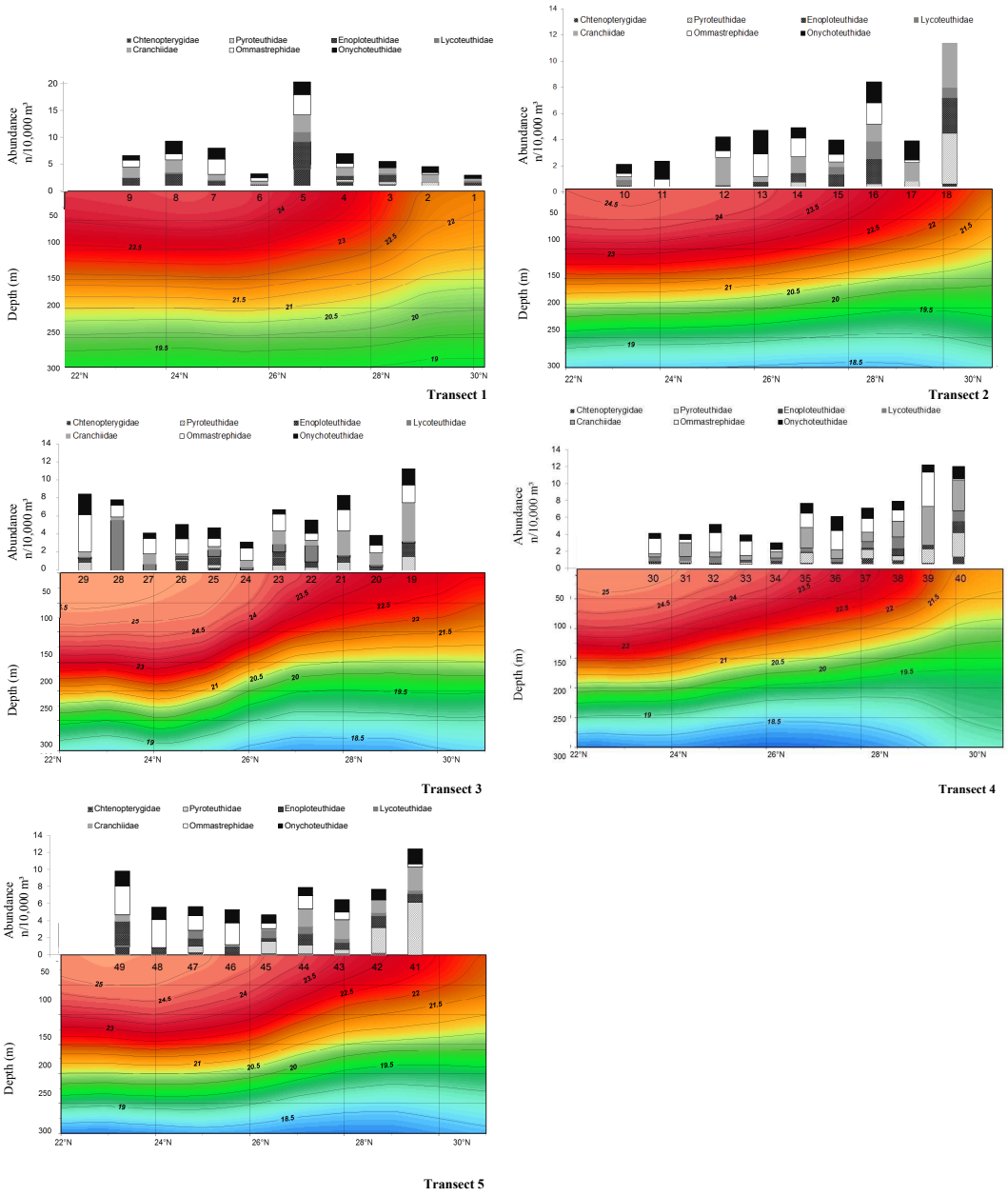


Fig. 50: Catch rates (n/10,000m^3) of cephalopods of the most abundant families at the 49 stations in relation to the latitudinal density along the five transects. Stations are shown from southern to northern latitudes.

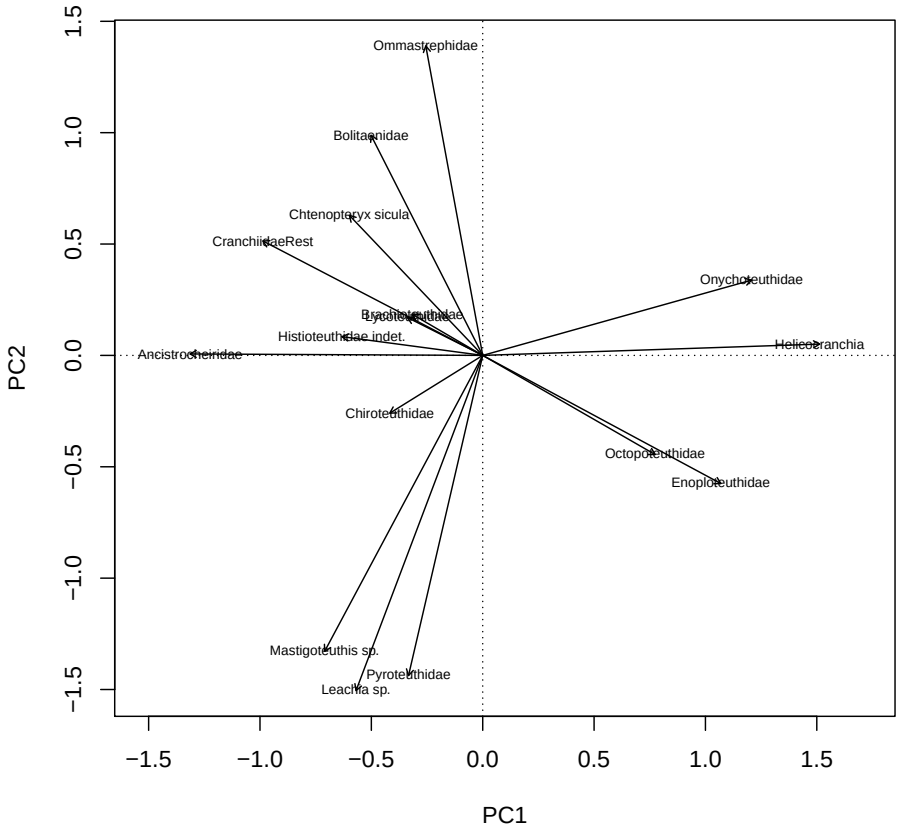


Fig. 51: Principal component analysis (PCA) ordination based on chord distances of cephalopod abundances. The first factorial plane explained 37.72% of the overall variance (PC1 = 19.12%. PC2= 18.6%).

PCA results for the scores (stations) showed a grouping of stations belonging to the first transect of the study area and an ordination pattern of stations of the third transect. Referring to the latitudinal distribution of the sampling locations, three areas were distinguished in relation to the convergence zone: a northern, southern and a central part. Species assemblages of northern and southern stations with stations of the central part grouped in between could be detected according to the PCA results (Fig. 52).

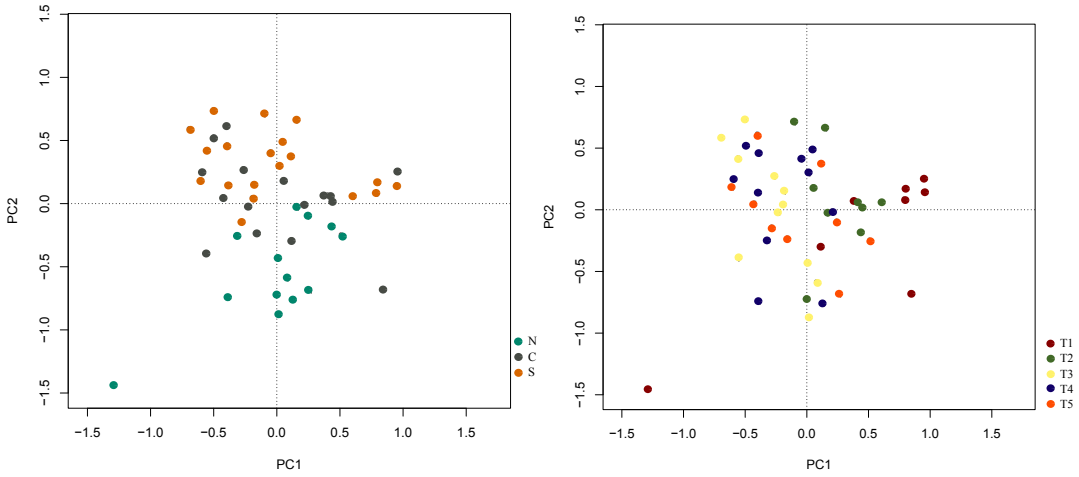


Fig. 52: Principal component analysis (PCA) ordination based on chord distances of cephalopod abundances showing scores (stations). Stations are dyed according to the longitudinal distribution, transects T1-T5, and their latitudinal position (North: 31-29°N. Central: 29-26°N. South: 25.5-23°N).

Redundancy Analysis

All variables (Surface, Temperature, Time, Longitude) explain 23.91% of the variance. The first three constrained axes (RDA1, RDA 2, RDA 3) explain 10.82, 6.71 and 3.99% of the variance. The variance explained by the first unconstrained axis (PCA1) is 11.41%. A permutation test for community data (reduced model. marginal effects) revealed significant relationships between the environmental factors and species assemblages (ANOVA. $p < 0.01$). Above all factors examined, sea surface temperatures correlated to the strongest extend with the first axis (table 9). Especially the distributions of Ommastrephidae and Bolitaenidae could be explained by this variable. As for the longitudinal distribution, the already observed occurrence of onychoteuthids at the eastern stations, 70° to 67°W, could be visualized by RDA (Fig. 53). Concerning the spatial variable, several families (Histioteuthidae, *Chtenopteryx sicula*, Lycoteuthidae) built one group that was more abundant at western stations up from 61°W. The explanatory variable time and the family Pyroteuthidae were negatively correlated with axis 1. The sea surface temperature (SST) was chosen as the environmental variable because this variable revealed a more significant relationship of species assemblage and temperature (ANOVA. $p < 0.01$). Temperatures at 150 m, 300 m or the mean exhibited a weaker correlation with permutation test for community data (direct model). Furthermore, individuals were caught in the upper 300 m and the SST seemed to have an influence for especially the ommastrephids.

Tab. 9: Correlations between the environmental variables and the canonical axes of the conducted RDA. Higest correlation with axis 1 showed SST.

Environmental variable	Correlation with axis			
	RDA1	RDA2	RDA3	RDA4
Sea Surface Temperature	0.94072	-0.1342	-0.1460	0.27517
Time Night	-0.28921	-0.2098	-0.8871	0.29232
East	-0.08135	0.9862	-0.1326	0.05591
West	0.05787	-0.6131	-0.1973	-0.76279

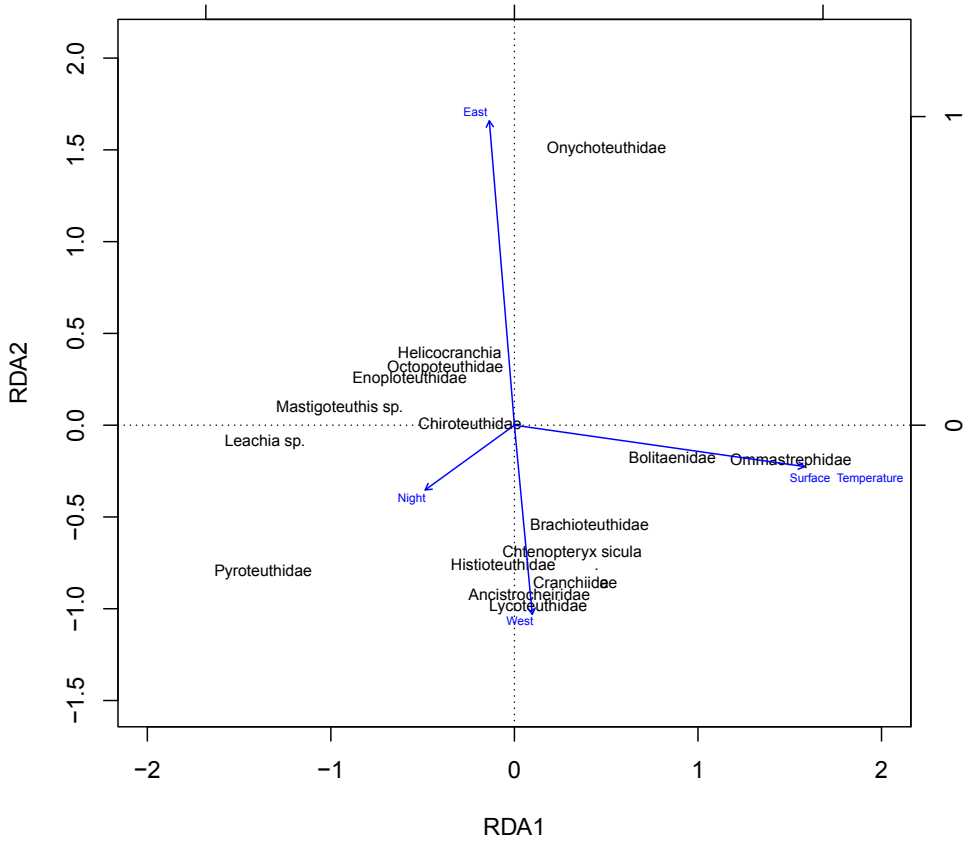


Fig. 53: Canonical Ordination (Redundancy Analysis) based on chord distances of cephalopod early life stages. Response variables were fourth rooted family abundances (n/10.000m^3), explanatory environmental variables are indicated by blue lines. The length of the correlation to the environmental variables is reflected by the arrow length.

Mapping of the RDA results showed that species assemblages at the southern stations were higher correlated to the sea surface temperature which was

indicated by red contours (fig. 54).

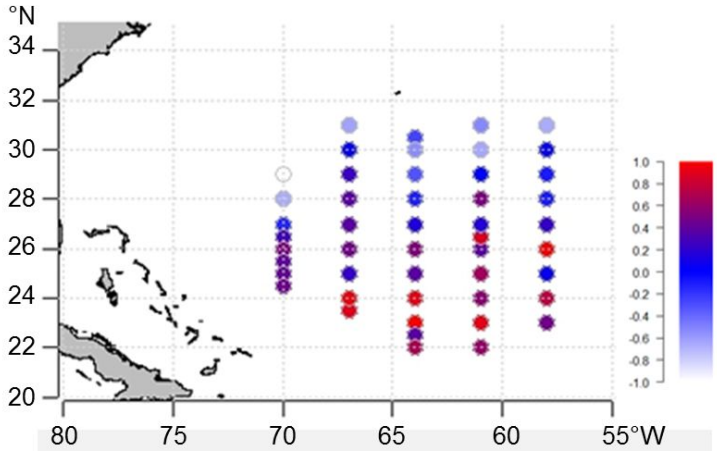


Fig. 54: Sample Scores of RDA based on chord distances of cephalopod assemblages along the study area in relation to sea surface temperature. The colours indicate the strength of correlation.

3.3.7. Comparison of day and night trawls

In total, more species and specimens were caught during night that during day hauls. The medians for the amount of individuals and species caught per 10^3 m^3 are presented in figure 55. Wilcoxon rank sum test for unpaired data showed a highly significant difference between the two sample times for the amount of specimens ($p < 0.001$) and a significant difference concerning species richness ($p = 0.003$). The median Shannon-Wiener index was slightly higher for the night hauls but not significantly (Wilcoxon rank sum test).

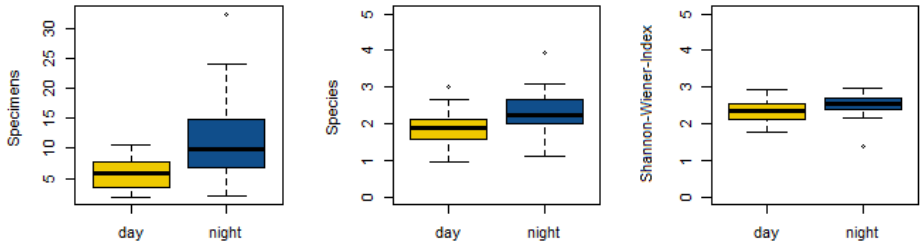


Fig. 55: Boxplots illustrating the median range of specimens and species caught as well as the Shannon-Wiener Index in relation to day and night hauls.

The MDS ordination plot shows a separation between day and night stations. Family assemblages of the different time points are grouped together (Fig. 56). Permutation analysis, ANOSIM, indicated a significant difference between day and night hauls (R =0.116. p-value= 0.008 **).

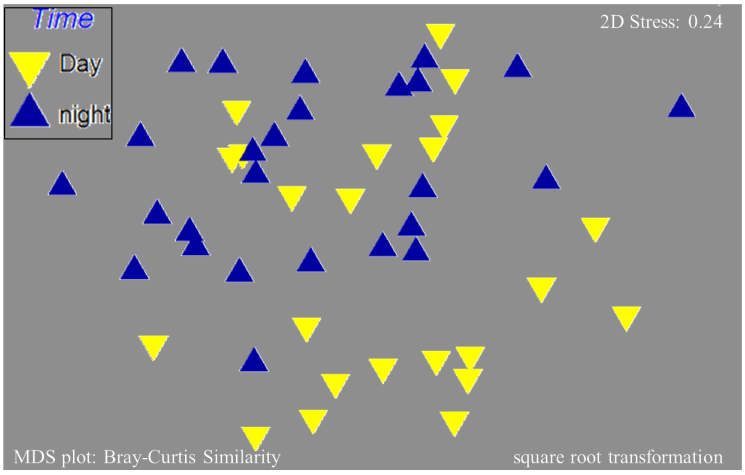


Fig. 56: Ordination of cephalopod assemblages during day and night using non-metric multidimensional scaling. Similarity was calculated based on Bray-Curtis measure of family abundances.

Concerning the species composition, differences between day and night trawls were observed for the Pyroteuthidae. Individuals of this family made up 13% of the total amount of individuals caught during night and 7% of the day catch. The contribution of the family Pyroteuthidae to the differences in time points was also shown by exploratory analysis (SIMPER). The families Lycoteuthidae and Enoploteuthidae were also more abundant during night than day time and strongly contributed to the differences in family composition (table 10).

Tab. 10: Discrimination of families between day and night hauls. Families are ordered according to contribution to the total dissimilarity after SIMPER analysis.

	Average abundance ($n/10^3m^3$)			
Family	Night	Day	Contribution (%)	Cumulative Contribution (%)
Average Dissimilarity	35.47 %			
Pyroteuthidae	1.27	0.72	12.01	12.01
Enoploteuthidae	1.37	0.92	9.71	21.72
Lycoteuthidae	1.05	0.86	9.69	31.42
Chtenopteryx sicula	0.9	0.52	8.55	39.97
Brachioteuthidae	0.72	0.75	8.39	48.35
Chiroteuthidae	0.65	0.51	7.66	56.02
Ancistrocheiridae	0.38	0.49	7.03	63.05
Ommastrephidae	1.48	1.56	6.94	69.99
Bolitaenidae	0.42	0.29	6.26	76.25
Cranchiidae	1.66	1.44	5.44	81.69
Onychoteuthidae	1.64	1.71	4.91	86.6
Histioteuthidae	0.12	0.21	3.21	89.81
Octopoteuthidae	0.19	0.05	2.83	92.64

4. Discussion

In the Sargasso Sea cephalopods and especially their early life stages form the bulk of the oceanic micronekton/macroplankton, together with euphausiids, decapod shrimps, and early life fishes. Although they are well-known top predators and essential members of pelagic food webs, our knowledge on the cephalopods of the Sargasso Sea is still very poor. This study reports on a huge dataset of cephalopods that was collected within the Sargasso Sea during two successive oceanographic expeditions in 2014 and 2015. It provides a profound insight into the faunal distribution and composition within this area. Understanding the distribution and diversity of cephalopods of the Sargasso Sea is important for several reasons. First of all, in marine habitats that are rapidly changing, all taxa need to be valued and preserved (Tittensor et al., 2010). Especially the pelagic ocean remains widely uninvestigated and detailed ecosystem related studies are lacking (Angel, 1993; Gray, 1997; Webb et al., 2010). The present study comprises the most comprehensive dataset of cephalopods sampled in the Sargasso Sea so far. It allows new and important conclusions about the abundance, distribution and diversity of cephalopod species of a major sub-tropical ocean. Secondly, the distinctive hydrographic features of the Sargasso Sea characterize the species composition and distribution pattern of the cephalopods. In an earlier study that was based on a much smaller dataset abundance and diversity of early life cephalopods in the Sargasso Sea decreased from north to south (Diekmann and Piatkowski, 2002). This observation was mainly pronounced for the cranchid squid, *Leachia* sp., whose distribution was shown to be affected by the subtropical convergence zone (STCZ), with a distinct decrease in abundance south of the STCZ. Such a clear trend in increasing cephalopod species richness and abundance towards stations north of the STCZ could not be observed for all transects of the present study area, probably due to the higher number of transects which covered a much larger area from west to east across the Sargasso Sea (Fig. 9). In addition, a trend of increasing species richness towards the eastern stations of the study area was observed in the 2015 research cruise (Fig. 10). Furthermore, in this study the suitability and limits of diverse sampling methods became apparent (Wormuth and Roper, 1983; Piatkowski, 1998). It was benefitted from the application of different sampling gear which sampled the different life stages of cephalopods in the study area more adequately.

Life in the Sargasso Sea

Within the Atlantic Ocean the Sargasso Sea has been described as a "crossroad", with the endemic algae Sargassum functioning as a feeding area for some

species and a migration route for other species (Laffoley et al., 2011). Despite low biomass and productivity, plankton communities in the Sargasso Sea are generally known for exhibiting high growth rates which are mainly restricted to the northern area (Goldman, 1993; Jackson, 1980). Abundance and species richness for several taxa, e.g. copepods (Deevey and Brooks, 1977; Roman et al., 1993) or mesopelagic fishes (Backus et al., 1969; Jahn and Backus, 1976) generally decrease in a north-southern gradient. During the 2015 cruise it was striking that phytoplankton densities were highest at 120 - 140 m depth and not at the surface (personal observations of M. Kaufmann). The very clear water of the Sargasso Sea could be an explanation because sufficient light reaches the epipelagic zone, which allows production and thus nutrient availability even at deeper layers (Menzel et al., 1960). The surface waters were dominated by cyanobacteria at the southern stations between 24°N and 22.5°N. Those bacteria use molecular nitrogen from the atmosphere as fertilizer for growth instead of nitrate, which is an explanation for their success in the commonly nutrient poor Sargasso Sea (Hanel et al., 2015). A positive correlation between zooplankton biomass and SST as well as a negative correlation between biomass and the mean 300-600 m water mass has been shown in the Sargasso Sea (Steinberg et al., 2012).

Concerning zooplankton, densities are lower compared to other regions, e.g. the Antarctic or the Indian Ocean (Pakhomov et al., 2000; Nair et al., 1981). For example, copepods were rarely found and euphausiids appeared in low densities, but high species numbers (C. Buchholz, H. Auel ,pers. observations). Especially krill species were found at night near the thermocline, supposedly hunting and "grazing". An increased biomass and abundance was shown for salp species in the presence of cyclonic mesoscale eddies within the Sargasso Sea (Stone and Steinberg, 2014). Eddies are a source of nutrients for the euphotic zone and enhance plankton growth (McGillicuddy et al., 1998). An impact on the cephalopod fauna cannot me excluded. Concerning the cephalopod fauna, on the one hand, density was lower compared to other oceanic regions like the Eastern Atlantic Ocean (Rosa et al., 2008). On the other hand, species richness was comparable to other Atlantic regions like the North-Eastern coast of Brazil (Haimovici et al., 2002). One of the reasons might be that more productive areas can support larger populations and strong vertical stratification limits the supply of nutrients in the euphotic layers. Due to their pronounced vertical migration cephalopods are able to occupy a larger area within the Sargasso Sea.

Effects of hydrography on cephalopod assemblages

Each of the five transects of the 2015 expedition crossed frontal features, which were also represented by the cephalopod assemblages. Cephalopod densities showed a general tendency to increase towards the northern latitudes, with lower sea surface temperatures (Fig. 50). Other faunal groups have also been reported to exhibit a distribution related to the STCZ. For example, greater species numbers of mesopelagic fish (Backus et al., 1969) or copepods (Colton et al., 1975) have been reported for areas north of the STCZ whereas leptocephali distributions seem to decrease in the northern areas (Miller and McCleave, 1994). From the mapping of Redundancy Analysis (RDA) sample scores, it can be assumed (Fig. 54) that species assemblages at southern stations were more sensitive to changing sea surface temperature than at northern stations. As reliable fluorescence measurements were not available for all stations, assumptions about the impact on the cephalopod communities cannot be made. It has been suggested that fluorescence is correlated with fish and cephalopod biomass, which might result in higher abundances in frontal regions which exhibit higher prey densities (Lansdell and Young, 2007).

In considering the island of Bermuda as a huge seamount, another explanation for the increased cephalopod density at the northern stations could be the "seamount-theory" (Boehlert and Genin, 1987). Seamounts are assumed to exhibit high species abundances of pelagic and benthic individuals as circulating currents or eddies might retain planktonic life stages (Diekmann and Piatkowski, 2004). Thereby stations located closer to the island, the northern sample locations, were more species and specimen rich due to enhanced primary production and acting as retention mechanisms for planktonic stages (Dower and Perry, 2001; Fock et al., 2002; Mullineau and Mills, 1997). In particular, the cranchiid *Leachia lemur* was mainly collected at stations north to the STCZ, an observation that was also made for the individuals sampled along the station grid of the Walther Herwig cruise (Fig. 57). This observation was conformable with the study conducted by Diekmann and Piatkowski in 2002.

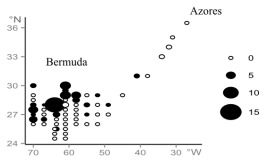


Fig. 57: *Leachia* sp.. General distribution along the station grid. Numbers idicated absolute catch rates

Even if several species were more abundant at northern stations, the octopod species, *Japetella diaphana*, showed a general tendency towards southern stations. *Japetella diaphana* individuals were mostly collected at stations in the range of the southern part of the STCZ with higher surface temperatures than in the north (temperature difference between 22° and 24°C). RDA results showed a positive correlation between surface temperatures and species assemblages which indicates that most of the cephalopods preferred warmer water masses. For the non-quantitatively collected individuals of the WH 373 IKMT trawls a similar pattern towards the southern latitudes was visible (Fig. 58).

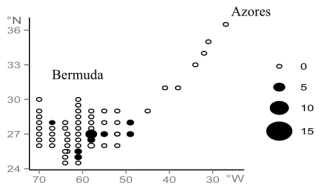


Fig. 58: *Japetella diaphana*. General distribution along the station grid. Numbers idicated absolute catch rates.

A longitudinal gradient with forming distinct clusters along the five transects from west to east was supported by the PCA results (Fig. 51). Several groups, e.g. Onychoteuthidae, Ommastrephidae, Enoploteuthidae, Cranchiidae (*Helicocranchia papillata*) or *Chtenopteryx sicula* were highly abundant at the first transect. In particular station no. 5 at the southern edge of the STCZ showed an increased species diversity, as well as increased species abundances. In the western central Atlantic, it is assumed that the Gulfstream acts as a transporter of paralarvae. Thereby, eastern central Florida shows the highest cephalopod species richness in the wider Carribean (Judkins et al., 2010). Zooplankton communities in the Sargasso Sea might have also been transported by jets and convergences along the STCZ.

An association of different cephalopod families with characteristic water masses has, for example, also been shown in the Pacific Ocean (Bower et al., 1998), where an increased abundance of pyroteuthids in subtropical water masses and of enoploteuthids in tropical waters has been observed. The Sargasso Sea cephalopod assemblages revealed by PCA showed a grouping of certain families, e.g. Pyroteuthidae, *Leachia* sp. specimens and Mastigoteuthidae. The conducted RDA supports the occurrence of paralarval ommastrephids and bolitaenids near the surface, which underlines their typical presence in the

upper water layers (Piatkowski et al., 1993; Vecchione, 1999).

The influence of the stratification in the water column on the cephalopod and fish assemblages has been investigated in the Arabian Sea (Röpke et al., 1993). Highest cephalopod densities were found close to the pycnocline, the boundary layer of two distinct water masses of different densities in the region. Hydrographic features of the Sargasso Sea also affected the cephalopod assemblage. The observations of the species distributions in the present study support that the STCZ acts as a marked faunal boundary region in the central Sargasso Sea.

Comparison of the two cruises
The survey of cephalopods along the station grid of the Walther Herwig 373 research cruise in 2014 resulted in a total sampling of 2,063 individuals, which belonged to at least 37 species. Thus, a higher species richness was observed than in the study by Diekmann and Piatkowski (2002), which reported 20 oceanic species from that area. The Walther Herwig 373 cruise illustrated the cephalopod community of the Sargasso Sea covering a broad east-to-west range from 30°W to 27°W. Because of a non-quantitative sorting, only information about presence of cephalopod species should be estimated from the IKMT hauls. The catches of the pelagic midwater trawl allow assumptions about the species abundances, but should be only interpreted for species presences. Nevertheless, information about depth-related occurrence of species can be drawn due to the depth stratified catches as well as information about subadult and adult specimens due to the large net mesh size. Furthermore, the WH 373 expedition covered a broad longitudinal section which provides additional information compared to the narrower station grid of the Marian S. Merian cruise in 2015. As sampling during the MSM 41 expedition was conducted quantitatively, information about species occurrence, relative abundance and distribution was collected. Diel vertical migrating species were distinguished, because hauls were conducted during different day times. During the MSM cruise 2,484 specimens (21 families, at least 36 species) were collected by different gear in total.

Fishing gear
Concerning the two expeditions, multiple sampling gears were deployed which allowed comparisons of their application ranges. Every sampling method has its constraints and a trade-off between sampling yield and its information has to be made. For catching of larger, fast-swimming organisms commercial trawls, like the pelagic midwater trawl used during the Walther Herwig cruise 373, are more suitable than nets with mouth openings below 10 m^2 (Roper and R. E. Young, 1975; Wormuth, 1985). One of the main problems that occurs

during sampling is the net avoiding behaviour of mobile nektonic organisms (Pearcy, 1978). Another observation emphasises that big large-meshed nets allwow smaller organisms the escape through the meshes (Castonguay and J. D. McCleave, 1987). Despite these problems, in filtering water volumes efficiently, big nets are suitable for the characterization of species composition of nekton along sparsely inhabited oceanic areas (Pearcy, 1978). For the assessment of the distribution of small and early life stages of cephalopods, mid-sized nets such as IKMT and MOCNESS have been recommended (Piatkowski, 1998). The small meshed net IKMT 0.5 used in the present studies, is able to sample relatively large water masses at towing speeds of 0.5 to 4 knots, which might decrease net avoidance. One disadvantage of the IKMT nets was the damage of the specimens due to the double hauls, which was not given for the MOCNESS catches. Specimens that were collected with this gear were sparse but in much better conditions than those collected by the IKMTs.

One striking observation was enabled by the Manta Trawl: Cephalopods collected by this neuston net, which only sampled surface waters, all belonged to the species *Onykia carriboea*. Thereby, it could be concluded that *Onykia* specimens are associated with the *Sargassum* seaweed, an observation that would not have been possible by single IKMT trawling. Vecchione et al. (2003) also reported the occurrence of this onychoteuthid species associated with *Sargassum* seaweed.

DNA sequencing

From the Walther Herwig 373 specimens for 33 of 42 individuals molecular barcoding studies were performed. Thereby sequences of the COI gene locus were obtained using the primers LCO1490 and HCO2198 (Folmer et al., 1994). Failing of the nine samples (*Onykia carriboea*, *Pyroteuthis margaritifera*, *Leachia* sp., *Ommastrephes batramii*, *Helicocranchia sp.*, *Thysanoteuthis* sp. and 2 individuals of *Ctenopteryx sicula*) could have been due to degradation of the material or, although less likely, caused by mutations in the primer binding sites.

Concerning the phylogenetic trees, the problematic status of *Onykia carriboea* within the phylogeny of onychoteuthids has been also observed by Bolstad et al. (2010). According to morphological differences, the possibility of *Onykia carriboea* comprising more than one species is highly likely (Kubodera et al., 1998; Wakabayashi et al., 2007). Further revision for this genus is needed.
As for the ommastrephids, the morphological distinction between early life stages of *Hylaoteuthis pelagica* and *Ommastrephes bartramii* was confirmed by the barcoding analysis. Both species are recorded to occur in the Sargasso

Sea (Diekmann and Piatkowski, 2002). The status of ommastrephids in the phylogenetic trees was largely consistent with recently published results (Dai et al., 2012; Franjević et al., 2015).
The position of the two octopod cephalopod species, *Japetella diaphana* and *Octopus* sp., compared to the decapod species in the phylogenetic trees of this study was highly comparable to previous studies from Carlini et al. (2001). Those intensely examined the phylogenetic relationships of octopods based on COI data.
In the NJ tree, the genera: *Octopoteuthis*, *Ancistrocheirus* and *Pyroteuthis*, were closely grouped which resembles the tree of Carlini and Graves (1999). It would have been interesting to see how the NJ tree would have looked like if the sequences for *Chtenopteryx sicula* could have beeen included. Furthermore, the *Brachioteuthis* spp. specimens could have been sequenced to detect if they affect the phylogenetic branching order.

Conclusion of the Barcoding study
The barcoding analysis represented in this phylogenetic study was helpful for supporting certain species identifications but misleading for especially rare species.
COI represents a gene that is helpful for species identification if a sequence reference set is available but may be problematic for the definition of species boundaries (Allcock et al., 2011), especially if the species diversity is unknown. Even if further sequences should be analysed for a more verifiable statement, a difficulty in identifying cephalopod species only by sequencing the COI gene locus was observed in this study. Sequencing results for the COI gene locus from diverse metazoans showed that approximately 23% of the taxa could not be clustered to their correct species group (Funk and Omland, 2003). Reasons for this observation can be poor morphological species identification, maternal inheritance, incomplete lineage sorting, introgression or other underlying genetic factors (Rubinoff et al., 2006).
From Carlini and Graves (1999) a significantly greater variation in the COI amino acid sequences within the Octopodiformes was reported than for the Decapodiformes, indicating a non-consisting rate of evolution for cephalopods (Strugnell and Lindgren, 2007). Nevertheless, for some species, e.g. *Illex* species from the Atlantic, identification based on COI seems to be more precise than morphological identification (Carlini et al., 2006).

Abundance
In this study a typical oceanic cephalopod community was found, that was dominated by representatives of the families Onychoteuthidae, Enoploteuthidae, Pyroteuthidae, Ommastrephidae and Cranchiidae. The species composition was similar to that one described for the Sargasso Sea by Diekmann and Piatkowski (2002). Similar cephalopod communities were described from other oceanic regions like the southwest Indian Ocean (Laptikhovsky et al., 2015), the Arabian Sea (Piatkowski, 1991; Piatkowski et al., 1993), or the Hawaiian Islands Waters (Bower et al., 1999). The early life stages of Enoploteuthidae, Ommastrephidae and Cranchiidae are the dominating epipelagic cephalopods in tropical oceanic seas (Haimovici et al., 2002).

Concerning cephalopod diversity, the collected paralarvae were exclusively pelagic or mesopelagic species. For the IKMT trawls of the 2014 cruise, the most abundant group was represented by the Onychoteuthidae. Specimens of this family are known to form schools and perform seasonal migrations (Nesis, 1979). As the two research cruises were conducted during the same season of the year, assumptions about the seasonal changes in the distribution pattern of the early life cephalopods are not possible.

The most abundant group of the IKMT catches in 2015 were again onychoteuthids with two co-occurring forms, *Onychoteuthis banksii* and representatives of the possible species complex *Onykia carriboea*. It is quite likely that more than two forms occurred. Further genetic analysis will help understanding the species diversity within the family. Both types are known to be abundant in the subtropical and tropical parts of the Atlantic Ocean (Roper and R. E. Young, 1975; Rosa et al., 2008). It was striking that the onychoteuthids were always in best condition compared to other sampled species which might be attributed to their more muscular body tissues.

Specimens of the family Ommastrephidae were also highly abundant in the samples. which has also been observed from catches of other oceanic regions like the Hawaiian waters (Bower et al., 1998), or the Arabian Sea (Piatkowski et al., 1993). In the western Iberian Sea, off the Portugese coast, ommastrephids were collected between 50 and 300 m and with an increased occurrence at northern latitudes (Moreno et al., 2009).

For the detection of species assemblages along the sample sites, principal component analysis (PCA) was chosen as the ordination method prior to multidimensional scaling (nMDS), because it was based on a chord-distance

matrix, which can deal with the occurrence of "null-abundances" (Legendre and Gallagher, 2001). Both methods minimize the dimensions of the data set with nMDS preserving the distance between the data points and PCA preserving the data point distances. In order to find a model, which could explain the species assemblages in relation to multiple environmental factors, the redundancy analysis (RDA) was chosen.

The analysis of the cephalopod assemblage by PCA revealed a grouping of certain families. The RDA indicated the occurrence of ommastrephid paralarvae near the surface, which underlines their high abundance in upper water layers (Vecchione, 1999). Diel vertical migrations were especially pronounced in families that bear light organs such as pyroteuthids; see RDA results.

According to this study, the paralarval cephalopod assemblage of the Sargasso Sea is comparable to cephalopod groupings from other subtropical or tropical oceanic regions. For example, studies from the Gulf of California (De Silva-Dávila et al., 2015) identified the same teuthoid families except for the Gonatidae, an oegopsid family with many representatives in the Pacific Ocean that was not found in the Sargasso Sea samples, although *Gonatus steenstrupi* is a common squid along the northern mid-Atlantic Ridge (Vecchione et al., 2010).

Within the Sargasso Sea *Pyroteuthis margaritifera* dominated the pyroteuthid family, whereas in the Gulf of California *Pterygioteuthis hoylei* dominated this family (De Silva-Dávila et al., 2013). In comparison to the study on early cephalopod life stages occurring off the north-eastern coast of Brazil and around tropical Atlantic seamounts slightly more enoploteuthids than ommastrephids seemed to dominate in those regions compared to the Sargasso Sea. Nevertheless, family compositions were highly comparable to those of the Sargasso area (Haimovici et al., 2002). In the study from the Hawaiian waters (Bower et al., 1999) where 57 species belonging to 21 families were collected, the diversity seemed slightly lower than in the Sargasso Sea, although thesampling effort was more than double size (10,375 paralarvae). Paralarval species assemblages around the epipelagic waters around Hawaii were similar to those described from the Sargasso Sea (e.g. genera were *Abraliopsis*, *Ancistrocheirus*, *Brachioteuthis*, *Chtenopetyx sicula*). Whereas in the Hawaiian waters two different species of *Enoploteuthis* sp. and *Pterygioteuthis* sp. were reported, in the Sargasso Sea only one species of each genus within was described. The most numerous species were *Ommastrephes bartramii* (18%), *Pterygioteuthis microlampas* (15%), *Chtenopteryx sicula* (8%), and *Onychoteuthis compacta* (6%).

Rare species

Some species were found in very low numbers, probably attributed to the sampling methods. For example, *Vampyroteuthis infernalis* (n=1) which is a deep-sea species, was only collected at the 1,000 m haul and the sepiolid *Heteroteuthis dispar*, a common species in the subtropical Atlantic Ocean (Vecchione et al., 2002), occurred only with three specimens. Other species, like the octopoteuthids, were also collected in small abundances. Specimens were mainly identified as *Taningia danae* or *Octopoteuthis* sp.. One *Lepidoteuthis* sp. specimen was collected. This genus has not been reported from the Sargasso Sea yet. Whether these species are truly rare, meaning widely distributed with patchy abundances (Vecchione et al., 2010), or poorly sampled, remains unclear.

Diurnal variance

Significant differences between day and night catches of the MSM 41 sampling were observed for the cephalopod assemblages and highlighted by MDS plot (Fig. 53). The median amount of sampled specimens highly increased during night as well as the median amount of species numbers, for which the difference was slightly lower between day and night samples (fig 55). Differences between the Shannon-Wiener indices, which were used as a biodiversity measurement, were also lower during day hauls. The Shannon-Wiener index considers species diversity as well as the general abundance of specimens and its decreased difference could indicate that sampling was influenced by diurnal vertical migration of species. Many mesopelagic cephalopods, like pyroteuthids, are known to perform vertically upward migrations (De Silva-Dávila et al., 2013; Roper and R. E. Young, 1975). They migrate into deeper waters during day and ascent to the epipelagic waters during night. Reasons for diurnal migration are predator avoidance as they are less exposed when light conditions are poor and increased feeding opportunities, because prey concentrates in the surface layers during nighttime. With integrated sampling (300 m), assumptions about depth occurrence of cephalopods could be made comparing day and night hauls. SIMPER analysis showed that in species bearing light organs, such as pyroteuthids, enoploteuthids and lycoteuthids, mostly contributed to the differences concerning day and night distribution (table 10). For example, the enoploteuthid *Abralia veranyi* uses its light organs for counter illumination. Thereby, the ventral side of the mantle is covered with photophores that impede the detection from predators hunting beneath the squid with incident moonlight. As photophores are usually dorsally lacking, squids are also camouflaged concerning above hunting predators (Herring, 1977). The influence of diel vertical migration during night time on cephalopods bearing light organs was also shown in the

Redundany analysis (RDA) results (Fig. 53). Thereby photophore-exhibiting species were closely grouped with the environmental variable “night time”.
For the Walther Herwig cruise in 2014, quantitative analysis between night and day hauls cannot be made due to the low number of catches obtained with the pelagic trawls. However, a difference in the species/family composition was visible concerning depth stratification. As ommastrephids dominated the 300 m catches, enoploteuthids were very abundant at the 1,000 m station (Fig. 18). Members of this family are known to undergo daily vertical migrations, which could be a reason why more specimens were collected in the deep layer during daytime (R. E. Young and Harman, 1985).

It has to be kept in mind that net avoiding behaviour can lead to misinterpretation of day and night catches as species occurrences are interpreted as diel vertical migration, but can also result of visual net avoidance during daytime (Ianson et al., 2004). Nevertheless, the SIMPER analysis results strongly support the assumption that differences between day and night catches are due to vertically migrating species.

Conclusion & Outlook

To conclude, a typical oceanic cephalopod community was described for the two expeditions. The thermal front seemed to represent a faunal frontier for several species and a generally higher species and specimen abundance was observed for the northern study area of the Sargasso Sea. It could be shown that sea surface temperature had a strong influence on populations of cephalopod early life stages. Oceanic cephalopods are mobile, actively swimming species and, also due to their planktonic life stages, inhabit different parts of the water column. Differences in species composition and vertical migration patterns are therefore difficult to detect. The information gained from the two research cruises to the Sargasso Sea is based upon the most comprehensive data set available for this area and will help improving the knowledge about the cephalopod assemblages of the western North Atlantic. Further study on paralarval assemblages in other oceanic regions, for example the Indian Ocean, is needed for a more comprehensive knowledge on the world's oceans cephalopod distributions and abundances.

The cephalopods collected in the Sargasso Sea can be used for further projects such as more comprehensive genetic studies, functional morphology studies such as histological examinations or imaging techniques of paralarval characters. It has to be kept in mind that this study represents a "snap-shot" of the Sargasso Sea cephalopod fauna of two following years. This can be, on the one hand, compared to the study conducted 20 years ago (Diekmann and Piatkowski, 2002) which emphasises consistencies in species abundances and distributions. On the other hand, this dataset can be used for future comparisons of this and other areas of the western Atlantic Ocean.

A. Species Tables

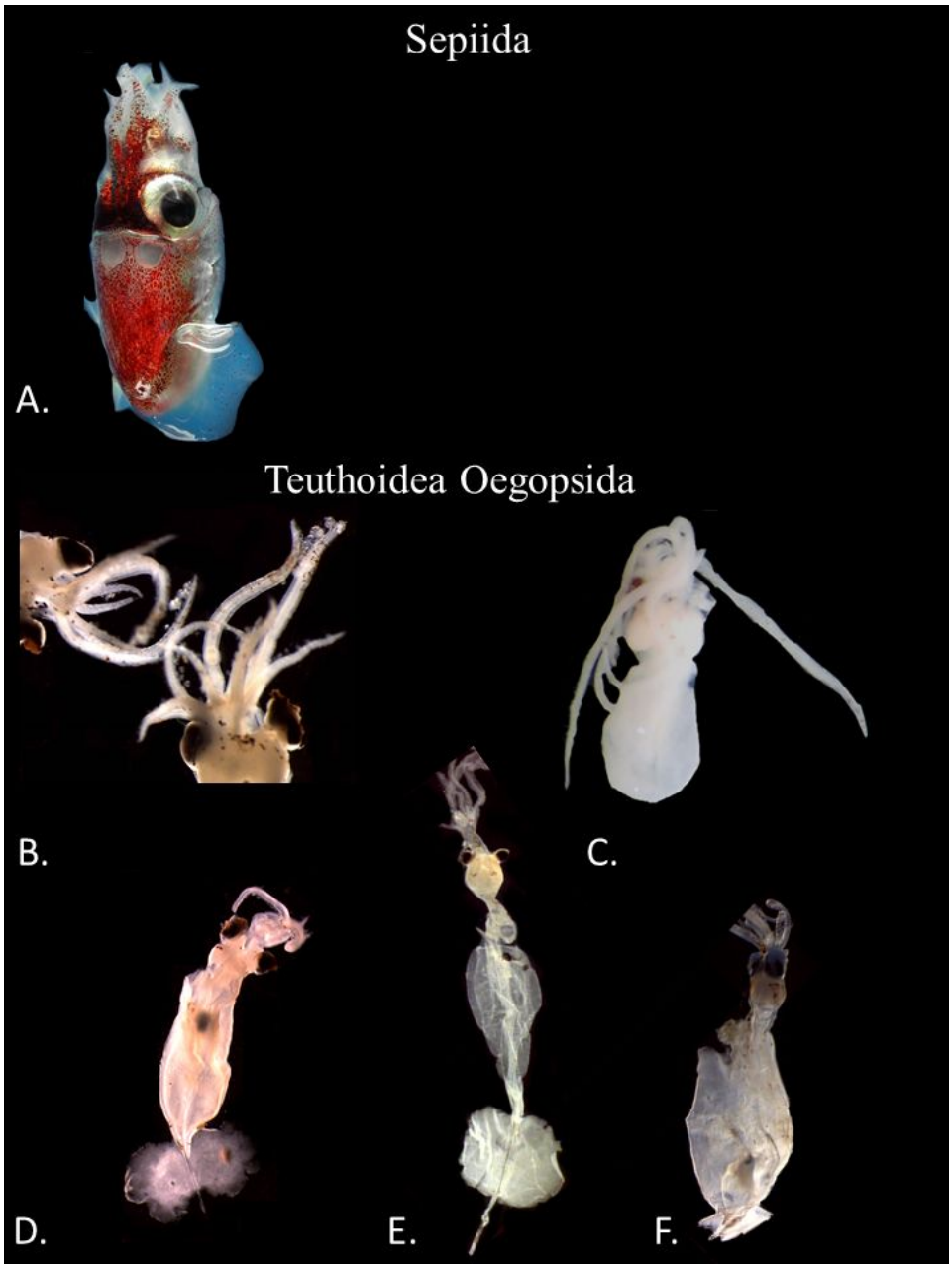


Fig. 59: A. *Heteroteuthis dispar* (5 mm), B. *Ancistrocheirus lesueurii* (3, 4 mm), C. *Architeuthis*-type (2 mm), D. *Brachioteuthis sp.* (11 mm), E. *Chiroteuthis veranyii* (15 mm), F. *Placoteuthis sp.* (17 mm).

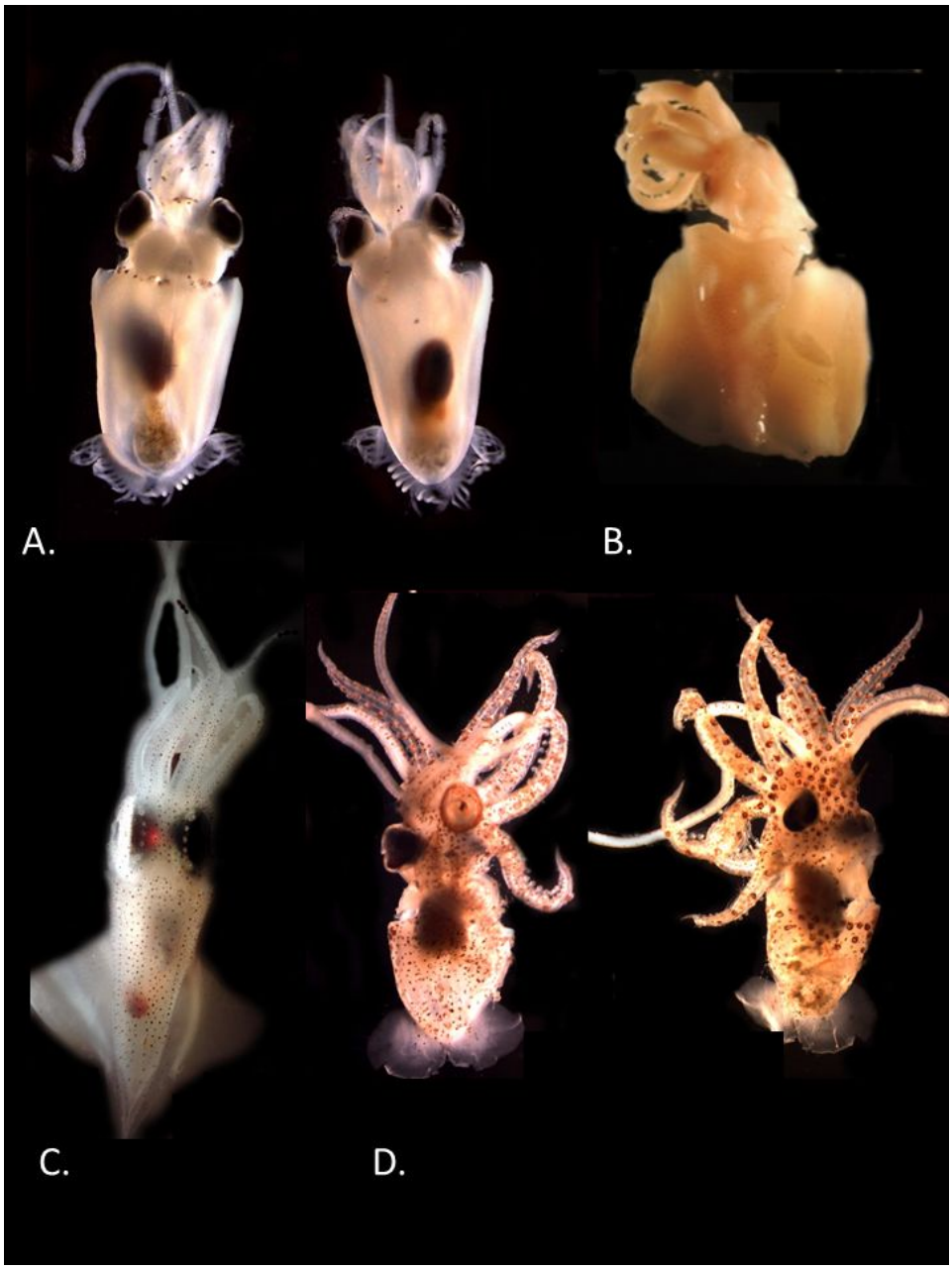


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Fig. 60: A. *Chtenopteryx sicula* (6 mm), B. *Discoteuthis sp.* (15 mm), C. *Abraliopsis morisii* (5 mm), D. *Histioteuthis sp.* (5 mm).

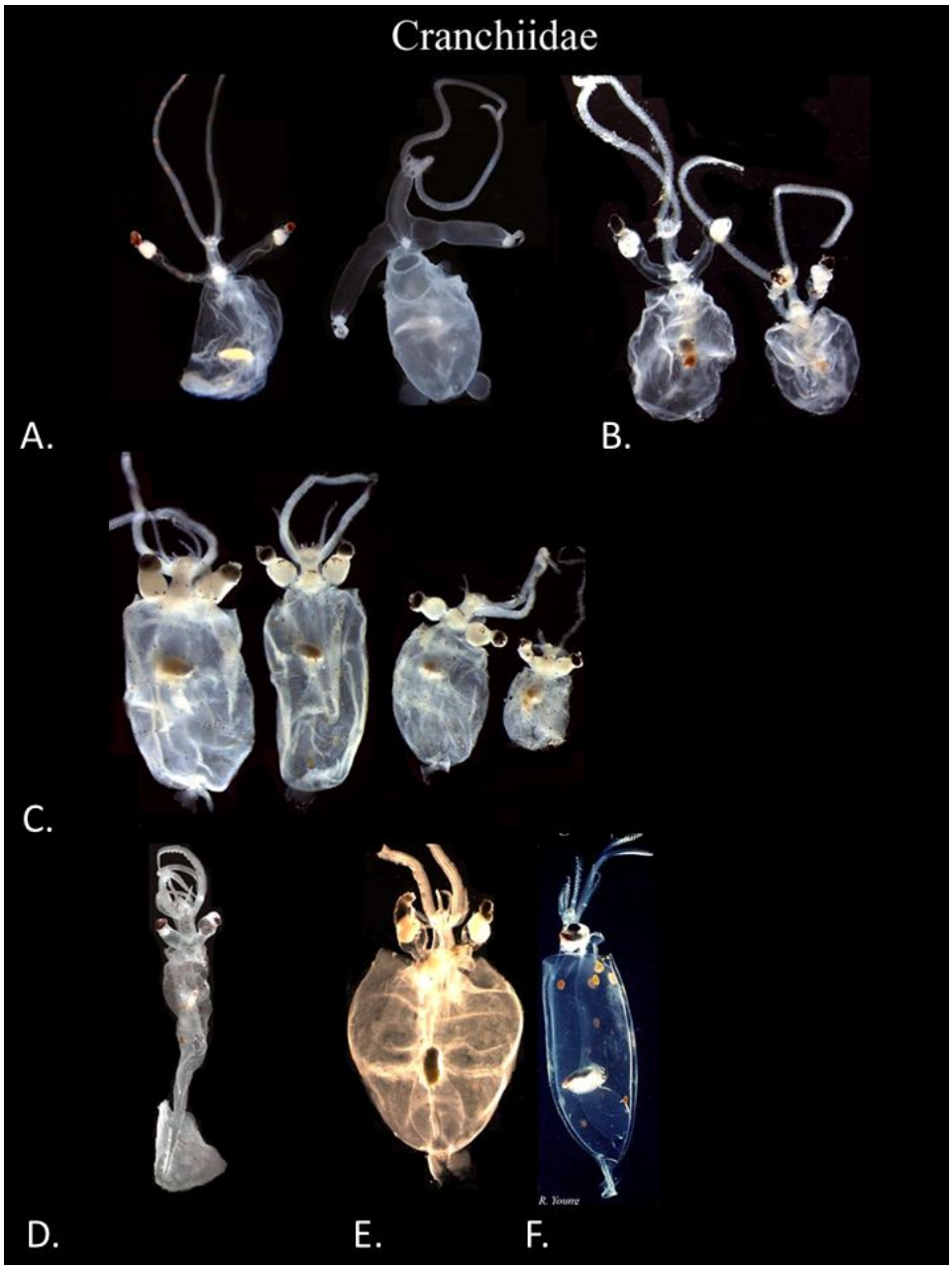

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Fig. 61: A. *Bathothauma lyromma* (8mm, 29 mm), B. *Cranchiidae indet.* (5, 4 mm), C. *Helicocranchia sp.* (3, 8 mm), D. *Leachia sp.* (76 mm), E. *Liocranchia sp.* (12 mm), F.*Megalocranchia oceanica* (20 mm).

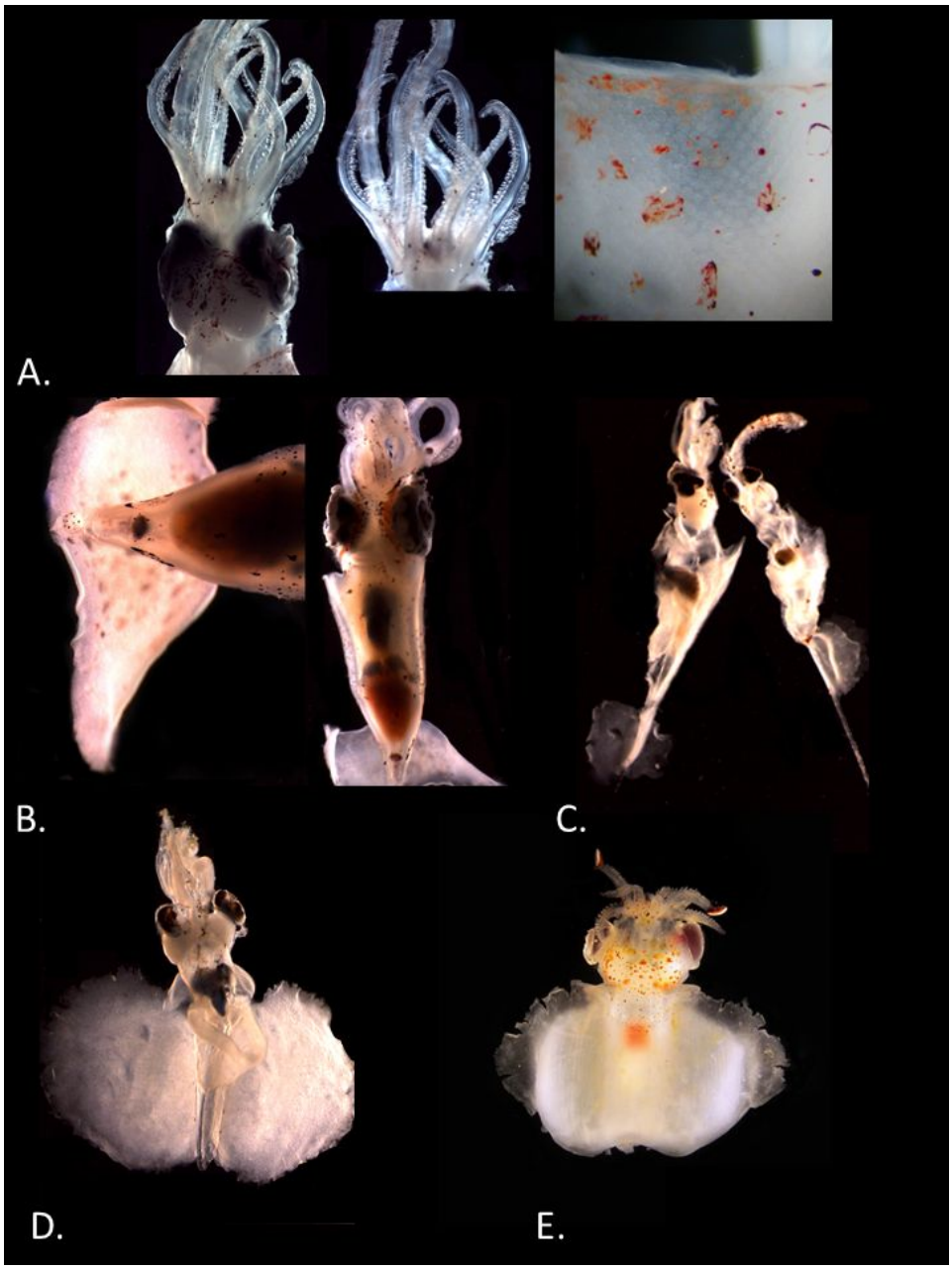

Fig. 62: A. *Lepidoteuthis grimaldii* (20 mm), B. *Selenoteuthis scintillans* (12 mm), C. *Mastigoteuthis sp.* (20 mm), D. *Octopoteuthis sp.* (4 mm), E. *Taningia danae* (15 mm).

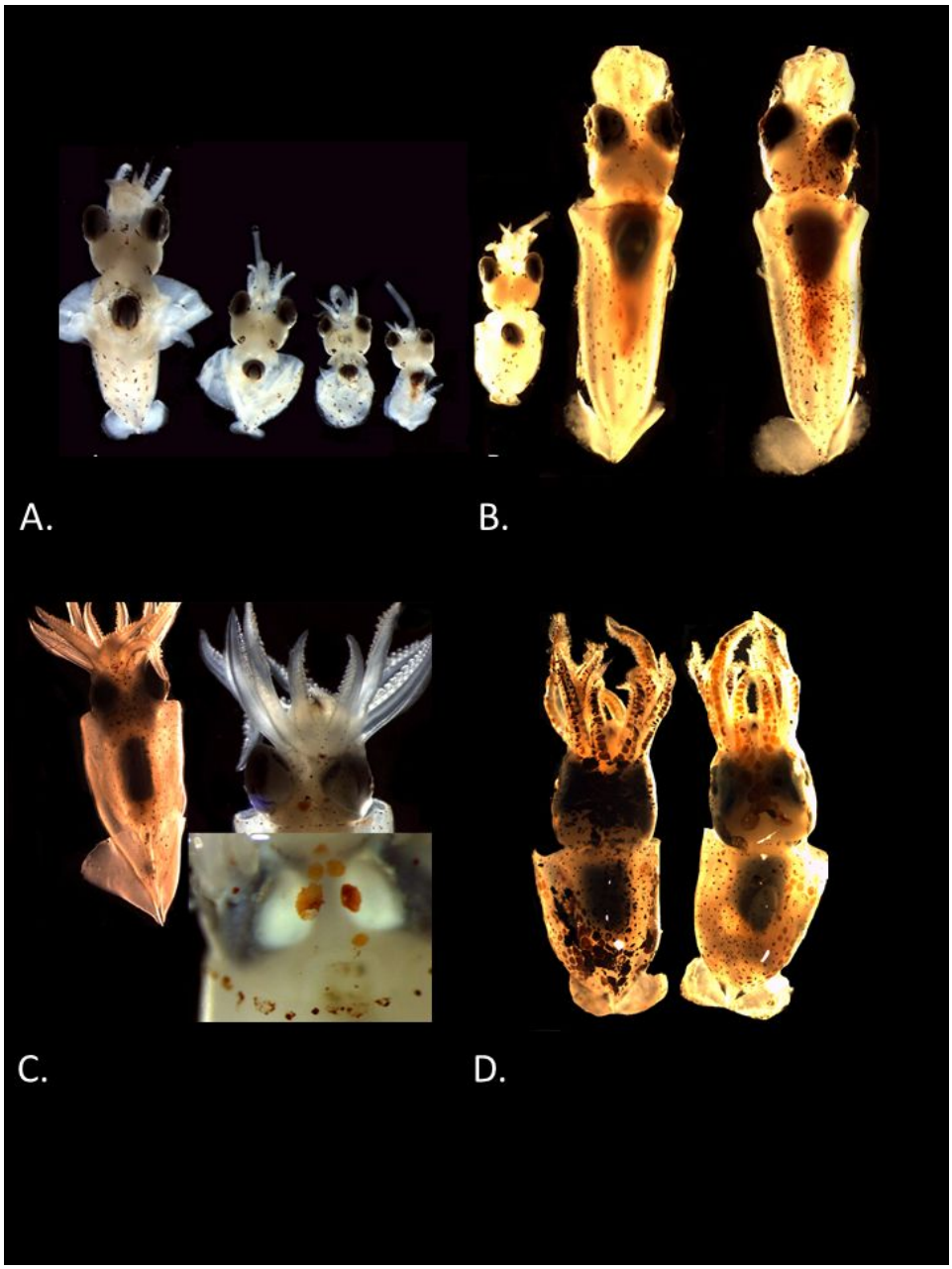

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Fig. 63: A. *Ommastrephes batramii* (2 – 3.5 mm), B. *Hyaloteuthis pelagica* (2- 6 mm), C. *Onychoteuthis banksii* (13.5 mm), D. *Onykia carriboea* (3 mm).

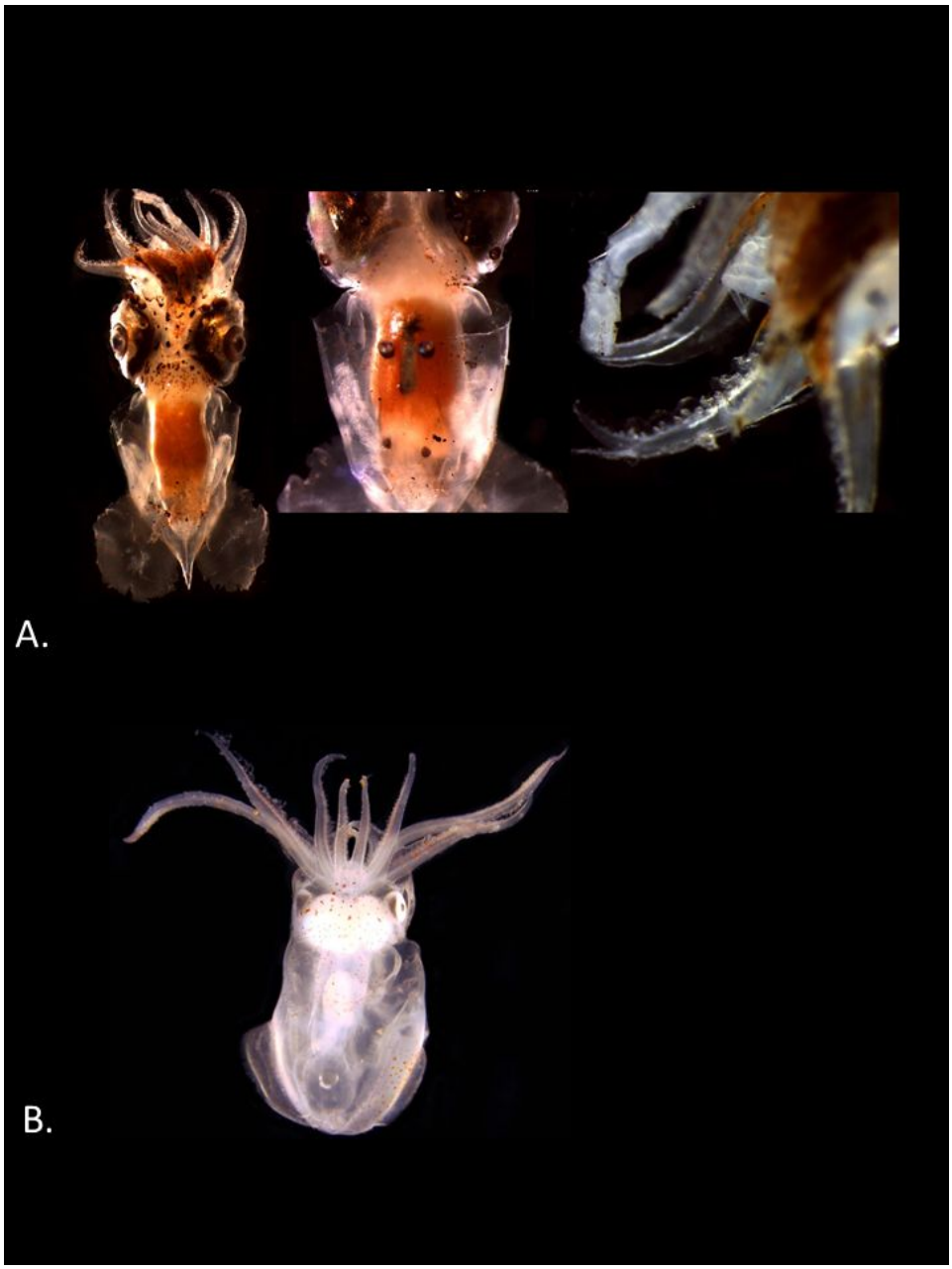

Fig. 64: A. *Pyroteuthis margaritifera* (6 mm), B. *Thysanoteuthis rhombus* (8 mm, U. Piatkowski).

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Fig. 65: A. *Argonauta argo* (4 mm), B. *Vitreledonella richardi* (20 mm; U. Piatkowski), C. *Japetella diaphana* (7 mm, U. Piatkowski), D. *Tremoctopus violaceus* (24 mm, M. Norman), E. *Octopoteuthidae indet.* (3.5 mm), F. *Vampyroteuthis infernalis* (40 mm).

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