Distribution patterns of oceanic micronekton at seamounts and hydrographic fronts of the subtropical Atlantic Ocean

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Chapter I

General Introduction

The pelagic environment of open oceans seems to be the most monotonous habitat on our planet. It is generally characterised by low productivity and a weak horizontal physical structuring. In the vertical plain variability is stronger in the upper parts of the water column, especially in the pycnocline, but small in the meso- and bathypelagic layers. Small physical discontinuities lead to only slight ecological differences at small spatial scales, and few obvious ecological niches exist. At biogeographic scales, Longhurst (1998) distinguished primary (biomes) and secondary hierarchical areas (provinces) of the upper ocean for which unique ecological characteristics may be predicted. His definition of boundaries between compartments is mainly based on observations of primary productivity in the world's oceans, that had become available in the past decades by remote sensing, imaging world-wide sea-surface chlorophyll concentrations. The boundaries between biomes, which stretch around the globe, are mainly congruent with major climatic zones. At this large scale typical latitudinal diversity gradients with high diversity in tropical seas and low diversity in polar regions have been postulated (*e.g.* Rex et al., 1993; Stehli et al., 1969). This latitudinal decline in species richness is particularly pronounced in the pelagic realm rather than in the benthos (Hillebrand, 2004). However, biodiversity patterns may be considerably more complex than was envisaged originally and deviations from this simple latitudinal trend can be found in various regions. As examples, diversity trends are not the same north and south of the equator (Gray, 2001, 2002), and regional 'hotspots' or coldspots' of diversity exist for different marine organisms (Price, 2002; Worm et al. 2003).

According to the Biodiversity Convention (*www.biodiv.org*), biodiversity is defined as ‘the variability among living organisms from all sources including *inter alia*, terrestrial, marine, and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems’. Definitions of biodiversity according to ecosystem structuring have been reviewed by Huston (1994), who emphasised the strong relationship between sampling scale and the processes that influence diversity. At small scales all species are assumed to interact with each other and compete for similar resources. Diversity within habitats has been called alpha diversity (Whittaker, 1960). When at slightly larger scales the sampling covers more than one habitat or community, it has been called between habitat or beta diversity (Whittaker, 1960, 1975). In contrast to this, gamma diversity describes patterns at a regional scale, when not ecological but rather evolutionary processes operate (Whittaker, 1960). According to Levin (1992) there is no single scale at which ecosystems should be described and it is difficult to scale up from the results of small-scale surveys to conclusions that are relevant to ecological patterns and processes at larger spatial scales (Thrush and Warwick, 1997). For the pelagic realm, Haury et al. (1978) were the first who emphasised the importance of scale by expressing the variability of plankton biomass by using a Stommel diagram, a three-dimensional presentation of biomass versus space and time. Stommel (1963) showed that there is an approximate linear relationship between the size and the longevity of eddy structures in the oceans. Any biological distribution patterns with similar space and time scales are, therefore, presumably determined by those hydrodynamic features. Deviating patterns were interpreted as being generated by biological processes like behaviour or recruitment or non-eddy related hydrographic features, such as frontal structures.

Physical gradients in the open ocean: Implications on spatial variability

Hydrographic features are the main abiotic factors influencing the structure of pelagic communities. Changes in distribution patterns and species diversity are expected to be sharpest where there are the strongest discontinuities in the physical environment. These regions characterised by ‘larger-than-average horizontal gradients’ are called fronts (Joyce, 1983). **Fronts** are generally supposed to act as barriers to distribution, although there are a variety of mechanisms of how parcels of water, containing biota, pass from one side to the other (Le Fèvre, 1986). Furthermore, horizontal gradients may be too weak to strictly limit distribution of most species, which make the definition of boundaries difficult. Therefore, fronts can be better described as leaky boundaries, rather than impermeable fences (Longhurst, 1998). Fronts are particularly pronounced where tidally mixed shelf water meets stratified water crossing the continental slope, and are often characterised by high biological productivity (Joyce, 1983; Le Fèvre, 1986). Tidal as well as shelf edge fronts are, however, not part of the present study that rather investigates, among other factors, the implications of **oceanic fronts** on the structure of species communities in the subtropical North Atlantic. In the open ocean two kinds of frontal systems are distinguished: (i) linear convergent zones, usually found at the confluences of two major currents, and (ii) linear features or filaments around or shed from meso-scale eddies. Especially at convergent zones enhanced levels of biomass have been observed (*e.g.* Le Fèvre, 1986). Some oceanic fronts like the conjunction between the cold Oyashio and the warm Kuroshio in the northern Pacific are particularly marked and represent a distinct boundary to the distribution of pelagic species (Hidaka et al., 2003; Nishikawa et al., 1995; Sassa et al., 2002a, b). A homologue feature can be observed in the Atlantic Ocean where the Gulf Stream faces the cold Labrador Current. The subtropical convergence zone of the North Atlantic is characterised by much less pronounced horizontal temperature gradients (Colton et al., 1975; Halliwell et al., 1991b; Voorhis, 1969). The convergence or ‘piling’ of water in these regions, as well as in the Pacific, is caused by a combination of surrounding atmospheric pressure systems, which produce winds that force Ekman transport. The subtropical convergence zone is produced by and thus situated between the eastward-flowing westerlies in the mid latitudes and the westward-flowing trade winds in the tropical latitudes of the North Atlantic. This combination of forces results in an eastward geostrophic flow and in a significant downwelling (Hanson et al., 1991). The concentration of floating organic matter along the front indicates an accumulation of surface-dwelling organisms (Pingree et al., 1974). Whether in these areas of enhanced frontogenesis the species composition and abundance varies or the front rather acts as a boundary to distribution remains largely unknown. The results of former studies were ambiguous. In the northern part of the Sargasso Sea, the thermal stratification of the euphotic zone is restricted to the summer period, which leads to north-south differences in net primary production (Ryther and Menzel, 1960). Correspondingly, higher abundances of mesopelagic fishes, fish larvae, or epipelagic copepods were found north of the subtropical convergent zone, but species compositions did not change consistently crossing the front (Backus et al. 1969; Boettger, 1982; Colton et al., 1975; John, 1984; Miller, 1995).

Strong horizontal gradients related to meso- and large-scale eddies form the second frontal system found in the open ocean. Eddies originate *e.g.* from meandering streams, and large-sized and long-persistent cold-core or warm-core rings can be frequently observed along the major western boundary currents, the Gulf Stream and the Kuroshio. They significantly contribute to primary production in the subtropics and mid-latitudes (Oschlies and Garçon, 1998) and are important mechanism in the exchange of biota across fronts or currents (Ashjian, 1992). The development of meso-scale eddies is on the other hand often related to abrupt topographic features, like islands and seamounts. **Seamounts** are topographic elevations of more than 1000 m above the deep ocean floor and are often of volcanic origin (Epp and Smoot, 1989). Their profile can show slopes up to 60° (Sagalevitch et al., 1992), thus representing a strong bathymetric gradient within the flat abyssal plains. Worldwide, approximately 30000 seamounts exist (Rogers, 1994) that can be found rather isolated or clustered in groups or linear rows, forming the so-called seamount chains. Only few of them have been investigated in detail and one comparatively well-studied seamount is Great Meteor Seamount located in the eastern subtropical North Atlantic, which is one of the core study areas within this work. Seamounts may act as topographic obstacles to the biota (Genin et al., 1988; Rogers, 1994) and to major current systems. Lying in the path of large-scale flows, they will cause current deflections and meanders, occasionally accompanied by the above mentioned eddy formation (Hogg, 1980; Roden and Taft, 1985; Royer, 1978). In addition, most seamounts have their own isolated micro-environment with flow and tracer distributions quite different from the surrounding deep ocean. The complex effects of seamounts on ocean circulation are still poorly understood, which can be partly related to the great diversity in seamount size, shape and distribution. However, recent studies have considerably improved our knowledge on dynamical processes at isolated seamounts and many of the former purely theoretical concepts have been confirmed by field and modelling studies (Beckmann and Haidvogel, 1997; Beckmann and Mohn, 2002; Chapman and Haidvogel, 1992; Mohn and Beckmann, 2002; Owens and Hogg, 1980). One of the basic principles related to isolated topographic features was proposed by Taylor

(1917). He showed that a steady flow impinging on closed depth contours follows isobaths, and a closed circulation forms above this topographic elevation, the so-called Taylor column. Taylor columns, more generally referred to as Taylor caps (Schär and Davies, 1988), have been observed over numerous seamounts including Great Meteor Seamount (Lueck and Mudge, 1997; Meincke, 1971, Mohn and Beckmann, 2002). They are usually accompanied by a pronounced doming of the isopycnals and are supposed to have several implications on the pelagic realm. Taylor columns of shallow seamounts, penetrating into the euphotic zone, could locally enhance primary production and, therefore, provide a significant source of energy for higher trophic levels (Dower et al., 1992). Furthermore, it is hypothesised that they maintain planktonic stages within the area and are, thus, acting as a retention mechanism essential for recruitment of seamount associated organisms (*e.g.* Mullineaux and Mills, 1997; Parker and Tunnicliffe, 1994). The persistence of such closed vortices is, however, critical to the development of *e.g.* fish larvae, and only few examples exist where Taylor caps were present over relevant biological time-scales (Owens and Hogg, 1980; Richardson, 1980). In addition, when they are confined to deeper water layers, Taylor caps may not be an effective retention mechanism to larvae, as highest densities are usually found within or above the pycnocline (Dower and Mackas, 1996). Other relevant hydrographic features at seamounts are the formation of trapped waves (Brink 1990), possibly leading to a dipole-structure of flows rotating anticyclonically over the seamount (Beckmann and Mohn, 2002), or the amplification of tidal currents and locally enhanced turbulent mixing (Eriksen 1991; Kunze and Toole, 1997).

Local upwelling, induced by impinging flows, has been initially presumed to be the responsible factor, governing high concentrations of commercially valuable fish species around seamounts (Rogers, 1994; Uda and Ishino, 1958). The uplifting of isotherms into the euphotic zones as a result of Taylor cap formation can introduce nutrient-rich waters into near surface layers and cause an increase in primary productivity. However, evidences for enhanced primary productivity over longer time periods remain scarce (Dower et al., 1992; Genin and Boehlert, 1985; Rogers, 1994), and other theories developed on how high standing stocks of fish are sustained. The most important hypothesis was first introduced by Isaacs and Schwartzlose (1965), who supposed that dense populations of fish fed upon diurnally migrating zooplankton that is swept onto seamounts by prevailing currents. Downwardly migrating zooplankton trapped over the seamount might be exposed to an increased predation pressure and, hence, gaps devoid of vertically migrating organisms develop every evening over abrupt shallow topography (Genin et al., 1988, 1994; Haury et al., 1995, 2000). This process would significantly increase the patchiness in the pelagic zone and would be a contrasting mechanism to the retention of organisms due to closed circulation cells and the increase of plankton biomass due to enhanced productivity. Consequently, equivocal descriptions of ‘seamount effects’ on the distribution of ichthyoplankton or mesozooplankton exist in the literature, as higher, lower or equal biomass was measured above seamounts in comparison to the adjacent open ocean (Dower and Mackas, 1996; Fedosova, 1974; Genin et al., 1994; Huskin et al., 2001; Nellen, 1973).

Finally, seamounts are perceived as areas of enhanced speciation rates and endemism. Speciation could be the result of geographic and reproductive isolation. Seamount populations can be separated from external populations by geographic distance and by hydrographic conditions that retain planktonic life stages within the vicinity of the spawning area and, thus, allowing self-recruitment (*e.g.* Taylor columns). 15% of all benthic species occurring at seamounts are considered as potential endemics (Wilson and Kaufmann, 1987) and recent studies even estimated that 29-34% of all species are new to science (Richer de Forges et al., 2000). Ehrich (1977) investigated three fish species at Great Meteor Seamount for morphological divergences between the seamount and the African Shelf population and concluded that the species are separated. Seamounts appear to provide ‘stepping stones’ to the trans-oceanic dispersal of species via active swimming behaviour or the passive drift of planktonic life stages to other shallow topographic regions, which, therefore, serve as ‘way stations’ for expanding populations.

Fish and cephalopods: Key players of the micronekton

The micronekton includes a large group of organisms, which are defined by their size and swimming capacity. A working definition of micronekton includes all mobile organisms that are capable to withstand significant current speeds and which have a size range from ~1-2 cm to ~12.5 cm (Pearcy, 1983 and reference therein). This comprises, among others, larval and juvenile fish, small pelagic fish (including mesopelagic species of the deep sound scattering layers), krill, and small cephalopods. Micronektonic organisms are an important component of oceanic ecosystems and are, like plankton and fish, structured in complex three-dimensional spatial patterns at all scales in the ocean, from metres to hundreds of kilometres.

Within the present study special attention is paid to representatives of two taxonomic groups whose adult states are dominating the oceanic nekton: Cephalopoda and bony fishes (Osteichthyes). Next to sharks, rays and marine mammals, both are among the dominant predators in the ocean. The hatchlings of both groups are usually pelagic and are accounted to the plankton community. They are characterised by weak swimming capabilities and can be viewed as passively drifting particles. They are, thus, directly subjected to ocean currents, which can influence the formation, maintenance or disruption of species assemblages. During larval development and with increasing mobility cephalopods and fish can be assigned to the micronekton or more generally to the nekton community. Many mesopelagic species of both groups do not exceed the above-mentioned size range and are consequently accounted to the micronekton throughout their entire life. Mesopelagic species dominate oceanic ichthyoplankton assemblages in various parts of the oceans (*e.g.* Cha et al., 1994; Nellen, 1973; Olivar, 1990; Richardson et al., 1980; Sassa et al., 2002b). Their larval stages are primarily found in the productive epipelagic zone, within the upper 200 m of the water column (Ahlstrom, 1959; Sassa et al., 2002b). 30 mesopelagic fish families have been described so far, of which Sternoptychidae (49), Stomiidae (228) and Myctophidae (235) were the most speciose (Nelson, 1994).

The class Cephalopoda is a small taxonomic group that is known to comprise about 700 species (Nesis, 2003) and is grouped into two subclasses, the outer shell bearing Nautiloidea and the Coleoidea containing the squids, cuttlefish, octopods and vampire squids. The coleoids are short lived, carnivorous animals that have rapid growth rates and occupy a wide variety of ecological niches in the pelagic open ocean, where highest diversification is found. However, in contrast to ecologically similar fishes even the most abundant cephalopod species seem underrepresented in samples of any size. The investigation of small-scale spatial distribution patterns poses, thus, additional difficulties as many samples do not contain any individuals and between-sample variability is consequently high. The early life stages of many species are virtually unknown, which makes the taxonomic investigation of cephalopods captured by plankton nets or small trawls problematic. Hence, an identification key was developed during the course of this study that specifically illustrates early life stages found around the investigated seamounts of the subtropical North-East Atlantic (see Appendix). It was based on available information from Sweeney et al. (1992), Nesis (1987) and Roper et al. (1984), but own descriptions and illustrations were added for a more comprehensive species characterisation. The following chapters depend on the exact identification of species and the key was, thus, an important tool to adequately describe distribution patterns.

The ontogenetic development of cephalopods is different from fish, and their planktonic young are often referred to as 'paralarvae' (Young and Harman, 1988). This term has been chosen, as many cephalopods do not go through a metamorphosis according to the definition of Geigy and Portmann (1941). Von Boletzky (1974) argued that cephalopods, in contrast to other molluscan groups, often have planktonic stages whose distinct 'larval characters' involve differences in morphometrics, but not in basic morphology. Young and Harman (1988) defined a paralarva as a cephalopod of the first post-hatching growth stage that is, similar to most fish species, pelagic in near-surface waters. Paralarvae are not supposed to perform diel vertical migrations (Vecchione et al., 2001) and, thus, have a distinctively different mode of life from that of older conspecific individuals. During their ontogenetic development many species move deeper into the water column (*e.g.* Griswald and Prezioso, 1981), and Roper and Young (1975) estimated that juvenile specimens generally exhibit the same distributional patterns as the adults.

Focus of the present study

The present work elucidates the heterogeneity in spatial distribution patterns of oceanic micronekton communities with respect to hydrographic and topographic gradients. All the investigated areas within this study are located in the subtropical North Atlantic (Fig. I.1), in the eastern or in the western part of the ocean basin, and are restricted to the 'North Atlantic Subtropical Gyral Province' (Longhurst, 1998). This province does not include the continental shelf and is only topographically disturbed by the island platforms of Bermuda, the Azores, the Canaries, as well as by the Mid-Atlantic Ridge and numerous seamounts. The work focuses on micronektonic cephalopods, their early life stages, and larval fish distribution patterns, which are partly investigated in parallel. The following chapters each highlight certain aspects of how pelagic assemblages are structured along physical gradients. Four major questions are addressed in each investigation area: (i) What species are present? (ii) What are the main distribution and abundance patterns, vertically as well as geographically? (iii) How and why did the patterns develop? (iiii) Do distinct species assemblages exist with some relation to topography and hydrography? An overview is given on small- to meso-scale spatial variability and, thus, to alpha and beta diversity patterns in different oceanic environments. Furthermore, early life stages of cephalopods occurring in the investigated regions are documented and illustrated in an identification key (see Appendix).

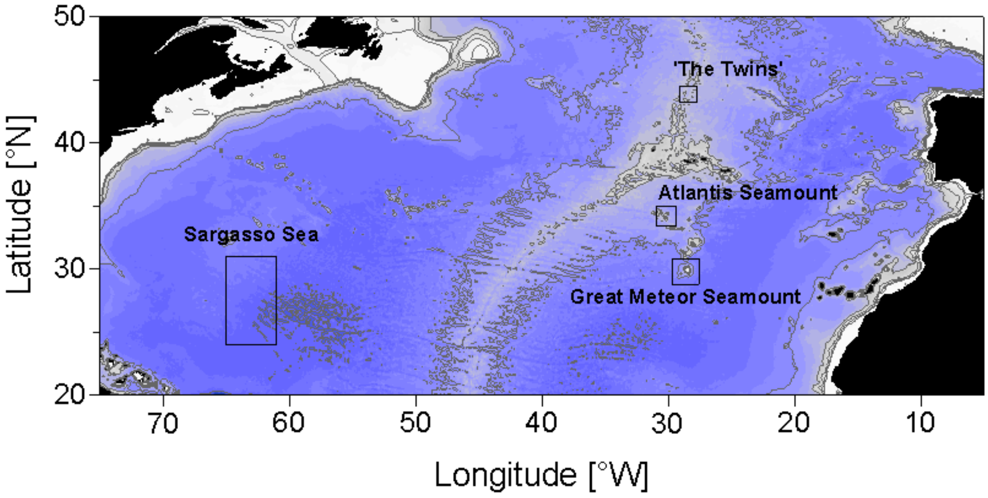

Fig. I.1: Investigation areas of the present study.

In the second chapter the influence of an oceanic front on the community composition of paralarval cephalopods in the Sargasso Sea is investigated. In the western North Atlantic the transition between the prevailing westerlies and the trade winds from the east drives convergences in surface waters, the Subtropical Convergence Zone (Halliwell et al., 1994; Voorhis, 1969). It separates the Sargasso Sea into a cooler, more-productive northern part and a warmer, less-productive southern part. The influence of this front on oceanic cephalopods in terms of community composition and abundance remained so far unclear. Hence, the cephalopod fauna based on paralarvae collections in relation to hydrographic features was investigated. The focus was to determine whether changes occur gradually or abruptly and to evaluate the importance of the Subtropical Convergence Zone as an ecological boundary.

Chapter III to V concentrate on the effects of abrupt shallow topographic features like seamounts on pelagic communities. The fieldwork was conducted at three seamounts of the subtropical eastern North Atlantic. The most extensive sampling was performed at Great Meteor Seamount during a multidisciplinary research cruise of RV Meteor (cruise M42/3). Great Meteor Seamount is one of the largest topographic elevations in the eastern North Atlantic and is widely isolated from other seamounts, islands or continental shelfs. In the course of the field sampling extensive hydrographic measurements were performed, thus allowing a detailed description of the complex topographic effects on ocean circulation.

Within the seamount studies, the third and fourth chapter emphasise distribution patterns of early life stages of cephalopods in the vertical as well as in the horizontal plain, partly including results from larval fish distribution. Paralarval cephalopods and larval fish are only to a certain extend capable to migrate actively within their three-dimensional environment. They are, thus, directly influenced by the current system that was affected by the seamount in numerous ways. The early life stages were sampled by a vertically resolving multi opening-closing net applied above the summit, the slope and in the adjacent open ocean. The third chapter gives a detailed overview about the cephalopod species composition in the area of Great Meteor Seamount. Vertical distribution patterns and diel vertical migration behaviour of selected taxa are investigated. The effect of seamount topography was tested in two different ways: (i) The vertically resolved abundances were compared between stations located above the plateau and in the open ocean; (ii) A non-metric multivariate analysis was performed to investigate the station specific species community in relation to topography and hydrographic features. In the fourth chapter a different approach was used to identify effects on the pelagic community induced by Great Meteor Seamount. Data for larval fish and paralarval cephalopods were combined and analysed by multivariate methods based on Principal Component Analysis and its canonical extension, Redundancy Analysis. Fine-scale spatial structuring of species assemblages were determined in the vertical and horizontal plain and were discussed in relation to aggregation, maintenance and disruption processes relevant at the seamount. In addition, the importance of Great Meteor Seamount as habitat to resident fish and cephalopod stocks and local recruitment is evaluated.

The fifth chapter deals with the distribution of micronektonic cephalopods at three different seamounts. Samples were collected with a pelagic Youngfishtrawl at Great Meteor Seamount, Atlantis Seamount and a smaller topographic feature called 'The Twins', all located in the eastern North Atlantic. Most oceanic cephalopod species represent highly mobile squids and, thus, during this part of the study less emphasis was given to the influence of small-scale oceanographic conditions but rather to the importance of seamounts as topographic obstacles. For this purpose a model was developed describing the vertical distribution patterns of dominant species in relation to daytime and water depth. On this basis the physical interaction of selected species with the upper slope and plateau is determined and the impacts on species ecology are discussed. Finally, the hypothesis of a seamount specific cephalopod fauna is investigated by comparing the three sampling locations.

Chapter II

Early life stages of cephalopods in the Sargasso Sea: Distribution and diversity relative to hydrographic conditions

Abstract

The distribution of early life stages of cephalopods was studied during a cruise of the German RV Poseidon to the Sargasso Sea in March 1993, covering an area south-east of Bermuda from 24°N to 31°N and 61°W to 65°W. Hydrographic measurements were carried out by conductivity, temperature and depth casts (CTD) and expendable bathythermographs (XBT). The subtropical convergence zone was detected at a latitude of approximately 27°20'N and divided the Sargasso Sea into a northern and a southern area. Zooplankton sampling with a 6m² Isaac-Kidd midwater trawl and Bongo nets yielded a total catch of 909 specimens of early life stages of cephalopods, representing at least 13 families and 20 mainly oceanic species. Multivariate statistical analyses were performed in order to compare the species composition and abundance of cephalopods. Two different assemblages were clearly identified, north and south of the front. According to the position of the front an analysis of similarity (ANOSIM) was applied, which confirmed the observed differences in species composition at a highly significant level. The Cranchiidae, mainly represented by the endemic species *Leachia lemur*, was the most abundant family, especially in the northern part of the Sargasso Sea, and was mainly responsible for the distinction between the cephalopod assemblages. In general, higher abundances of early life stages and a higher diversity were observed north of the subtropical convergence zone, which is assumed to form a faunal boundary.

Introduction

Central oceanic regions such as the Sargasso Sea have traditionally been thought to be low productive areas and have been compared with terrestrial deserts (Ryther, 1963). Recent studies have shown that this assumption is partially wrong. In historical data sets the primary production in the oligotrophic central gyres has been underestimated by a factor of 2-4 (Goericke and Welschmeyer, 1998), though productivity and biomass are still relatively low. A contrasting view is that the Sargasso Sea is characterised by a dynamic phytoplankton community, with low biomass but high growth rates that are balanced by high rates of grazing (Goldman, 1993; Jackson, 1980). Compared to slope and shelf waters, however, the Sargasso Sea shows consistently lower biomass concentrations in zooplankton (Ashjian et al., 1994; Deevey, 1971; Deevey and Brooks, 1977; Ortner et al., 1978; Wiebe et al., 1985). The distribution is less patchy and the average mean depth of the biomass concentration is similar during both day and night (Ashjian et al., 1994).

The Sargasso Sea, however, is not a homogeneous oceanic region. It lies within the North Atlantic Subtropical Convergence Zone (STCZ), a transition zone between the prevailing westerlies and the easterly trades (Halliwell et al., 1994; Voorhis, 1969). The convergence zone is characterised by enhanced meridional gradients of near-surface temperature and a decreasing depth of the upper (seasonal) thermocline from south to north (Halliwell et al., 1994). During winter and spring an extensive large-scale thermal front develops, which meanders in east-west direction (Voorhis, 1969; Voorhis and Hersey, 1964). The thermal gradient is only marginally detectable during summer (Halliwell et al., 1991b), but there is also some evidence that the front may persist throughout the year (Backus et al., 1969; Colton et al., 1975). It separates the central part of the Sargasso Sea into a cooler, more-productive northern part and a warmer, less-productive southern part. The enhanced primary production north of the front, which may be up to ten-times higher than in the south, may be due to a deeper winter mixing compared with a stronger stratification of the water column south of it (Ryther and Menzel, 1960). In correspondence with the differences in productivity, a general decline in abundance and differences in species composition has been observed in north-south direction, *e.g.*, epipelagic copepods (Colton et al., 1975) and mesopelagic fishes (Backus et al.,1969).

Cephalopods have been frequently investigated in the western North Atlantic, but hardly any work has been performed in the Sargasso Sea. Expeditions at the beginning of the last century investigated the cephalopod fauna around Bermuda (*e.g.*, Berry, 1920; Peile, 1926; Pfeffer, 1912), but the number of hauls and the catchability of their nets were limited. The first intensive study was carried out by Voss (1960), who described the cephalopod fauna around the Bermudian islands. Catches with different net types yielded 21 cephalopod species, of which at that time only three had previously been reported from that area; however, detailed distribution patterns were not analysed. Since then the cephalopod fauna of the oceanic parts of the western North Atlantic have not been further studied. Investigations have concentrated rather on the Florida Current (Cairns, 1976; Lea, 1984) and the Gulf Stream system (Dawe and Stephen, 1988).

In the present paper the cephalopod fauna of the Sargasso Sea is examined for the first time. In order to reduce avoidance effects and to ensure a nearly quantitative sampling (Piatkowski, 1998), early life stages of cephalopods have been considered. The sampling was conducted with two different standard zooplankton nets (IKMT6, Bongo), essentially in north-south directions, and, thus, crossing the STCZ. Distribution patterns of oceanic cephalopods are described, and species assemblages are identified. Observed spatial differences in species composition are discussed with regard to hydrographic features of the region.

Materials and Methods

Sampling

Data were collected in the Sargasso Sea during the RV Poseidon cruise 200/1 in March 1993, which had been initiated to detect spawning grounds of the European eel *Anguilla anguilla* (Schnack et al., 1994). Stations were located south-east of Bermuda, covering an area from 24°N to 31°N and 61°W to 65°W (Fig. II.1). Early life stages of cephalopods were sampled using a Bongo net (500 µm mesh size, 27 hauls), essentially on a north-south transect at 62°W, and an Isaac-Kidd midwater trawl (IKMT6, 300 µm mesh size, 11 hauls at 9 stations). The Bongo net was towed for approximately 90min at downward oblique hauls between 100 m depth and the surface. The IKMT6 was applied in different depths from 300 m to 80m; towing time was approximately 60min. Ship speed during sampling was kept at 3 kn. Filtered water volumes were estimated using calibrated flowmeters, which were mounted in the centre of the net openings. All samples were initially preserved in 4% formalin, buffered with borax. Cephalopods were sorted and identified to the lowest taxonomic level possible. Cephalopod densities (N/1000m³) were then estimated and used in the initial species-station table for the spatial analysis of cephalopod community structure.

Hydrographic data were collected using expendable bathythermographs (XBTs; 10 stations) and conductivity, temperature and depth casts (CTD, model ME OTS 1500; 38 stations). XBTs were only deployed on the northern part of the 65°W transect (not illustrated in Fig. II.1). The CTD was launched at all other stations, always in advance of the zooplankton tows.

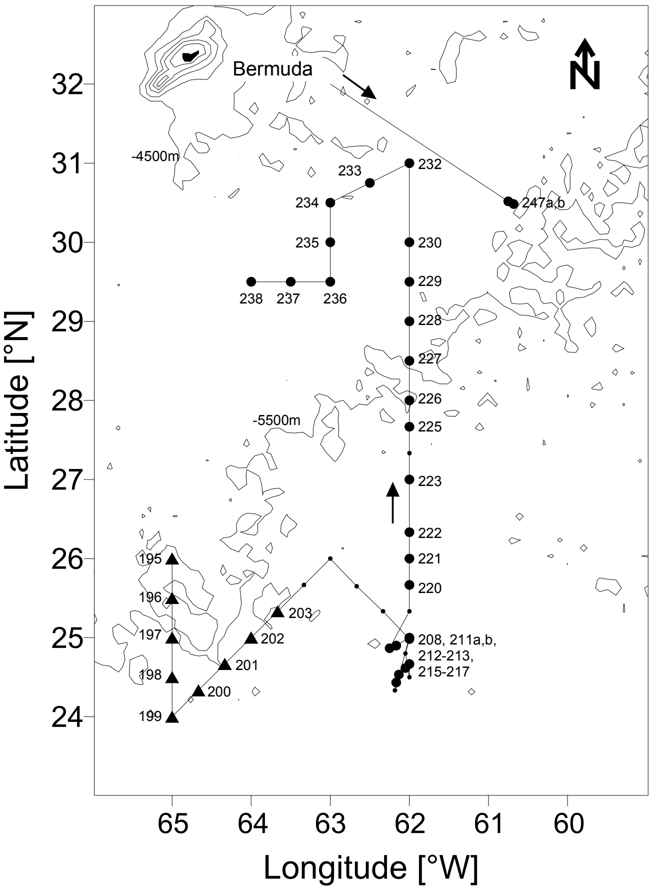

Fig. II.1: RV Poseidon cruise 200/1, March 1993. Sampling area in the Sargasso Sea. Bold points represent Bongo hauls, triangles IKMT6 hauls. CTD was applied on all marked stations.

Data analysis

Multivariate statistical analyses were performed to examine differences in species composition and abundances of early life stages of cephalopods. IKMT6 hauls were not included in these analyses, since only a few hauls in the southern Sargasso Sea were performed. Prior to analysis, the densities of cephalopod species (N/1000m^3) at each 'Bongo station' were fourth-root transformed. The transformation reduced the weighting of dominant species and increased the importance of rare ones (Field et al., 1982). The similarity between stations was calculated by means of the Bray-Curtis measure (Bray and Curtis, 1957; Field et al., 1982). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method and ordinated using non-metric multi-dimensional scaling techniques (MDS; Kruskal, 1964).

According to the prevailing hydrographic regimes, the Sargasso Sea was separated into a northern and a southern region divided, by the position of the thermal front (see results). The cephalopod catches in these two regions were compared using different subroutines of the Primer-E. (5) computer program (Clarke and Warwick, 2001). Analysis of similarities (ANOSIM; Clarke and Warwick, 1994) was employed to test for differences in species composition between the two areas. In cases when the ANOSIM showed significant results, the similarity percentage routine (SIMPER; Clarke and Warwick, 1994) was applied to examine which cephalopod species were most responsible for contrasts in the community analysis. In addition various univariate indices, the Magalef species richness index (D), the Shannon-Wiener diversity index (H') and Pielou´s evenness index (J), were calculated for the samples north and south of the thermal front.

Results

Oceanographic conditions

Oceanographic data were measured on two transects in a north-south direction from 24°N to 31°N at a longitude of 65°W and 62°W, respectively. On both sections a sharp near-surface temperature gradient was detected, which demonstrated the location of the thermal front. South of the front the water was stratified, whereas northward the surface layer was mixed. In Fig. II.2 the temperature profile at 62°W, the transect of intensive sampling, is illustrated. The temperature gradient was encountered at approximately 27°20'N. South of this front the 21°C isotherm was measured below 100 m water depth. To the north this isotherm reached the surface at approximately 29°30'N. The northern area was characterised by a mixed layer of approximately 50-100 m depth. At 65°W the stratification in the southern area was slightly intensified, and the most pronounced temperature gradient was again found at approximately 27°20'N.

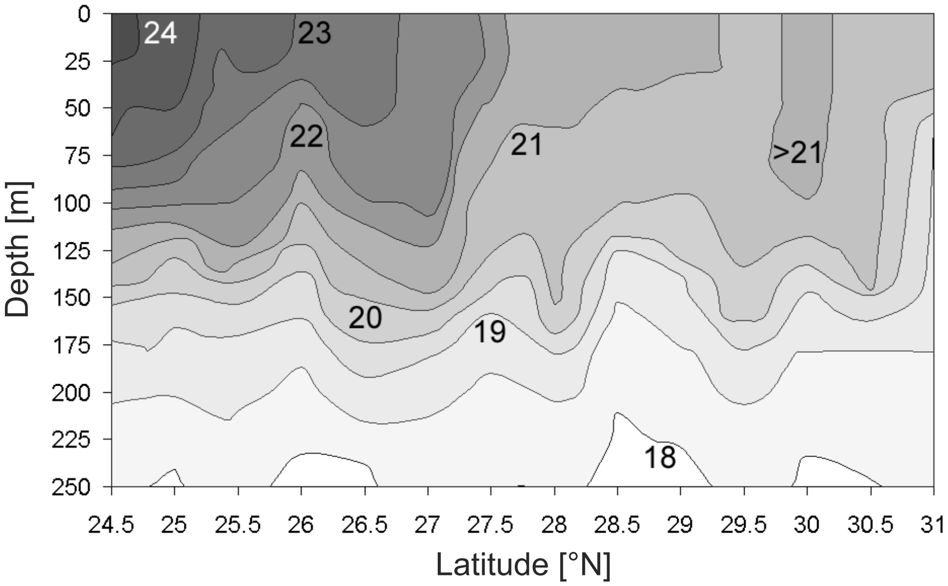

Fig. II.2. RV Poseidon cruise 200/1, March 1993. North-south temperature section at 62°W from 250 m water depth to the surface.

Cephalopod families and major species

A total of 909 specimens of early life stages of cephalopods were caught in 11 IKMT6 and 27 Bongo hauls. 13 families and 20 species were identified (Tab. II.1). Since many specimens could only be assigned to higher taxa, the number of families and species must be considered as minimal. All specimens belonged to the Oegopsida and the incirrate Octopoda. In the Bongo hauls the Cranchiidae were dominant (38.2%), mainly represented by the endemic species *Leachia lemur*. The Enoploteuthidae and the Onychoteuthidae were moderately abundant, with 18.2 and 9.0%, respectively. In terms of density the most abundant species were *L. lemur* (0.72 ind. per 1000m^3), followed by *Abraliopsis pfefferi*

(0.38 ind. per 1000m³), *Onychoteuthis banksii* (0.26 ind. per 1000m³), *Megalocranchia* sp. (0.22 ind. per 1000m³) and *Selenoteuthis scintillans* (0.21 ind. per 1000m³).

Specimens sampled with the IKMT6 were generally larger compared to specimens from the Bongo catches. With the exception of *Thysanoteuthis rhombus*, which was only found in the IKMT6 samples, the same species were identified in the collections of both net types; however, the relative composition was different. Highest abundances in the IKMT6 samples were observed for the Enoploteuthidae and Onychoteuthidae, each comprising 21.6% of the total catch. Rhynchoteuthion stages of Ommastrephidae accounted for 15.7%. Cranchiidae were less abundant (9.9%) and were dominated by *Helicocranchia* sp, mainly identifiable as *H. papillata*. Species densities were not calculated because of inaccurate flowmeter readings. Differences in the total abundance of early life stages in day- or night-time samples were not detected. Therefore, diel effects on the catchability of the two nets were not taken into consideration.

Tab. II.1. Early life stages of cephalopods collected during the RV Poseidon cruise 200/1, March 1993. Numbers of higher taxa only include specimens that could not be further identified, N_{abs}: total catch in numbers; rel. N [%]: percentage of total catch according to gear type; mean species density: N/1000m³ (only Bongo net).

Order, Family	Species	Bongo net			IKMT 6	
		N_{abs}.	Rel. N [%]	N/1000m³	N_{abs}.	Rel. N [%]
Order Teuthida						
Sub-O. Oegopsina	Oegopsina indet.	50	9.36	7.22	52	13.87
Family Ancistrocheiridae	*Ancistrocheirus lesueurii*	4	0.75	0.60	5	1.33
Family Brachioteuthidae	*Brachioteuthis* sp.	8	1.50	1.24	2	0.53
Family Chiroteuthidae	*Chiroteuthis* sp.	8	1.50	1.10	3	0.80
Family Chtenopterygidae	*Chtenopteryx sicula*	3	0.56	0.57	5	1.33
Family Cranchiidae	Cranchiidae indet.	3	0.56	0.42		
Cranchiinae	*Leachia lemur*	126	23.60	17.59	6	1.60
Taoninae	Taoninae indet.				5	1.33
	Helicocranchia papillata	24	4.49	4.10	15	4.00
	Helicocranchia sp.	10	1.87	1.28	2	0.53
	Taonius pavo	3	0.56	0.88	1	0.27
	Megalocranchia sp.	38	7.12	5.25	8	2.13
Family Enoploteuthidae	Enoploteuthidae indet.	27	5.06	4.13	51	13.60
	Enoploteuthis leptura leptura	3	0.56	0.56		
	Abraliopsis pfefferi	67	12.55	10.34	30	8.00
Family Lycoteuthidae	*Selenoteuthis scintillans*	36	6.74	5.65	19	5.07
Family Ommastrephidae	Ommastrephidae indet.	13	2.43	1.94	25	6.67
Ommastrephinae	*Ommastrephes bartramii*	7	1.31	1.12	16	4.27
	Hyaloteuthis pelagica	6	1.12	0.96	18	4.80
Family Onychoteuthidae	*Onychoteuthis banksii* complex	45	8.43	6.96	70	18.67
	Onykia cariiboea	3	0.56	0.48	11	2.93
Family Pyroteuthidae	Pyroteuthidae indet.	4	0.75	0.55	7	1.87
	Pyroteuthis margaritifera	29	5.43	5.37	18	4.80
	Pterygioteuthis giardi giardi	8	1.50	1.20	1	0.27
Family Thysanoteuthidae	*Thysanoteuthis rhombus*				2	0.53
Order Octopoda						
Family Argonautidae	*Argonauta argo*	6	1.12	0.83		
Family Tremoctopodidae	*Tremoctopus violaceus violaceus*	3	0.56	0.42	3	0.80
Sum		534			375	

Distribution of cephalopods in relation to the thermal front

The investigation of early life stages of cephalopods in the Bongo hauls revealed marked north-south differences in abundance. North of the thermal front, at 27°20'N, densities of cephalopods increased from an average of 1.70 ind. per 1000m³ in the southern part of the Sargasso Sea to 4.03 ind. per 1000m³ in the north (Fig. II.3). Highest abundances were encountered north of 29°N, with a maximum of 8.92 ind. per 1000m³.

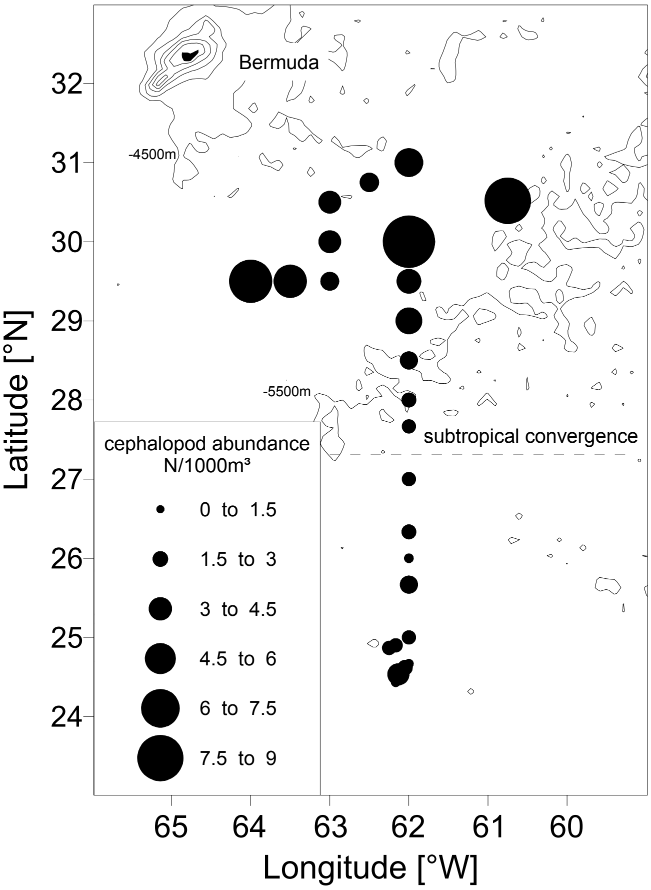

Fig. II.3. RV Poseidon cruise 200/1, March 1993. Densities of cephalopod early life stages at each Bongo station (N/1000m³). The horizontal line indicates the position of the thermal front at 62°W.

Classification of the cephalopod densities in the Bongo hauls separated the 27 samples at an arbitrary level of 65% dissimilarity into two large (I and II) and one small cluster (III) (Fig. II.4). The first (I) and the third (III) cluster included all samples south of the subtropical convergence and three further stations north of it. The second cluster (II) comprised exclusively samples taken in the northern area of the Sargasso Sea. Ordination (MDS) of the same data confirmed this finding (Fig. II.5): All samples from the northern

Sargasso Sea were grouped to the right of a line drawn in a nearly vertical direction, whereas samples from the southern area were positioned to the left of this line. The sample from station 221, which formed a single cluster (III) in the classification, was slightly separated from the other samples in the MDS plot (Fig. II.5).

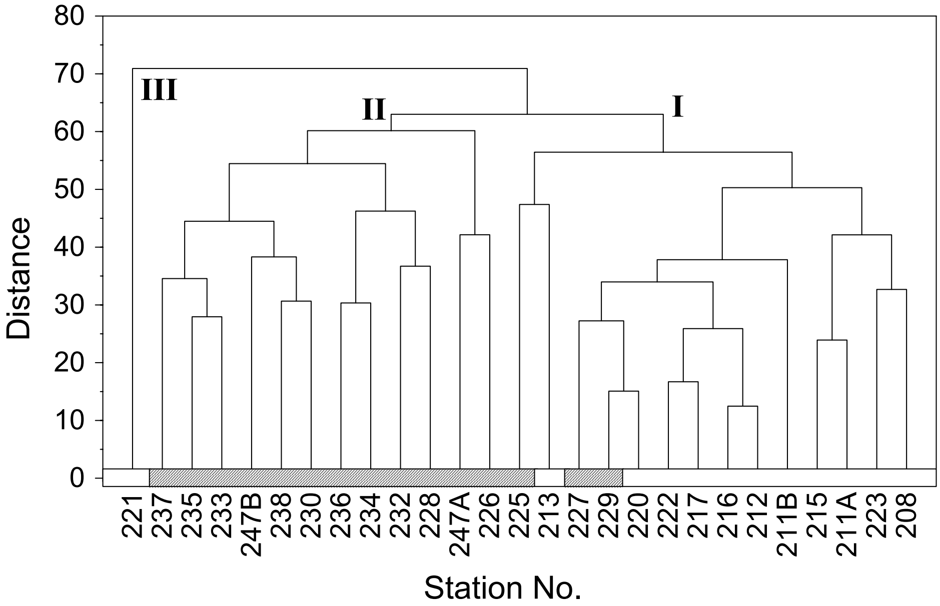

Fig. II.4: Classification of the 27 Bongo stations according to cephalopod assemblages. Hatched bars indicate samples north of the thermal front.

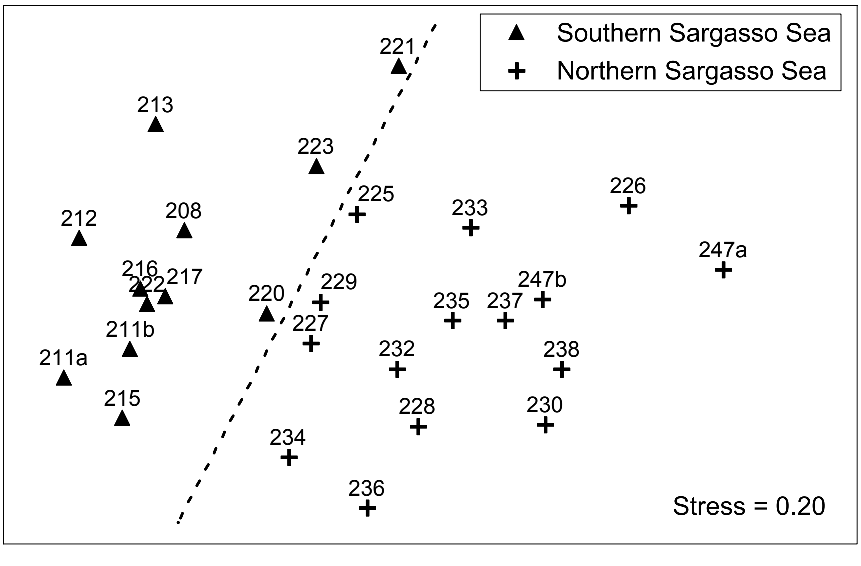

Fig. II.5: Ordination of the 27 Bongo stations according to cephalopod assemblages. The line separates samples north of the thermal front from samples south of it. Stress = 0.20.

In order to test the *a priori* hypotheses that there are differences in the species composition between the northern and the southern part of the Sargasso Sea, an ANOSIM was performed. It showed that the species compositions of both areas, separated by the STCZ, did significantly differ (global R = 0.481; p<0.001) and, thus, supported the results from the classification and ordination. The following exploratory analysis (SIMPER) indicated which species contributed most to the differences between the samples from the northern and the southern stations (Tab. II.2). The Cranchiidae dominated in the north; the family was mainly represented by *L. lemur*, *Megalocranchia* sp. and *Helicocranchia* sp., mostly identifiable as *H. papillata*. Other characteristic species in the northern part of the sampling area based on absolute abundances, were *A. pfefferi*, *Pyroteuthis margaritifera*, and *O. banksii*. Samples south of the STCZ were characterised by relatively high abundances of *A. pfefferi*, rhynchoteuthion stages of Ommastrephidae, *O. banksii* and *S. scintillans*. The cephalopod fauna of the southern Sargasso Sea differed from that of the northern area by relatively higher abundances of *S. scintillans* and ommastrephid species as well as by low numbers of cranchiid species, especially *L. lemur*.

Tab. II.2: SIMPER-Analysis: Discriminating species between the northern and the southern part of the Sargasso Sea. Species are ordered in decreasing contribution (%) to the total dissimilarity up to 90% cumulative contribution.

Species	Average Abundance		Contribution [%]	Cumulative contribution [%]
	Southern Sargasso Sea	Northern Sargasso Sea		
Leachia lemur	0.04	1.14	17.86	17.86
Selenoteuthis scintillans	0.31	0.12	8.96	26.82
Helicocranchia sp.	0	0.36	8.24	35.05
Ommastrephidae	0.22	0.09	7.9	42.95
Onychoteuthis banksii	0.21	0.29	7.64	50.59
Pyroteuthis margaritifera	0.05	0.32	7.17	57.76
Megalocranchia sp.	0.08	0.29	7.03	64.79
Abraliopsis pfefferi	0.25	0.49	5.99	70.78
Brachioteuthis sp.	0	0.08	5.63	76.41
Pterygioteuthis giardi	0.03	0.06	4.03	80.43
Chiroteuthis sp.	0	0.07	3.08	83.51
Ancistrocheirus lesueuri	0	0.04	2.98	86.49
Argonauta argo	0	0.06	2.94	89.43

Taxa which exclusively occurred north of the subtropical convergence, though mostly in low abundances, were *Ancistrocheirus lesueuri*, *Chtenopteryx sicula*, *Brachioteuthis* sp., *Chiroteuthis* sp., *H. papillata*, *Taonius pavo* and *Argonauta argo*.

The calculation of different dominance and diversity indices for the pooled species densities north and south of the front reflected the observed differences between the two areas (Tab. II.3). A total of 18 different species, compared to 10 in the southern part of the Sargasso Sea, were identified in the north (Ommastrephidae were not included at the species level), and the density of early life stages of cephalopods was more than three-times higher. The Magalef index (D) and Shannon's diversity index (H') showed higher values for the northern part of the Sargasso Sea, whereas Pielou´s evenness index (J) was slightly smaller. This was due to the dominance of just one species, *L. lemur*, in the northern area and the relatively even distribution of species abundances in the south.

Tab. II.3: Univariate indices of the northern and the southern Sargasso Sea regions. Rhynchoteuthion stages of the family Ommastrephidae were not included on the species level.

	Southern Sargasso Sea	Northern Sargasso Sea
No. of species	10	18
Density [N/1000m³]	14.832	53.614
Magalef species richness (D)	3.337	4.269
Pielou's evenness (J)	0.832	0.781
Shannon [H'(log e)]	1.917	2.257

Discussion

Sampling methods

The collection of early life stages of cephalopods with zooplankton nets has advantages and limitations. Advantages are the considerably lower avoidance effects of young and small planktonic cephalopods in comparison to their rapidly swimming adults (Piatkowski, 1998; Piatkowski et al., 1993). The sampling devices used in this study, Bongo net and IKMT6, are supposed to sample small paralarvae, even of the muscular type, effectively (Rodhouse et al., 1992; Roper, 1977). Limitations are caused by the seasonal occurrence of early life stages of those species, which do not spawn year round, making them susceptible to plankton sampling only shortly after spawning events. Furthermore, spawning areas are not always identical with the distributional range of the adults. Hence, the distribution patterns of the early life stages do not necessarily reflect those inhabited by older stages.

Cephalopod families and major species: Bongo and IKMT6 catches

In this study the cephalopod fauna was investigated for the first time in an extensive area of the Sargasso Sea. Mesopelagic cephalopods such as the Cranchiidae and Enoploteuthidae dominated the catches, because most of their hatchlings occur in near-surface waters before they exhibit a marked ontogenetic descent to develop into the juvenile and adult stages (Roper and Young, 1975; Young, 1978). In general, a typical oceanic cephalopod community was present. The species composition was similar to other collections of pelagic cephalopods in the subtropical western North Atlantic (Dawe and Stephen, 1988; Gibbs and Roper, 1970; Lea, 1984; Lu and Roper, 1979; Voss, 1960), but was depauperate of shelf-associated species such as Myopsida and some Ommastrephidae (*e.g.*, *Illex illecebrosus*) as well as early life stages of benthic Octopoda. The same families, Cranchiidae and Enoploteuthidae, dominated in this study and in earlier collections of a one degree square area south east of Bermuda (Gibbs and Roper, 1970). A comparison of the species composition between this investigation and former studies, which mainly collected juvenile to adult specimens, indicated that most of the cephalopod species seem to spawn in early spring or year round, respectively. For most oceanic cephalopods only scattered information about spawning periods exists. For instance, the peak spawning time of *Abraliopsis pfefferi*, investigated at Deepwater Dumpsite 106 (Lu and Roper, 1979), was estimated to take place primarily in summer, though spawning females occurred already in spring. In the present collection early life stages of *A. pfefferi* represented the second most-abundant species. Therefore, spawning was likely to have started already in the early months of the year. From records of *Megalocranchia megalops* collected during their study, Lu and Roper (1979) concluded that this species spawns from winter to early spring, which agrees with the occurrence of recently hatched specimens in the present investigation.

Distribution of cephalopods in relation to the thermal front

In the eastern North Atlantic, Lu and Clarke (1975) observed an increase of cephalopod abundances and species number from north to south, and from temperate to subtropical and tropical regions. This also seems to be true for the western North Atlantic. Dawe and Stephen (1988) considered the north wall of the Gulf Stream to be a boundary that restricts the distribution of tropical-subtropical cephalopod species to higher latitudes. The sampling in the relatively small area of the Sargasso Sea south of the Gulf Stream core revealed reverse relationships: abundances and species diversity were significantly higher in the northern part of the investigated area. This pattern has also been demonstrated for small invertebrate zooplankton (Böttger, 1982), epipelagic copepods (Colton et al., 1975) and mesopelagic fishes (Backus et al., 1969). These studies related the differences to the position of the STCZ, characterised by a distinct thermal front.

In March 1993 the front was located at a latitude of approximately 27°20’N. This lies within the region of pronounced frontogenesis, which has been described in the latitude range of 22°-32°N (Voorhis and Hersey, 1964) or, in more recent studies, between 26°N and 32°N (Halliwell et al., 1991a, b, 1994). The front forms in the upper 200 m, where the colder water of the northern Sargasso Sea converges with the warmer mixed layer of the southern Sargasso Sea (Halliwell et al., 1991b; Wegner, 1982). It is usually detectable by a temperature gradient of 1°C within a distance of 10 km (Voorhis and Hersey, 1964). The most obvious feature during the Poseidon cruise in March 1993 was the strong stratification of the water mass south of the STCZ, which limited the mixing of the surface layer. In the same season as the present investigation, Ryther and Menzel (1960) measured distinct differences in primary production near Bermuda. South of 30°N they detected a rapid decline in productivity to approximately ten percent of that found at stations at the northern end of their transect (35°N). This strong gradient of primary production, coinciding with the position of the front, is likely to have an influence on the distribution of zooplankton, as proposed by Backus et al. (1969). Cold core rings, separated from the Gulf Stream and enclosing cold and nutrient rich slope water, possibly enhance this effect (Ortner et al., 1978). Niermann (1986) observed a decreasing abundance of species and individuals of *Sargassum natans* epibionts in the southern part of the Sargasso Sea. He attributed this decrease to lower primary production and, thus, a lack of suitable food in this region. In the waters north of the thermal front, Böttger (1982) measured a two- to three-times higher microzooplankton biomass than in the stratified waters south of it. This small size fraction of zooplankton is an important food resource for fish larvae (Arthur, 1977) and likely sustains higher abundances of early life stages of cephalopods, supporting the remarkable increase in the cephalopod densities north of 29°N. Previous studies have also noted north-south differences in the biota of the Sargasso Sea (Backus et al., 1969;

Böttger, 1982; Colton et al., 1975), with species diversity being higher in the northern area. This was also observed for the early life stages of cephalopods. Seven species/ genera were exclusively found in the north. Furthermore, different species dominated the cephalopod assemblages. In the north the cranchiid *Leachia lemur* was by far the prevailing species. According to Voss et al. (1992) it is restricted to the North Atlantic Subtropical Region west of about 50°W and seems to be endemic to the northern and southern Sargasso Sea. The high abundance and the centre of distribution of *L. lemur* north of the STCZ is probably attributable to the putative higher productivity in that area. Although the genus *Leachia* is generally confined to low-productive subtropical waters, increased abundances of cranchiids always appear to be related to areas of intensified productivity (Voss, 1988).

In comparison, *Selenoteuthis scintillans*, which besides *L. lemur* is mainly responsible for the north-south differences in species composition (SIMPER), was relatively scarce in the northern area. Its geographical distribution in the western North Atlantic extends from approximately 8°N to 41°N (Voss and Stephen, 1992), completely covering the investigated part of the Sargasso Sea. The conspicuous low abundances of *S. scintillans* found north of the STCZ correspond to the densities estimated by Lu and Roper (1979). Their results and the present study indicate that the northern Sargasso Sea represents the northern boundary of distribution for this species. Supported by the observation that the occurrence of *S. scintillans* north of the Gulf Stream is restricted to warm core eddies (Voss and Stephen, 1992), temperature seems to be the limiting factor.

In conclusion, the distribution patterns of early life stages of cephalopods confirm that the thermal front represents a distinct boundary, both in species composition and in abundance, with a considerable decrease from north to south (Backus et al., 1969; Böttger, 1982; Colton et al., 1975; Lea, 1984). The latitudinal decrease is not gradual, but pronounced at the front. Whether this is also true for adult cephalopods is still in question. As juvenile and adult squids are highly mobile and mesopelagic species inhabit completely different parts of the water column compared to their hatchlings, possible north-south differences are more difficult to detect. In order to understand the influence of hydrography on distribution patterns of oceanic cephalopods, it is necessary to achieve a better picture of the overall distribution of cephalopods in the western North Atlantic and to improve the knowledge about their biology, *i.e.*, spawning periods, sites and feeding habits.

Chapter III

Species composition and distribution patterns of early life stages of cephalopods at Great Meteor Seamount (subtropical NE Atlantic)

Abstract

The distribution of early life stages of cephalopods was studied during a cruise of RV Meteor in September 1998 at Great Meteor Seamount, an isolated flat-topped seamount in the subtropical eastern North Atlantic. Zooplankton sampling was conducted with a multiple opening-closing-net (modified MOCNESS, 1 m² net opening, 335 µm mesh size) in seven depth strata between 290 m depth and the surface. 1180 early life stages of cephalopods were collected, representing at least 18 families and 31 mainly oceanic species. Most of the identified cephalopods comprised mesopelagic species (*e.g.*, representatives of the families Enoploteuthidae and Pyroteuthidae) that showed diel vertical migration patterns. Hydrographic measurements in parallel to zooplankton sampling revealed slow anticyclonic recirculation around the seamount forming a Taylor column and, thus, some retention potential for passive particles. Nevertheless, multivariate statistical analysis revealed no differences in the cephalopod community between the area in the proximity of the summit and the adjacent oceanic region. This was partly related to the depth of the plateau (< 300 m), which resulted in a hardly enhanced primary production, as well as to the low retention potential for active vertical migrators. However, reduced numbers of cephalopods over the summit at night-time sampling were observed indicating gap formation above the seamount.

Introduction

Seamounts are striking features in all oceans contrasting with the vast surrounding abyssal plains. They attract biological oceanographers, because they are supposed to increase productivity and, therefore, host comparatively large stocks of pelagic and benthic organisms in regions which are commonly regarded as oceanic deserts (Boehlert and Genin, 1987; Koslow, 1997; Rogers, 1994). Seamounts are elevations of more than 1000 m, which are mainly of volcanic origin (Epp and Smoot, 1989). Approximately 30000 seamounts are assumed to exist worldwide but only a few of them have been studied in detail (Rogers, 1994). Seamounts are known to affect prevailing oceanic circulation patterns (Beckmann, 1999; Roden, 1987). On a mesoscale spatial level, they can enhance the formation of trapped waves (Brink, 1990), deflect ocean currents along isobaths, amplify tidal currents (Eriksen, 1991), and produce eddies that may form closed circulation cells, so-called Taylor columns or Taylor caps (*e.g.*, Chapman and Haidvogel, 1992; Lueck and Mudge, 1997).

Hydrographic conditions such as recirculating currents appear to be important for the retention of planktonic larval stages and may even support speciation and endemisms of faunal components (Calder, 2000; Mullineaux and Mills, 1996; Richer de Forges et al., 2000). In contrast, topography and hydrography may also act as dispersal mechanisms (Dower et al., 1992; Leal and Bouchet, 1991; Parker and Tunnicliffe, 1994). Recently, exploratory fisheries at seamounts revealed large and economically valuable fish stocks (Koslow et al., 1994; Moore, 1999; Uchida and Tagami, 1984). Whether these comparatively large stocks of demersal fish are a consequence of either higher productivity or better transfer efficiency compared to the adjacent open ocean is still under discussion (Comeau et al., 1995; Dower and Mackas, 1996; Haury et al., 2000; Mouriño et al., 2001; Rogers, 1994) and depends on local conditions, *e.g.*, the varying minimum depth of the seamount plateau, extent of the summit, steepness of the slope, and the degree of isolation from the continental shelf and major oceanic currents.

One of the most striking isolated submarine features in the North East Atlantic is Great Meteor Seamount (GMS), located east of the Mid-Atlantic Ridge at approximately 30°N and 28.5°W. This seamount rises from depths of almost 4800 m to about 275 m below sea level. GMS is characterised by an elliptical base, a steep slope with a gradient of up to 45°, a relatively flat and large plateau area of about 1130 km², and an average depth of 330 m. In 1998 an interdisciplinary research cruise was conducted to study biological and hydrographical features at GMS. One focus of the sampling was the investigation of the influence of topography on the pelagic fauna, from microzooplankton to macronekton. Cephalopods are one component of the pelagic fauna, which form an important link in oceanic food webs (Piatkowski et al., 2001). Most oceanic species have in common that their hatchlings develop within the plankton, mainly in the upper layers. The early life stages are, thus, susceptible to zooplankton sampling and can be caught more quantitatively than their fast swimming adult stages which are difficult to sample representatively even with large pelagic trawls (Piatkowski, 1998). This may be a reason why relatively few studies on cephalopods in the open ocean and especially at seamounts have been conducted (Nesis, 1994; Parin et al., 1988). Nesis (1993a) provided an overview on the various association modes of cephalopod species at seamounts, but specific distribution patterns remained unclear. In the present study the cephalopod fauna at GMS was investigated for the first time and the distribution of the early life stages was related to topography and special hydrographic features. Corresponding to recent findings on seamount specific zooplankton and demersal fish communities (Dower and Mackas, 1996; Fock et al., 2002b), the main objective was to demonstrate whether a characteristic cephalopod fauna exists at GMS and to what extent the seamount influences distribution patterns and dispersal strategies of early life stages of cephalopods. Furthermore, specific vertical distribution and diel migration patterns are described.

Material and Methods

Sampling

Cephalopod specimens were obtained from zooplankton samples collected at Great Meteor Seamount (GMS) in September 1998 during cruise 42/3 of the German research vessel Meteor. Sampling was carried out with a BIOMOC, *i.e.*, a modified MOCNESS (Wiebe et al., 1976) with a 1 m² net opening that allows consecutive opening and closing of nine nets during one haul. The gear was equipped with an electronic flowmeter to estimate the net specific filtered volume. The nets had a length of 6 m and a mesh size of 335 µm.

In total, 22 stations were sampled, covering the flat-topped summit of the seamount, the slope and the surrounding oceanic region (Tab. III.1). At each station sampling was conducted from 290 m depth to the surface in 7 discrete depth strata (290-250 m, 250-200 m, 200-150 m, 150-100 m, 100-50 m, 50-10 m, 10-0 m). The net was towed in each water layer in a threefold oblique tow at a ship's speed of approximately 3 knots. On average 1500 m³ of water were filtered in each depth stratum. All samples were initially preserved on board in sodium borate buffered formalin, diluted in seawater to 4 %.

Tab. III.1: Numbers of stations sampled with BIOMOC net above the summit, the slope, and in the adjacent deep sea at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Listed are the corresponding water depth, daytime of sampling, and haul numbers. Haul numbers sampled at 'shallow' and 'deep water stations' correspond to the same sampling but to a different categorisation applied within parts of the analysis. At all stations depth stratified tows were conducted from 290 m depth to the surface.

Location	Water depth [m]	No. of tows		
		Day	Twilight	Night
Plateau	<350m	5	1	4
Slope	350-1500m	0	2	3
Deep-Sea	>1500m	2	2	3
Shallow	<350m	5		4
Deep water	>1000m	2		2

Cephalopods were sorted and identified to the lowest feasible taxonomic level. For each station cephalopod species densities (N/1000 m³) were calculated per depth stratum and integrated for the entire water column. Water column densities (0-290 m) were calculated for each station by weighting the samples according to the extension of the corresponding depth stratum (equal to numerical integration). Only water column densities were used in the initial species-station table for the spatial analysis of the cephalopod community.

Hydrography

GMS is positioned within the flow system of the wind-driven subtropical gyre of the North East Atlantic. Hydrographical measurements performed on the M42/3 cruise of RV Meteor revealed that the seamount lies within a weak south-westerly current and is strongly influenced by diurnal and semidiurnal tides (Mohn and Beckmann, 2002). The authors also detected a Taylor cap formation above the seamount. Furthermore, Mohn and Beckmann (2002) and Beckmann and Mohn (2002) developed a numerical model simulating the three-dimensional circulation at GMS. In different experiments passive tracers and Lagrangian trajectories with passive floats and actively vertically migrating particles were used. The authors concluded that the region hydrographically influenced by GMS extends to about 4 times the area of the summit plain and generally includes an area of less than 4400 m water depth. They defined an inner (circumscribed by the 1500 m depth contour) and an outer seamount regime (covering an area from 1500-4400 m water depth). A strong retention potential of passive tracers was confined to the summit area, delimited by the 350 m depth contour.

Data analysis

Zooplankton stations were categorised according to different abiotic variables (sampling time of day; position in relation to the seamount or distance from the plateau margin; water depth). Three different daytimes were distinguished: Day, night and twilight (dusk/ dawn), with the concurrent global radiation measured on board RV Meteor as a proxy. The position of the stations was assigned to plateau (<350 m water depth), slope (350-1500 m water depth) and deep sea stations (>1500 m water depth) according to the findings of Beckmann and Mohn (2002) (Tab. III.1).

Multivariate statistical analyses were performed to examine differences in species composition and abundances of cephalopods at the sampling sites. For this purpose families which mainly comprised specimens that could not be identified to species level, were treated as entities. Species/ group densities (N/1000 m^3) were calculated for each station (integrated over the water column). Densities were fourth root transformed in order to reduce the effect of dominating species/ groups and increase the importance of rare ones (Field et al., 1982). Similarity between stations was calculated by means of the Bray-Curtis coefficient (Bray and Curtis, 1957). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method (CLUSTER; Field et al., 1982) and ordinated by non-metric multidimensional scaling (nMDS; Kruskal and Wish, 1978). Two-dimensional ordination plots were performed on the resulting similarity matrix to illustrate the relationships among cephalopod assemblages at different stations around the seamount. Relationships between cephalopod assemblages and various subsets of environmental variables were examined using the BIOENV procedure (Clarke and Ainsworth, 1993). Light intensity at sea level (indicating time of day), distance from the plateau margin and water depth were applied as continuous variables possibly influencing distribution patterns. Measures for light intensity were log transformed to validate the use of normalised Euclidean distances for the calculation of a similarity matrix based on abiotic information. The Spearman rank correlation was used as a measure of agreement between each of the abiotic matrices and the biotic Bray-Curtis similarity matrix (Clarke and Ainsworth, 1993). The above non-parametric multivariate techniques are included in the PRIMER software package (Clarke and Warwick, 1994).

For species occurring in sufficient numbers in zooplankton catches at different times of the day (>10 individuals per time of day) the weighted mean depth (WMD) was calculated as $WMD = \left(\sum n_i d_i\right) / \sum n_i$, where n_i is species/ family density (N/1000m^3) at depth d_i (Bollens and Frost, 1989). WMDs were not compared statistically between different times of the day due to the low number of stations. In a second approach differences between the average day and night distribution patterns of the most abundant species were investigated by the Kolmogorov-Smirnov two sample test, as this test is known to be robust against so-called shift alternatives (Darling, 1957).

In order to investigate the effect of the topographic elevation on the densities of early life stages of cephalopods two different approaches were chosen. Specimens of all cephalopod species were summed up, as numbers at the species level would be too low for statistical analysis. Because of the pronounced diel vertical migration of some cephalopod groups, day and night samples were considered separately. Firstly, the depth-variation in cephalopod density between plateau (<350 m water depth) and deep water stations (>1000 m water depth) (Tab. III.1) was examined by using a two-way ANOVA: Original data were log (x+1) transformed to achieve homogeneous variances (Bartlett´s test, p>0.05). Normal distribution of data could not be tested directly because of low station numbers. Therefore, data were pooled after using a z-transformation and investigated graphically and statistically for deviations from normal distribution (Kolmogorov-Smirnov test, p>0.2). Secondly, the mean vertical distribution of cephalopods above the plateau and in deep water was analysed by the Wilcoxon matched pairs test by comparing the mean densities in each depth stratum. As no differences between the distribution patterns were detectable, the requirement for the test were met. All statistical tests were considered to be significant at a probability level of $p<0.05$.

Results

Species composition

22 BIOMOC hauls yielded a total of 1180 early life stages of cephalopods, comprising 18 families and 31 species (Tab. III.2). All specimens belonged to the order Oegopsida and the octopod sub-order Incirrata. Since many specimens could not be identified to species level the total number of species must be considered as minimal. As an example morphological characters of rhynchoteuthion larvae indicated 4 different species of the family Ommastrephidae in the collection that can be reliably distinguished only into two different larval types (Vecchione et al., 2001), rhynchoteuthion type A' (probably representing *Ommastrephes bartramii*) and type B' (including paralarvae of *Hyaloteuthis pelagica*, *Sthenoteuthis pteropus*, and *Ornitoteuthis antillarum*). Densities per family, integrated over 0-290 m water depth (N/1000 m^3) (Tab. III.2) showed a dominance of two families, the Enoploteuthidae (25.8 % of the total catch) and the Onychoteuthidae (16.9 %; Fig. III.1). Both families were mainly represented by one species: *Abraliopsis pfefferi* (Enoploteuthidae) and *Onychoteuthis banksii* (Onychoteuthidae), respectively. Other moderately abundant groups were small bodied mesopelagic squids of the families Pyroteuthidae (10.7 %), Ancistrocheiridae (5.7 %), and Lycoteuthidae (5.7 %). The meso- to bathypelagic Cranchiidae amounted to 5.2 % of the total catch. Besides the Ommastrephidae (4.5 %) and the Chtenopterygidae (4.0 %), all other oegopsid families contributed less than 2.5 % to the overall abundance of cephalopods (Fig. III.1). The Octopoda (7.5 %) were represented by at least four families, three of them comprising pelagic species (*Argonauta argo, Bolitaena pygmaea*, *Tremoctopus violaceus*). Specimens belonging to the Octopodidae were probably hatchlings of the deep-water species *Scaeurgus unicirrhus*, as benthic juveniles and adults were caught four times by concurrent bottom trawl hauls and bottom traps during the Meteor expedition at GMS (Diekmann, unpublished data).

Tab. III.2: Early life stages of cephalopods collected by BIOMOC net during RV Meteor cruise 42/3 in September 1998. Numbers for higher taxa only include specimens that could not be further identified. Identification of Ommastrephidae into rhynchoteuthion types was performed according to Vecchione et al. (2001). N_{abs}: total catch in numbers; N/1000 m^3: I. average species density in specimens per 1000 m^3 filtered water volume and II. average family density (as before). Percentage of positive tows indicate the frequency of species at the 22 stations.

Order, Family	Species	$N_{abs.}$	N/1000m^3	N/1000m^3 per family	Positive tows [%]
Order Oegopsida	Oegopsida indet.	183	13.42		
Family Enoploteuthidae	Enoploteuthidae indet.	136	23.71	33.31	
	Abralia veranyi	1	0.12		4.5
	Abraliopsis pfefferi	86	8.81		86.4
	Enoploteuthis leptura	7	0.67		18.2
Family Onychoteuthidae	Onychoteuthidae indet.	6	0.89	21.85	
	Onychoteuthis banksii	194	19.78		81.8
	Onykia carriboea	14	1.18		27.3
Family Pyroteuthidae	Pyroteuthidae indet.	28	3.54	13.84	
	Pterygioteuthis giardi	2	0.14		4.5
	Pyroteuthis margaritifera	77	10.16		81.8
Family Lycoteuthidae	Lycoteuthidae indet.	8	0.94	7.41	
Subfamily Lycoteuthinae	*Selenoteuthis scintillans*	54	6.47		68.2
Family Ancistrocheiridae	*Ancistrocheirus lesueuri*	70	7.30	7.30	72.7
Family Cranchiidae	Cranchiidae indet.	10	1.45	6.72	
Subfamily Cranchiinae	Cranchiinae indet.	8	0.71		
	Cranchia scabra	4	0.55		13.6
	Leachia sp.	1	0.03		4.5
	Liocranchia reinhardti	2	0.18		9.1
Subfamily Taoninae	Taoninae indet.	5	0.40		
	Bathothauma lyromma	3	0.23		13.6
	Helicocranchia sp.	3	0.30		
	Helicocranchia papillata	21	2.26		50.0
	Helicocranchia pfefferi	4	0.24		9.1
	Liguriella sp.	3	0.36		9.1
Family Ommastrephidae	Ommastrephidae indet.	7	0.78	5.85	
Subfamily Ommastrephinae	*Rhynchoteuthion Type A´*	38	3.93		50.0
	Rhynchoteuthion Type B´	17	1.14		40.9
Family Chtenopterygidae	*Chtenopteryx sicula*	52	5.19	5.19	72.7
Family Chiroteuthidae	Chiroteuthidae indet.	2	0.34	2.65	
	Chiroteuthis sp.	11	1.77		36.4
	Valbyteuthis sp.	8	0.54		18.2
Family Thysanoteuthidae	*Thysanoteuthis rhombus*	8	0.93	0.93	22.7
Family Brachioteuthidae	*Brachioteuthis* sp.	5	0.35	0.35	13.6
Family Mastigoteuthidae	*Mastigoteuthis* sp.	3	0.24	0.24	13.6
Family Histioteuthidae	*Histioteuthis* sp.	1	0.15	0.24	4.5
	Histioteuthis celetaria celetaria	1	0.09		4.5
Family Cycloteuthidae	*Discoteuthis* sp.	3	0.13	0.13	4.5
Order Octopoda	Octopoda indet.	1	0.14	9.71	
Family Argonautidae	*Argonauta argo*	21	2.57		50.0
Family Bolitaenidae	*Bolitaena pygmaea*	43	4.43		72.7
Family Octopodidae	Octopodinae sp.	27	2.29		40.9
Family Tremoctopodidae	*Tremoctopus violaceus*	2	0.28		9.1
Sum		1180			

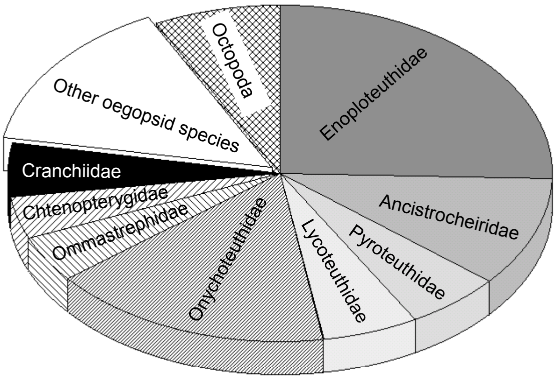

Fig. III.1: Catch composition of cephalopods as percentage of the total relative abundance of major cephalopod groups from BIOMOC samples at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Unidentified specimens and oegopsid species/ families which contributed less than 2.5 % to the total cephalopod abundance were summarized as ‘other oegopsid species’.

Cephalopod distribution in relation to GMS

Cephalopod densities in BIOMOC hauls standardised to 290 m water depth varied between 1.5–16.7 specimens per 1000 m^3 (Fig. III.2). Night and twilight sampling yielded up to 200 % more specimens compared to daytime sampling. If diurnal patterns were not taken into account densities were higher in the south-western region, *i.e.*, leeward of the seamount, than above its summit (Fig. III.2). Separate consideration of day and night hauls revealed differences between shallow (<350 m water depth) and deep water stations (>1000 m water depth) in average densities and vertical distribution of early life stages of cephalopods. During daytime lower densities were measured at deep water stations compared to stations above the summit (Fig. III.3); in all seven depth strata lower densities were found at deep-water stations and differences were statistically significant ($p<0.05$; Wilcoxon matched pairs test). At night the reverse pattern was observed. Higher densities were measured in deep water hauls compared to sampling above the summit. However, below 200 m water depth densities were generally low and even fewer specimens were caught at deep water stations compared to the plateau. Thus, no statistical difference was revealed ($p>0.05$; Wilcoxon matched pairs test). The same results were obtained using densities per depth stratum separately for each station (two-way ANOVA, Tab. III.3). Densities were significantly different ($p<0.05$) between shallow and deep water stations by day, but not at night. Significant differences between depth strata were demonstrated at any sampling time.

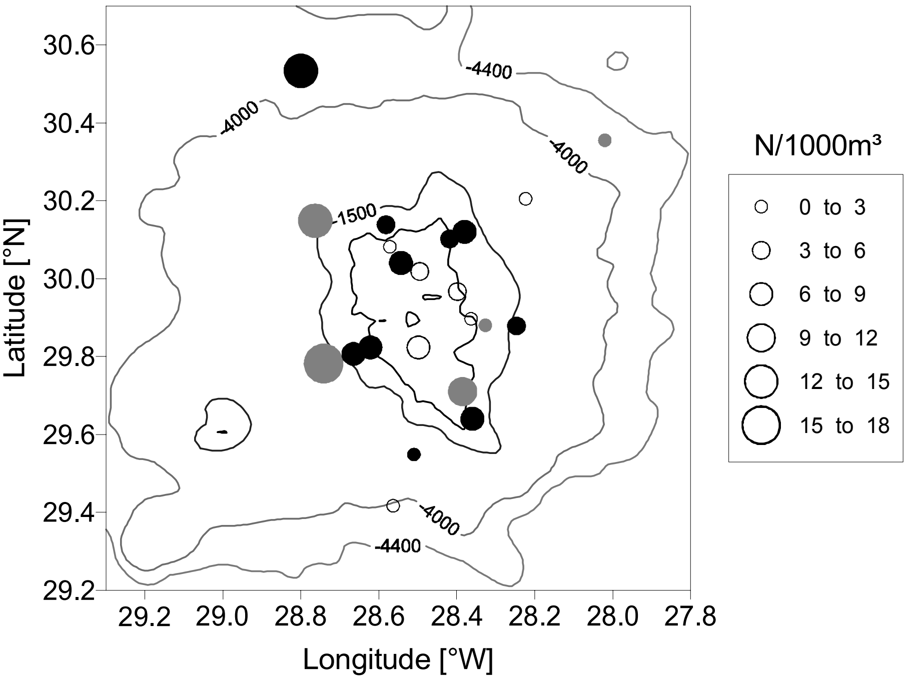

Fig. III.2: Cephalopod densities (N/1000 m³) in BIOMOC samples from 290 m depth to the surface, collected during the RV Meteor-cruise 42/3 in September 1998 at Great Meteor Seamount. Bathymetry of Great Meteor Seamount is displayed in 350 m, 1500 m, 4000 m, and 4400 m depth contours. Diameters of the circles, representing cephalopod densities, increase linearly from 0–18 specimens/1000 m³ filtered water volume. Shading of circles indicates time of day during sampling (open circles: day; grey circles: twilight; black circles: night).

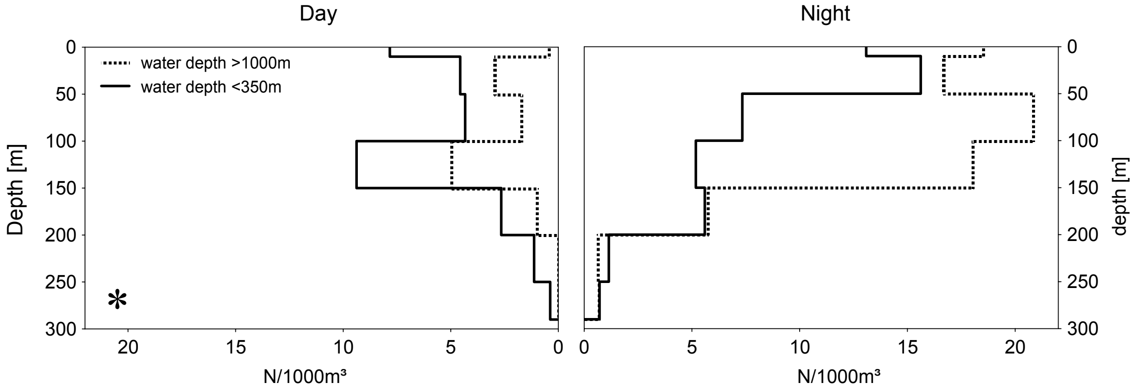

Fig. III.3: Vertical distribution of early life stages of cephalopods in seven discrete depth strata sampled by BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Distribution patterns between stations sampled above the summit (<350 m water depth, solid line) and in deep waters (>1000 m water depth, dotted line) are compared separately for day and night sampling. Asterisk indicates significant difference between two sampling series at the 0.05 probability level (Wilcoxon matched pairs test).

Tab. III.3: Results of two-way ANOVAs testing for differences in density of cephalopod early life stages by position (shallow stations: <350 m water depth, deep stations: >1000 m water depth) and sampling depth (7 depth strata from 290 m depth to the surface). Day and night distributions were tested separately. Significant differences ($p<0.05$) are in italics. Sampling was performed by BIOMOC net during RV Meteor cruise 42/3 in September 1998.

Source of variation	df	MS	F-ratio	p-value	Number of vertical series
Day					
Position	1	0.716	7.899	*0.00805*	7
Depth stratum	6	0.394	4.347	*0.00222*	
Position x depth	6	0.044	0.488	0.81255	
Error	35	0.091			
Night					
Position	1	0.001	0.018	0.894	6
Depth stratum	6	0.792	12.903	*0.000*	
Position x depth	6	0.082	1.336	0.275	
Error	28	0.061			

Hierarchical, agglomerative classification (CLUSTER) and ordination (nMDS) of species densities at BIOMOC stations indicated three different groups, separated at an arbitrary level of 53 % dissimilarity, and one ungrouped station (Fig. III.4). The largest group contained 14 of the 22 stations. When additional information on position (plateau, slope, deep sea) and daytime (day, twilight, night) were superimposed on the graph no direct dependence from any factor was obvious (Fig. III.4). This observation was additionally tested by the BIOENV procedure, using continuous data for water depth, light intensity, and distance from the plateau margin. A maximum of 15.8 % correlation to the similarity matrix based on species abundances could be achieved combining all three factors, indicating no detectable interrelation between cephalopod community structure and the tested abiotic variables.

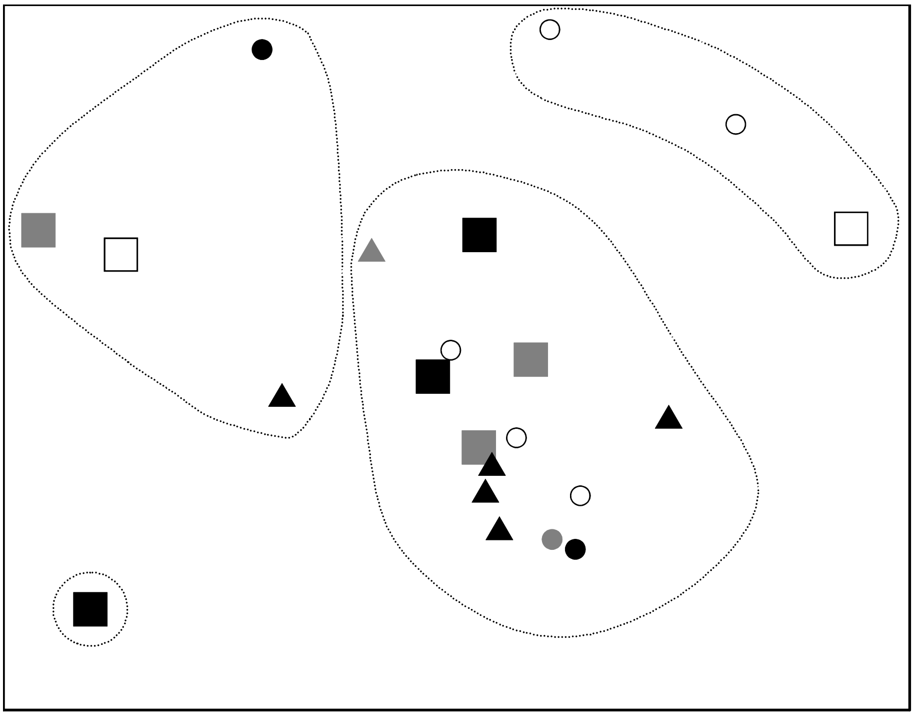

Fig. III.4: Ordination of the 22 BIOMOC stations according to cephalopod assemblages, sampled at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Symbols represent stations categorised as plateau (circles), slope (triangles), and deep sea stations (squares). Colour of the symbols represent the time of sampling (white: day; grey: twilight; black: night). Grouping (dotted lines) was indicated by cluster analysis. Stress = 0.12.

Diel vertical migration patterns

The comparison of the weighted mean depth (WMD) between different times of the day resulted in similar vertical migration patterns for most investigated species groups. For major cephalopod species/ families and for the total of all early life stages of cephalopods the WMD by day was found to be deeper than at night (Tab. III.4). The biggest differences between day and night distribution were observed for Enoploteuthidae (±43 m), Ancistrocheiridae (±30 m) and Pyroteuthidae (±29 m), of which the latter additionally showed the deepest distribution of all investigated cephalopod groups. However, the variability within stations sampled at the same daytime was high. Migration magnitudes may have been underestimated, as the samples were not necessarily obtained when specimens were at their maximum or minimum depth distribution. Twilight sampling mostly resulted in an intermediate depth distribution except for Ancistrocheiridae and Cranchiidae. No upward migration at night could be demonstrated for Ommastrephidae and *Selenoteuthis scintillans* (Lycoteuthidae). Both occurred in shallower mean depths during the day than at night (Tab. III.4). However, the vertical distribution patterns did not confirm this observation (Fig. III.5). The Ommastrephidae were exclusively found in the upper 150 m of the water column without any upward migration at any time of the day. The same was observed for *S. scintillans* and partly for *O. banksii,* although for this species abundance increased during night in the near surface layer. An upward migration at night was revealed for the Enoploteuthidae, the most abundant family in the samples, and the Pyroteuthidae, although only the latter showed statistically significant differences between day and night vertical distribution patterns.

Tab. III.4: Average weighted mean depth (WMD) at day, twilight, and night of all early life stages of cephalopods and the most abundant species/ families sampled with BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Additionally listed are one standard deviation (s) of the WMD and the total number of specimens (n), on which the analysis was based.

Species group	Daytime	WMD	s_{WMD}	n
All species	twilight	95.0	21.5	354
	day	101.9	18.2	230
	night	93.8	20.7	585
Enoploteuthidae	twilight	68.6	8.2	67
	day	109.6	33.4	47
	night	66.8	26.8	111
Ommastrephidae	day	46.5	25.3	18
	night	64.9	18.9	23
Onychoteuthis banksii	twilight	73.6	26.1	77
	day	78.4	22.2	45
	night	61.7	22.7	73
Pyroteuthidae	twilight	150.2	33.7	20
	day	165.1	67.0	14
	night	135.9	40.7	64
Ancistrocheirus lesueuri	twilight	51.5	7.1	21
	day	85.0	35.1	15
	night	55.2	32.2	24
Selenoteuthis scintillans	twilight	92.5	76.9	11
	day	70.3	4.4	14
	night	94.6	47.1	37
Cranchiidae	twilight	102.8	16.7	14
	day	138.4	43.3	12
	night	112.9	43.8	35

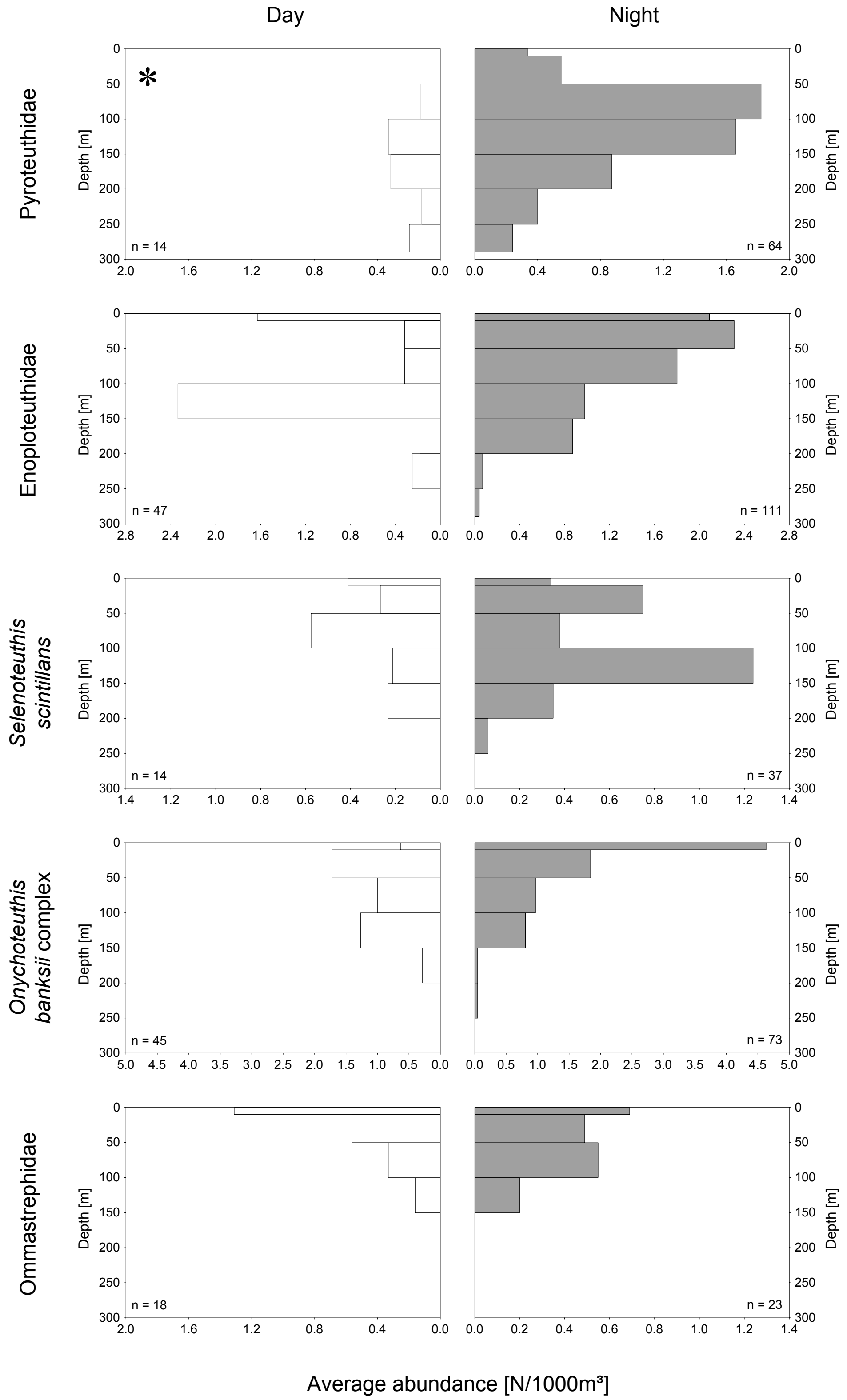

Fig. III.5: Vertical distribution of the most abundant cephalopod species/ families sampled by BIOMOC net at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998. Bars are mean abundances per 1000 m³ at each depth interval of 7 day (clear bars) and 10 night (shaded bars) vertical series of samples. Asterisk indicates significant difference between day and night distribution at the 0.05 probability level (K-S test).

Discussion

In the present study the cephalopod fauna at Great Meteor Seamount (GMS) and its surrounding water masses was investigated for the first time. The sampling strategy aimed originally at the investigation of the zooplankton distribution within the euphotic zone. Therefore, only early life stages of cephalopods that were distributed within the upper 290 m of the water column could be taken into account and benthic and bathypelagic species are consequently missing in the faunal description.

Although the sampling in September 1998 was not repeated and, thus, the findings of this study can only be interpreted as a first snapshot of the cephalopod community, the provided information is quite comprehensive. In general, a typical oceanic subtropical cephalopod fauna was found. All species occurred within their known distributional range. No neritic species, *e.g.*, myopsid squids or some representatives of the family Ommastrephidae (*e.g.*, *Illex coindetii, Todaropsis eblanae*), which are abundant at the west African shelf and slope waters, were identified in the samples. A detailed comparison of the cephalopod fauna with other investigations was not possible as no information is available on the distribution of early life stages in the subtropical eastern North Atlantic. Kluchnik (1978) recorded a cephalopod community similar to the present study in an area from 30°N to 37°S, east of the Mid-Atlantic Ridge. However, the relative species composition was different, because the sampling expanded south of the equator. Main differences were found within the Ommastrephidae, which was one of the dominating groups in the investigation of Kluchnik (1978) but less abundant in the collection at hand.

All specimens found in zooplankton samples belonged to cephalopods known to remain pelagic during their whole life except of one form of the family Octopodidae, which can be related to benthic adults, presumably of the species *Scaeurgus unicirrhus*. This octopod that lives in the upper bathyal zone is a typical inhabitant of seamounts (Nesis, 1993a). Because GMS is widely isolated from other shallow topographic features and the water depth increases rapidly from 300 m at its top to about 5000 m at its flanks, it is very likely that the early life stage Octopodidae originated from an octopod stock inhabiting the seamount. The major component of the cephalopod fauna was represented by diurnal vertical migrators that may be advected by currents over the summit and descend near to the bottom during day (*e.g.*, *Pyroteuthis margaritifera, Abraliopsis pfefferi, Selenoteuthis* *scintillans*). The extensive diurnal vertical migratory behaviour of the adults is well known and was described by Clarke and Lu (1974) and Roper and Young (1975). According to Roper and Young (1975) early life stages of those species occur in near surface waters, whereas the juvenile and adult forms live in deeper water layers. Nevertheless, the early life stages of some species investigated in the present study already demonstrated significant diurnal vertical migrations (Pyroteuthidae) or showed at least a tendency for dispersing downwards during daytime (*e.g.*, Enoploteuthidae, *S. scintillans*).

The zooplankton sampling in the area of GMS revealed a combination of short-term temporal and small-scale spatial variability. During the cruise of RV Meteor the field work profited from favourable weather conditions and weak but constant winds. The assumptions about the flow field around GMS (Mohn and Beckmann, 2002) and the distribution of passively advected and actively migrating organisms in a numerical model (Beckmann and Mohn, 2002) were based on such constant weather conditions, because strong winds largely affect the direction and the velocity of near-surface currents. Thus, the hydrographic models very likely represented the real situation during the research cruise and deviations from model predictions due to short-term shifts in circulation patterns were expected to be low. However, no clear indications were found for an influence of the seamount hydrography on cephalopod abundance. The relatively high species densities measured south-westward of the plateau may be related to weaker small-scale turbulence leeward of the seamount (Beckmann and Mohn, 2002), but could also be an effect of the time of sampling, as all hauls in this area were performed at dusk or during the night, favouring the catch of upward migrating species. Nevertheless, a similar observation was made in a study by Huskin et al. (2001). They found a general tendency of increasing zooplankton biomass and copepod abundance following a transect from east to west of GMS, but could also not relate this phenomenon to hydrography nor an increased primary production. During the present study slightly enhanced phytoplankton biomass was measured above the summit of GMS, but not leeward of it (Kaufmann, 2004). Phytoplankton biomass concentrations seemed to be only weakly increased and a direct response of higher trophic levels was unlikely. Furthermore, for measurable effects on secondary production physical anomalies above tropographic elevations have to be maintained for a few weeks (Genin and Boehlert, 1985; Rogers, 1994).

Specimens without extensive vertical migration behaviour (*e.g.*, early life stages of *Onychoteuthis banksii*) could be retained above the summit because the water mass above the seamount was virtually isolated, laterally and vertically (Beckmann and Mohn, 2002). An influx of early life stages into this water body via ocean currents is, thus, hardly possible. An increased density of cephalopods above the summit could only be expected if the seamount was an area of high spawning activity, viz cephalopod production. According to the generally low abundances of early life stages, especially above the plateau, this was obviously not the case at GMS, at least not during the sampling period. Therefore, it was concluded that the distribution patterns of cephalopods were attributed to the interaction of currents, topography and vertical migration behaviour of zooplankton rather than to retention potential or enhanced primary and secondary production above the plateau. The comparison of the vertical distribution patterns of all cephalopod species between GMS and the surrounding open ocean indicated an influence of the seamount on their overall abundance. The higher abundance of cephalopods during the day above the summit seemed to be related to 'trapping' of vertical migrators (*e.g.*, Pyroteuthidae) that are usually concentrated in the water layers below the summit depth during the day (Rogers, 1994). At night higher abundances in the open ocean compared to the plateau area indicate that vertically migrating species became susceptible to the sampling, whereas above the plateau their number might have been reduced by predation of *e.g.*, demersal fish species inhabiting the summit. Genin et al. (1994) and Haury et al. (2000) hypothesised that higher predation pressure on zooplankton organisms in the seamount area might be responsible for daily 'gap formation'. They assumed that these gaps are transported downstream and, accordingly, higher zooplankton patchiness can be found leeward of the seamount. The comparison of cephalopod abundances above and adjacent to the plateau gives rise to the assumption that a similar mechanism exists at GMS. Unfortunately, gap formation and patchiness downstream of the seamount could not be investigated directly due to the restricted sampling grid. However, the potential trapping of vertically migrating zooplankton organisms could support high concentrations of predatory benthopelagic fishes, as has been reported from GMS (Uiblein et al., 1999) and other seamounts (Dower and Perry, 2001; Uchida and Tagami, 1984).

In contrast to the influence on species abundances, no 'seamount-effect' was revealed for the species composition as shown by the MDS analysis. Differences between stations were not related to topographic or hydrographic features. Octopodid early life stages, which were presumably spawned above the summit or the slope of the seamount, were distributed within the whole investigated area and occurred even at deep water stations. Possible effects might also be masked by the selected station grid. According to Beckmann and Mohn (2002) the influence of GMS extends to about four times the area of the summit plain, which means that no stations were sampled outside the vicinity of the seamount. Dower and Mackas (1996) demonstrated a seamount effect on the mesozooplankton community that extended to about one seamount diameter into the surrounding oceanic waters, and even beyond this area the similarity between off- and above-seamount communities was relatively high. The high diversity of the cephalopod catches at GMS and the large variability among consecutive tows made it extremely difficult to detect any differences between station groups. Similar large variability has been reported from early life cephalopod assemblages in Hawaiian Island waters (Bower et al., 1999) and from tropical seamounts and near oceanic islands off the north-eastern coast of Brazil (Haimovici et al, 2002).

In order to answer the question whether seamounts have a positive effect on cephalopod assemblages, especially on their early life stages, additional sampling of the surrounding oceanic region would be required and stations would need to be repeatedly sampled, covering the entire day-night cycle. So far, commercially valuable cephalopod stocks have only been reported from around the shallow Saya de Malha Bank (14.7 m average water depth) in the western Indian Ocean (Nesis, 1993b). Whether seamounts that do not reach into the productive euphotic zone provide a similar suitable environment for cephalopod aggregations and serve as recruitment areas remains, however, still debatable.

Chapter IV

Fish larvae and cephalopod paralarvae assemblage structures at Great Meteor Seamount

– A multivariate approach –

Abstract

Assemblage structures and distribution patterns of larval fish and paralarval cephalopods were examined in September 1998 at Great Meteor seamount, an isolated seamount located in the subtropical eastern North Atlantic. Early life stages of fish (n=18555) and cephalopods (n=1200) were collected at 23 stations with a multiple opening-closing net in seven discrete depth strata from 290 m depth close to the seamount plateau to the surface. Oceanic species dominated in both taxonomic groups. A peak in diversity was determined at an intermediate depth, in the 100-150 m water layer. Species assemblages were investigated by different multivariate analytical methods using indirect and direct gradient analyses. Distinct assemblages were identified in the upper and lower part of the water column, separated at approximately 150 m water depth. The division was statistically robust although a considerable overlap between species was observed. Indications for the formation of gaps above the summit were found for the deeper communities likely to be caused by an increased predation pressure of benthopelagic fishes inhabiting the seamount. Horizontal distribution patterns of fish and cephalopod assemblages were remarkably similar and corresponded to the structure of closed circulation cells detected above the

flanks and the flat plateau area. Species assemblages of fish were significantly different between the inner and outer seamount regime, separated by hydrographic features at the 1500 m depth contour, whereas differences in community composition of cephalopods were less pronounced. The study confirms that the water column above the upper slopes and the seamount summit provide a significant retention potential to facilitate local recruitment of resident stocks with self-sustainable populations isolated from the continental shelf and oceanic islands. ‘Seamount effects’, reflected in the species composition, appeared to be smaller for cephalopods than for fish, because of the occurrence of the pelagic stage of only one bottom-dwelling octopod, for which a direct association to the seamount is assumed.

Introduction

In the last decades several studies focused on the oceanography and ecology of seamounts (reviewed by Boehlert and Genin, 1987; Roden, 1987; Rogers, 1994). Two aspects were of particular importance: (i) Large standing stocks of economically valuable fish species were discovered (Fonteneau, 1991; Genin et al., 1988; Gerber, 1993; Hubbs, 1959; Sibert et al., 2000), and (ii) higher attention was paid to biodiversity in the oceans; and isolated topographic elevations are usually supposed to serve as stepping stones and to represent areas of enhanced endemism (Richer de Forges et al., 2000; Wilson and Kaufmann, 1987).

At seamounts and oceanic islands substantial aggregations of demersal and pelagic fish communities are found that differ from the surrounding open ocean (*e.g.*, Koslow et al., 2000; Musyl et al., 2003; Parin, 1991; Uiblein et al, 1999). Lacking an upstream source population, resident stocks rely on local recruitment and physical or behavioural mechanisms maintaining larvae within the vicinity of the appropriate habitat. Within marine systems barriers to dispersal are relatively weak and it was, thus, hypothesised that larval retention around islands and seamounts occurs by means of mesoscale oceanographic features (Boehlert and Mundy, 1993). Taylor caps, defined as closed-streamline anticyclonic vortices above topographic obstacles in an impinging flow (Chapman and Haidvogel, 1992), and mesoscale eddies, shed from seamounts or seamount chains and remaining in the proximity of the shallow topography (Cheney et al., 1980), are potential mechanisms for larval retention. The residence time of water masses above the seamount summit or within eddies is, thus, increased, possibly affecting passively drifting particles and free-floating larvae (Boehlert and Mundy, 1993; Boehlert et al., 1992; Lobel and Robinson, 1986; Parker and Tunnicliffe, 1994). However, the description of 'seamount effects' on the distribution of ichthyoplankton or mesozooplankton remained equivocal, as *e.g.*, higher, lower or equal biomass was measured above topographic elevations in comparison to surrounding waters (Dower and Mackas, 1996; Fedosova, 1974; Genin et al., 1994; Haury et al., 2000; Huskin et al., 2001; Nellen, 1973). Investigations dealing with larval fish and early life stages of cephalopods mostly failed to identify a seamount associated ichthyo- or teuthofauna in the plankton that differs from the surrounding open ocean (Belyanina, 1984; Belyanina, 1993; Boehlert et al., 1992; Haimovici et al., 2002; Nesis, 1994). The analyses usually remained at the stage of describing the general species composition or focused on distribution patterns of single taxa. The formal testing of general hypotheses concerning ‘seamount effects’ is still lacking. The main problem common to most biological investigations at seamounts is the restricted spatial and/or temporal coverage of the sampled area. In being generally isolated from continental land masses, sampling at seamounts is mostly limited to a snapshot, and seasonal differences as well as the impact of extreme weather effects cannot be resolved. Furthermore, steep topographic elevations or seamount chains strongly influence hydrography far beyond the immediate vicinity of the plateau, sometimes extending to about four times the area of the summit plain (Beckmann and Mohn, 2002; Dower and Mackas, 1996). A comparison of only a few sites between areas may be, thus, insufficient and an appropriate biological sampling needs to cover the far field, which is often beyond the scope of interdisciplinary research cruises.

In this investigation of larval fish and paralarval cephalopods in the area of Great Meteor Seamount, an isolated seamount located in the subtropical North Atlantic, a slightly different approach than in former studies was used, to circumvent the above mentioned problems. Instead of comparing on-off seamount abundances and biomass values, either combining all taxa or selecting dominating species, multivariate statistical methods were chosen to define species assemblages in the horizontal as well as in the vertical plain. Distribution patterns of larval fish and paralarval cephalopods were examined in the light of physical oceanographic conditions. The ichthyoplankton composition of Great Meteor Seamount was described in detail before (Nellen, 1973; Nellen and Ruseler, 2004), but only single species were assumed to be affected by topography. Relatively high abundances of larvae from neritic species were found above the plateau and were indirectly related to resident fish populations, observed from parallel trawl catches at the upper slope and summit. By taking the whole community into account rather than selected species, assemblage structures were identified by modified principal component analyses and investigated if their vertical and horizontal distribution patterns could be spatially associated to topography and hydrography. Subsequently, potential explanatory variables, based on hydrographic and other environmental measurements at Great Meteor Seamount, were related to the species composition by redundancy analysis enabling significance testing. Assemblage structures of planktonic fish and cephalopods were compared, assuming corresponding influences on larval dispersal. Possible mechanisms forming, maintaining or disrupting the observed assemblages are discussed.

Material and Methods

Investigation area

Great Meteor Seamount (GMS) is located in the subtropical North Atlantic east of the mid-Atlantic Ridge at approximately 30°N and 28.5°W. It is one of the largest isolated topographic elevations in the Atlantic Ocean and rises steeply from depths of almost 4800 m to about 275 m below sea level. It is characterised by a large flat-topped plateau area of about 1130km² at an average depth of 330 m. The average slope is around 29% but locally exceeds up to 40%. The flow system of GMS is dominated by the wind-driven subtropical gyre of the North East Atlantic, *i.e.*, it lies within a mainly south-westward flowing current (Fig. IV.1). Diurnal and semidiurnal tidal constituents are also of importance. Hydrographical measurements had been performed in detail in parallel to the present study, and Mohn and Beckmann (2002), and Beckmann and Mohn (2002) described the hydrographic situation at GMS based on observations and three-dimensional numerical models. Topography affected the flow field by about four times the area of the summit plain, and an inner and outer seamount regime was distinguished along the 1500 m and 4400 m isobaths, respectively. The time-mean circulation within the inner seamount regime differed between the upper thermocline layer and the layer above the seamount summit. In near bottom layers an anticyclonic circulation cell of significant magnitude encompasses the plateau with some sub-mesoscale variability at the seamount periphery (Fig. IV.1). In the upper mixed layer including the thermocline a closed anticyclonic cell was observed that was located in the centre of the summit plain and extends above the southern hill. It was accompanied by a number of counterrotating cells above the rim (Fig. IV.1). Overall, a Taylor cap formation was detected above the summit and a strong retention potential of passive tracers within the 350 m depth contour was revealed. Although a slight upwelling at the slope of the seamount was found, it was not assumed to influence the primary or secondary production, as the doming of isopycnals did not reach into the euphotic zone.

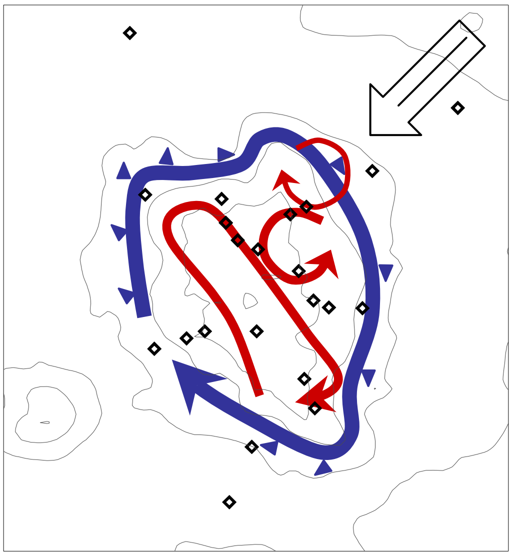

Fig. IV.1: Schematic view of the time-mean circulation in the upper thermocline layer (red arrows) and the seamount summit layer (blue arrows) at GMS in relation to Biomoc sampling stations (rhombic symbols). Arrow thickness indicates current velocities of 6 up to 10cm*s^{-1}. The block arrow represents the south-westward flowing current as a branch from the subtropical gyre. Bathymetry of Great Meteor Seamount is displayed in 350 m, 1500 m, 3000 m, and 4400 m depth contours. The figure is modfied from Mohn and Beckmann (2002).

Data collection

A total of 23 zooplankton stations were sampled in the area of Great Meteor Seamount (GMS) during September 1998 on board the German research vessel Meteor. Sampling was performed approximately along two orthogonal transects, crossing GMS in the area of the summit plain (Fig. IV.2).

Hydrographic conditions were recorded at every station by means of a CTD-cast. Since the density in this region is mainly determined by temperature and not salinity, temperature profiles were produced for each transect.

Fish larvae as well as early life stages of cephalopods (subsequently referred to as ‘fish’ and ‘cephalopods’) were collected by BIOMOC, a modified MOCNESS (Wiebe et al. 1976). The gear has a 1 m² net opening equipped with 9 nets of 335 µm mesh size that can be subsequently opened and closed. An electronic flowmeter was mounted in the frame to estimate the net specific filtered water volume. Samples from 23 stations (Fig. IV.2), covering the flat-topped summit of the seamount, the slope and the surrounding oceanic region were analysed. At 22 of these stations sampling was conducted from 290 m depth to the surface in 7 discrete depth strata (290-250 m, 250-200 m, 200-150 m, 150-100 m, 100-50 m, 50-10 m, 10-0 m). At an additional oceanic station samples were obtained from 1000 m water depth to the surface. However, only samples from 0-250 m were considered within this study, to allow comparison between stations. The BIOMOC was towed within each water layer in a threefold oblique tow at a ship's speed of approximately 3 knots. Plankton samples were initially preserved on board in 4% seawater-diluted formalin, buffered with sodium borate. In the laboratory fish and cephalopods were separated from the samples. Each specimen was identified to the lowest possible taxonomic level. Species densities (N/1000 m³) were calculated for each depth stratum as well as for the whole water column, integrating from 290 m depth to the surface, and were subsequently used in the initial tables of multivariate analyses.

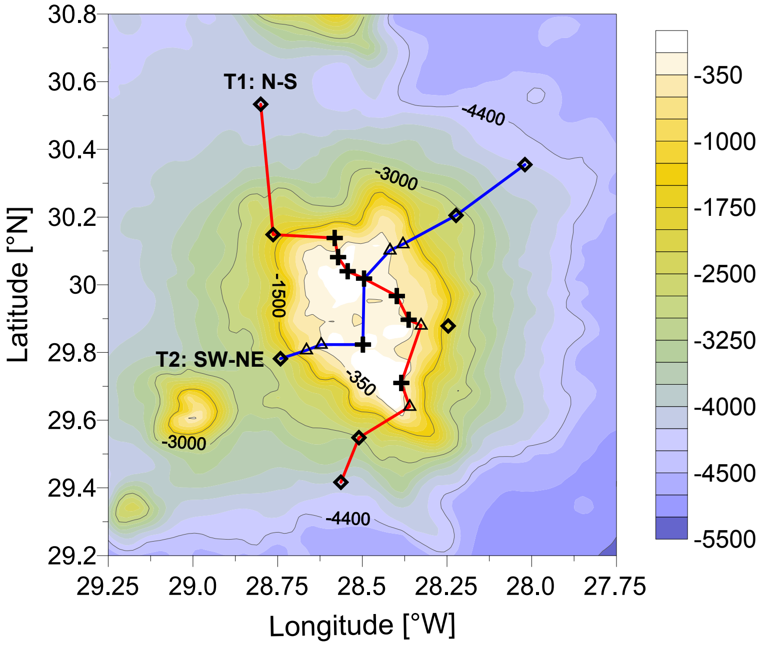

Fig. IV.2: BIOMOC stations sampled from 290 m depth to the surface, collected during the RV Meteor-cruise 42/3 in September 1998 at Great Meteor Seamount. Stations were classified into three categories, plateau (✚), slope (△), and deep sea (◇), indicated by symbols. Bathymetry of Great Meteor Seamount is displayed in 350 m, 1500 m, 3000 m, and 4400 m depth contours. The red (T1) and blue (T2) lines indicate transects mapped in relation to PCA results of depth resolved samples (Fig. IV.6 and IV.8).

Species diversity

The Shannon-Wiener diversity index (Shannon and Weaver, 1949) was calculated for fish and cephalopod taxa within each depth stratum using the following formula:

$$H' = \sum_{i=1}^{s} p_i(\ln p_i) \qquad \text{with } p_i = n_i \Big/ \sum_{i=1}^{s} n_i$$

where n_i is the number of individuals of the ith species in the sample and s is the number of species.

The Shannon-Wiener index was plotted against average sample depth to illustrate the change in species diversity from to 290 m water depth to the surface.

Multivariate data analysis

Sample specific densities of fish and cephalopods were analysed by Principal Component Analysis (PCA). The output was used for summarizing the spatial patterns of species communities by few orthogonal (*i.e.*, uncorrelated) principal components (PCs). Cephalopods were grouped to family or subfamily level, as a large portion of specimens was not identifiable to species. Fish larvae that could not be identified to species were assigned to higher taxa. Furthermore, in case only one species could be identified within a family, family- instead of species-specific densities were used. Taxa contributing less than 0.5% to the total abundance were excluded from the analysis. From 150 (fish) and 31 (cephalopods) taxa, 26 and 14 remained for gradient analyses. Prior to the PCA, densities were ln(x+1) transformed in order to reduce the relationship between the mean and the variance and to linearise the relationship between variables. Subsequently, a chord distance transformation was applied (Legendre and Gallagher, 2001; Orlóci, 1967) that allows the use of Euclidean-based ordination methods with community data containing many zero values. A standardized PCA based on the correlation matrix was performed on the transformed values to reduce the representation of distribution patterns from initially 26 and 14 variables for fish and cephalopods, respectively, to few orthogonal PCs. The number of significant PCs retained was determined from a scree-plot, by examining it for a clear break in the slope, *i.e.*, a significant change from high explained variation to low explanation, indicated by eigenvalues. Species vectors were displayed on the first factorial plane, and species loadings on single PCs were used to identify groups of species that tend to co-occur. Sample scores of PC1 and PC2 were subsequently mapped along the two transects for different depth strata or were mapped horizontally for integrated abundance values.

Furthermore, the agreement between the two community compositions (fish and cephalopods) at each station was tested by a Mantel test (Mantel, 1967) based on Spearman nonparametric correlation coefficient (Clarke and Ainsworth, 1993). In accordance with the previously performed PCA, first the Chord distance was calculated among sites to obtain two comparable distance matrices. Afterwards, the rank correlation between the distances among stations in the cephalopod- and fish-larvae matrix was calculated. By permuting the objects (stations) in one of the original data matrices repeatedly (999 permutations), the distribution of the test statistic was obtained and the significance of the determined relationship was tested. The permutation test was performed with the help of the 'Relate' module of the Primer 5 program (Clarke and Warwick, 1994).

Direct comparisons between the species composition in the samples (either fish or cephalopods) and environmental data were tested by canonical analysis using Redundancy analysis (RDA). RDA is a linear eigenvector ordination technique related to PCA, which constrains the axes to be linear combinations of explanatory variables. The importance of those variables can be subsequently evaluated by significance tests. As not all potential factors influencing the species composition could be quantified and included in the canonical analysis (*e.g.*, sub-mesoscale circulation cells), RDA was only performed as an add-on to the PCA.

Four or five different environmental variables were considered. In case vertically stratified samples were analysed, mean depth of sampling was included. As an additional variable sun height (-90 to +90°) was used. Sun height follows a sinusoidal curve over 24 hours and should reflect diel vertical migrations. Assuming a linear relationship between sun height and the migration magnitude implies that the extent of vertical movement within a certain time period is supposed to be largest during sunset and sunrise and nearly zero during midnight and noon. Sun height values from any time of the day at the date of sampling and the approximate position of the seamount were obtained from the freely available 'Sundi' software (V 1.1, *http://emsolar.ee.tu-berlin.de/simulation/sundi.html*). Finally the flow field allowed a classification of stations according the respective water depth into three categories, ‘plateau’ (<350m), ‘slope’ (350-1500m), and ‘deep sea’ (>1500m), whereas the first two categories refer to the inner and the latter to the outer seamount regime.

Temperature, salinity and nutrient measurements were not used as explanatory variables. Temperature was highly correlated to water depth and salinity hardly varied within the upper 300 m of the water column. As nutrient concentrations were generally low (Kaufmann, 2004), no influence on secondary production was assumed.

A weighted standardisation was applied to the environmental variables and species data were used according to the transformations already applied for PCA. To avoid collinearity between the binary-coded nominal variables ‘plateau’, ‘slope’ and ‘deep sea’ one variable (‘slope’) needed to be omitted from the analysis. Results were displayed as a correlation biplot, showing the relationship between species and environmental data. The significance of the relationship was investigated at two levels by Monte Carlo permutation tests: First a general test was applied concerning the null hypothesis of independence between species and environmental data using the sum of all canonical eigenvalues. Second, a forward selection process was performed, which is an analogous procedure to the selection process in stepwise multiple regression, to identify the most important environmental variables. Each environmental variable was first treated as a single predictor and the variance explained represented, hence, ‘marginal effects’. Thereafter, the best variable was selected and all other environmental variables were ranked according to the additional explained variance that was given in conjunction with the already selected variable (-s). This process was repeated until all variables were included, with the explained variance representing ”conditional effects”. At each step, the significance of the added variables was tested by permuting randomly the rows of the species matrices (999 unrestricted permutations of raw data) and recomputing the RDA.

Unless otherwise noted, all multivariate analyses were performed using the Brodgar 2.3.1 program.

Results

Vertical temperature profiles

Temperature ranged from 15°C near the seamount summit to about 26°C in surface water layers (Fig. IV.3). A seasonal thermocline was only weakly established at approximately 50-75 m depth. Systematic temperature anomalies were measured which reflected the presence of the seamount. A 'dome-like' deformation of the temperature field was recognized at both transects that weakened between 100 and 200 m water depth and was partly converted to a slight depression. However, according to Mohn and Beckmann (2002) the upward displacement of isotherms above the relatively shallow seamount plain did not exceed 30 m and was, thus, below the resolution of the plankton sampling scheme. Additionally, a pronounced depression of isotherms in the slope area was found. This depression comprised the whole seamount summit (Mohn and Beckmann, 2002) but was less pronounced in the southern slope area. It extended from water layers near the seamount summit into near surface waters.

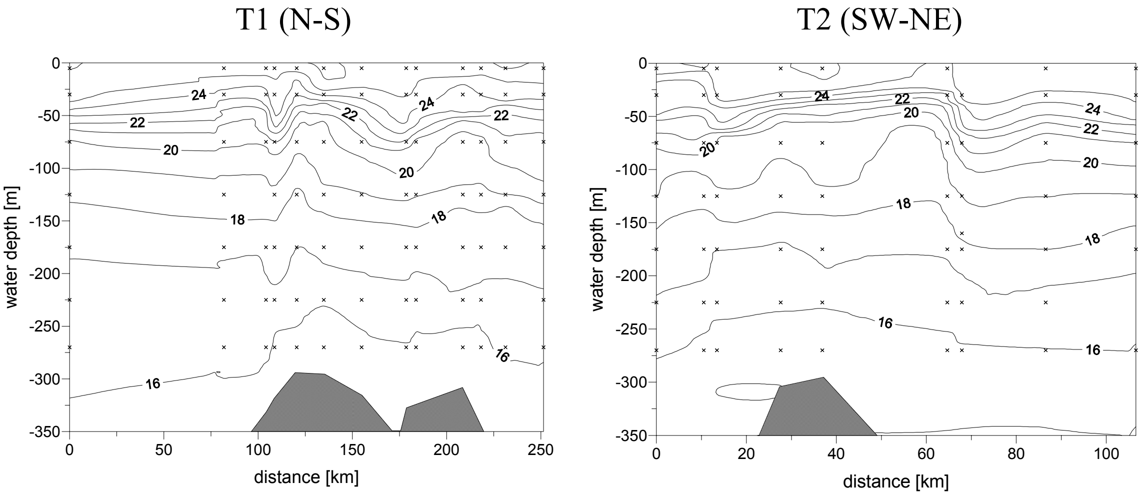

Fig. IV.3: Vertical temperature profiles along both transects, T1 and T2 (see Fig. IV.2). Crosses indicate the average depth of available Biomoc-samples. Interpolation between data points was done by kriging.

Species composition and diversity

The analysis of 156 discrete samples collected at 23 stations amounted to 18555 individual fish larvae and 1200 cephalopod paralarvae. 150 different fish taxa of 53 families were identified, which presumably corresponded closely to the actual number of species present at Great Meteor Seamount in September 1998 (Nellen and Ruseler, 2004). Most specimens belonged to typical oceanic and mesopelagic fish species, e.g the two clearly dominating taxa *Cyclothone* sp. and *Vincinguerria* sp. that accounted for 18.2% and 16.8% of the total catch, respectively (Tab. IV.1). Most important families were the Myctophidae, Gonostomatidae and Photichthyidae, which representatives amounted to a total of 75% of all collected specimens. Few larvae were found that belonged to neritic or demersal adults. The only numerically significant species was *Chlorophthalmus agassizii* with a percent contribution of approximately 5%. The family Myctophidae was the most speciose (22 species), followed by Paralepididae (six species), Gonostomatidae, Melanostomiidae and Sternoptychidae (five species each). 26 species or taxa contributed more than 0.5% to the overall fish larval density and amounted to nearly 74% of the total catch.

Cephalopods comprised at least 31 species of 18 families. Most specimens belonged to mesopelagic families, mainly Enoploteuthidae (25.6%) and Pyroteuthidae (10.7%) (Tab. IV.1). Dominant species were *Abraliopsis pfefferi* (Enoploteuthidae) and *Onychoteuthis banksii* complex (Onychoteuthidae). The Octopoda were composed of at least four different families of which three were of major importance: The pelagic groups Argonautidae and Bolitaenidae, as well as the Octopodidae, which were presumably represented by only one species, the deep-water octopod *Scaeurgus unicirrhus*. 14 families were identified to be numerically most important, each contributing at least 0.5% to the total catch. The meso- to bathypelagic family Cranchiidae was additionally splitted to subfamily level, into Taoninae and Cranchiinae. All identified taxa included in the analyses represented approximately 80% of the total cephalopod catch.

Tab. IV.1: Average densities of fish and cephalopod taxa, the percentage contribution to the overall densities and the taxon abbreviation, used for PCA and RDA. Only taxa contributing at least 0.5% to the overall densities of fish or cephalopods are listed.

Fish larvae				**Cephalopod larvae**			
Taxon	Abbreviation	Average N/1000m³	% contribution	Taxon	Abbreviation	Average N/1000m³	%-contribution
Cyclothone sp.	Cyclo	19.54	18.16	Enoploteuthidae	Enoplo	1.02	17.57
Vinciguerria sp.	Vincin	18.07	16.80	Onychoteuthidae	Onych	0.95	16.27
Lampanyctus spp.	Lampan	5.37	4.99	Pyroteuthidae	Pyro	0.62	10.61
Chlorophthalmus agassizii	Chloro	5.30	4.93	Lycoteuthidae	Lyco	0.34	5.75
Hygophum spp.	Hygop	5.12	4.76	Ancistrocheiridae	Ancist	0.32	5.45
Diaphus sp.	Diaphus	4.34	4.03	Ommastrephidae	Ommas	0.26	4.50
Bolinichthys sp.	Bolin	2.24	2.08	Taoninae	Taoninae	0.23	3.91
Nannobrachium spp.	Nann	1.96	1.82	Chtenopterygidae	Chteno	0.23	3.87
Notolychnus valdiviae	Notol	1.93	1.79	Bolitaenidae	Bolitae	0.20	3.39
Lepidophanes gaussi	Lepido	1.74	1.61	Chiroteuthidae	Chiro	0.14	2.43
Diogenichthys atlanticus	Diogen	1.67	1.55	Argonautidae	Argo	0.11	1.92
Sternoptyx sp.	Stern	1.56	1.45	Octopodidae	Octo	0.10	1.70
Scopelarchus spp.	Scopel	1.19	1.11	Cranchiinae	Cranchiinae	0.06	1.10
Chauliodus sp.	Chau	1.10	1.03	Thysanoteuthidae	Thysano	0.04	0.69
Diplospinus multistriatus	Diplos	0.93	0.87	Histioteuthidae	Histio	0.03	0.53
Sudis sp.	Sudis	0.89	0.83				
Symbolophorus rufinus	Symbol	0.83	0.77				
Alepisauridae	Alepis	0.75	0.69				
Magnisudis atlantica	Magni	0.72	0.67				
Lampadena spp.	Lampad	0.67	0.62				
Oneirodidae	Oneir	0.60	0.56				
Ceratoscopelus sp.	Cerato	0.60	0.56				
Myctophum spp.	Myct	0.59	0.55				
Aulopus filamentosus	Aulop	0.58	0.54				
Maurolicus muelleri	Maurol	0.56	0.52				
Lestidiops jayakari	Lestid	0.50	0.43				

Species diversity in relation to sampling depth revealed similar patterns for fish and cephalopods (Fig. IV.4). For both taxonomic groups highest diversity was measured from 100-150 m. Below this layer, the Shannon-Wiener index decreased steadily. Diversity of paralarval cephalopods at the deepest stratum reached almost zero, meaning that usually only one species was found in this water depth. In contrast to this, diversity of fish was generally much higher and even in the deepest layer several different species were encountered.

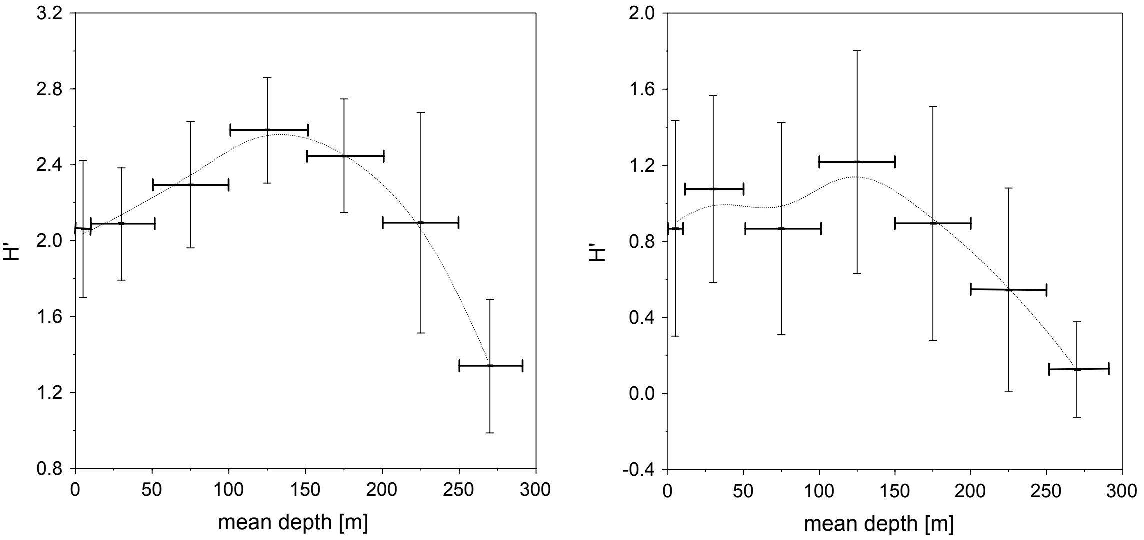

Fig. IV.4: Shannon-Wiener Diversity measure (H' based on natural logarithm) of larval fish (left) and paralarval cephalopods (right) in relation to sample depth. Horizontal lines indicate the average diversity measure at the respective depth stratum, vertical lines the standard deviation. A distance-weighted least squares smoothing procedure was applied. All distinguishable taxa, identified to the lowest taxonomic level were included. Samples containing no fish or cephalopod specimens were excluded from the analysis.

Species assemblages identified by PCA and RDA

Three fish species assemblages could be defined by a PCA analysis of the Chord distances between depth-stratified samples (Fig. IV.5). The first group was positively, the second negatively related to PC1. A third group was generally characterised by high positive species loadings on PC2 but was nearly uncorrelated to the first axis. The mapping of sample scores along transect 1 and transect 2 revealed a distinct relationship between the first axis (explaining 20.9% of total variance) and sampling depth (Fig. IV.6). Species with positive loadings on PC1 were concentrated in the upper 150 m of the water column, species with negative loadings dominated the assemblage in water depth below 150 m.

Furthermore, the negative correlation between assemblages indicated that both groups possibly excluded each other in the shallowest or deepest depth stratum. Characteristic taxa of the upper water assemblages were the numerically dominating species *Cyclothone* sp., genera of the myctophid subfamily Lampanyctinae such as *Lampanyctus* and *Diaphus*, as well as the neritic *C. agassizii*. *Scopelarchus* spp. and the sternoptychid species *Maurolicus muelleri* and *Sternoptyx* sp. were negatively correlated to this species group. High sample scores of PC2 (10.5%) were mainly found in intermediate water layers. In this layer the fish community was characterised by high diversity (Fig. IV.4), indicating an overlap between the upper and lower species assemblages. Several myctophid species of the subfamily Myctophinae, such as *Hygophum* spp. and *Diogenichthys atlanticus*, characterised this group. The only species of the Lampanyctinae was *Notolynchus valdiviae*. The vector lengths of most taxa were generally high, indicating a good representation within the first factorial plane (Fig. IV.5). However, the vector apex of the second most abundant genus *Vincinguerria* was located near the origin of the diagram. Individuals of this genus are, thus, only weakly related to any of the species assemblages and are presumably abundant at every site and sampling depth. At certain stations the clear vertical structuring of sample scores was slightly disturbed (Fig. IV.6). At transect 1 irregularities were mainly found above the shallowest part of the seamount summit, at depth below 150 m. Species with negative loadings along PC1, *i.e.*, the assemblage comprising *Scopelarchus* spp., *M. muelleri* and *Sternoptyx* sp., were partly replaced by other fish taxa, *e.g.*, characterised by higher loadings on PC2. This change in species composition co-occurs with a pronounced upward displacement of isotherms (Fig. IV.3). In contrast to this, PC1 sample scores of transect 2 (Fig. IV.6) deviated from the vertical pattern in the upper 150 m of the water column north-eastward of the plateau and not above it. In this area, which is located upstream of the seamount, species with hardly any correlation to PC1 intruded in near surface layers.

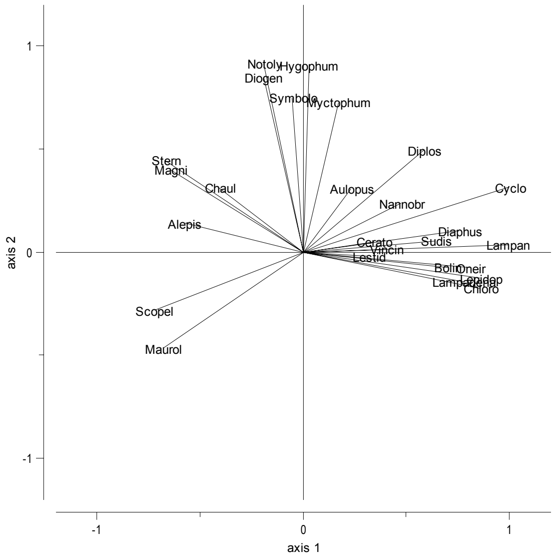

Fig. IV.5: Principal component analysis (PCA) ordination diagram based on chord distances of vertically resolved fishlarvae abundance data. Only taxa contributing >0.5% to the overall abundance were included. 31.4% of overall variance was explained by the first factorial plane (PC1 = 20.9%; PC2 = 10.5%). Abbreviations of species names can be deduced from table IV.1.

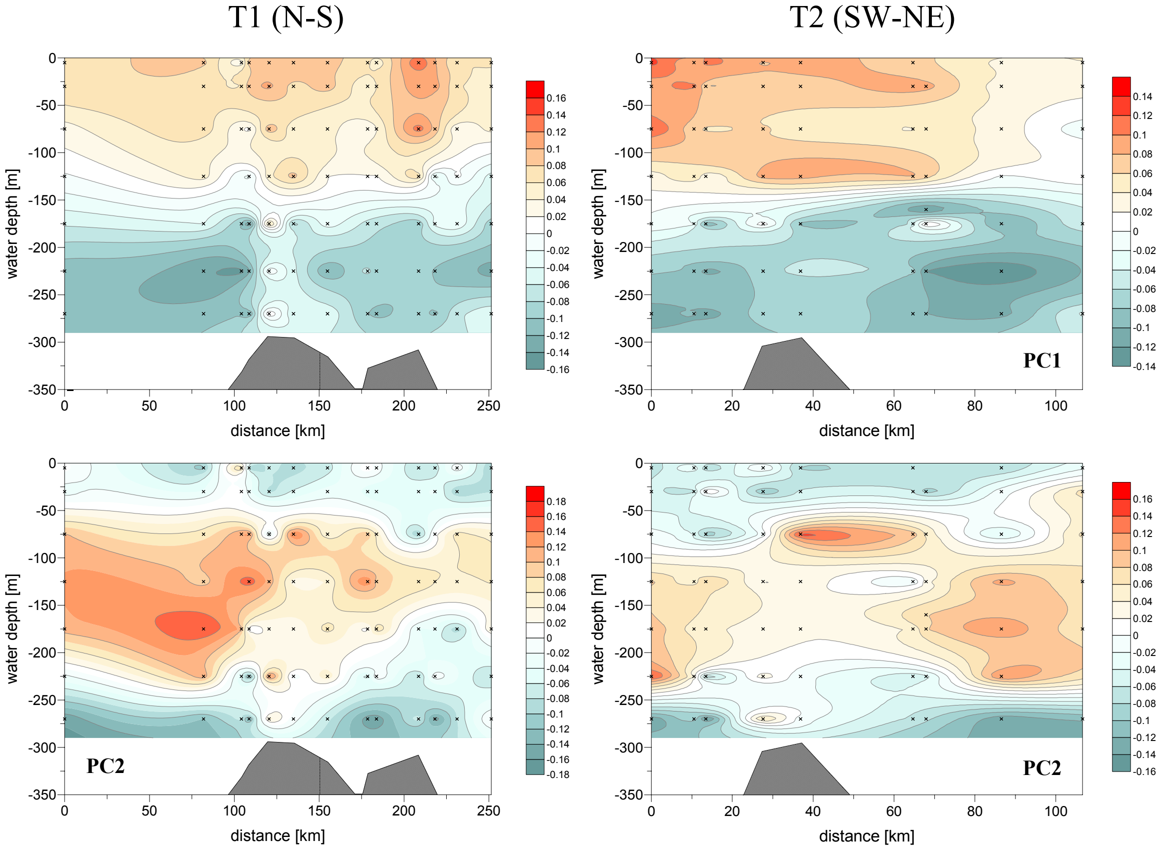

Fig. IV.6: Sample scores of PC1 (upper graphs) and PC2 (lower graphs) of the principal component analysis (PCA) based on chord distances of vertically resolved larval fish abundance data. Scores are mapped according to average sampling depth and the distance along Transect 1 (N-S; left) and Transect 2 (W-E; right) indicated in Fig. IV.2. Crosses indicate available data points, interpolation between points was done by kriging.

PCA analysis of the cephalopod community yielded comparable results to fish although the formation of groups, because of weaker correlations between taxa, was less pronounced (Fig. IV.7). Positive loadings along the first axis were measured for example for Pyroteuthidae, Bolitaenidae and Octopodidae, negative loadings for Onychoteuthidae, Ancistroteuthidae or Ommastrephidae. Samples scores of the first PC (15.9%) showed, similarly to fish, a strong relationship to sampling depth (Fig. IV.8) indicating that the first species group was more confined to deeper, the latter group more to upper water layers. Taxa occurring in relatively low densities showed the highest correlation with the second axis. According to the expected higher variability of these taxa, PC2 sample scores (9.1%) were not spatially structured at any of the two transects. They may be, thus, arbitrarily distributed within the upper 290 m of the water column. Anomalies were consequently only detectable for the PC1 sample scores. The deviation of isolines from the general vertical structure corresponded closely to the patterns found in the larval fish community (Fig. IV.6 and IV.8). However, it has to be noted that less variability was explained by the first axis and that cephalopods were not found in all samples collected below 200 m water depth. The interpolation of sample scores resulted, therefore, in highly variable patterns.

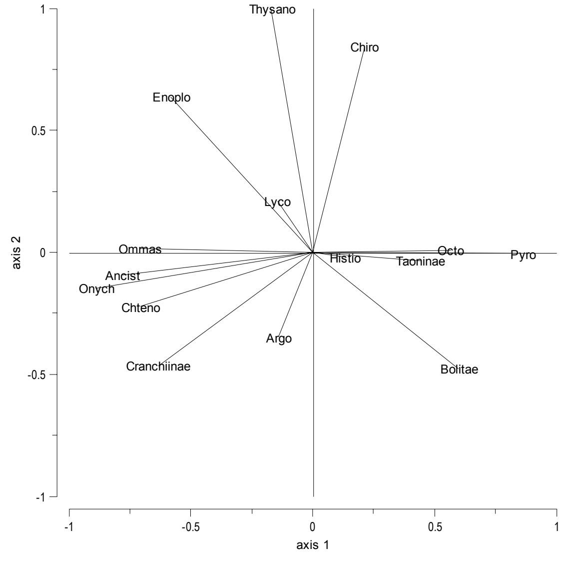

Fig. IV.7: Principal component analysis (PCA) ordination diagram based on chord distances of vertically resolved cephalopod paralarvae abundance data. Only families contributing >0.5% to the overall abundance were included. 26.3% of overall variance was explained by the first factorial plane (PC1 = 15.9%; PC2 = 9.1%). Abbreviations of species names can be deduced from table IV.1.

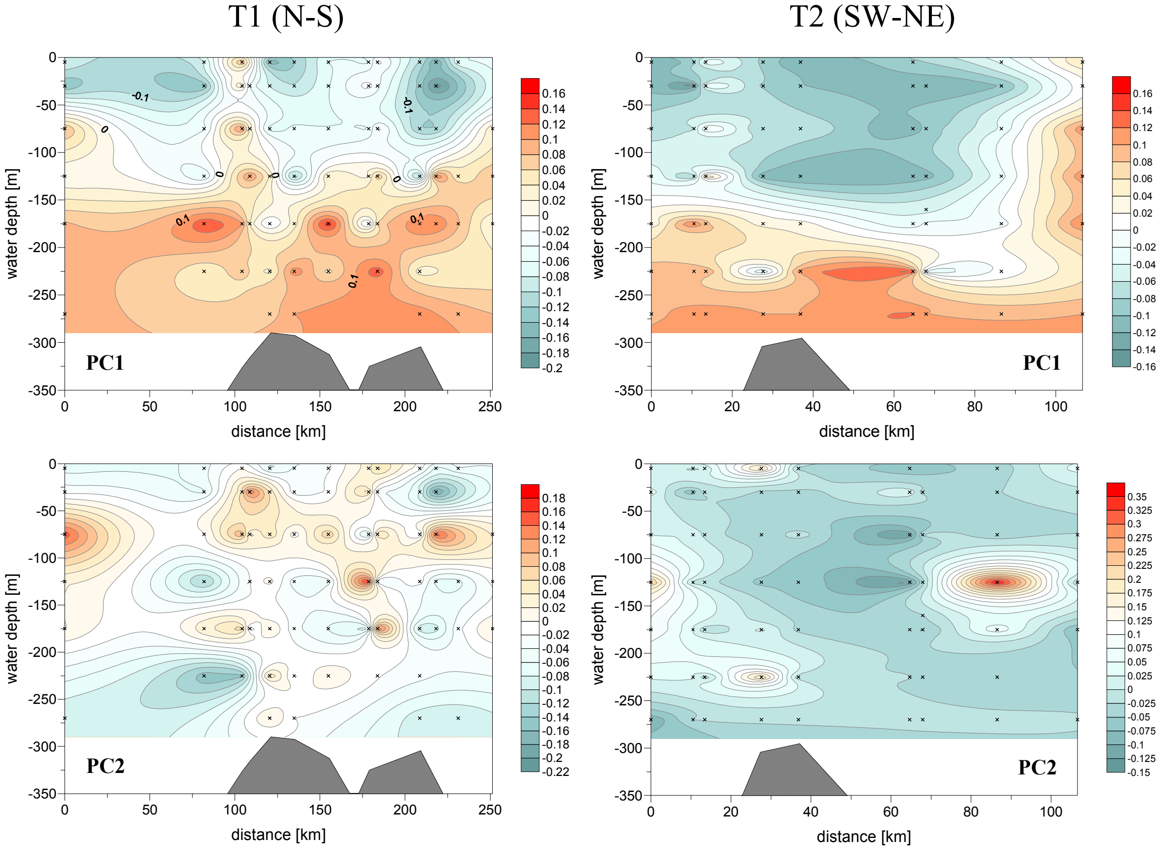

Fig. IV.8: Sample scores of PC1 (upper graphs) and PC2 (lower graphs) of the principal component analysis (PCA) based on chord distances of vertically resolved paralarval cephalopod abundance data. Scores are mapped according to average sampling depth and the distance along Transect 1 (N-S; left) and Transect 2 (W-E; right) indicated in Fig. IV.2. Crosses indicate available data points, interpolation between points was done by kriging.

Analysing the horizontal patterns of the fish and cephalopod assemblages by means of a PCA using integrated abundance values yielded no obvious grouping of taxa. However, fish species that were characterised by negative loadings on the first axis in the PCA on vertically resolved samples (Fig. IV.5), showed also the highest correlation to each other in this PCA plot (Fig. IV.9). As an example *Scopelarchus* spp. were still related to *M. muelleri* and *Sternoptyx* sp., although other species like *Symbolophorus rufinus* were integrated in this group. An analogous observation was made for cephalopods where among others Onychoteuthidae, Chtenopterygidae and Cranchiinae showed a strong correlation to PC1 in both PCAs, based on abundances of vertically resolved (Fig. IV.7) as well as of vertically integrated samples (Fig. IV.9). The grouping of taxa is, thus, a matter of sampling depth, but also depends on the horizontal distribution at the seamount.

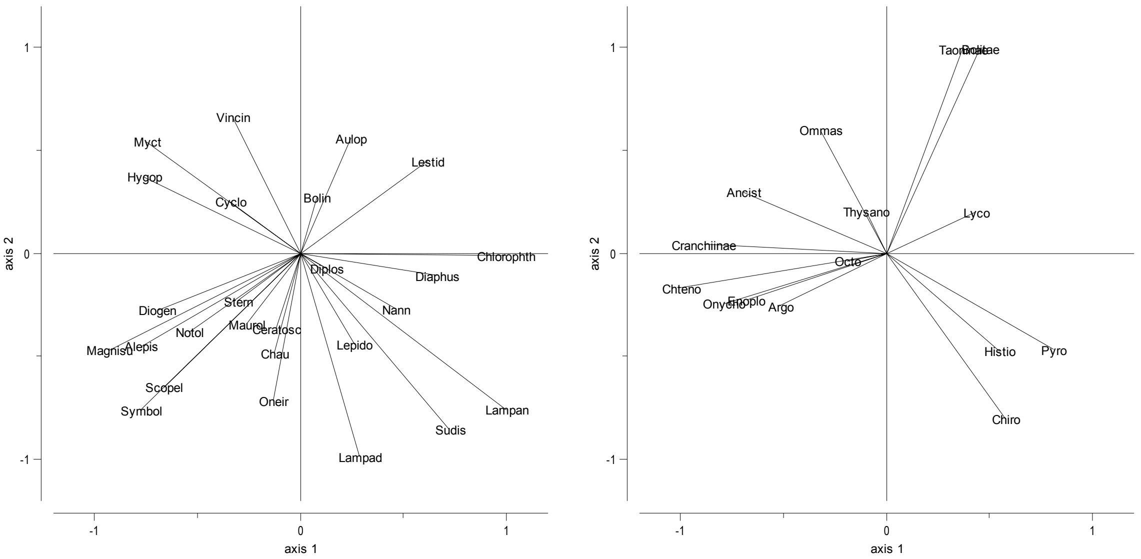

Fig. IV.9: Principal component analysis (PCA) ordination diagram based on chord distances of station specific larval fish (left) and paralarval cephalopod (right) abundance data. Only families contributing >0.5% to the overall abundance were included. 31.8% of the overall variance was explained by the first factorial plane for larval fish (PC1 = 17.8%; PC2 = 14.0%), 38.0% for paralarval cephalopods (PC1 = 22.6%; PC2 = 15.3%). Abbreviations of species names can be deduced from table IV.1.

The mapping of sample scores at the first PC showed similar spatial patterns taking the fish (17.8%) or the cephalopod community (22.6%) as a basis (Fig. IV.10). The outermost stations as well as stations located at the northern edge of the summit differed clearly from stations above the centre of the plateau or the north-eastern and south-eastern plateau and slope areas of the seamount. Concerning the species vectors in the PCA plots (Fig. IV.9), the latter station group was characterised by *e.g.*, the neritic fish species *C. agassizii* and *Lampanyctus* spp. as well as by cephalopod families with negative loadings on PC1, namely Cranchiinae, Onychoteuthidae or Ommastrephidae. All these taxa were related to upper layer assemblages in the first PCAs. The species communities on the outermost sites were, on the other hand, more dominated by fish and cephalopod taxa that were, according to the previous analyses (Figs. 5 and 7), positively related to water depth, as *e.g.*, *Scopelarchus* spp. or Pyroteuthidae. Sample scores of the second PC of the fish (14%) and cephalopod (15.3%) analysis differed, however, markedly from each other (Fig. IV.10). Concerning the fish community, the outermost stations still resembled each other but also showed some similarities to stations above the summit. Samples scores resulting from the PCA based on cephalopod species composition revealed only small differences between stations with the exception of one station south of the summit, where mainly Taoninae and

Bolitaenidae were identified. The similarities observed between horizontal patterns of sample scores were confirmed by a mantle test. The Chord distances among stations calculated from fish abundances were correlated with the corresponding distances based on cephalopod abundances with a correlation coefficient of 0.4. This rank correlation was proved to be highly significant (p<0.001).

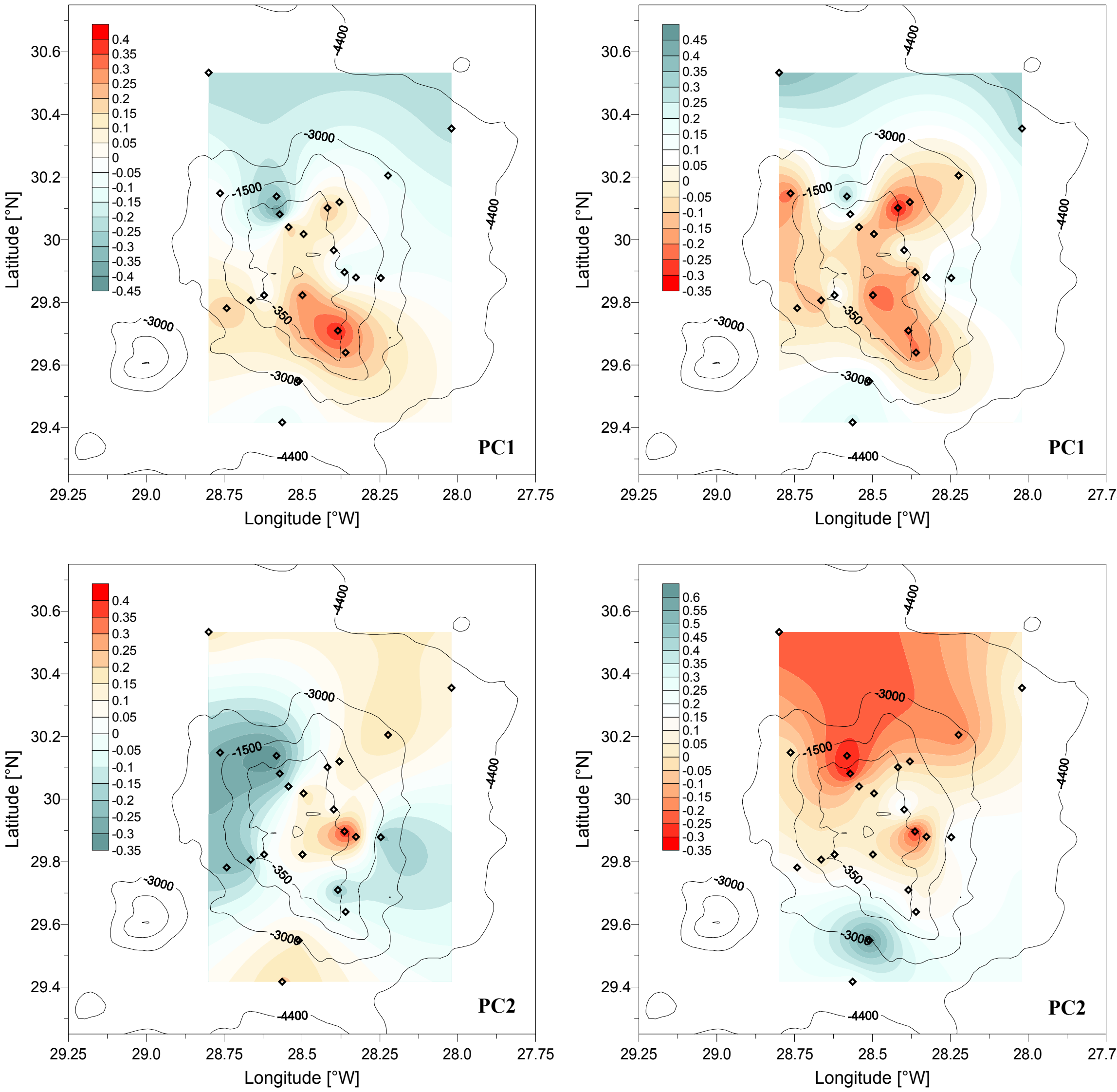

Fig. IV.10: Sample scores of PC1 (upper graphs) and PC2 (lower graphs) of the principal component analyses (PCA) based on chord distances of station specific larval fish (left) and paralarval cephalopod (right) abundance data. Scores are mapped according to the geographical position of the stations in the area of Great Meteor Seamount. Rhombic symbols indicate available data points, interpolation between points was done by kriging.

The concluding redundancy analyses (RDAs) confirmed the observations that species assemblages changed vertically as well as horizontally within the area of GMS. Sampling depth was the main influencing variable for fish and cephalopod species, taking the vertically resolved data into account (Fig. IV.11, Tab. IV.2a-b). Groupings of species were essentially the same as in the previously described PCAs (Fig. IV.5, IV.7 and IV.9). Although marginal effects were small 'sunheight' was also a significant factor in the fish RDA, indicating vertical migratory behaviour of some species. The nominal variable 'deep sea' explained a significant amount of variation for both, the fish and the cephalopod community. This supports the results of similar sample scores among the outermost stations, which are, thus, presumably characterised by comparable species compositions. RDA of site specific abundance data was only significant for fish but not for cephalopods, although for both communities 'deep sea' was again the main influencing variable (Fig. IV.12, Tab. IV.3a-b).

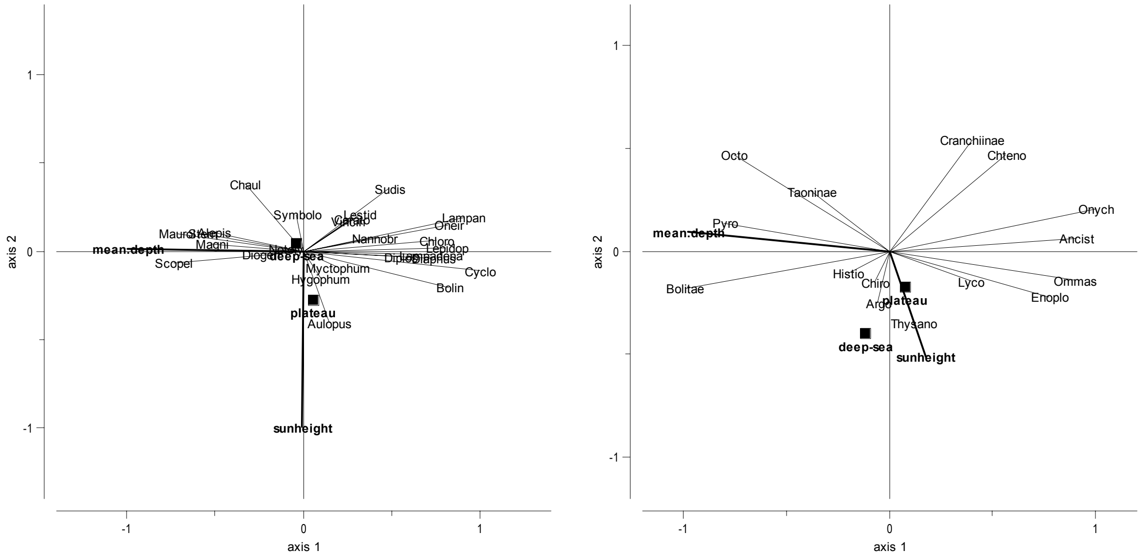

Fig. IV.11: Redundancy analysis (RDA) ordination diagram based on chord distances of vertically resolved larval fish (left) and paralarval cephalopod (right) abundance data. Only families contributing >0.5% to the overall abundance were included. Abbreviations of species names can be deduced from table IV.1. Environmental variables are indicated by bold lines for continuous variables (mean sampling depth, sunheight) or bold squares for nominal variables (plateau, deep sea). The length of vectors indicate the contribution of the descriptors to the formation of PC1 and PC2. 19.0% of the overall variance was explained by environmental factors for fish larvae, 11.0% for cephalopod paralarvae. The relationships between species and environmental variables were statistically significant (Monte Carlo permutation test; p<0.001) for both species communities. For detailed results of the RDA see table IV.2.

Tab. IV.2: Results of Redundancy analysis (RDA) for larval fish (a) and paralarval cephalopod (b) abundance data based on depth stratified sampling in the area of Great Meteor Seamount. Correlations between canonical axes and environmental variables are additionally presented. The marginal effect gives the eigenvalue and percentage of explained variance if only one explanatory variable is used. Conditional effects show the increase in the total sum of eigenvalues after including a new variable during a forward selection. Environmental variables are listed according to the inclusion in the forward-selection model. Significance levels are based on a Monte Carlo permutation test of raw data with 999 unrestricted permutations.

a)

Axis	1	2	3	4
Eigenvalues	0.157	0.014	0.012	0.007
Cumulative % variance of species data	15.724	17.159	18.325	18.996
Cumulative % variance of species-environment relationship	82.772	90.330	96.464	100.000

Environmental variable	Correlations with axis				Marginal effects [eigenvalues]	Conditional effects [eigenvalues]
	1	2	3	4		
catch depth	-0.99	0.01	0.04	0.11	0.16 (81.63%)	0.16 (p = 0.001)
sunheight	-0.01	-1.00	-0.05	0.06	0.01 (7.55%)	0.01 (p = 0.001)
deep sea	-0.06	0.07	-0.72	-0.69	0.01 (5.18%)	0.01 (p = 0.006)
plateau	0.08	-0.40	-0.11	0.91	0.01 (4.72%)	0.01 (p = 0.564)

b)

Axis	1	2	3	4
Eigenvalues	0.08	0.02	0.01	0.00
Cumulative % variance of species data	8.22	9.82	10.52	10.95
Cumulative % variance of species-environment relationship	75.11	89.74	96.11	100.00

Environmental variable	Correlations with axis				Marginal effects [eigenvalues]	Conditional effects [eigenvalues]
	1	2	3	4		
catch depth	-0.98	0.09	-0.02	0.19	0 08 (72.00%)	0.08 (p = 0.001)
deep sea	-0.18	-0.62	-0.28	-0.71	0.01 (10.60%)	0.01 (p = 0.041)
sun height	0.18	-0.51	-0.44	0.72	0.01 (9.40%)	0.01 (p = 0.271)
plateau	0.12	-0.28	0.55	0.78	0.01 (6.54%)	0.01 (p = 0.732)

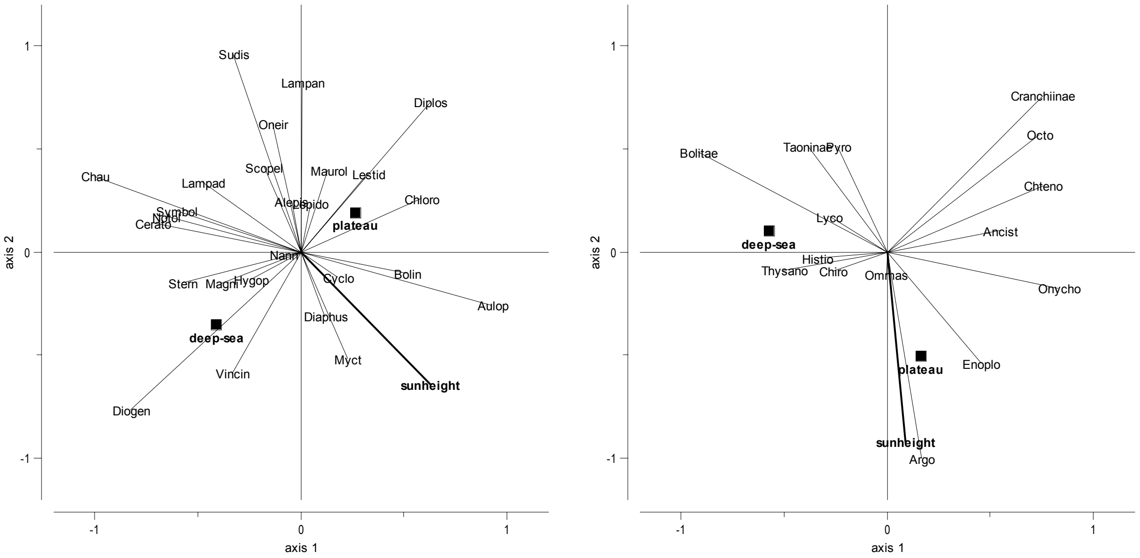

Fig. IV.12: Redundancy analysis (RDA) ordination diagram based on chord distances of station specific larval fish (left) and paralarval cephalopod (right) abundance data. Only families contributing >0.5% to the overall abundance were included. Abbreviations of species names can be deduced from table IV.1. Environmental variables are indicated by bold lines for continuous variables (sunheight) or bold squares for nominal variables (plateau, deep sea). The length of vectors indicate the contribution of the descriptors to the formation of PC1 and PC2. 18.9% of the overall variance was explained by environmental factors for fish larvae, 15.9% for cephalopod paralarvae. The relationships between species and environmental variables were statistically significant (Monte Carlo permutation test; p = 0.04) for larval fish but not for paralarval cephalopods. For detailed results of the RDA see table IV.3.

Tab. IV.3: Results of Redundancy analysis (RDA) for larval fish (a) and paralarval cephalopod (b) station specific abundance data based on 23 stations collected in the area of Great Meteor Seamount. Correlations between canonical axes and environmental variables are additionally presented. The marginal effect gives the eigenvalue and percentage of explained variance if only one explanatory variable is used. Conditional effects show the increase in the total sum of eigenvalues after including a new variable during a forward selection. Environmental variables are listed according to the inclusion in the forward-selection model. Significance levels are based on a Monte Carlo permutation test of raw data with 999 unrestricted permutations.

a)

Axis	1	2	3
Eigenvalues	0.08	0.06	0.05
Cumulative % variance of species data	7.77	14.07	18.88
Cumulative % variance of species-environment relationship	41.15	74.53	100.00

Environmental variable	Correlations with axis			Marginal effects [eigenvalues]	Conditional effects [eigenvalues]
	1	2	3		
deep sea	-0.76	-0.65	-0.05	0.07 (37.83%)	0.07 (p = 0.046)
sunheight	0.63	-0.64	0.44	0.07 (34.89%)	0.06 (p = 0.059)
plateau	0.44	0.32	0.84	0.06 (29.36%)	0.05 (p = 0.856)

Tab. IV.3: continued from previous page

b)

Axis	1	2	3		
Eigenvalues	0.08	0.06	0.02		
Cumulative % variance of species data	7.97	13.58	15.93		
Cumulative % variance of species-environment relationship	50.05	85.25	100.00		
Environmental variable	Correlations with axis			Marginal effects [eigenvalues]	Conditional effects [eigenvalues]
	1	2	3		
deep sea	-0.90	0.16	-0.40	0.07 (44.13%)	0.07 (p = 0.069)
sunheight	0.09	-0.92	-0.38	0.05 (32.38%)	0.05 (p = 0.262)
plateau	0.23	-0.72	0.65	0.04 (27.31%)	0.04 (p = 0.947)

Diel vertical distribution patterns

Vertical distribution patterns of key taxa, characteristic for one of the assemblages identified in the PCAs based on vertically resolved abundance data (Fig. IV.5 and IV.7), were additionally investigated. Irrespective of sampling position day and night distributions were compared to each other (Fig. IV.13). Diel vertical migration was observed for *Scopelarchus* spp., Pyroteuthidae and Enoploteuthidae, although for none of the taxa a pronounced correlation with sunheight was detected by the RDAs (Fig. IV.11). *Scopelarchus* spp. and Pyroteuthidae were, however clearly related to sampling depth and showed accordingly the deepest distribution of all investigated taxa. Both were regularly encountered in the deepest layer, at day and night. *Cyclothone* sp. and Onychoteuthidae were mainly found in the upper 150 m of the water column and were, according to the PCAs (Figs. 5-8), typical representatives of the upper layer assemblages. *Hygophum* spp. and Enoploteuthidae that were both related to the second PC (Fig. IV.3 and IV.5) were more confined to intermediate water layers although Enoploteuthidae showed a weaker correlation to the axis because of their diel vertical migration behaviour. The distribution patterns of all taxa overlapped mainly between 50 to 150 m water depths, which coincides with the strata showing highest species diversity.

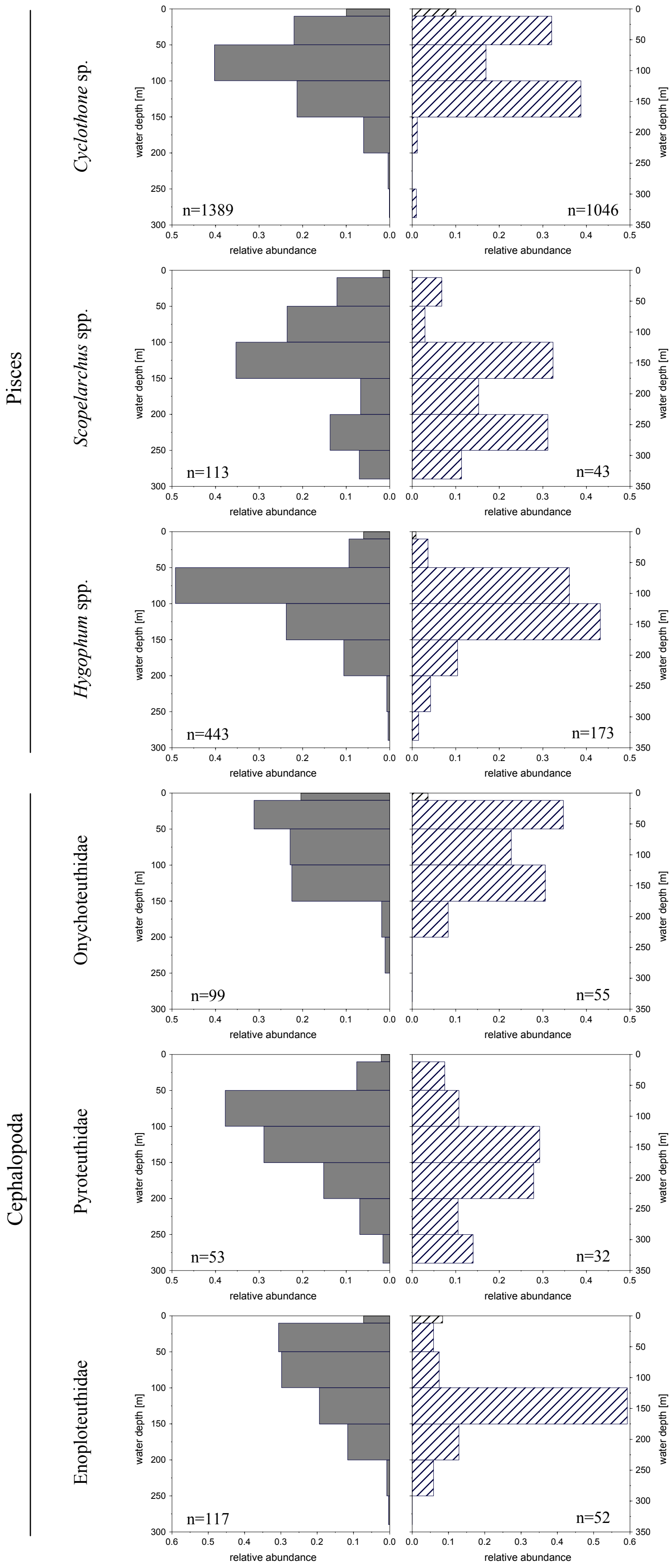

Fig. IV.13: Average vertical distribution of key fish and cephalopod species at night (left, 11 hauls) and day (right, 7 hauls) during RV Meteor-cruise 42/3 in September 1998 at Great Meteor Seamount.

Discussion

Oceanic seamounts are supposed to provide habitats for demersal and pelagic fish and cephalopod communities that are usually not found in the open ocean. The maintenance of populations is dependent on local recruitment or the advection of eggs and larvae from shelf areas or neighbouring oceanic islands and seamounts. Eggs and larvae added to the background of the oceanic plankton are assumed to alter the species composition with some relation to the topographic elevation. However, most studies failed to identify seamount associated larval fish or cephalopod communities (Belyanina, 1984; Boehlert and Mundy, 1993; Haimovici et al., 2002) and there is little evidence that persistent ichthyoplankton assemblages distinct from those in the surrounding ocean, exist near deep (>200m) and isolated seamounts (Boehlert and Mundy, 1993). The minimum distance between GMS and the African shelf amounts to more than 750 nm and the seamount summit rises to a minimum water depth of 275 m. Consequently, the ichthyo- and teuthofauna in this study was dominated by widespread oceanic taxa and only few topographically associated species were found. In general, the larval fish community resembled the fauna known from the Canary region or south of the Azores (Bekker et al., 1982; John et al., 2002; Rodríguez et al., 2000), whereas paralarval cephalopods belonged almost exclusively to circumatlantic oceanic species with a pelagic lifecycle. Hatchlings of Octopodidae, presumably originating from the deep-water octopod *Scaeurgus unicirrhus* caught above the plateau (Diekmann, unpublished data), were the only specimens related to bottom dwelling adults. Nellen and Ruseler (2004) accounted approximately 84% of all fish taxa collected at GMS during Meteor cruise 42/3 to oceanic species, and only 5% or 9% were assumed to be slope- or shelf-bound, respectively. *Cyclothone* and *Vincinguerria* were the most abundant mesopelagic genera in the present and earlier ichthyoplankton studies of GMS (Belyanina, 1984; Nellen, 1973). Differences in species composition between these studies are partly explainable by seasonality of reproduction. As an example, *Macroramphosus* spp. larvae were numerically dominant in February 1970 (Nellen, 1973), but no larvae of this type were found in plankton samples collected in September 1998, although adult specimens represented one of the most important groups in parallel trawl catches (Fock et al., 2002b; Uiblein et al., 1999). Similarly, the neritic species *Trachurus picturatus* represented a significant part of the trawl catches during all field campaigns in 1967, 1970 (Ehrich, 1977) and 1998 (Uiblein; 1999) and were abundant in plankton samples in 1970 (Nellen, 1973), but no larvae were collected in the present collection (Nellen and Ruseler, 2004).

In addition to neritic species, some mesopelagic fish and squid taxa might also show restricted distributions and occur almost exclusively in boundary zones, where mesopelagic waters impinge on the continental slopes or on seamounts and oceanic islands. This mesopelagic-boundary community was described by Reid et al. (1991) around the Hawaiian Islands in a zone of approximately 400 to 700 m depth. Mesopelagic fish species that had been reported to be associated with land summarised by Reid et al. (1991) were *e.g.*, *Benthosema* spp., *Diaphus* spp. or *Maurolicus muelleri*, whereas the latter two were also regularly encountered at GMS. *M. muelleri* was shown to be most abundant near continental slopes and was rarely found in the open ocean (Barnett 1984; Hulley and Prosch, 1987; Kawaguchi and Mauchline 1987). However, large oceanic populations of this species were observed before from seamounts in the Central North Pacific (Boehlert et al., 1994). Boehlert et al. (1994) proposed that these isolated populations were most likely maintained by a combination of local recruitment and periodic replenishment by advection of eggs and larvae. The authors considered the areas of the seamount located above 500 m depth as suitable habitat for *M. muelleri* and suggested that stable populations beyond the continental slopes might be present at large seamounts and seamount chains. GMS is one of the largest topographic elevations in the Atlantic Ocean and its plateau covers an area of more than 1100km². It is thus likely that those larvae found at GMS originated from local production. The occurrence of *M. muelleri* larvae during other times of the year, in February (Nellen, 1973) and May-July (Belyanina, 1984), indicates a consistent, year-round recruitment. Advection of eggs and larvae from the continental slopes along the south-eastward flowing Canary current might additionally complement the standing stock, although most larvae found at GMS were too small to be advected from the shelf.

Assuming that some of the species, assigned to the neritic or mesopelagic-boundary community, represent self-sustaining stocks, higher larval abundances would be expected leeward of the seamount than upstream of it. Unfortunately, only few samples had been taken beyond the slope and plateau area. Furthermore, the influence of GMS on the circulation extends, according to Beckmann and Mohn (2002), to about four times the area of the summit plain and, thus, far beyond the area that had been sampled during this study.

Hence, a direct comparison of single species abundances between the inner seamount regime and the far field was not expected to yield comprehensive results. Because of the high diverse, irregular spaced plankton samples, a multivariate rather than a single species approach was used to identify distribution and abundance patterns in relation to seamount structures.

The investigation of the vertically resolved fish and cephalopod composition by PCA and RDA yielded roughly three assemblages for each taxonomic group. The distinct vertical zonation of these groups was quite obvious from the mapping of sample scores, although some degree of overlap also existed. The neritic fish species *Chlorophthalmus agassizii* and *Aulopus filamentosus*, the dominating gonostomatid fish *Cylothone* sp., as well as the epipelagic squid families Ommastrephidae and Onychoteuthidae are only some examples of the bulk of taxa concentrated in the upper 150 m of the water column. Within this layer most species of the subfamily Lampanyctinae were distributed at shallower depth than those of the Myctophinae, which has been reported in former studies throughout the oceans (*e.g.* Cha et al., 1994; Sassa et al., 2004). In contrast, only few taxa occurred below 150 m, which was also indicated by a strong decrease in species diversity with increasing water depth. Species found in this layer, like the *Chauliodus* sp., *Scopelarchus* spp. and the sternoptychids *Sternoptyx* sp. and *M. muelleri*, as well as the squid family Pyroteuthidae showed a diel vertical migration behaviour or were accounted to the deep meso- to bathypelagic fauna (e.g Badcock, 1989; Gibbs, 1989; Johnson, 1989; Kinzer and Schulz, 1988). Their vertical distribution extended into near bottom layers, thus increasing the possibility of a physical interaction with the seamount summit and upper slopes.

Corresponding to the vertical structuring of species assemblages, two distinct flow systems were identified, one in the near-surface mixed layer including the upper seasonal thermocline and one in the lower seamount summit layer (Mohn and Beckmann, 2002; Beckmann and Mohn, 2002). The circulation within these strata was largely decoupled and vertical velocity of local up- and downwelling events were generally weak. An exchange of species between the upper and lower part of the water column would, thus, only be possible by active vertical movement. As the majority of species did not show vertical migration behaviour, the separation of layers by distinct circulation cells might additionally contribute to the abrupt change in species composition observed at 150 m. The vertical zonation of species further implicates that the identified assemblages were subjected to different hydrographic regimes and advection processes. According to Beckmann and Mohn (2002), passive particles released in numerical experiments in the shallow areas of the seamount (<350m) concentrated above the summit plain, but, according to the prevailing flow systems, particles in the mixed layer behaved differently from those located in the central water column above the summit. The general vertical structure of species assemblages showed some irregularities above the plateau, which were also confined to either the upper or the lower part of the water column. Most striking were variations in sample scores at the northern one of two small pinnacles that overtop the central summit plain by nearly 100 m (transect 1). At this position a slight shift in community composition towards species, generally distributed in intermediate water depths, was observed in the lower seamount summit layer. Mohn and Beckmann (2002) discovered that the vertical time-mean flow above the summit plain was downward, which might be one reason for the divergent pattern. However, the station showing the most conspicuous irregularities was located above the shallowest part of the seamount and was one of the few stations sampled at night. This means that the species composition might have been influenced by vertically upward migrating taxa like *Scopelarchus* or squids of the family Pyroteuthidae. The observed pattern of PC1 sample scores, indicating a numerical decrease of the deep distributed species assemblage above the pinnacle, is, thus, even more remarkable. It is, therefore, supposed that the prevailing process would not be the passive vertical transport but rather the exclusion of organisms by the physical interference with shallow topography and the reduction of vertically migrating organisms through predation during previous daylight hours. Pusch et al. (2004) measured significantly lower densities of mesopelagic fish species above the summit and slopes of GMS and Atlantis seamount and concluded that the truncation of the vertical migration range and enhanced predation by benthopelagic fishes were the main reasons for the observed gaps. Early life stages of fish and cephalopods are generally found at shallower water depths than their adults, but post-larvae may be still obstructed by the upper slope and plateau. Furthermore, gaps of migrating plankton organisms, formed during evening over the summits of abrupt shallow topography, had been reported *e.g.*, by Genin et al. (1988, 1994) and Haury et al. (2000). Rogers (1994) reviewed the structure of pelagic communities over seamounts and assumed that diurnally migrating plankton layers advected over seamounts by prevailing currents get trapped on the shallow bottom and are exposed to higher predation pressure by *e.g.*, benthopelagic fish. At GMS *Macroamphosus* sp. and *Capros aper* occurred in extremely dense aggregations in all areas of the plateau (Uiblein et al., 1999) and might particularly benefit from the allochthonous energy source of entrapped zooplankton and micronekton. It is, thus, very likely that vertically migrating fish and cephalopod species suffer from increased mortality above the plateau. In this case species composition would be expected to change to a predominance of non-migrating organisms, which corresponds to the observations in the seamount summit layer.

Along transect 2, anomalies in the vertical structure of species assemblages were less obvious above the plateau than north-eastward of it. The outermost station, located upstream of the seamount, was the one that was least affected by the flow system encircling GMS. Hence, topographically associated species were expected to be less abundant there than at other stations above and leeward of the plateau. This was partly supported by the observation that at this position the deep distributed assemblage was of relatively high importance. The PCA analysis of station specific abundance values gave further indications for this assumption. The three sites lying in the far-field of GMS, including the one located north-eastward of the plateau, were characterised by similar sample scores along the first and second PCs, indicating corresponding species assemblages. According to the species loadings, the outermost stations showed *e.g.*, comparably low abundances of the presumably seamount associated *C. agassizii* and *Diaphus* sp. and high abundances of vertically migrating and deep distributed fish and cephalopod taxa. Sample scores of most stations located above the seamount summit showed opposite signs compared to the far-field, pointing to a partly contrasting species composition. Nellen and Ruseler (2004) investigated distribution patterns of selected larval fish taxa and assumed that GMS is most likely to be a nursery ground for neritic species like *C. agassizii*. Similar conclusions were drawn from sample analyses collected in 1970, where lower plankton biomass and lower abundance of fish larvae belonging to mesopelagic species were measured above the plateau, whereas larvae of neritic species were even more abundant compared to the surrounding waters (Nellen, 1973). An effective retention potential is required to maintain higher larval abundances of resident fish species above GMS. Beckmann and Mohn (2002) determined that the residence time of passively advected organisms was significantly increased within the inner seamount regime, *i.e.*, within the 1500 m isobath. The RDAs investigating vertically stratified samples revealed significant effects on the fish and cephalopod species composition induced by sampling depths and the ‘deep sea’ factor, meaning that assemblages differed between the inner and outer seamount regime, but not between the plateau and slope area. However, the spatial patterns of PC1 sample scores within the 1500 m depth contour resembled substantially the counterrotating time-mean circulation cells, identified in the upper thermocline layer above the summit of GMS (Fig. IV.1), where species, generally confined to the upper part of the water column, dominated. The remarkable agreement between the station specific sample score patterns of the fish and cephalopod community, revealed by the PCA and the subsequently performed Mantel test, indicates that the topographic and hydrographic perturbations have significant and comparable influences on both assemblage structures. Correspondingly, similar effects on the whole planktonic ecosystem at the seamount must be assumed.

It is concluded that the flow field of GMS becomes more manifested in the species composition of fish and cephalopods than initially expected by Nellen and Ruseler (2004) and Diekmann and Piatkowski (2004), although the spatial variability of the less abundant cephalopods was higher than for fish. The reduction of deep-distributed and vertically migrating organisms above the plateau probably intensifies the structuring of species assemblages and leads to the clear separation of an inner and outer seamount assemblage.

To summarise, GMS was, in contrast to other studies performed at shallow seamounts that may penetrate into the euphotic zone (Dower et al., 1992; Genin and Boehlert, 1985), not deemed to have positive effects on early larval survival, as primary productivity and biomass of planktonic organisms was not increased in the area of the plateau (Kaufmann, 2004; Martin and Nellen, 2004; Mouriño et al., 2001). Multivariate analyses rather indicated influences on planktonic stages of fish and cephalopods by three main interacting processes that generate vertically and horizontally structured assemblages.

First, GMS acts as a ‘topographic obstacle’ to species, where water depth interferes with their overall vertical distribution. Deep-distributed taxa like *Scopelarchus* spp. can be excluded from the upper summit layer or are exposed to higher predation pressure by benthopelagic fish species because of their diel vertical migration behaviour. An ontogenetic descent, characteristic for most mesopelagic fish and cephalopod taxa, can additionally strengthen disruption processes, which leads to gaps of certain species and increased patchiness above and downstream of the plateau.

Second, reproduction of resident fish and cephalopod species, leads to higher larval abundances in the area of GMS in comparison to the surrounding oceanic region. The significant retention potential for non-migrating specimens caused by anticyclonic currents enclosing the bank can keep at least parts of the larvae over biological relevant time scales in the area of the seamount and is supposed to enable self-sustainability of stocks. Because of seasonal reproduction the identification of local recruitment by a single sampling effort remains, however, difficult.

Third, diffusive and advective forces at GMS, including some eddy-like variability especially at the periphery of the seamount, influence the structure of species assemblages and can establish distribution patterns deviating from the general topography of the seamount. Despite of the clear spatial structuring of fish and cephalopod assemblages, lots of variation remained unexplained and needs to be investigated by future studies, implementing a combination of small- and large-scale sampling schemes.

Chapter V

Vertical distribution and migration behaviour of cephalopods: Implications on distribution patterns around seamounts

Abstract

Micronektonic cephalopods were investigated at three seamounts located in the subtropical eastern North Atlantic: Great Meteor Seamount, Atlantis Seamount and 'The Twins'. Sampling was conducted with a pelagic Youngfishtrawl in discrete depth strata from 25 to 800 m, covering summit and slope of the seamounts as well as the adjacent open ocean. A total of 612 cephalopods were collected in 86 hauls, representing 40 species of 23 families. All seamounts were characterised by a typical oceanic community and differences in species composition were rather small. However, species numbers and absolute abundances became significantly lower with decreasing water depth, *i.e.* stations located over the plateau were more impoverished in terms of abundance and species richness. This was caused by the vertical distribution patterns of dominant species that occurred below the seamount summit depth at least during some times of the day. In order to describe the daily cycle of vertical movements, a logit regression model using sun height and water depth as explanatory variables was developed. The results of the model corresponded well to former studies, which examined vertical distribution and migration patterns, although the dataset comprised a limited amount of samples.

Introduction

Diel vertical migration is a characteristic feature of nektonic cephalopods (Hanlon and Messenger, 1996). During their ontogenetic development they undertake horizontal and vertical migrations to achieve optimal conditions concerning food concentration, growth, predator avoidance, and spawning. Information on vertical distribution and migration behaviour of cephalopods is, however, scattered and most descriptions remain tentative (Roper and Young, 1975). Two reasons are responsible for this: First, oceanic cephalopods are often large and fast swimming squids capable to avoid sampling gear such as big trawls, and, second, vertically resolving multi opening-closing nets are seldom used and sample only early life stages representatively. Consequently, the precise depth of capture is often not available. Light is generally regarded as the most likely cue used by aquatic organisms to regulate their vertical movements through the water column (*e.g.* Bollens and Frost, 1991; Ringelberg et al., 1991). The most common pattern is that they stay deeper during day than at night, when they migrate towards the surface. This ‘normal diel vertical migration’ can be *e.g.* observed for the mesopelagic squid families Enoploteuthidae and Pyroteuthidae (Lu and Roper, 1979; Nesis, 1993c; Roper and Young, 1975; Young, 1978). Their distribution pattern and migration amplitude are assumed to be similar to that of many mesopelagic fishes, such as myctophids (*e.g.* Roe, 1974; Watanabe et al. 1999).

In the wide open ocean the extent of vertical migration is usually not restricted by bottom depth. Continental shelfs, banks, ridges, seamounts and islands represent boundaries in the otherwise unstructured environment and limit the distribution of mesopelagic species. Because of their relatively small dimension and the summit depth, which is often located well below the euphotic zone, oceanic seamounts probably have only a small influence on the pelagic life. However, at various seamounts throughout the world large standing stocks of commercially valuable fish species have been found (Fonteneau, 1991; Hubbs, 1959; Ushida and Tagami, 1984). Depending on topographic and hydrographic features the high fish biomass is supposed to be sustained by enhanced primary productivity and/or by energy transport via the entrapment of diurnally migrating zooplankton swept over the shallow topography by prevailing currents (Boehlert and Genin, 1987; Rogers, 1994). The latter hypothesis was first proposed by Isaacs and Schwarzlose (1965) and several indications were later found for the formation of patches devoid of vertically migrating zooplankton above and downstream of seamounts (Genin et al., 1988, 1994; Haury et al.,1995, 2000). These gaps develop when layers of downwardly moving zooplankton intercept with topography and then are exposed to an enhanced predation pressure by resident fish species living close to the seamount. Mobile nektonic squids are probably not passively advected above seamount summits, but may be excluded by topography. Drastically reduced abundances of myctophids at seamounts with 250 to 275 m minimum water depth were recently observed by Pusch et al. (2004), and it is assumed that similar features may be identified for cephalopods.

In the present study, the cephalopod fauna at three seamounts, located in the subtropical north-eastern Atlantic Ocean, was investigated. The field work was designed to test two hypothesis: (i) Seamounts are characterised by a special cephalopod fauna, depending on the depth of the summit and the ecological region; (ii) The depth distribution and diel vertical migration behaviour influences the abundance of cephalopods in the vicinity of seamounts. Sampling was performed with a small-meshed Youngfishtrawl. Assuming that light is the main factor influencing vertical migration behaviour, sun height is used to predict the probability of occurrence of dominant species in relation to maximum sampling depth. Vertical distribution patterns and the migration amplitude of single species are investigated and the implications on distribution and abundance at abrupt shallow topography are described. Furthermore, the cephalopod fauna was compared between seamounts and bathymetric zones and mechanisms influencing the species composition are discussed.

Material and Methods

Investigation area

Three seamounts with different topographic morphology were investigated, which are located in the subtropical north-east Atlantic (Fig. V.1). Two seamounts are characterised by a flat plateau area and steep slopes, defined as guyots: Atlantis Seamount at 34°09'N and 30°15'W and Great Meteor Seamount (GMS) at 30°00'N and 28°30'W. Both belong to the Atlantis-Meteor Seamount complex located 700 km south of the Azores and are lying within the flow system of the wind-driven subtropical gyre of the North East Atlantic. Prevailing currents in the area are relatively weak and flow into a south-westerly direction (Mohn and Beckmann, 2002; Pusch et al., 2004). At the time of sampling surface temperatures ranged between 24.5 and 26.3 °C at GMS and between 23.5 and 25.0 °C at Atlantis Seamount. The plateau area of GMS, reaching 275 m below surface, covers more than 1100 km² and is nearly three times larger than the Atlantis Seamount plateau (410 km²), with a minimum depth of 250 m. The third topographic elevation, 'The Twins' (43°57'N, 28°32'W), is located north of the Azores at the eastern margin of the Mid Atlantic Ridge. It is characterised by two needle-like peaks of less than 0.5 km² extension, one reaching 387 m below surface. Surface temperatures were slightly lower than south of the Azores, ranging between 19.4 and 20.1 °C. Detailed current measurements are lacking but the North Atlantic current system presumably results in a weak, easterly directed flow field (Schmitz and McCartney, 1993).

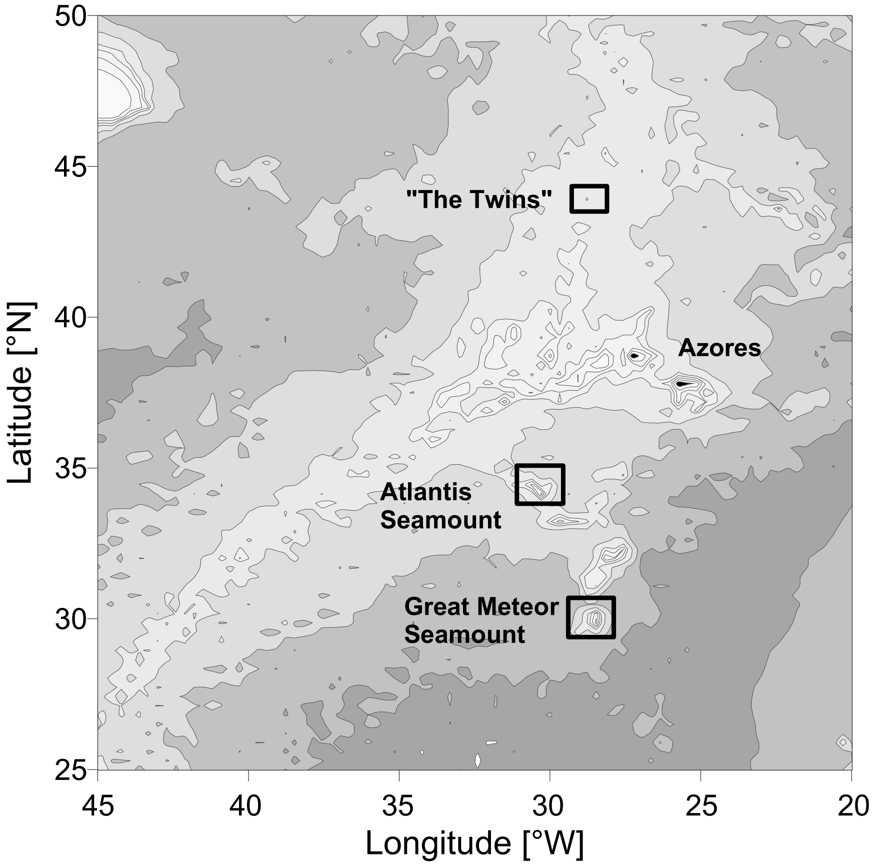

Fig. V.1: Investigation areas in the subtropical north-east Atlantic.

Data collection

Cephalopods were sampled during two research cruises, in September 1998 with RV Meteor (M42/3) at Great Meteor Seamount (GMS), and in August 2000 with RV Heincke (He135) at Atlantis Seamount and 'The Twins'. A Youngfishtrawl (YFT) with an effective net opening of 80 m² and a mesh size of 11 mm in the cod end (von Westernhagen et al., 2000) was applied on all stations. The YFT was towed with approximately 3 knots. The swept area was calculated from the distance between the positions where the net reached or left target depth multiplied with the net wing-spread (10m). During He135 a datalogger (minilog; V3.02, Vemco Ltd. ©1999) was mounted in the cod end, which constantly recorded depth and ambient temperature. These data were used to calibrate catch depth and swept areas.

At GMS, samples were obtained along a transect extending from the seamount plateau into north-easterly direction towards the adjacent open ocean. 12 YFT hauls were performed with a maximum fishing depth ranging from 130-440 m. At 'The Twins' and Atlantis Seamount three stations, near or above the summit, at the slope and in the adjacent open ocean, were sampled repeatedly at different times of the day. A depth stratified sampling scheme was adopted with the following strata: 25, 100, 200, 250, 400, 600, and 800 m. 38 samples were collected near 'The Twins', 36 samples in the area of Atlantis Seamount. Cephalopods were sorted immediately on board. Individuals were preserved in seawater-diluted formalin (4%), buffered with sodium borate, and species identification was done during laboratory analyses. Abundances (N/km²) were calculated by standardising species numbers to 1-km² swept area.

Data analysis

Modelling of vertical distribution patterns – Vertical distribution patterns of cephalopods were modelled as probability of occurrence in relation to catch depth and mean sun height (-90 to +90°). Sun height shows a sinusoidal curve over 24 hours and should reflect diel vertical migration. Using sun height instead of ambient solar radiation in the model implies that specimens move vertically throughout the full day-night cycle. However, migration magnitude versus time is supposed to be largest during sunset and sunrise and nearly zero during midnight and noon. Sun height values for each sampling time at the approximate position of each seamount were obtained from the freely available ‘Sundi’ software (V 1.1, *http://emsolar.ee.tu-berlin.de/simulation/ sundi.html*).

For the model, species data were reduced to presence-absence data. This reduction was necessary as numbers per species were relatively low, thus, introducing large variation to abundance estimates. Only species that had been caught in sufficient numbers during all cruises were considered, *i.e.* more than 20 individuals on at least 5 different stations. Furthermore, stations sampled at less than 800 m total water depth, which also represented the maximum fishing depth, were excluded. It was assumed that vertically migrating species are not influenced by topography if water depth exceeded this level.

The probability of occurrence was estimated by logistic regression and estimation of parameters was done using the maximum likelihood method. Regression coefficients were tested by Wald´s Chi-square statistic. The significance level of the parameters was set to 0.05, and the model was additionally checked for overdispersion. Differences in migration behaviour between the most abundant species were visualised with three-dimensional surface plots, displaying probability of occurrence in relation to sun height and catch depth. The best subset of parameters was additionally estimated with the help of Akaike’s information criterion (AIC), an analogon to the adjusted r^2 used in linear regression.

Bathymetric comparisons and multivariate statistical analyses – Stations were classified into three bathymetric depth zones, defined as plateau (<500 m water depth), slope (500-1000 m), and oceanic (> 1000 m). Total cephalopod abundances (N/km²) were compared between bathymetric zones according to daytime and depth stratum to reveal seamount effects on abundance values. Because of its small summit region, no plateau stations were available for ‘The Twins’.

Species composition in trawl catches was compared between sampling sites and between seamounts by non-metric multivariate analytical techniques. As daytime and sampling depth quantitatively and qualitatively influenced the catch composition, the original dataset was reduced. Only samples obtained during night in 100-440 m water depth were used, enabling comparability of samples from both cruises. Additionally, species that appeared only once were omitted from the initial numerical matrix. Due to low sample sizes causing large variance in abundance values, data were fourth root transformed prior to the analysis.

The similarity between stations was calculated by means of the Bray-Curtis measure (Bray and Curtis, 1957). Samples were classified by hierarchical agglomerative cluster analysis using the group-average linking method (Field et al., 1982), and ordinated using non-metric multi-dimensional scaling techniques (MDS; Kruskal and Wish, 1978). Subsequently, analysis of similarities (ANOSIM; Clarke and Warwick, 1994) was performed to test for differences in species composition between factor levels (bathymetric zones, seamounts). The test was considered to be significant at a probability level of $p<0.05$. All multivariate analyses were carried out using subroutines of the Primer-E. (5) computer program (Clarke and Warwick, 2001).

Results

Species composition and abundances

86 YFT hauls yielded a total of 612 cephalopods (Tab. V.1). By far highest abundances were measured at GMS, where nearly half of all individuals (292) were caught in 12 hauls amounting to an average abundance of 16.8 ind. per km^2. Sampling at Atlantis Seamount and 'The Twins' yielded low abundances of 3.8 and 5.0 ind. per km^2, respectively. Combining all samples, 40 species of 23 families were identified, which are all widely distributed in oceanic areas of the tropical and subtropical Atlantic Ocean. Taxonomic richness in terms of species numbers was highest at Atlantis Seamount with 27 species, and slightly lower at 'The Twins' (23 species) and GMS (22 species) (Tab. V.1). Half of all taxa were considered to be rare and nine species were even encountered only once. The relative abundance of the dominant taxa was, however, largely comparable between seamounts. In all investigation areas the cephalopod fauna was dominated by mesopelagic squid species of the families Enoploteuthidae and Pyroteuthidae as well as by the epipelagic species complex *Onychoteuthis banksii*. Some taxa like *Bathyteuthis* sp. and representatives of the family Histioteuthidae are known to be deep meso- to bathypelagic and were, thus, mainly detected in samples collected within and below the 600 m water layer. As these strata were only sampled at 'The Twins' and Atlantis seamount, deep distributed species were consequently rare in the collection of GMS. Main differences between cephalopod collections were found for the lycoteuthid squid *Selenoteuthis*

scintillans, which was relatively abundant at GMS but was completely missing at the other two seamounts. The Pyroteuthidae clearly dominated the fauna at ‘The Twins’ and amounted to more than one third of the total catch, which was more than twice as much compared to Atlantis seamount and GMS.

Tab. V.1: Cephalopod taxa collected by Youngfishtrawl at Great Meteor Seamount during RV Meteor cruise 42/3 in September 1998, and at ‘The Twins’ and Atlantis Seamount during cruise HE135 with RV Heincke in August 2000. Numbers for higher taxa only include specimens that could not be further identified. N_{abs}: total catch in numbers; relative N [%]: percentage of total cephalopod catch; Average N/km2: Mean abundance, taking the whole sampling at the seamount into account.

Order, Family	Species	Great Meteor Seamount			"The Twins"			Atlantis Seamount		
		N_{abs}	rel. N [%]	Average N/km²	N_{abs}	rel. N [%]	Average N/km²	N_{abs}	rel. N [%]	Average N/km²
Order Spirulida										
Family Spirulidae	*Spirula spirula*	1	0.34	0.97						
Order Sepiolidae										
Family Sepiolidae	*Heteroteuthis dispar*				6	3.45	2.95	12	8.16	8.88
Order Teuthida										
Sub-O. Oegopsina	Oegopsina indet.	6	2.05	8.21	5	2.87	3.56	2	1.36	1.38
Family Bathyteuthidae	*Bathyteuthis* sp.							1	0.68	0.76
Family Brachioteuthidae	*Brachioteuthis* sp.	1	0.34	1.48				1	0.68	0.43
Family Chiroteuthidae	Chiroteuthidae indet.	1	0.34	2.66						
Family Cranchiidae										
Subfamily Cranchiinae	*Cranchia scabra*	2	0.68	3.28				1	0.68	1.57
	Liocranchia reinhardti							1	0.68	1.32
SubfamilyTaoninae	*Batothauma lyromma*				5	2.87	2.93	2	1.36	1.66
	Helicocranchia sp.	2	0.68	2.95						
	Helicocranchia papillata	2	0.68	2.95						
	Helicocranchia pfefferi	4	1.37	5.89	2	1.15	0.87	3	2.04	1.64
	Megalocranchia sp.				1	0.57	1.99	6	4.08	6.96
	Taonius pavo				5	2.87	2.49	10	6.80	6.52
Family Ctenopterygidae	*Chtenopteryx sicula*	20	6.85	31.66	8	4.60	6.96	1	0.68	0.43
Family Cycloteuthidae	*Discoteuthis discus*				1	0.57	1.74	1	0.68	0.97
Family Enoploteuthidae	Enoploteuthidae indet.							1	0.68	1.53
	Abralia veranyi	3	1.03	5.33						
	Abraliopsis pfefferi	106	36.30	135.80	9	5.17	8.22	39	26.53	31.59
	Enoploteuthis leptura	6	2.05	9.21				1	0.68	1.16
Family Grimalditeuthidae	*Grimalditeuthis* sp.	1	0.34	1.79						
Family Histioteuthidae	*Histioteuthis* sp.	1	0.34	1.79	4	2.30	3.29	1	0.68	1.22
	Histioteuthis arcturi							6	4.08	4.95
	Histioteuthis bonellii				4	2.30	3.52			
	Histioteuthis celetaria celetaria				4	2.30	2.39	1	0.68	0.76
	Histioteuthis meleagroteuthis				2	1.15	1.51	3	2.04	1.85
	Histioteuthis reversa				10	5.75	7.66			
Family Lycoteuthidae										
Subfamily Lampadioteuthinae	*Lampadioteuthis megaleia*	1	0.34	1.91	2	1.15	2.30	1	0.68	0.43
Subfamily Lycoteuthinae	*Selenoteuthis scintillans*	20	6.85	33.37						
Family Mastigoteuthidae	*Mastigopsis hjorti*				3	1.72	2.55			
	Mastigoteuthis atlantica				1	0.57	0.85	3	2.04	2.14
Family Octopoteuthidae	*Taningia danae*							1	0.68	0.65
Family Ommastrephidae	Ommastrephidae indet.	3	1.03	5.22	2	1.15	1.52	2	1.36	1.36
Subfamily Ommastrephinae	*Hyaloteuthis pelagica*	2	0.68	3.48						
	Ommastrephes bartramii	18	6.16	31.34	4	2.30	3.38	4	2.72	2.71
Family Onychoteuthidae	*Onychoteuthis banksii*	52	17.81	82.76	27	15.52	19.68	16	10.88	15.81
Family Pyroteuthidae	Pyroteuthidae indet.	2	0.68	1.62						
	Pterygioteuthis giardi	12	4.11	18.77	20	11.49	2.14	9	6.12	1.27
	Pyroteuthis margaritifera	18	6.16	31.19	42	24.14	42.49	13	8.84	12.63
Order Octopoda										
Sub-O. Incirrina										
Family Alloposidae	*Alloposus mollis*				1	0.57	1.60	1	0.68	0.97
Family Argonautidae	*Argonauta argo*				1	0.57	1.16			
Family Bolitaenidae	*Bolitaena pygmaea*	5	1.71	8.48				2	1.36	1.75
	Japetella diaphana							1	0.68	0.62
Family Ocythoidae	*Ocythoe tuberculata*				3	1.72	1.49			
Family Tremoctopodidae	*Tremoctopus violaceus*	1	0.34	1.91						
Family Vitreledonellidae	*Vitreledonella richardi*	2	0.68	2.89	1	0.57	0.85	1	0.68	0.76
Sum		292			173			147		

Vertical distribution and migration behaviour

Distinct diel vertical migration patterns were revealed for species of the mesopelagic families Enoploteuthidae and Pyroteuthidae (Fig. V.2, Tab. V.2). The enoploteuthid squid *Abraliopsis pfefferi* showed a significant relationship to both explanatory variables catch depth and sun height (Fig. V.2a, Tab. V.2). At noon the probability of occurrence was close to zero from 0-800 m water depth and the only positive tows during daylight were made at maximum sampling depth (800 m). The highest probability of nearly one was detected at midnight, when *A. pfefferi* dispersed over the entire investigated water column and could be even encountered in surface layers. Vertical migration behaviour of the pyroteuthid species *Pyroteuthis margaritifera* and *Pterygioteuthis giardi* was observed to be very similar (Fig. V.2b, c; Tab. V.2). According to the model, their distribution patterns were not dependent on water depth, but on daytime. During daylight, positive tows were only recorded below 400 m water depth and the probability of occurrence was found close to zero at noon. Highest probability values were calculated for midnight in water layers from 600 m to the surface. Values already exceeded 0.5, *i.e.* a 50% chance to observe these species in hauls throughout the water column, right after sunset. A contrasting vertical distribution was observed for the family Histioteuthidae (Fig. V.2g). Their occurrence was independent of daytime, *i.e.* specimens of this family did not seem to perform diel vertical migrations, but was clearly related to catch depth (Tab. V.2). From 0-800 m depth the probability of occurrence increased monotonically and did not approach a maximum value. This indicates that the distribution of Histioteuthidae extends to water depths below 800 m. The vertical distribution patterns of Ommastrephidae, *O. banksii*, and *Chtenopteryx sicula* did not show significant relationships to any of the two factors (Fig. V.2d, e, f; Tab. V.2). The probability of occurrence of *C. sicula* and Ommastrephidae remains generally low over the entire investigated water column and throughout the entire day-night cycle. *O. banksii* was encountered more frequently and showed a tendency towards higher probabilities with increasing water depth.

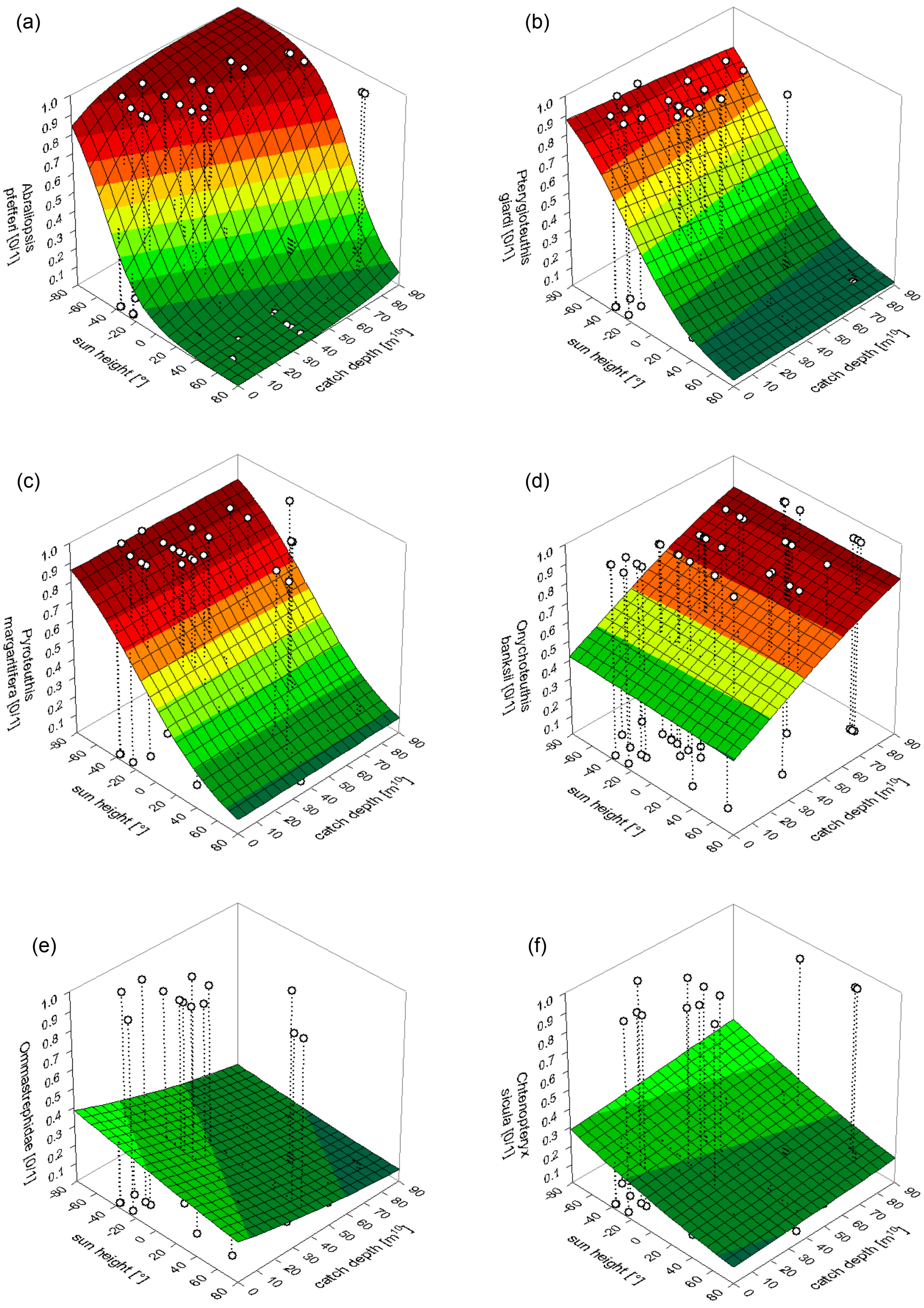

Fig. V.2: Probability of occurrence in YFT hauls in relation to maximum catch depth and sun height. Coloured planes visualize logistic models fitted to the presence absence data. Circles represent raw data (0/1). For parameter estimates and model development the reader is referred to table V.2. (a) *Abraliopsis pfefferi*, (b) *Pterygioteuthis giardi,* (c) *Pyroteuthis margaritifera*, (d) *Onychoteuthis* banksii, (e) Ommastrephidae, (f) *Chtenopteryx sicula.* Figures are continued on the following page.

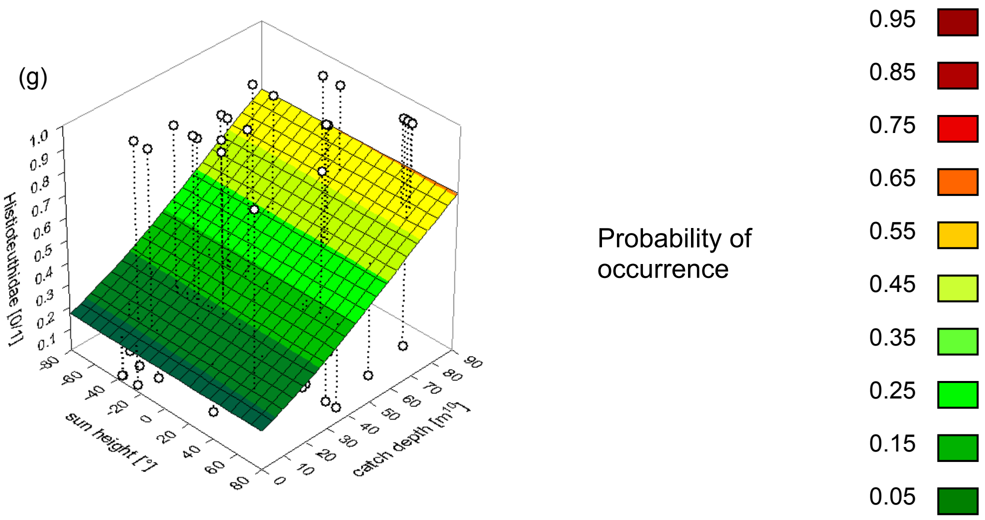

Fig. V.2:**continued** from the previous page: (g) Histioteuthidae.

Tab. V.2: Parameter estimates of logistic models predicting probability of occurrence in YFT hauls in relation to maximum catch depth and sun height. The significance of the parameters is given as well as the theoretically best subset of explanatory variables in the model according to the AIC.

Species/ group	Parameter	Parameter estimate	SE	Wald's Χ² statistic	p-level	best subset according to AIC
Abraliopsis pfefferi	Intercept	2.827	0.871	10.53	*0.00117*	sunheight x catch depth
	sun height	0.056	0.016	12.48	*0.00041*	
	catch depth	-0.005	0.002	7.12	*0.00762*	
Pyroteuthis margaritifera	Intercept	0.348	0.594	0.34	0.55863	sun height
	sun height	0.027	0.010	6.78	*0.00920*	
	catch depth	0.000	0.001	0.01	0.93753	
Pterygioteuthis giardi	Intercept	0.680	0.659	1.06	0.30221	sun height
	sun height	0.033	0.013	6.63	*0.01003*	
	catch depth	0.001	0.002	0.21	0.64603	
Onychoteuthis banksii	Intercept	-0.376	0.547	0.47	0.49204	catch depth
	sun height	-0.001	0.009	0.01	0.94191	
	catch depth	0.002	0.001	2.66	0.10273	
Ommastrephidae	Intercept	0.885	0.654	1.83	0.17578	catch depth
	sun height	0.005	0.011	0.20	0.65190	
	catch depth	0.002	0.002	0.86	0.35474	
Chtenopteryx sicula	Intercept	1.619	0.688	5.53	*0.01866*	sun height
	sun height	0.009	0.011	0.63	0.42612	
	catch depth	-0.001	0.002	0.11	0.74020	
Histioteuthidae	Intercept	1.571	0.600	6.85	*0.00885*	catch depth
	sun height	0.000	0.009	0.00	0.98179	
	catch depth	-0.003	0.001	4.07	*0.04371*	

Cephalopod abundances in relation to bathymetry

The effects of daytime and topography were investigated by comparing cephalopod abundances between samples. The realization of rigorous statistical analyses was not possible, due to limited sample sizes and only few depth strata were directly comparable. Daytime catches in most cases were quite small and allowed only a tentative comparison between bathymetric zones. In contrast, abundances increased significantly in samples obtained during darkness and differences between bathymetric zones were pronounced. At GMS and Atlantis seamount, abundances measured during night above the plateau were principally lower than in the open ocean and, with only one exception, also lower than at slope stations (Tab. V.3a, c). Correspondingly, abundances at slope stations were reduced compared to oceanic stations. Daytime samples at the two guyots indicate, in contrast, a slightly increased abundance above the summit in comparison to slope and oceanic stations, although sampling depth at theses positions were not identical. At 'The Twins', which does not have an extended plateau area, abundances measured above the slope or in the far field are generally of the same order of magnitude and did not show a tendency towards lower values at shallower bottom depth (Tab. V.3b).

Tab. V.3: Mean abundances of cephalopods (N/km²) at Great Meteor Seamount, (b) 'The Twins', and (c) Atlantis Seamount in relation to daytime, bathymetric zones and maximum sampling depth. Index numbers refer to the number of samples used in the calculation of the mean. If index numbers are missing, only a single sample was available.

(a)

		Oceanic		Slope		Plateau	
Great Meteor Seamount	Max. sampling depth [m]	Mean abundance [N/km²]		Mean abundance [N/km²]		Max. sampling depth [m]	Mean abundance [N/km²]
day	400	50.9	>	36.6	<	260	118.6
	420	53.7		<		330	66.0
dusk	300			1005.1			
night	250	1052.9	>	642.6	>	130	314.1
	400	986.4	>	447.1	>	275	461.4

Tab. V.3: continued from the previous page.

(b)

"The Twins"	Max. sampling depth [m]	Mean abundance [N/km²]		
		Oceanic		slope
day	100			67.6 (2)
	200			14.5 (2)
	250	81.3	>	7.1 (2)
	400	85.9 (3)	>	38.9 (2)
	600	65.8 (2)	<	79.6 (3)
	800	155.4 (2)	>	100.5 (2)
dawn	250	49.2	<	60.6
night	25	218.3	>	67.3
	100	242.1 (2)	<	354.5 (2)
	200			129.3
	250	201.2 (2)	<	254.2 (3)
	400	169.7	>	35.1
	600			201.8

(c)

Atlantis Seamount	Max. sampling depth [m]	Mean abundance [N/km²]				
		Oceanic		Slope		Plateau
day	100					62.7
	250			53.9	>	20.4 (2)
	400	0.0	<	8.2 (2)		
	600	17.6	<	36.8 (2)		
	800	83.3	<	93.4 (2)		
night	25	140.3	>	69.6 (2)	>	32.9
	100	301.4	>	31.4 (2)	<	150.9 (2)
	250	232.4	>	116.7 (2)	>	55.7 (3)
	400	191.5	>	44.2 (2)		
	600	392.5	>	140.8 (2)		
	800	217.2	<	262.5		

Species assemblages

Classification of YFT samples according to their species composition resulted in four small (Ia-d) and four large clusters (II-V), separated at a level of 45% (Fig. V.3). Five of the six samples in group I were collected at Atlantis seamount of which four were sampled above the plateau. Cluster II consisted exclusively of samples collected at Atlantis seamount in the area of the slope, whereas cluster III comprised, with one exception, all hauls performed at GMS. Cluster IV and V were dominated by samples collected at 'The Twins', and all hauls were performed above the slope or in oceanic areas. Correspondingly, slope and oceanic stations could not be separated on the MDS-ordination plot, while plateau stations hardly overlapped with these two bathymetric zones (Fig. V.4a). However, distances between single plateau samples indicated a high variability in species composition. Superimposing labels for seamounts on the same ordination plot (Fig. V.4b) showed, similar to the cluster analysis, that samples collected at GMS were clearly grouped together irrespectively of the sampled bathymetric zone. Stations sampled at 'The Twins' also formed a group, which partly overlapped with GMS-samples. Hauls performed at Atlantis seamount were dispersed over the whole plot area, thus showing the strongest variability between samples according to their species composition.

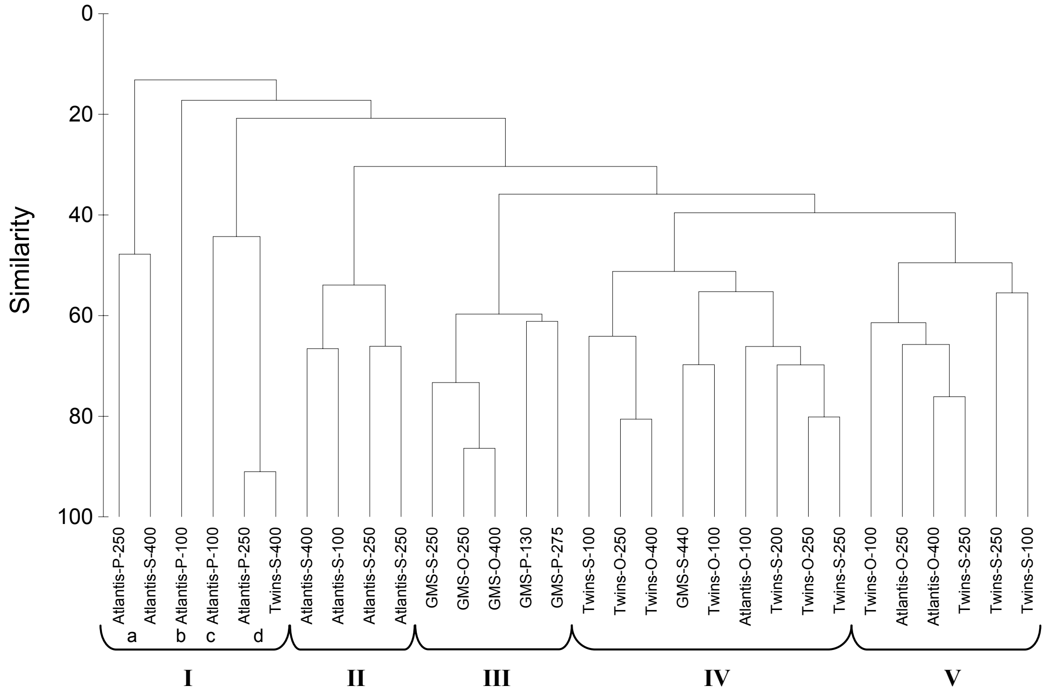

Fig. V.3: Classification of cephalopod assemblages at three different seamounts using hierarchical agglomerative cluster analysis based on the group-average linking method. Similarity between stations was calculated by means of the Bray-Curtis measure of fourth root transformed species abundances (N/km^2). Labels indicate the seamount (Great Meteor Seamount (GMS), Atlantis Seamount (Atlantis), and 'The Twins' (Twins)), bathymetric zones (plateau (p), slope (s), oceanic (o), and the fished depth stratum in meters. Only samples collected during darkness in 100-440 m water depth were used in the analysis.

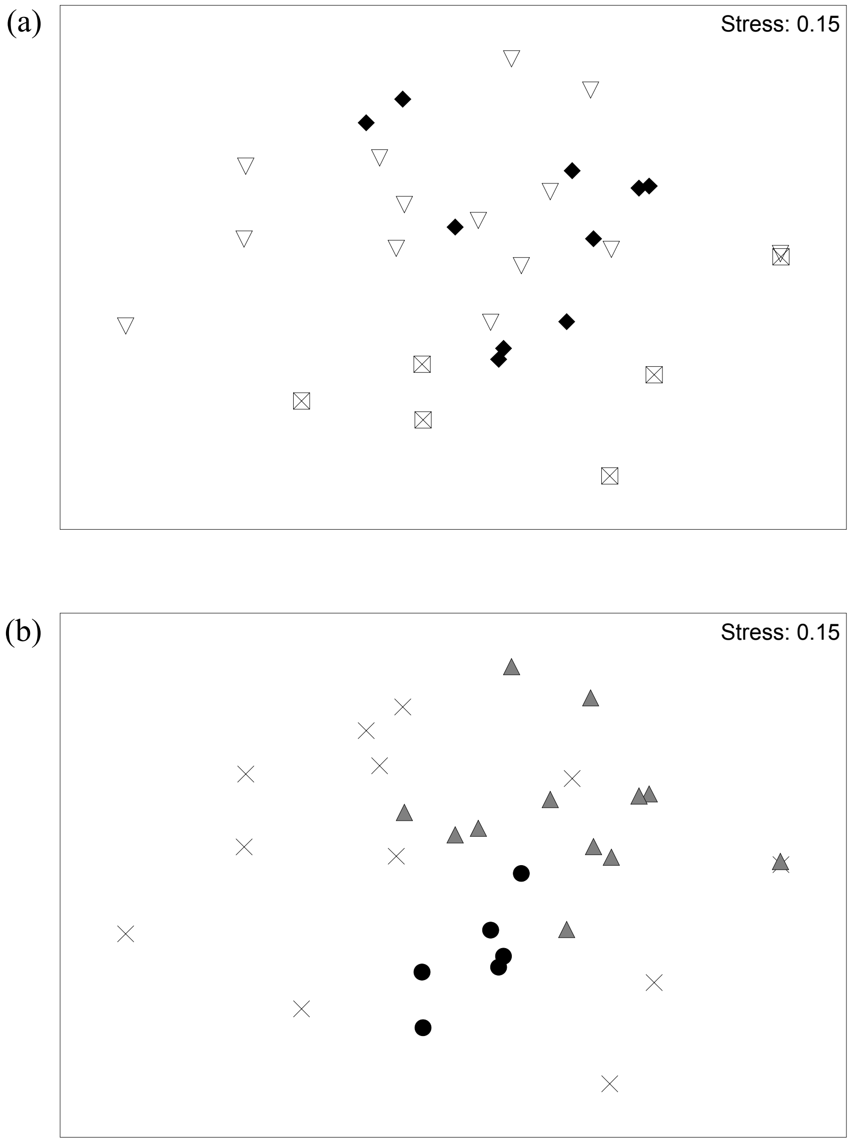

Fig. V.4: Ordination of cephalopod assemblages at three different seamounts using non-metric Multidimensional scaling. Similarity between stations was calculated by means of the Bray-Curtis measure of fourth root transformed species abundances (N/km²). Labels indicate (a) bathymetric zones, and (b) the seamount. (a): Plateau (☒), slope(▽), oceanic (◆); (b): Great Meteor Seamount (●), Atlantis Seamount (×), 'The Twins' (▲). Only samples collected during darkness in 100-440 m water depth were used in the analysis.

The observed separation between samples according to bathymetric zones and seamounts was confirmed by the subsequent ANOSIM, using the same similarity matrix as a basis. Comparing bathymetric zones revealed that the species composition at plateau stations was significantly different from slope (p = 0.002) or oceanic stations (p = 0.009), whereas the two deeper zones could not be statistically distinguished. The decreasing abundances of the mesopelagic squids *A. pfefferi*, *P. giardi*, and *P. margaritifera* with declining water depth mainly caused the observed differences, as all species were completely missing or were rarely encountered above the plateau (Tab. V.4). In contrast to this, Ommastrephidae and *O. banksii* were found in similar or partly higher abundances at plateau stations compared to slope and oceanic sampling positions. Representatives of the family Histioteuthidae were not captured above the plateau, but in the two deeper bathymetric zones.

Tab. V.4: Mean abundances of the dominant cephalopod taxa (N/km²) sampled at Great Meteor Seamount, Atlantis Seamount, and 'The Twins' in different bathymetric zones defined as oceanic (> 1000 m), slope (500-1000 m), and plateau stations (<500 m water depth). Only samples collected during darkness in 100-440 m water depth were used for calculations. Dashes indicate that the respective taxon was missing in the seamount collection.

Mean Abundance [N/km²]	Great Meteor Seamount			Atlantis Seamount			"The Twins"	
	Oceanic	Slope	Plateau	Oceanic	Slope	Plateau	Oceanic	Slope
Abraliopsis pfefferi	627.95	43.41	31.31	34.9	27.93	0	24.21	14.84
Chtenopteryx sicula	39.81	34.43	64.45	0	0	0	14.01	4.33
Heteroteuthis dispar	-	-	-	11.07	19.25	9.48	0	7.42
Histioteuthidae	0	0	0	41.07	0	0	7.23	29.6
Omma-strephidae	0	11.48	17.75	19.15	0	0	0	12.28
Onychoteuthis banksii	89.01	100.79	131.25	12.56	7.91	61.02	37.04	12.05
Pterygioteuthis giardi	47.81	50.4	0	12.56	0	27.05	42.43	34.87
Pyroteuthis margaritifera	55.01	93.81	8.87	67.67	14.19	0	86.32	107.57
Selenoteuthis scintillans	51.41	61.87	33.65	-	-	-	-	-

As plateau stations were not available at 'The Twins', they were eliminated from the ANOSIM comparing the cephalopod fauna between the three seamounts. No significant differences in species composition were found between the largest (GMS) and the smallest seamount ('The Twins'), but both were discovered to be significantly different from Atlantis Seamount ('The Twins': $p = 0.007$; GMS: $p = 0.012$). This was attributed to a higher variability in species composition between hauls and to a slightly lower catch rate at

Atlantis Seamount, that was mainly expressed by comparatively low abundances of *P. margaritifera* and *P. giardi* (Tab. V.1, V.4).

Discussion

Cephalopods are a common element of the oceanic nekton and are both, important as predators of mesozooplankton and as prey for fish, marine mammals and birds (Clarke, 1987). It is, therefore, not surprising that some species exhibit strong diel vertical migrations exploiting the similarly migrating food source, while at the same time minimising their stay in surface layers and, thus, their own risk of predation from visually orientating predators. In this study carried out in the subtropical eastern North Atlantic, a model was developed to investigate depth distribution and migration behaviour of dominant cephalopod taxa. The applied logit regression implies a monotonous relationship between the occurrence of species and the explanatory variables sun height and sampling depth. With reference to the latter variable this means that the occurrence of species restricted to intermediate water depth cannot be adequately described. Furthermore, using a conventional trawl, the occasional capture of specimens during setting or retrieval of the net cannot be avoided and may result in biased depth records below the animal's normal depth distribution. For species, which are regularly encountered in the samples, the influence of contamination on the results is, however, assumed to be low, and model parameters calculated for the dominant taxa described their distribution patterns reasonably well. Representatives of the mesopelagic families Enoploteuthidae and Pyroteuthidae were captured more often during night than during day and the highest change in probability of occurrence was consequently around sunset or sunrise. The enoploteuthid squid *Abraliopsis pfefferi* showed pronounced vertical migration behaviour with a clearly shallower depth distribution during night than during day. These results of the model correspond well to the observations from Roper and Young (1975) and Lu and Roper (1979), who concluded that this species is dispersed throughout the water column to about 1000 m during day, whereas it concentrates in the upper 100 m at night. Diurnal vertical migration was also reported for the pyroteuthids *Pterygioteuthis giardi* and *Pyroteuthis margaritifera*. According to Roper and Young (1975) daytime captures of pyroteuthids were made as deep as 1200 m, although they predominated between 300 and 600 m. Nesis (1993c) found a complete separation of habitat depth from day to night, with a concentration of specimens between 50-200 m during darkness and 400-800 m at daylight. However, similar to the present study, no tows were performed below 800 m water depth and it is, therefore, possible that parts of the population even migrate below the maximum sampling depth. This might have contributed to the fact that the model failed to reveal a change in depth distribution from day to night, whereas a significant relationship to sun height was revealed. It is, therefore, assumed that the low number of positive tows during day is not related to net avoidance but rather to a descent into deeper layers.

The information on vertical distribution of *Onychoteuthis banksii* in the literature is still equivocal, because adult specimens are hardly captured in trawls. Paralarvae are generally confined to the upper 150 m of the water column (Diekmann and Piatkowski, 2004), but juveniles and adults are possibly found at greater depth. A juvenile of 20 mm mantle length was *e.g.* captured at 800 m with a closing trawl (Roper and Young, 1975), and in Hawaiian waters specimens of the genus *Onychoteuthis* were encountered down to 1350 m water depth (Young, 1978). Roper and Young (1975) postulated that this species is not restricted to epipelagic regions because of the presence of photosensitive vesicles. Correspondingly, the model indicated a spreading of individuals throughout the water column with a higher probability of occurrence with increasing water depth. In accordance with former studies (Clarke and Lu, 1975; Lu and Roper, 1979; Roper and Young, 1975) distinct diurnal vertical migration behaviour could not be revealed.

Juvenile and adult ommastrephids are, similar to *O. banksii*, difficult to sample due to their high swimming speed and, thus, information on their exact distribution patterns is scarce. Observations were made from below 1000 m water depth up to the surface with highest occurrences during night (Clarke, 1966; Roper and Young, 1975). Although the probability of occurrence slightly increased during darkness no direct relationship to sun height and water depth could be discovered, indicating a broad vertical depth range inhabited by ommastrephids independent of daytime. Furthermore, the overall low probability of occurrence suggests that these muscular squids are probably not adequately sampled with the YFT. Corresponding conclusions were drawn from the model output for *Chtenopteryx sicula*. Young (1978) found in Hawaiian waters some indications for diurnal vertical migration, whereas Roper and Young (1975) reported a broad depth distribution, from near surface layers down to 800 m water depth.

The vertical distribution of Histioteuthidae was rarely investigated so far. Young (1978) analysed the day-night distribution of three different species in the Pacific Ocean and although most individuals were found at shallower water depth during night, results remained ambiguous for each species, and vertical habitats between congeners could not be distinguished. Therefore, all specimens identified within the monogeneric family Histioteuthidae were combined in the model and a higher encounter rate in samples collected during night could not be revealed. The probability rather increased significantly with depth, thus showing that the genus inhabits deeper layers, which presumably reach even below the maximum sampling depth of 800 m and, thus, far beyond the seamount summit.

The depth range inhabited by the investigated taxa overlaps significantly with the minimum summit depths of the three seamounts, and shows that the cephalopods appear in close proximity to the seafloor. Because of the shallower and much larger plateau areas, the strongest impact on cephalopod distribution was expected for GMS and Atlantis Seamount, rather than for ‘The Twins’, which is confirmed by the gradual decline in the pooled abundance values with decreasing water depth (Nesis, 1993a). For deep distributed taxa such as the Histioteuthidae, the seamounts represent a topographic obstacle in the surrounding flat abyssal plain. Bottom depth presumably governs their horizontal distribution and accordingly no histioteuthids were captured over the seamount plateaus. In contrast to this, the sound scattering layer interception hypothesis, first described by Isaacs and Schwartzlose (1965), might be important to vertically migrating species. This hypothesis suggests that local fish populations on seamounts feed on zooplankton that undergoes normal diurnal vertical migration. It is assumed that zooplankton and possibly also micronekton are laterally advected by prevailing currents onto the plateau and slope and are trapped by the seafloor when they descend to deeper water layers at sunrise. The higher predation pressure in near bottom layers by epibenthic fish was indirectly proved by the formation of gaps of vertically migrating zooplankton that develop every evening over abrupt shallow topography (Genin et al., 1988, 1994; Haury et al., 2000). At GMS, remains of micronektonic squids were found in the stomachs of several benthopelagic fish species such as *Zenopsis conchifer* (Zidowitz et al., 2002) and *Antigonia capros* (Fock et al., 2002a), and cephalopods even prevailed in the diet of the latter species. Although stomach contents were only identified to suborder level (Decapodiformes), small-bodied mesopelagic squids were most likely the dominant prey organisms. Abundances of cephalopods during darkness were generally reduced over the plateau but also at slope stations in comparison to oceanic areas, and these differences were especially pronounced for enoploteuthids and pyroteuthids. This gives rise to the conclusion that not only physical exclusion but also a high predation pressure influence distribution patterns of vertically migrating species at seamounts. Furthermore, according to Fock et al. (2002a) the interception probability of predatory fishes with the sound scattering layer is supposed to be highest at plateau margins, as vertically migrating species pass this habitat twice a day, around sunrise and sunset. Muscular squids like *O. banksii* and Ommastrephidae are probably less vulnerable to predation but rather act as major predators themselves. Fish and euphausiids were identified in the diet of *O. banksii* in the eastern Gulf of Mexico as main prey items (Pasarella and Hopkins, 1991). This implies that *O. banksii* feeds on sound scattering layer organisms, and the higher abundances measured above the plateau of GMS and Atlantis Seamount in comparison to surrounding waters might indicate that the shallow areas are preferential feeding grounds.

The spatial distribution of most oceanic cephalopods is strongly influenced by water depth, which was shown to have consequences on the species composition at seamounts. The shallow plateau areas were, however, not characterised by a special cephalopod fauna but by reduced abundances and lower species richness. The gradual decline in overall abundance values with decreasing water depth is comparable to the down-slope structuring observed for myctophid fishes at the continental shelf (Hulley, 1992) or at seamounts (Pusch et al., 2004). Bathymetric effects were less prominent at 'The Twins' compared to the shallower guyots Atlantis Seamount and GMS. However, taking only slope and oceanic stations into account, differences in species composition between seamounts were rather small. Longhurst (1998) divided the Atlantic Ocean into different ecological provinces and defined the 'North Atlantic Subtropical Gyral Province' to be roughly located between 25-30°N and 42°N. 'The Twins' are located at the northern edge of this province and are probably more influenced by westerly winds than the seamounts in lower latitudes, *i.e.* the primary production is supposed to be slightly higher there due to deeper winter convection. Nevertheless, the cephalopod fauna was not found to differ between the southernmost seamount GMS and 'The Twins', which was partly attributed to the time of sampling, which took place in summer, when adequate temperature conditions for subtropical species are shifted further up to the north. In general, the northern limit of the province, approximately determined by the Azores front, is supposed to represent a zoogeographic distribution boundary for *e.g.* decapod crustaceans and mesopelagic fishes (Badcock and Merret, 1977; Fasham, 1979). In contrast to this, Pusch (2004) found a high proportion of subtropical and tropical myctophid species at 'The Twins', indicating that the Azores front represents a leaky boundary. Similarly, the species composition of mesozooplankton and decapod crustaceans and was observed to change gradually rather than abruptly crossing the Azores front (Domanski, 1986; Huskin, 2001). Vecchione et al. (2001) investigated the cephalopod distribution in the western North Atlantic and revealed that the latitudinal variability was relatively small compared to faunal differences perpendicular to the continental shelf. Correspondingly, meso-scale topographic elevations like seamounts induced a higher variability to cephalopod species composition than the latitudinal distance between sampling locations. Distributional variability associated with latitude may only become more important when taking additional seamounts of temperate areas into account rather than restrict the study to subtropical regions.

Chapter VI

General Discussion

How are micronekton communities structured in the open ocean? This is the central question of the present study and different areas within the subtropical Atlantic Ocean, each characterised by specific topographic or hydrographic conditions, were investigated. The key taxon of this study is the molluscan class Cephalopoda. Cephalopods, especially large-bodied squids, are difficult to sample adequately and results of scientific field studies often underestimate their abundance because of their strong net avoidance. The present study, therefore, focuses on early life stages, called paralarvae (Young and Harman, 1988), which can be effectively sampled by various types of plankton gears (Piatkowski, 1998). In addition to cephalopods, fish larvae distribution patterns were investigated in chapter IV, as it is generally assumed that the same biotic and abiotic processes affect early life stages of both taxonomic groups.

Cephalopod and fish larvae community compositions in subtropical oceanic environments of the North Atlantic

Information on the biogeography of oceanic cephalopods is scattered, and relatively little effort has been spent on this topic since the comprehensive work of Clarke (1966). Most studies investigating cephalopods are restricted to small areas or at best to biogeographic provinces, and often geographic distribution patterns have been summarised in taxonomic reviews of selected taxa (*e.g.* Nesis, 1987; Sweeney et al., 1992; Voss et al. 1998). The reliability of distributional limits highly depends on a widespread sampling effort.

Consequently, a larger amount of information is available for coastal areas and, thus, for neritic species than for oceanic animals. The subtropical North Atlantic is relatively well-studied concerning oceanic cephalopods and fish (Backus et al., 1977; Clarke and Lu, 1974, 1975; Hulley, 1981; Lu and Roper, 1979; Vecchione et al., 2001). Backus et al. (1977) defined zoogeographic boundaries in the North Atlantic based on the distribution patterns of myctophid fish species and his 'North Atlantic Subtropical Region' is more or less congruent to the 'North Atlantic Subtropical Gyral Province' described by Longhurst (1998). The four sampling areas investigated in this study were all located within this region, and the cephalopod species compositions turned out to be very much alike. The cephalopod communities were generally characterised by widespread oceanic taxa, of which most are distributed on both sides of the Mid-Atlantic Ridge and the equator (Nesis, 1987, 2003; Roper et al., 1984). Only one species with a limited geographical range was identified. The cranchiid *Leachia lemur* was exclusively found in the western North Atlantic and is, according to Voss et al. (1992), restricted to subtropical Atlantic regions west of 50°W and possibly is endemic to the Sargasso Sea. On the whole, the collections were dominated by midwater oceanic squids of the families Enoploteuthidae, Pyroteuthidae or Cranchiidae. Myopsid squids, which are entirely neritic (Clarke, 1966), were completely missing, and Octopoda were only found in low abundances. Most identified octopods are pelagic during their whole life and are confined to the meso- to bathypelagic realm (Hochberg et al., 1992), which is another indication for the oceanic characteristics of the investigated areas. Only at Great Meteor Seamount (GMS) some octopod hatchlings were found that belonged to the bottom-dwelling species *Scaeurgus unicirrhus*. According to Nesis (1993a), this octopod is a typical inhabitant of seamounts, and due to the isolation of GMS from the continental shelf it is very likely that the hatchlings originate from a local stock. *S. unicirrhus* was, thus, the only species found in the pelagic cephalopod community, which showed a direct association to shallow topography.

Similar to cephalopods, the larval fish community at GMS was dominated by widespread midwater species, and according to Nellen and Ruseler (2004) less than 10% belonged to the neritic or shelf-bound ecological group. Differences in species composition compared to former studies performed at GMS were rather small (Belyanina, 1984; Nellen, 1973) and could be explained by the seasonal reproduction of some subtropical species. The larval fish community at GMS largely resembled those known from the Canary or Azores regions (Bekker et al., 1982; John et al., 2002; Rodríguez et al., 2000). Most likely the local fish community is complemented with species from the Macaronesian islands or the North African shelf by the prevailing currents, which flow into south-westerly direction. However, species composition did not vary substantially between years (Belyanina, 1984; Nellen, 1973; Nellen and Ruseler, 2004), and neritic species were presumably too small to have been advected from remote populations. This indicates that faunal assemblages are to some degree associated with the seamount, which has been so far only identified in few larval fish studies (Boehlert and Mundy, 1993).

Processes structuring communities of fish and cephalopod early life stages

Pelagic communities are structured by different biotic and abiotic factors acting in various ways and extents on each individual species and its developmental stages. The factors can be classified into those affecting the formation, maintenance or disruption of species assemblages. The full coverage of all relevant mechanisms and their influences is beyond the scope of the present study, but some important aspects should be highlighted that were derived from results presented in chapters II to V and that especially refer to the planktonic stages of cephalopods and fish.

Assemblages of larval fish and paralarval cephalopods are by definition ephemeral and are restricted to a short life-span, before individuals metamorphose or adapt to the ecological niches inhabited by their juveniles and adults. The **formation** of assemblages primarily depends on adult spawning behaviour, but is additionally influenced by water mass characteristics and the immediate flow field. In general, distinct assemblages are often associated with different water masses (*e.g.* Grioche et al., 1999; Sassa et al. 2002a), but the processes why these patterns occur remain often unclear. In the oceanic environment convergences and fronts may accumulate drifting plankton (Franks, 1992), and correspondingly may have profound effects on the distribution and survival of fish and cephalopod early life stages. At small-scales convergences can develop by Langmuir circulation or, at larger scales, can be caused by atmospheric pressure systems like the subtropical convergence zone observed in the Sargasso Sea. Macro-scale eddies that emerge *e.g.* from Gulf Stream meanders and pinch off large volumes of water, are important circular currents that are well known to aggregate distinct assemblages (Ortner et al., 1978; Roman et al., 1985; Wiebe et al., 1976). Furthermore, current-topography interactions may also induce circular currents, *e.g.* Taylor columns, that similarly concentrate buoyant plankton at the meso-scale level (Wolanski and Hamner, 1988). The high primary productivity, frequently observed at seamounts and fronts (*e.g.* Dower et al., 1992), may additionally confer an advantage in survival to larvae and paralarvae. The principal biological processes affecting **maintenance** are those promoting growth and survival. Physical factors maintaining species assemblages are usually the same as the one influencing formation, because they concentrate particles. Circular currents and eddies retain organisms within a particular water mass and outward diffusion is limited (Lobel and Robinson, 1986). Advection by consistent currents does not necessarily disrupt assemblages as passively drifting plankton may move as an entity. It is, however, very obvious that hydrographic features will only have pronounced effects on early life stages if they exist over biologically relevant time scales. Biotic factors influencing **disruption** of species assemblages apply to predator-prey interactions and, for larvae and paralarvae, to metamorphosis and an ontogenetic habitat change. High predation pressure can indisputably have severe effects on planktonic assemblages. At shallow seamounts vertical migration behaviour might enhance this effect due to physical interactions of organisms with topography. Vertically migrating species can be laterally displaced around seamounts (Genin et al., 1988) or are, in the proximity to the seafloor, exposed to higher predation pressure by benthopelagic fishes (Isaacs and Schwartzlose, 1965). The lack of appropriate prey may have similar disruption effects, as, first, mobile individuals may leave the area or, second, organisms that are not capable to migrate over larger distances suffer from starvation. Divergence fronts represent a physical process that disrupts assemblages and has the opposite effect of convergences. Furthermore, assemblages are dispersed if mechanisms forming and maintaining structures disappear. As an example, extreme wind events can cause turbulent mixing and may initiate the break down of Taylor column structures (Beckmann and Mohn, 2002). Particles and organisms previously retained by circular currents above or in the vicinity of seamounts would be then advected by wind induced currents.

Community structures at hydrographic fronts and seamounts

In the present study different spatial scales have been investigated, from small-scale patchiness to large-scale distribution patterns, covering adjacent ecological regions. Within each investigated area the cephalopod and larval fish communities were spatially structured and the observed patterns could be partly related to topographic or hydrographic gradients. At a regional scale, the cephalopod species composition changed across the subtropical convergence zone in the Sargasso Sea, and diversity and abundance increased significantly from south to north. The subtropical convergence zone is characterised by enhanced meridional gradients in near surface temperature (Voorhis and Hersey, 1964) and a shoaling of the upper thermocline in the poleward direction (Halliwell et al., 1994). This temperature gradient, often referred to as seasonal thermal front, is confined to a zonal band located at approximately 26°N to 32°N (Halliwell et al., 1991a, b, 1994). It separates the southern part of the Sargasso Sea, with a year round stratification of the water column, from its northern part, where stratification is restricted to the summer period. Convection during winter regulates the distribution of nutrients in the water column and results in a higher primary productivity north than south of the thermal front (Menzel and Ryther, 1960). This increase in productivity was related to higher abundances of *e.g.* epipelagic copepods, mesopelagic fishes or epibionts on *Sargassum natans* (Backus et al., 1969; Colton et al., 1975; Niermann, 1986), and possibly supported higher cephalopod paralarval densities north of the subtropical convergence zone. The increase in species diversity in the northern Sargasso Sea might be attributed to incursions of Gulf Stream cold core rings. The rings enclose cold slope water within a remnant of the Gulf Stream and were also shown to increase heterogeneity in zooplankton composition (Ortner et al., 1978). Due to their persistence and numbers identified in the northern Sargasso Sea (Lai and Richardson, 1977), it is very likely that the rings significantly influenced the cephalopod community.

In contrast to this large-scale comparison, where distinct faunal regions were identified, distribution patterns of planktonic cephalopods and fish at seamounts showed a high variability and patchiness on smaller horizontal scales. Numbers of cephalopod paralarvae were generally low and not comparable to abundances of fish larvae, which made the detection of small-scale assemblage structures extremely difficult. Density distribution of paralarvae at GMS was, therefore, investigated on pooled abundances and not on species level. Analyses revealed differences between samples collected over the seamount and samples from the adjacent open ocean. During day significantly higher abundances were measured at all discrete depth strata above the plateau than beyond it. This was presumably caused by the entrapment of vertically migrating species during their daily descent, which had been described as a common effect for the sound scattering layer at submarine elevations (Genin et al., 1988, 1994; Rogers, 1994). During night the opposite observation was made. Higher abundances were measured in the open ocean than atop of the seamount. Several authors found nocturnal reductions in zooplankton biomass over seamounts and concluded that shallow topographic features are an important source of local zooplankton patchiness (Genin et al., 1988, 1994; Haury et al., 2000). They supposed that the formation of gaps is caused by predation, and, thus, can be interpreted as a process disrupting assemblages. Because of the high standing stocks of benthopelagic fishes (Uiblein et al., 1999) and their preference for mesopelagic and micronektonic prey (Fock et al., 2002a), it is assumed that such mechanisms also exist at GMS. Irregularities, detected above the shallowest parts of the seamount plateau by principal component analysis based on larval fish and paralarval cephalopod species compositions, supported this hypothesis. Deep distributed and vertically migrating species were less dominant in this area compared to other stations. As passive vertical transport was of minor importance it was assumed that predation was the main process causing these patterns. In contrast, larval fish, whose adult stages are probably associated to the seamount, were distributed in shallower water depth and were observed to be particularly abundant near or above the summit region. Similar observations were made in a former investigation at GMS, although this was based mainly on larvae of the neritic species *Trachurus picturatus*, which was due to seasonal reproduction not found in the present larval collection (Nellen, 1973). Beckmann and Mohn (2002) revealed a strong retention potential at GMS and showed that the residence time of passively drifting organisms is prolonged within the water column approximately enclosed by the 1500 m isobath. It was, therefore, assumed that early life stages of fish and cephalopods could be retained in the vicinity of the seamount. Furthermore, assemblage structures investigated by principal component and redundancy analysis reflected the circular current system reasonably well, which highlights the importance of seamount induced currents on the formation of planktonic assemblages.

However, most significant environmental gradients and discontinuities occur in the vertical plain. At GMS the temperature dropped from about 26 °C at the surface to 15 °C near the seamount summit, whereas the thermocline was approximately positioned at 50-75 m depth. It is, therefore, not surprising that fish and cephalopod assemblages were mainly vertically structured. Three larval fish assemblages were identified: In the upper 150 m of the water column specimens of the myctophid subfamily Lampanyctinae dominated, whereas species performing diel vertical migrations or are confined to the deep meso- to bathypelagic fauna had their centre of distribution below 150 m down to the maximum sampling depth. Most representatives of the myctophid subfamily Myctophinae were distributed in intermediate layers, like it has been shown from other studies investigating distribution patterns of oceanic fish larvae (Cha et al., 1994; Sassa et al., 2004). Cephalopods formed only two distinct vertical assemblages. Most paralarvae concentrated in the upper 150 m of the water column, which is known to be the typical depth range inhabited by early life stages (Roper and Young, 1975; Vecchione et al., 2001). Only two species belonging to the family Pyroteuthidae were regularly encountered below 150 m water depth, and showed even at their early developmental stage diel vertical migration behaviour, which is in contrast to earlier studies (Clarke and Lu, 1974; Roper and Young, 1975).

Micronektonic cephalopods, which are usually capable to withstand major currents and actively migrate large horizontal and vertical distances, are less influenced by seamount induced circulation systems or by small- to mesoscale physical gradients. Their distribution patterns rather changed in relation to water depth, *i.e.* the seamount interferes with the vertical distribution of various species. Cephalopods, which are generally distributed below the seamount summit depth are simply excluded from the area, as the seamount acts as a topographic obstacle. For specimens, passively advected or actively migrated above the seamount summit and slopes, the influence might be twofold. First, similar disruption processes already discussed for planktonic paralarvae exist. Above the seamount, vertically migrating squids cannot accomplish their diel descent and might get trapped at the seafloor, where they are exposed to higher predation pressure (Isaacs and Schwartzlose, 1965; Rogers, 1994). At GMS this was partly confirmed by the detection of squid remains in the stomach contents of demersal fish species caught above the plateau (Fock et al., 2002a; Zidowitz et al., 2002) and by considerable lower abundances of micronektonic squids in the area of the seamount in comparison to surrounding waters. At the same time, the mechanism of entrapment might secondly improve the feeding conditions for cephalopods. This applies to the muscular squids as well as to the small micronektonic groups that *e.g.* prey on vertically migrating copepods (Pasarella and Hopkins, 1991), observed to concentrate during day close to the seafloor of the GMS plateau (Martin and Nellen 2004).

Importance of seamounts to recruitment processes

Seamounts support stocks of commercially valuable fish species and have been subjected to increasing levels of fishing effort within the last two decades (Koslow, 1997). Two important fish species that have been or that still are heavily exploited at seamounts are the Pelagic Armourhead (*Pseudopentaceros wheeleri*) in the northern Hawaiian Ridge and the Orange Roughy (*Hoplostethus atlanticus*) around New Zealand and southeastern Australia. The armourhead has a complex life history with the adults spawning at the seamounts. The neustonic larvae are dispersed by ocean currents and adults return to the seamount at an age of 1.5 - 2.5 years (Boehlert and Sasaki, 1988). The life history of orange roughy is still poorly understood, but it is known that they form large spawning aggregations near banks, pinnacles and canyons (Pankhurst et al. 1987). Orange roughy and several other fish species aggregating at seamounts are characterised by extreme longevity (Koslow, 1997), which is supposed to be beneficial in case recruitment may be highly episodic. These examples, as well as the high standing stocks of benthopelagic fishes *e.g.* found at GMS (Uiblein et al., 1999) suggest that specific life cycles have evolved that possibly use seamount current systems, with larval phases concentrating in the Taylor column and the adult phases spawning in the immediate vicinity of the seamount. Dower and Perry (2001) found extremely large abundances of larval rockfishes (*Sebastes* spp.) at Cobb Seamount and supposed that, unlike other fish present in the sampling area, the rockfish population may be self-recruiting. Former studies measured long-persistent anticyclonic currents around Cobb Seamount that are consistent with a stratified Taylor column (Dower and Mackas, 1996; Freeland, 1994). Dower and Perry (2001), thus, assumed that the physical conditions in combination with the release depth of larvae makes it almost certain that rockfish larvae are retained over the seamount. Hydrographic conditions at GMS were largely comparable to Cobb Seamount, and Beckmann and Mohn (2002) suggested a corresponding high retention potential for that area, although this is restricted to certain depth strata and only valid for non-migrating particles. The particular higher larval abundances of some neritic fish taxa observed over the upper slope and summit compared to surrounding waters give further evidence that eggs and larvae spawned in the area of the seamount are retained by recirculating currents. Similar observations were made by Nellen (1973) and it is, therefore, concluded that some of the resident fish stocks are self-recruiting. Although it cannot be excluded that the populations are supplemented with larvae advected from the continental slope, recruitment seems to be highly dependent on local hydrographic conditions. Extreme wind events probably have profound effects on the year class strength of resident species. The disintegration of meso-scale eddies may lead to a dispersion of larvae and a transport away from the appropriate habitat occupied by their adults. The recruitment to the isolated population would be, therefore, highly episodic, leading to a greater vulnerability of seamount fishes to exploitation.

Future prospects

The present study outlines several aspects of what kind of cephalopod and ichthyoplankton communities exist, how they are structured and what processes regulate the formation, maintenance and disruption of assemblages. The key taxa within this study were the cephalopods and their early life stages, of which many at present cannot be identified to species level (Sweeney et al., 1992). Progress in taxonomy is, thus, the principal challenge in proceeding within this field in the future. The large variation in species composition found within and between samples of any investigated region showed that intensive sampling efforts are required to characterise assemblages. The occurrence of many rare species, which is typical for any oceanic cephalopod community, represents an additional statistical challenge. Some of the problems were overcome by multivariate statistical methods and in this respect by applying a new approach on the plankton samples collected at GMS by simultaneously investigating larval fish and paralarval cephalopods (see Chapter IV). However, it should be stressed that a better resolution of the station grid would have resulted in a more precise picture, providing more detailed information on the regulating mechanisms. Generally, sampling has to be conducted at spatial scales appropriate to the processes under investigation. With reference to sampling efforts at seamounts and fronts, this means that a large-scale spatial and temporal synoptic sampling is needed to untangle the main processes, while sampling at smaller scales can focus on particular mechanisms, acting *e.g.* over shorter time-periods. The temporal persistence of the observed distribution patterns could not be investigated in the present study, and it might be that certain mechanisms were overlooked analysing only a snapshot of the communities. The temporal coverage is especially important when seasonal effects should be taken into account. Although seasonality is much less pronounced in subtropical regions compared to higher latitudes, it is supposed to have at least effects on the relative species compositions of fish and cephalopods (*e.g.* Ditty et al., 1988; Vecchione et al., 2001). In future studies it is, thus, of vital importance that sampling is not only intensified on spatial but also on temporal scales. Nevertheless, the regional investigations presented in this work gave considerable insight into the range of processes that structure cephalopod and ichthyoplankton assemblages and, furthermore, into the communities themselves, which are still hardly known in the oceanic environment.

Summary

In the past the oceanic environment has often been compared with terrestrial deserts and until today relatively little is known about the ecology of the high seas. Within the present study pelagic oceanic communities of cephalopods and fish in the subtropical North Atlantic were investigated. The response of communities to physical gradients and hydrographic processes is addressed at different spatial scales. The primary goal of any scientific sampling is to catch a cross-section of the fauna present. Sampling of mobile species with nets is in general subjected to bias, and this is particularly evident for many muscular squids. This study, therefore, focussed on early life stages of cephalopods and fish, because they are easily quantitatively and qualitatively assessed with traditional sampling gear. Both taxonomic groups, cephalopods as well as fish, were dominated by mid-water species and few neritic species with bottom-dwelling adults were found.

In the western North Atlantic the cephalopod fauna of the Sargasso Sea was investigated for the first time. Zooplankton samples were collected essentially in north-south direction by two different net types, a 6 m² Isaac-Kidd Midwater trawl and a Bongo net. A total of 909 cephalopod specimens were captured belonging to 13 families and 20 species. In spite of the proximity to Bermuda Island, the fauna exclusively comprised oceanic taxa. Hydrographic measurements in parallel to the plankton sampling revealed a meridional thermal gradient at approximately 27°20'N. This frontal feature has been described as 'subtropical convergence zone' and separates the Sargasso Sea into a cooler more productive northern part and a warmer less productive southern part. Correspondingly, the abundances and species composition of cephalopods changed abruptly at the front, from a less diverse fauna characterised by low species densities in the south to higher densities and an increased diversity in the north. The presumably endemic cranchiid *Leachia lemur* was by far the dominant species in the northern part and contributed substantially to the differences detected in the community composition. In contrast to this, the mesopelagic

squids *Selenoteuthis scintillans* prevailed in the southern part of the Sargasso Sea but only rarely occurred in the north. It was, therefore, concluded that the subtropical convergence zone represents a distinct faunal boundary to the early life stages of cephalopods and separates two different ecological areas, not only distinguished by primary productivity but also by its faunal components.

In the eastern North Atlantic the cephalopod fauna was investigated at three seamounts, each of different topographic morphology. The seamount studied in greatest detail was Great Meteor Seamount (GMS), one of the largest topographic elevations throughout the Atlantic Ocean. GMS has an elliptical base, rises steeply from water depth of more than 4000 m up to less than 300 m below the surface, and is characterised by a large, flat plateau area. A multiple opening-closing plankton net with a 1 m² opening was applied in seven discrete strata from 290 m depth to the surface at 23 stations, covering the plateau, the flanks and the adjacent deep sea. 1200 early life stages of cephalopods were captured altogether, comprising 31 species of 18 families. In a first approach the station-specific cephalopod species composition was investigated by non-metric multidimensional scaling and related techniques. No differences between the open ocean and the community in the immediate vicinity of the seamount were detected. However, during night densities of cephalopods were reduced above the plateau compared to deep stations, whereas on the other hand slightly higher abundances were measured in the summit region during day. This was interpreted as an indication of current-topography interactions, which lead to a concentration of vertically migrating organism above the summit during the daily descent. Near the seafloor they are exposed to enhanced predation pressure of *e.g.* resident fish stocks. During night and upward migration, patches develop, diminished or devoid of vertically migrating species. Some of the mesopelagic squid species performed diurnal vertical migrations, although, due to their developmental stage, the observed migration amplitudes were less pronounced than those of their adults. The reduced cephalopod densities above the plateau found during night, therefore, indicated gap formation processes, and it was assumed that deep distributed species were more vulnerable to predation above GMS than in the surrounding waters.

In a second approach, results of paralarval cephalopods in combination with larval fish in the plankton catches at GMS were investigated by direct and indirect gradient analysis. Although larval fish were much more abundant (n=18555) and much more diverse than paralarval cephalopods (n=1200), the general distribution patterns were remarkably similar. For both taxonomic groups highest diversity was measured in the 100-150 m water layer. Significantly different assemblages were found in the upper 150 m of the water column and in the lower part, from 150-290 m. An additional larval fish assemblage was identified at intermediate water depth. The mapping of sample scores of a modified principal component analysis revealed deviations from this general vertical assemblage structure above the plateau, which was related to the gap formation processes mentioned above. Horizontal distribution patterns of both taxa corresponded well to the structure of closed circulation cells detected above the upper slope and plateau area. Statistical tests revealed a significant difference of larval fish assemblages between the inner, *i.e.* within the 1500 m depth contour, and the outer seamount regime, whereas these differences were less pronounced for cephalopods. Because of the strong relationship between community composition and the seamount current system, it was concluded that a retention potential at GMS exists, that is capable to retain early life stages in the vicinity of the seamount and, thus, enable self-sustaining populations. These effects are supposed to be pronounced for fish, which is due to the frequent occurrence of neritic larvae within the samples. In contrast to this, only one species with bottom-dwelling adults was identified in the cephalopod community, and, thus, a weaker association to the seamount was assumed.

Finally, the species compositions of micronektonic cephalopods were compared between three seamounts of the eastern subtropical Atlantic: GMS, Atlantis Seamount, and ‘The Twins’. Atlantis Seamount has, similar to GMS, a flat plateau, although this amounts only to approximately one third of the area of GMS. ‘The Twins’ is characterised by two needle-like peaks that are reaching at maximum 387 m below the surface. At all seamounts a pelagic Youngfishtrawl was applied in discrete depth strata from 25 m to 800 m water depth, covering stations located over the summit, the slope, and in the adjacent open ocean. A total of 612 cephalopods were collected. 40 species of 23 families were identified, of which many species were extremely rare. All seamounts were characterised by a typical oceanic community and in spite of the latitudinal distance of more than 13° between GMS and ‘The Twins’ faunal differences were rather small. However, species numbers and abundances became significantly lower with decreasing water depth, *i.e.* stations above the plateau and upper slope were impoverished in terms of abundance and species richness. This was related to the pronounced diel vertical migrations performed by most of the

species or their overall vertical distribution well below the depth of the seamount summit. In order to describe vertical migration behaviour of the most abundant species, a logit regression model was developed using sun height and water depth as explanatory variables. The results of the model corresponded well to former studies and, thus, presented a new method to estimate vertical distribution of relatively rare species.

Zusammenfassung

In der Vergangenheit wurden ozeanische Gebiete häufig mit terrestrischen Wüsten verglichen, und bis heute ist relativ wenig über die Ökologie der offenen Ozeane bekannt. In der vorliegenden Arbeit wurden pelagische ozeanische Tintenfisch- und Fischgemeinschaften im subtropischen Nordatlantik untersucht. Es wurde analysiert, wie diese Gemeinschaften in Resonanz zu physikalischen Gradienten und hydrographischen Prozessen variieren. Das primäre Ziel jeder wissenschaftlichen Beprobung ist es, einen Querschnitt der vorhanden Fauna zu besammeln. Die Beprobung von beweglichen Organismen mit Netzen ist generell durch systematische Fehler gekennzeichnet, wobei dieses besonders auf die Fängigkeit von Kalmaren zutrifft. Die vorliegende Studie konzentrierte sich daher auf frühe Lebensstadien von Fischen und Cephalopoden, die mit herkömmlichen Netztypen qualitativ und quantitativ erfasst werden können. Beide taxonomische Gruppen, Tintenfische wie auch Fische, wurden von mesopelagischen Arten dominiert und es wurden nur wenige neritische Arten, die bodenlebenden Adulttieren zuzuordnen sind, gefangen.

Im westlichen Nordatlantik wurde zum ersten Mal die Cephalopodenfauna der Sargasso See untersucht. Zooplanktonproben wurden im wesentlichen in Nord-Süd Richtung mit zwei verschiedenen Netztypen gesammelt, einem 6 m² Issac-Kidd Midwater Trawl und einem Bongonetz. Insgesamt wurden 909 Tintenfische gefangen, die zu 13 Familien und 20 Arten gehören. Trotz der Nähe zu der Insel Bermuda, umfasste die Fauna ausschließlich ozeanische Taxa. Hydrographische Messungen, die parallel zur Zooplanktonprobennahme durchgeführt wurden, zeigten einen bei 27°20'N gelegenen meridionalen Temperaturgradienten. Dieses in diesem Zusammenhang als subtropische Konvergenzzone beschriebene Charakteristikum für Fronten teilt die Sargasso See in einen kühleren, produktiveren nördlichen Teil und einen wärmeren, weniger produktiven südlichen Teil. Die Häufigkeit und Diversität von Cephalopoden veränderte sich abrupt an der Front, von

einer weniger diversen Fauna mit niedrigen Abundanzen im Süden zu höheren Abundanzen und einer größeren Diversität im Norden. Der als endemische eingestufte Gallertkalmar *Leachia lemur* war die vorherrschende Art im nördlichen Teil und trug damit wesentlich zu den Unterschieden bei, die in der faunistischen Analyse der Gemeinschaftszusammensetzung aufgedeckt wurden. Im Gegensatz dazu war die mesopelagische Art *Selenoteuthis scintillans* im südlichen Teil der Sargasso See am häufigsten, während sie äußerst selten im nördlichen Teil angetroffen wurde. Aus den Ergebnissen wurde geschlossen, dass die subtropische Konvergenzzone eine deutliche Faunengrenze für die frühen Lebensstadien von Tintenfischen darstellt. Sie trennt zwei ökologisch verschiedene Gebiete voneinander, die sich nicht nur hinsichtlich ihrer Primärproduktion, sondern auch hinsichtlich ihrer Faunenkomponenten unterscheiden.

Im östlichen Nordatlantik wurde die Tintenfischfauna an drei Seebergen untersucht, die jeweils durch unterschiedliche topographische Merkmale gekennzeichnet sind. Am Genauesten wurde dabei die Große Meteorbank beprobt, die eine der größten topographischen Erhebungen im Atlantischen Ozean darstellt. Die Große Meteorbank hat eine elliptisch geformte Basis, erhebt sich steil von Tiefen unterhalb von 4000 m bis weniger als 300 m unter die Wasseroberfläche, und besitzt ein großes, weitgehend flaches Plateau. Ein Mehrfachschließnetz mit einer 1 m² Öffnung wurde in sieben verschiedenen Stufen von 290 m Tiefe bis an die Oberfläche auf 23 Stationen eingesetzt, die über dem Plateau, an den Flanken oder in den angrenzenden Tiefseebereichen gelegen waren. Insgesamt wurden 1200 frühe Lebensstadien von Tintenfischen gefangen, die 31 Arten und 18 Familien umfassten. Zunächst wurden die integrierten Artenzusammensetzungen der jeweiligen Stationen mit nicht-metrischer Multidimensionaler Skalierung und verwandten Methoden untersucht. Unterschiede zwischen den Gemeinschaften des offenen Ozeans und denen in unmittelbarer Nähe zum Seeberg konnten nicht entdeckt werden. In der Nacht waren die Dichten von Tintenfischen waren über dem Plateau im Verhältnis zur Tiefsee reduziert, während im Gegensatz dazu am Tage leicht erhöhte Abundanzen über dem Seeberggipfel gemessen wurden. Dieses wurde als Hinweis auf Strömungs-Topographie Interaktionen gedeutet, die während des Tages zu einer Konzentration vertikal migrierender Organismen über dem Gipfel führt. In der Nähe des Meeresbodens sind diese Organismen dann einem erhöhten Prädationsdruck durch lokale Fischbestände ausgesetzt. In der Nacht und während der Wanderung in flachere Wasserschichten entstehen dadurch

Bereiche, in denen vertikal wandernde Arten in Ihrer Häufigkeit reduziert sind oder vollkommen fehlen. Einige mesopelagische Kalmararten führten diurnale vertikale Wanderungsbewegungen durch. Aufgrund des frühen Entwicklungsstadiums dieser Cephalopoden waren die Wanderungen allerdings weniger ausgeprägt als die der adulten Individuen. Reduzierte Dichten von Cephalopoden während der Nacht über dem Plateau deuten auf Prozesse hin, die Lücken in den Verteilungen bewirken (‚gap formation'). Es wurde angenommen, dass die tief verteilten Individuen über der Bank gefährdeter durch Räuber waren als dies in den umliegenden Regionen des Seeberges der Fall war.

In einem zweiten Ansatz wurden die Ergebnisse von Cephalopodenparalarven und Fischlarven aus den Planktonfängen an der Großen Meteorbank zusammen ausgewertet und mit direkten und indirekten Gradientenanalysen untersucht. Obwohl Fischlarven sehr viel häufiger (n=18555) und in ihrer Zusammensetzung sehr viel diverser als Tintenfischparalarven (n=1200) waren, zeigten sich doch bemerkenswerte Ähnlichkeiten in den generellen Verteilungsmustern. In beiden taxonomischen Gruppen wurde die höchste Diversität in der Wasserschicht zwischen 100-150 m Tiefe gemessen. Signifikant verschiedene Artenansammlungen wurden in den oberen 150 m der Wassersäule und dem darunter liegenden Teil, von 150 bis 290 m Tiefe gefunden. Eine weitere Gruppierung von Fischlarvenarten wurde in mittleren Wassertiefen identifiziert. Die Kartierung der Probenwerte, basierend auf einer modifizierten Hauptkomponentenanalyse, zeigte über dem Plateau Abweichungen von der generellen vertikalen Gemeinschaftsstruktur. Dies wurde auf die Prozesse der bereits oben genannten ‚gap formation' zurückgeführt. Die horizontalen Verteilungsmuster beider Taxa stimmten gut mit der Struktur geschlossener Zirkulationszellen überein, die sich über dem Hang und dem Seebergplateau entwickelt hatten. Signifikante Unterschiede wurden in den Fischlarvenansammlungen zwischen dem inneren, d.h. innerhalb der 1500 m Linie gelegenen Bereich, und dem äußeren Seebergregime gefunden. Diese Unterschiede waren für die Paralarven von Tintenfischen weniger ausgeprägt. Der deutliche Bezug zwischen der Gemeinschaftszusammensetzung und dem Seeberg-Strömungssystem lässt auf ein ausgeprägtes Retentionspotential an der Großen Meteorbank schließen, das frühe Lebensstadien in der Nähe des Seeberges zurückhalten kann und damit sich selbst-erhaltende Populationen ermöglicht. Da neritische Larven verhältnismäßig häufig in den Proben auftraten sind diese Effekte für Fischlarven vermutlich besonders stark ausgeprägt. Im Gegensatz dazu wurde nur eine Tintenfischart mit bodenlebenden Adulttieren identifiziert, so dass eine schwächere Assoziation von Cephalopoden mit dem Seeberg angenommen wurde.

Abschließend wurden die Artenzusammensetzungen von Tintenfischen des Mikronektons zwischen drei Seebergen des östlichen subtropischen Nordatlantiks miteinander verglichen: Die Große Meteorbank, Atlantisbank und ‚The Twins'. Die Atlantisbank ist ähnlich wie die Große Meteorbank durch ein flaches Plateau charakterisiert, obwohl dieses nur ungefähr ein Drittel der Fläche der Großen Meteorbank einnimmt. ‚The Twins' ist durch zwei Felsnadeln gekennzeichnet, die maximal 387 m unter die Wasseroberfläche reichen. Alle drei Seeberge wurden mit einem Jungfischtrawl in diskreten Tiefenstrata von 25 bis 800 m Wassertiefe beprobt, wobei die Stationen über dem Seeberggipfel, dem Hang und dem angrenzenden offenen Ozean gelegen waren. Insgesamt wurden 612 Tintenfische gefangen. Viele der 40 Arten aus 23 Familien waren extrem selten. Alle Seeberge waren durch eine typisch ozeanische Gemeinschaft charakterisiert und zeigten trotz der latitudinalen Distanz zwischen der Großen Meteorbank und ‚The Twins' von mehr als 13° lediglich geringe Unterschiede in der Faunenzusammensetzung. Die Artenzahlen und Abundanzen waren allerdings deutlich mit abnehmender Wassertiefe reduziert, d.h. Stationen über dem Plateau und dem oberen Hangbereich waren hinsichtlich der Abundanz und des Artenreichtums verarmt. Ausgeprägte diurnale Vertikalwanderungen, die von den meisten Arten durchgeführt wurden, oder eine insgesamt tiefere Verteilung unterhalb der Wassertiefe des Seeberggipfels lieferten dazu eine mögliche Begründung. Um das vertikale Wanderungsverhalten der häufigsten Arten zu beschreiben wurde ein logistisches Regressionsmodell entwickelt, das den Sonnenstand und die Wassertiefe als erklärende Variablen benutzt. Die Ergebnisse des Modells stimmten gut mit früheren Studien überein und stellen somit eine neue Methode zur Bestimmung der Vertikalwanderung von relativ seltenen Arten dar.

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Early life and juvenile cephalopods around seamounts of the subtropical eastern North Atlantic:

Illustrations and a key for their identification

Rabea Diekmann, Uwe Piatkowski & Matthias Schneider

Abstract

Early life stages of cephalopod species were identified from zooplankton and nekton samples collected near seamounts of the subtropical eastern North Atlantic, especially at the Atlantis-Meteor Seamount Chain. Samples were taken during two recent German oceanographic expeditions into the region. In total, 1811 specimens, mainly posthatchlings and juveniles, were found, comprising 26 families and 49 species. A comprehensive species list is given as well as detailed illustrations of the major forms. A key was developed for an easy identification of the early life stages of oceanic cephalopods that dominated the cephalopod fauna from seamount regions of the subtropical eastern North Atlantic.

Contents

Introduction

Pelagic regions of the subtropical Atlantic Ocean are often regarded as „deserts“, because they are characterised by low primary productivity and low standing stocks of zooplankton and nekton. However, there are various seamounts and islands in this region which may provide productive environments with appropriate conditions for all trophic levels of the marine food chain (Rogers 1994). As it has been shown for the Southwest Pacific, seamounts can harbour unique ecosystems that are inhabited by characteristic living communities and higher standing stocks of commercially exploitable pelagic and benthic fishes and invertebrates, which support traditional fishing grounds (Koslow 1997).

However, little is known about the distribution of cephalopods near seamounts, although these active pelagic predators are a major nektonic group occurring in all open oceans. They are essential elements of pelagic food chains (Piatkowski et al., 2001), their early life stages can occur in exceptionally high densities (Vecchione, 1999), and their distribution is often closely related to hydrographic conditions (Diekmann & Piatkowski, 2002). In the present study we examine a comprehensive collection of oceanic cephalopods sampled near various seamounts of the subtropical eastern Atlantic Ocean. They were caught with zooplankton nets and pelagic trawls during the Meteor-cruise M42/3 in September 1998, and the Heincke-cruise He135 in summer of 2000 (Fig. 1). The epi- and mesopelagic early life cephalopods of these expeditions are described in detail, the most abundant families and species are illustrated, and a key for their identification is given.

Materials and methods

Cephalopods were collected during two research cruises (Meteor 42/3, September 1998; and Heincke 135, August 2000) at four seamounts east of the Mid-Atlantic Ridge (Fig. 1). Sampling was conducted with zooplankton nets (BIOMOC (modified MOCNESS); 1m² opening; 335µm mesh size) and a pelagic youngfish trawl (YFT; 10x10m net opening; 11mm mesh size in the cod end) in different depths to a maximum depth of 800 m. All samples were initially preserved in 4% formalin, buffered with borax. 1811 cephalopods, essentially comprising early life stages, were sorted and identified to the lowest feasible taxonomic level. The cephalopod systematic followed the classification of Sweeney & Roper (2001) (see chapter 3, 4). Besides our own descriptions and illustrations, information and descriptions from Sweeney et al. (1992), Nesis (1987) and Roper et al. (1984) were considered for the identification key.

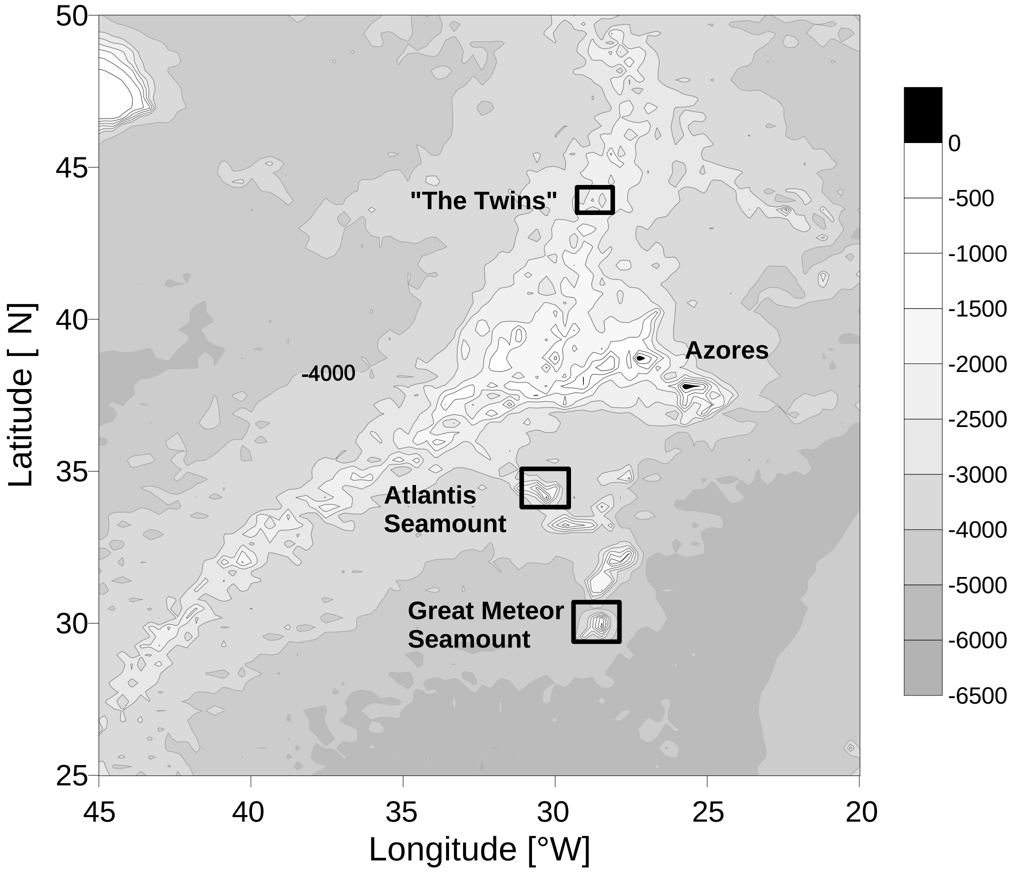
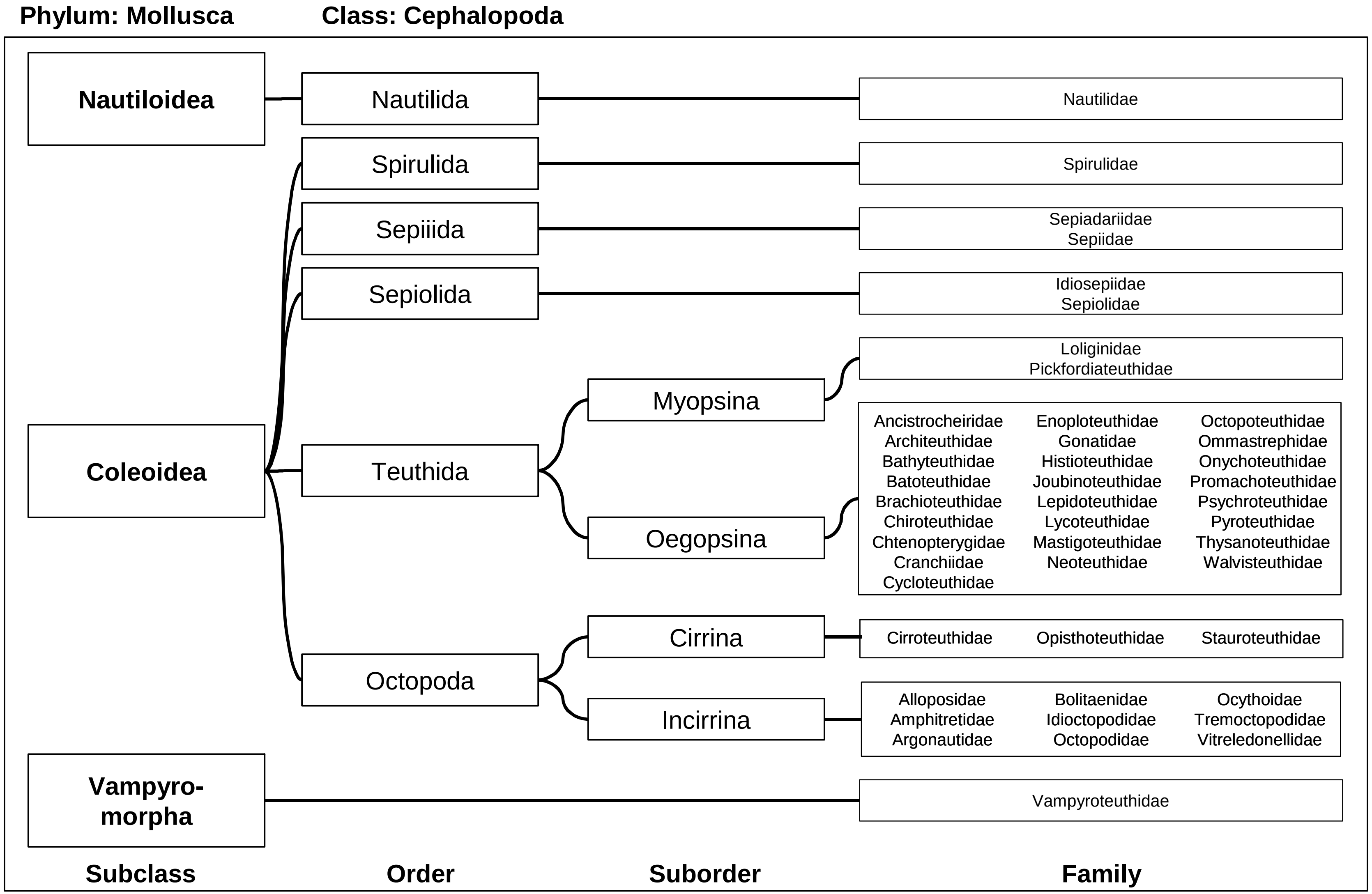


Fig. 1: Seamounts of the eastern subtropical North Atlantic investigated during two German research cruises (M42/3, HE135). Cephalopod early life stages and juveniles were sampled with zooplankton nets (Great Meteor Seamount only) and a pelagic youngfish trawl (all seamounts).



Classification of recent cephalopods

Checklist

Cephalopods around seamounts of the subtropical eastern North Atlantic:

Class Cephalopoda
Subclass Coleoidea
- Order Spirulida
    - Family Spirulidae
        - *Spirula spirula* (Linnaeus, 1758)
- Order Sepiolida
    - Family Sepiolidae
        - Subfamily Heteroteuthinae
            - *Heteroteuthis dispar* (Rüppel, 1844)
- Order Teuthida
    - Suborder Oegopsina
        - Family Ancistrocheiridae
            - *Ancistrocheirus lesueurii* (Orbigny, 1842)
        - Family Bathyteuthidae
            - *Bathyteuthis abyssicola* (Hoyle, 1885)
        - Family Brachioteuthidae
            - *Brachioteuthis riisei* (Steenstrup, 1882)
        - Family Chiroteuthidae
            - *Chiroteuthis* sp. (Orbigny, 1841)
            - *Grimalditeuthis bonplandi* (Vérany, 1839)
            - *Valbyteuthis* sp. (Joubin, 1931)
                - [Synonymous to *Plancoteuthis* sp. (Pfeffer, 1912)]
        - Family Chtenopterygidae
            - *Chtenopteryx sicula* (Vérany, 1851)
        - Family Cranchiidae
            - Subfamily Cranchiinae
                - *Cranchia scabra* (Leach, 1817)
                - *Liocranchia* sp. (Pfeffer, 1884)
                - *Leachia atlantica* (Degner, 1925)
            - Subfamily Taoninae
                - *Bathothauma lyromma* (Chun, 1906)
                - *Helicocranchia pfefferi* (Massy, 1907)
                - *Helicocranchia papillata* (Voss, 1960)
                - *Liguriella* sp. (Issel, 1908)
                - *Megalocranchia* sp.(Pfeffer, 1884)
                - *Taonius pavo* (LeSueur, 1821)
        - Family Cycloteuthidae
            - *Discoteuthis discus* (Young & Roper, 1969)
        - Family Enoploteuthidae
            - *Abralia veranyi* (Rüppel, 1844)
            - *Abraliopsis pfefferi* (Joubin, 1896)
            - *Enoploteuthis* sp. (Orbigny, 1844)
        - Family Histioteuthidae

- *Histioteuthis arcturi* (Robson, 1948)
- *Histioteuthis bonellii* (Férussac, 1834)
- *Histioteuthis celetaria celetaria* (Voss, 1960)
- *Histioteuthis meleagroteuthis* (Chun, 1910)
- *Histioteuthis reversa* (Verrill, 1880)

Family Lycoteuthidae
  Subfamily Lampadioteuthinae
    Lampadioteuthis megaleia (Berry, 1916)
  Subfamily Lycoteuthinae
    Selenoteuthis scintillans (Voss, 1959)
Family Mastigoteuthidae
    Idioteuthis hjorti (Chun, 1913)
    Mastigoteuthis atlantica (Joubin, 1933)
Family Octopoteuthidae
    Taningia danae (Joubin, 1831)
Family Ommastrephidae
  Subfamily Ommastrephinae
    Ommastrephes bartramii (LeSueur, 1821)
    Hyaloteuthis pelagica (Bosc, 1802)
    Sthenoteuthis pteropus (Steenstrup, 1855)
    Ornithoteuthis antillarum (Adam, 1957)
Family Onychoteuthidae
    Onychoteuthis banksii (Leach, 1817)
    Onykia carriboea (LeSueur, 1821)
Family Pyroteuthidae
    Pterygioteuthis giardi giardi (Fischer, 1896)
    Pyroteuthis margaritifera (Rüppel, 1844)
Family Thysanoteuthidae
    Thysanoteuthis rhombus (Troschel, 1857)

Order Octopoda
  Suborder Incirrina
    Family Alloposidae
      Alloposus mollis (Verril, 1880)
        [Synonymous to *Haliphron atlanticus* (Steenstrup, 1861)]
    Family Argonautidae
      Argonauta argo (Linnaeus, 1758)
    Family Bolitaenidae
      Bolitaena pygmaea (Verril, 1884)
      Japetella diaphana (Hoyle, 1885)
    Family Octopodidae
      Subfamily Octopodinae
        c.f. *Scaeurgus unicirrhus* (Orbigny, 1840)
    Family *Ocythoidae*
      Ocythoe tuberculata (Rafinesque, 1814)
    Family Tremoctopodidae
      Tremoctopus violaceus violaceus (Chiaje, 1830)
    Family Vitrelledonellidae
      Vitrelledonella richardi (Joubin, 1918)

Tab. 1: Early life stages of cephalopods collected with zooplankton nets (BIOMOC) and a pelagic youngfishtrawl (YFT) during the RV Meteor cruise 42/3 (September 1998) at Great Meteor Seamount (GMS) and during the RV Heincke cruise 135 (August 2000) at Atlantis Seamount, at "The Twins" and at a small seamount near the Azores. Numbers are absolute numbers, irrespective of effort and daytime. Numbers for higher taxa only include specimens that could not be further identified.

Order, Family	Species	Great Meteor Seamount		"The Twins"	Atlantis Seamount	Azores
		N_{abs} (Biomoc)	N_{abs} (YFT)	N_{abs} (YFT)	N_{abs} (YFT)	N_{abs} (YFT)
Order Spirulida						
Family Spirulidae	*Spirula spirula*		1			
Order Sepiolida						
Family Sepiolidae	*Heteroteuthis dispar*			6	12	3
Order Teuthida						
Sub-O. Oegopsina	Oegopsina indet.	183	6	5	2	
Family Ancistrocheiridae	*Ancistrocheirus lesueurii*	70				
Family Bathyteuthidae	*Bathyteuthis abyssicola*				1	
Family Brachioteuthidae	*Brachioteuthis* c.f. *riisei*	5	1		1	1
Family Chiroteuthidae	Chiroteuthidae indet.	2		1		
	Chiroteuthis sp.	11	1			
	Valbyteuthis sp.	8				
Family Chtenopterygidae	*Chtenopteryx sicula*	52	20	8	1	
Family Cranchiidae	Cranchiidae indet.	10				
Subfamily Cranchiinae	Cranchiinae indet.	8				
	Cranchia scabra	4	2		1	
	Leachia atlantica	1				
	Liocranchia sp.	2			1	
Subfamily Taoninae	Taoninae indet.	5				
	Bathothauma lyromma	3		5	2	3
	Helicocranchia pfefferi	4	4	2	3	
	Helicocranchia papillata	21	2			
	Helicocranchia sp.	3	2			
	Liguriella sp.	3				
	Megalocranchia sp.			1	6	
	Taonius pavo			5	10	2
Family Cycloteuthidae	*Discoteuthis discus*	3		1	1	1
Family Enoploteuthidae	Enoploteuthidae indet.	136			1	
	Abralia c.f. *veranyi*	1	3			
	Abraliopsis pfefferi	86	106	9	39	
	Enoploteuthis sp.	7	6		1	
Family Grimalditeuthidae	*Grimalditeuthis* c.f. *bonplandi*		1			
Family Histioteuthidae	*Histioteuthis* sp.	1	1	4	1	
	Histioteuthis arcturi				6	
	Histioteuthis bonellii			4		
	Histioteuthis celetaria celetaria	1		4	1	
	Histioteuthis meleagroteuthis			2	3	
	Histioteuthis reversa			10		
Family Lycoteuthidae	Lycoteuthidae indet.	8				
Subfamily Lampadioteuthinae	*Lampadioteuthis megaleia*		1	2	1	
Subfamily Lycoteuthinae	*Selenoteuthis scintillans*	54	20			
Family Mastigoteuthidae	*Idioteuthis* c.f. *hjorti*			3		
	Mastigoteuthis c.f. *atlantica*	3		1	3	1
Family Octopoteuthidae	*Taningia danae*				1	
Family Ommastrephidae	Ommastrephidae indet.	7	3	2	2	2
Subfamily Ommastrephinae	*Hyaloteuthis pelagica*	8 (Type B')	2			
	Ommastrephes bartramii	38 (Type A')	18	4	4	
	Ornithoteuthis antillarum	3 (Type B')				
	Sthenoteuthis c.f. *pteropus*	6 (Type B')				
Family Onychoteuthidae	Onychoteuthidae indet.	6				
	Onychoteuthis banksii complex	194	52	27	16	3
	Onykia carriboea	14				
Family Pyroteuthidae	Pyroteuthidae indet.	28	2			
	Pterygioteuthis giardi giardi	2	12	20	9	
	Pyroteuthis margaritifera	77	18	42	13	1
Family Thysanoteuthidae	*Thysanoteuthis rhombus*	8				
Order Octopoda	Octopoda indet.	1				
Sub-O. Incirrina						
Family Alloposidae	*Alloposus mollis*			1	1	
Family Argonautidae	*Argonauta argo*	21		1		1
Family Bolitaenidae	*Bolitaena pygmaea*	43	5		2	
	Japetella diaphana				1	
Family Octopodidae	Octopodinae c.f. *Scaeurgus unicirrhus*	27				
Family Ocythoidae	*Ocythoe tuberculata*			3		
Family Tremoctopodidae	*Tremoctopus violaceus violaceus*	2	1			
Family Vitreledonellidae	*Vitreledonella richardi*		2	1	1	
Sum		1125	292	174	147	18

Identification key of early life stages of oceanic cephalopods in the eastern subtropical North Atlantic (identification to family level)

1. • mantle without fins; arm crown without tentacles ⇒ **Order Octopoda** ⇒ **21.**
   • mantle with fins or fin rudiments; one pair of tentacles or a trunk-like structure (proboscis) exists ⇒ **2.**

2. • mantle with lateral fins ⇒ **3.**
   • mantle with subterminal or terminal fins, sometimes dorsally attached ⇒ **Order Teuthida** ⇒ **4.**

3. • coiled chambered shell in posterior mantle; fins or fin rudiments tiny and widely separated; huge buccal mass; well developed beak ⇒ **Spirulidae**
   • no coiled chambered shell; each fin at least as wide as long; buccal mass inconspicious ⇒ **Sepiolidae**

Order Teuthida

4. • eye covered by a transparent membrane (cornea) ⇒ Sub.-O. Myopsina (no species of this suborder found around the seamounts)
   • eye without cornea, thus, in contact with seawater ⇒ Sub.-O.Oegopsina ⇒ **5.**

5. • tentacles fused into trunk like structure (proboscis) ⇒ **Ommastrephidae**
   • pair of tentacles; no proboscis ⇒ **6.**

6. • head with long neck ⇒ **7.**
   • head without long neck ⇒ **8.**

7. • neck with dorsal hump; arm crown not stalked ⇒ **Brachioteuthidae**
   • neck multiple chambered and without dorsal hump; long tail with secondary fin (often missing); arm crown stalked ⇒ **Chiroteuthidae**

8. • body elongated with long pointed tail; tentacles greatly enlarged/ streched; funnel locking-cartilage oval with small projection (tragus) ⇒ **Mastigoteuthidae**
   • other features than above; if body elongated and/ or tentacles enlarged the funnel locking-cartilage is permanently fused with the mantle ⇒ **9.**

9. • funnel locking cartilage and mantle permanently fused ⇒ **10.**
   • funnel locking cartilage and mantle not fused; mantle always free in nuchal region ⇒ **11.**

10. • mantle free in nuchal region ⇒ **Grimalditeuthidae**
    • mantle fused in nuchal region ⇒ **Cranchiidae**

11. • transverse T-shape funnel locking-cartilage; mantle densely covered with small chromatophores, even visible in preserved specimens ⇒ **Thysanoteuthidae**
• funnel locking-cartilage of other shape (straight, round or subtriangular) ⇒ **12.**

12. • fins with muscular ribs; tentacular club in small larvae spatulate, nearly round and out-turned; funnel locking-cartilage straight ⇒ **Chtenopterygidae**
• fins without ribs ⇒ **13.**

13. • mantle sharply pointed posteriorly; funnel locking-cartilage straight; head often withdrawn into mantle up to eye lenses; in young stages arm pair IV rudimentary ⇒ **Onychoteuthidae**
• features other than above ⇒ **14.**

14. • no photophores on the skin (external) nor on intestine ⇒ **15.**
• photophores on mantle, arms, head and/ or eyes and intestine ⇒ **16.**

15. • fins nearly oval in outline, grow up to 100% ML (*Discoteuthis*); fin musculature separated in the midline by the gladius; funnel locking-cartilage subtriangular; 4 rows and more than 15 suckers on club ⇒ **Cycloteuthidae**
• fins very broad in specimens >3mm ML; fin musculature not separated by gladius; funnel locking-cartilage straight; tentacles present only in early juveniles (<12 suckers on club), generally lost in later stages ⇒ **Octopoteuthidae**

16. • ventral side of mantle, head and arms covered with usually big photophores (late paralarval stages), which are directed anteriorly; left eye is considerably larger than the right one; integumental light organs around margin of eye lid ⇒ **Histioteuthidae**
• other structure and pattern of photophores; eyes of equal size ⇒ **17.**

17. • light organs at base of arms; entire animal of dark reddish-brown colour ⇒ **Bathyteuthidae**
• no light organs at base of arms but on mantle, arms and/ or eyes and intestine ⇒ "Enoploteuthid" group of families and Lycoteuthidae ⇒ **18.**

18. • no light organs on eyes ⇒ **Ancistrocheiridae**
• light organs on eyes, well defined even in youngest stages ⇒ **19.**

19. • no light organs on viscera ⇒ **Enoploteuthidae**
• light organs present on viscera but absent from surface of mantle, funnel, head and arms (not considering tentacles) ⇒ **20.**

20. • ventral surface of eyes with 3 to 5 light organs; central one develops first, is always enlarged and of different colour and surface texture ⇒ **Lycoteuthidae**
• ventral surface of eye with unequal sized light organs (12-15 light organs in older stages); young with very small tentacular clubs, that generally curl dorsally at the tip and are covered with small suckers ⇒ **Pyroteuthidae**

Order Octopoda

21. • mantle gelatinous; web between all arms ⇒ **22.**
• mantle muscular ⇒ **24.**

22. • eyes large and hemispherical; mantle to arm ratio 1:1; suckers uniserial within the deep web and biserial beyond ⇒ **Alloposidae**
• eyes smaller and of different shape than above; suckers on arms uniserial ⇒ **23.**

23. • eyes elliptical; web not very deep in youngest stages; mantle to arm ratio approximately 3:1; ovoid digestive gland; gelatinous mantle often appears “hairy” ⇒ **Bolitaenidae**
• eyes rectangular; mantle to arm ratio approximately 2:1; digestive gland very long and slender, pointed at the posterior end ⇒ **Vitreledonellidae**

24. • arms of equal length or only slightly enlarged ⇒ **25.**
• arm pairs I, or I and IV greatly enlarged ⇒ **26.**

25. • specialised funnel locking cartilage present (groove with a small knob below), conspicuous even in hatchlings; in young females arm pair I slightly enlarged; dwarfed males with hectocotylus enveloped in a small sac ⇒ **Argonautidae**
• no specialised funnel locking cartilage (roughly a small “bump”), mantle locking apparatus absent; arms not modified in young males; arms equal in length and generally short and compact ⇒ **Octopodidae**

26. • arm pairs I and IV greatly enlarged, in youngest stages not enclosed in brachial membrane; funnel elongated ⇒ **Ocythoidae**
• arm pair I greatly enlarged and robust, arm pair III reduced; in hatchlings head and arms enveloped by brachial membrane ⇒ **Tremoctopodidae**

Description and illustration of major species

Order Spirulida
Family Spirulidae

Only one species, *Spirula spirula*, is recognised within this family. This cephalopod is small (up to 4.5cm ML) and distributed worldwide in tropical and subtropical waters. There are indications that *S. spirula* is associated with continental slopes and oceanic islands. The species is characterised by an internal shell, that is calcareous, coiled and chambered. The shell lies within the posterior half of the mantle and is already visible at 1.5mm ML (no metamorphosis during development). Fins are round and small. The arms are short and connected by a deep web. In hatchlings the head may be retracted entirely into the mantle. During further development the huge buccal mass becomes visible and fins are only recognisable as small rudiments.

Order Sepiolida
Family Sepiolidae

The family is characterised by a short, broad mantle with large, round fins. The funnel locking-cartilage is simple and straight. The shell is reduced to a chitinous gladius or completely absent. Adults are relatively small in body size. Only one species (*Heteroteuthis dispar*) was identified at the seamounts of the subtropical eastern North Atlantic.

H. dispar (Subfamily Heteroteuthinae, Fig. 2) is characterised by a deep web, joining the first three pairs of arms. The ventral arms are not connected. Fins are large and extend to the posterior end of the mantle. The dorsal edge of the mantle is free (not fused like in some related species). The light organ inside the mantle cavity (partly covered by the funnel) is rounded. The maximum mantle length of *H. dispar* is around 2.5cm (Bello, 1995).

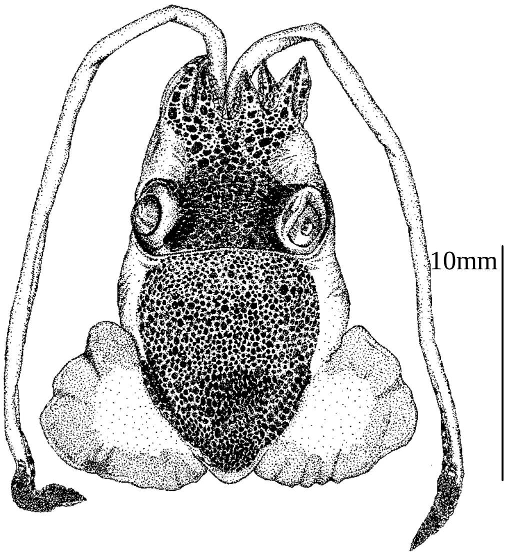


Fig. 2: *Heteroteuthis dispar*. Dorsal view of juvenile (ML=11mm).

Order Teuthida, Suborder Oegopsina

Enoploteuthid group of families:

The Enoploteuthidae, Ancistrocheiridae and Pyroteuthidae have traditionally been classified as subfamilies within the family Enoploteuthidae (Pfeffer, 1912). According to Clarke (1988) and Young & Harman (1998) they are now treated as separate families and are currently comprised to the enoploteuthid group of families. Because of some similarities in the identification characteristics the Lycoteuthidae are discussed together with the enoploteuthid group:

The representatives of all four families are small to medium sized squids. They are widely abundant but of minor importance to fisheries. Common to all is their mesopelagic lifestyle and the extended diurnal vertical migrations performed by the adults. In older stages hooks can be found on arms (two rows) and tentacular clubs (one or two rows; apart from the genus *Pterygioteuthis*).

Families of the group are characterised by highly complex photophores and can be distinguished by their arrangement and numbers on various body parts (Tab. 2).

Tab. 2: Key to families of the enoploteuthid group and the Lycoteuthidae based on photophore patterns.

Photophores	Enoploteuthidae	Ancistrocheiridae	Pyroteuthidae	Lycoteuthidae
Mantle, head, arms	+ (in rows)	+	–	(arms & tentacles partly with integumentary ph.)
Tentacles	–	+	+ (embedded in stalk)	
Eyes	+	–	+	+
Viscera	–	–	+	+

Family Enoploteuthidae:

The Enoploteuthidae are among the most abundant small squids of the open ocean. Three of the four genera (*Enoploteuthis*, *Abralia*, *Abraliopsis*) are distributed in the Atlantic Ocean and are especially numerous in the subtropical region (Nesis, 1987). Several small photophores on the ventral side of the mantle and head are mostly arranged in rows. Young stages are difficult to separate, because the characteristic photophore patterns do not develop before 4-5mm mantle length.

Table 3 comprises characteristics to distinguish between the two genera *Abralia* and *Abraliopsis*.

Tab. 3: Key to the early life stages of the genera *Abraliopsis* and *Abralia* (partly following Young et al., 1992).

	Abraliopsis sp.	*Abralia* sp.
Arms, tentacles	Extremely long, sometimes as long as or longer than mantle length	Very long, never longer as mantle length
Arm formula	III > II > I > Iς (3mm ML) Iς > III > II > I (juveniles)	II > I > III > Iς
Iς arm pair	3 terminal light organs (~black), first visible as swelling	No light organs on armtips
Photophores on eyes	5 photophores; 1>5>3 develop first; anlagen 2 and 4 visible juveniles: photophores of similar structure. Size: 1 = 5 > 2 = 3 = 4	5 photophores; 1>5>3 develop first; no anlagen visible juveniles: posterior photophore different from others

***Abralia* cf. *veranyi*:**

Abralia veranyi is distributed in the tropical and subtropical eastern and western North Atlantic Ocean and the Mediterranean Sea. It is associated with the continental shelf and does not occur in the open ocean. Nevertheless a few specimens were recognised around seamounts of the Atlantis-Meteor Chain. In addition to the features listed in Table 3 late juveniles and adults of the genus *Abralia* are characterised by one series of hooks and two series of suckers on the manus of the club.

Abraliopsis pfefferi (Fig. 3)*:*

The distribution of *Abraliopsis pfefferi* is limited to the tropical and subtropical Atlantic Ocean as also to the adjacent seas of the Gulf of Mexico and the Mediterranean (Nesis, 1987). Along the seamounts of the Mid-Atlantic Ridge the genus *Abraliopsis* was the most abundant enoploteuthid squid and dominated, aside from *Onychoteuthis banksii*, the cephalopod fauna.

The genus *Abraliopsis* is the easiest enoploteuthid to identify. It is characterised by three conspicuous dark photophores (green in living specimens) on the tip of the 4th armpair. Arms and tentacles are extremely long and mostly exceed mantle length. In juveniles and adults five round photophores of similar structure develop on the ventral side of each eye. They form a typical row with the posterior and anterior photophore enlarged. The manus of the club is armed with two series of hooks.

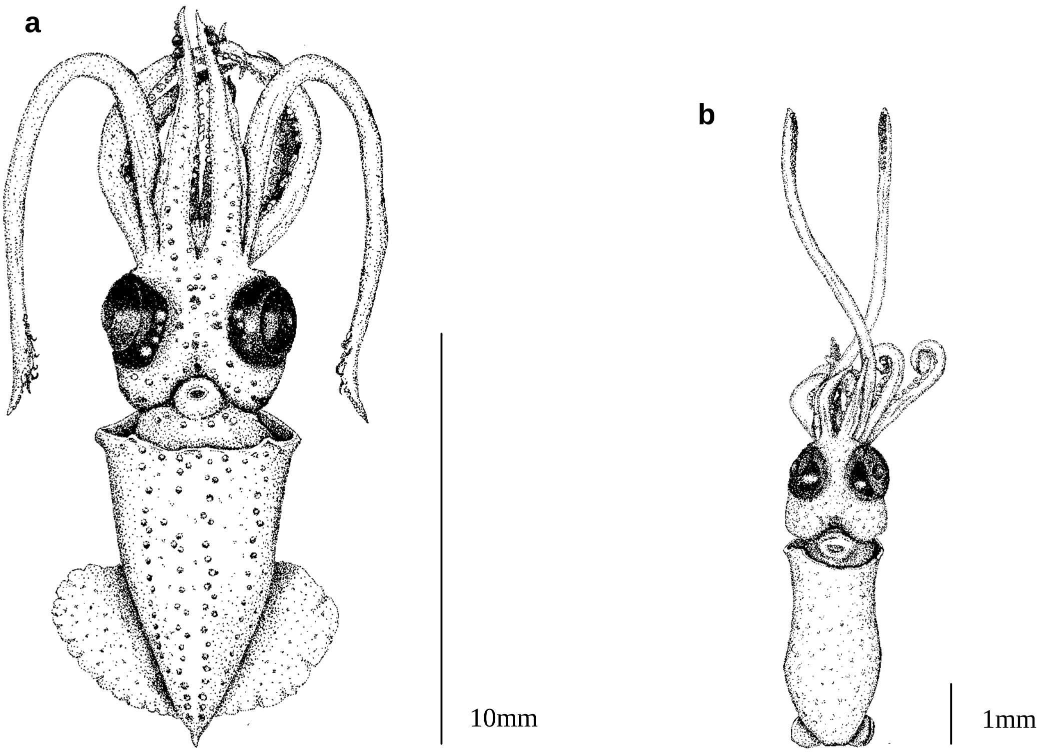


Fig. 3: *Abraliopsis pfefferi.* Ventral view of (a) late juvenile (ML=8.5mm) and (b) early juvenile (ML=3.6mm).

Enoploteuthis **sp.** (Fig. 4)*:*

Similar to the other two enoploteuthid species *Enoploteuthis* or the species *E. leptura leptura*, respectively, is distributed in the tropical Atlantic Ocean, from Bermuda to Madeira and Brazil to southwestern Africa (Nesis, 1987). Adults display a similar photophore pattern on the eyes as *Abraliopsis*, with the posterior and anterior one enlarged and the remaining three photophores small. In Hawaiian species of this genera the development of the ocular photophores begins with the two enlarged photophores. Apart from the other genera, *Enoploteuthis* is characterised by a tail-like projection beyond the posterior end of the fins. It can be detected at a mantle length of 10-15mm (Young et al., 1992). The manus of the tentacular club is armed with two series of hooks.

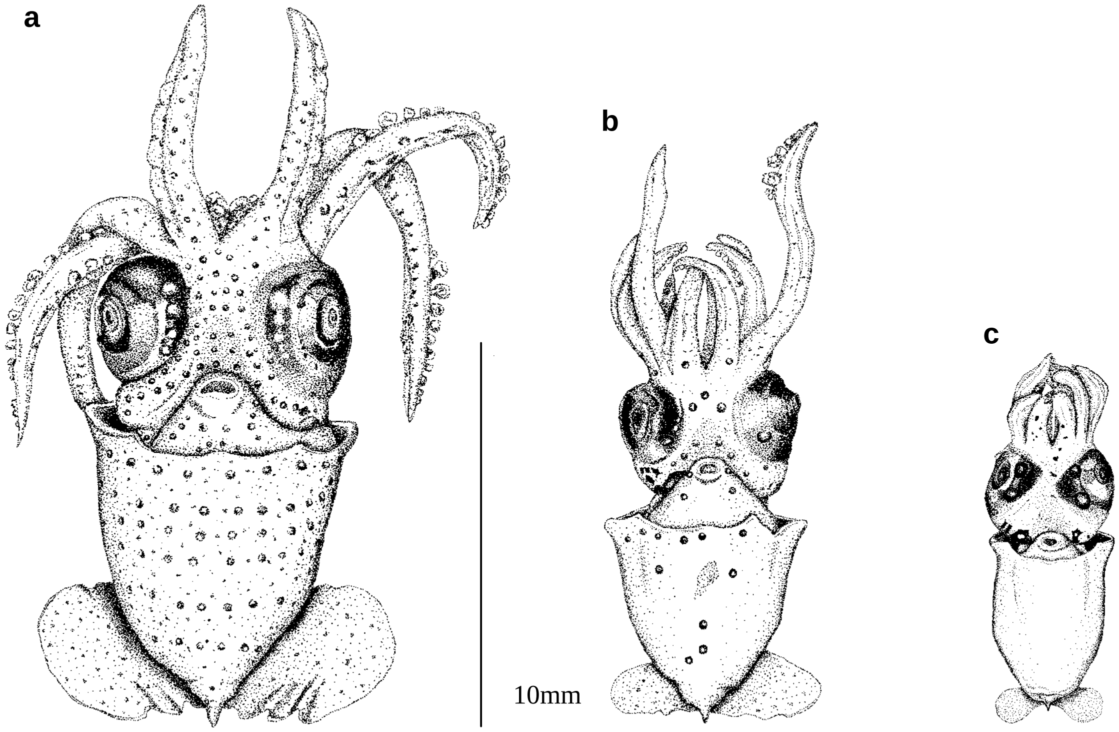


Fig. 4: *Enoploteuthis* sp. Ventral view of (a) late juvenile (ML=9.2mm), and early juveniles (b) ML=5.5mm), (c) ML=4.3mm.

Family Ancistrocheiridae:

Only one species, *Ancistrocheirus lesueurii*, is currently recognised in this family. It is circumglobally distributed but mainly restricted to tropical and subtropical waters. Differences in the morphology of early life stages from various oceans suggest, that more than one species exist (Young et al., 1992).

A. lesueurii can be easily distinguished from all other forms of the enoploteuthid group. Eyes are small, separated from the arm bases and are widely divergent. The head tissue is gelatinous. Tentacles are covered with photophores (not in youngest stages) and the tentacular club bears a few but very large suckers (Fig. 5).

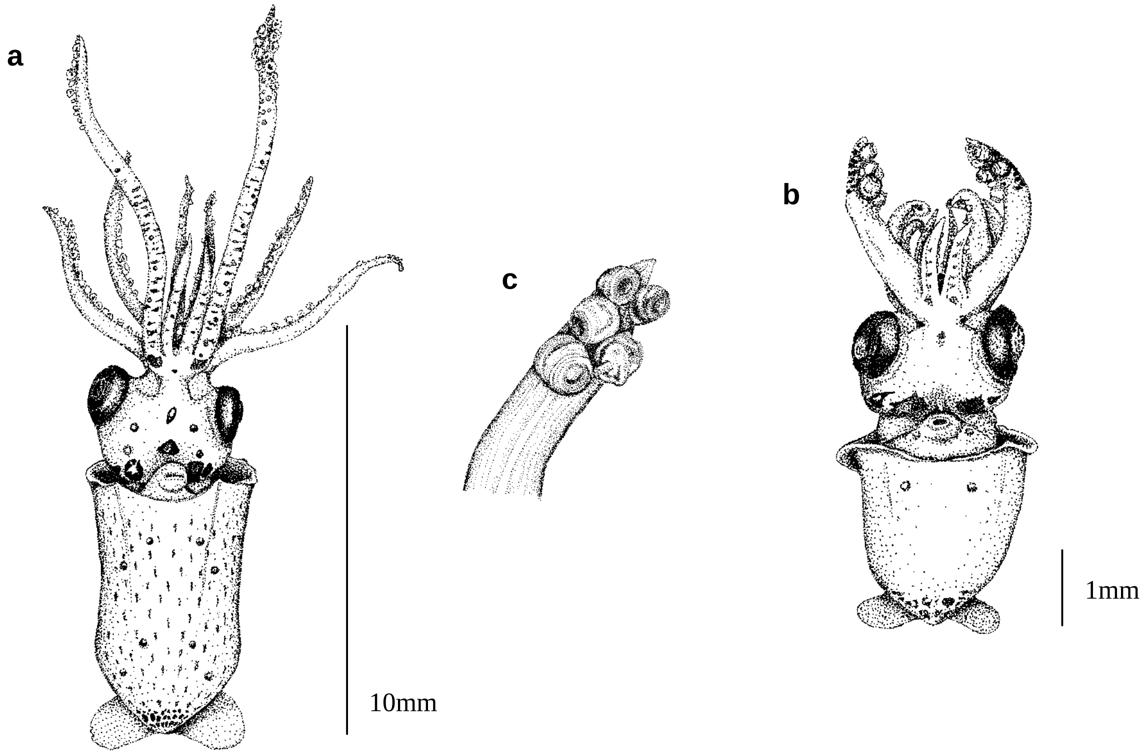


Fig. 5: *Ancistrocheirus lesueurii*. Ventral view of (a) juvenile (ML=6.9mm), (b) early juvenile (ML=2.8mm) and (c) tentacular club of juvenile (ML=1.9mm).

Family Pyroteuthidae:

Two genera (*Pyroteuthis, Pterygioteuthis*) are comprised in this family. Pyroteuthids are cosmopolitan mesopelagic species and are mainly found in tropical to subtropical waters. Their paralarvae are among the most abundant cephalopods in the plankton.

In addition to the photophore patterns, described in Table 4, young specimens of this family are characterised by very small tentacular clubs that generally curl at the tip and are covered with very small suckers. The tentacular stalk usually has a ventrally directed bend. In specimens larger than approximately 5mm ML the posterior end of the mantle is sharply pointed, the terminal conus of the gladius becomes visible (equivalent to the adults) and the fins show their typical appearance (rounded with two free lobes).

The two genera can be distinguished following Table 4.

Tab. 4: Key to the genera *Pyroteuthis* and *Pterygioteuthis*.

	Pyroteuthis	*Pterygioteuthis*
Gill photophores (<4-5mm ML)	absent	Present (at 1.5mm ML)
Gill photophores (>5mm ML)	Smaller than anal photophores	As large or larger than anal photophores
tentacle (freshly caught specimens)	Pink patch at the base of each tentacle and at the carpus	No pink patches

Early life stages of these genera can be hardly identified to species. Nevertheless, additional catches of larger Pyroteuthidae at the same locations allowed to identify the species *Pyroteuthis margaritifera* and *Pterygioteuthis giardi giardi* (Fig. 6) in the plankton catches of the subtropical eastern North Atlantic.

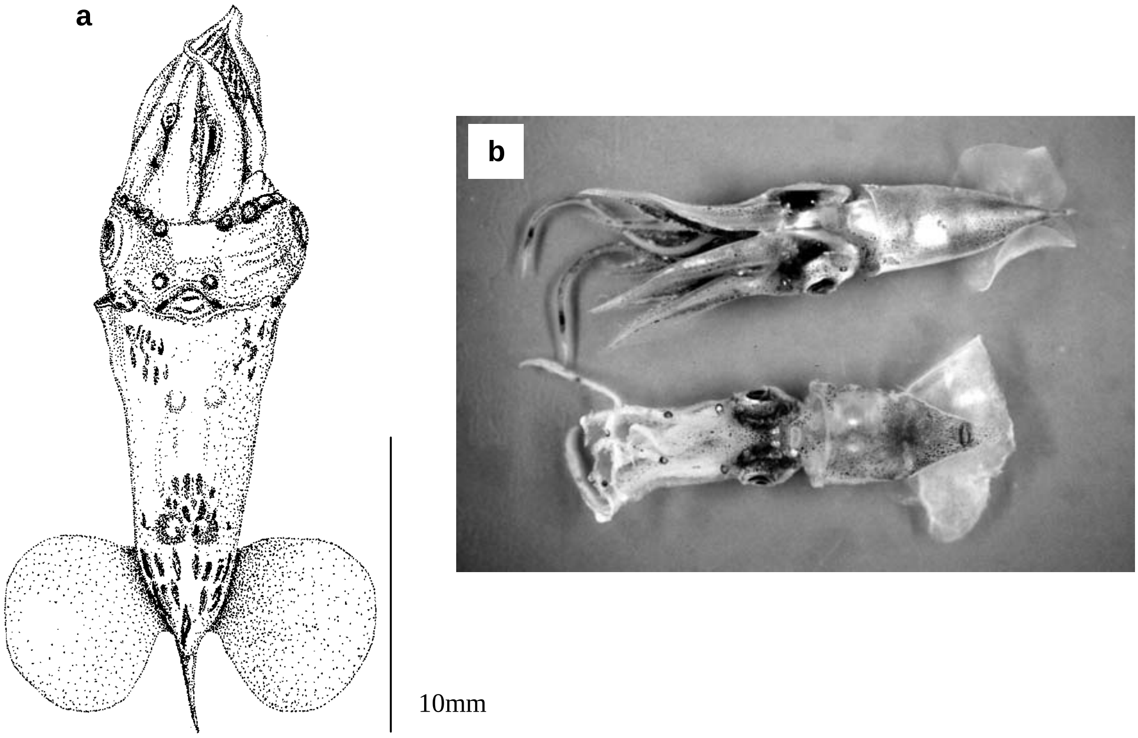


Fig. 6: Pyroteuthidae. (a) *Pterygioteuthis giardi giardi*; ventral view of adult (ML=14mm); (b) ventral view of adult *Pyroteuthis margaritifera* (top) and *Lampadioteuthis megalaia* (bottom).

Family Lycoteuthidae

Young Lycoteuthidae are relatively easy to separate from the enoploteuthid group by the early development of one large and exceptionally coloured photophore on the centre of each eyeball (apart from *Lampadioteuthis megalaia*). Two species of two subfamilies occurred in the eastern subtropical North Atlantic Ocean. They are identifiable by the arrangement and the colour of the photophores around their eyes:

- Subfamily Lampadioteuthinae: This monotypic subfamily (*Lampadioteuthis megaleia*; Fig. 6) is known from the subtropical waters of the western South Pacific and the North Atlantic. *L. megaleia* is characterised by four photophores on the eyeball: Three are in a line, the fourth is positioned posterior to the other photophores and next to the eye lens.
- Subfamily Lycoteuthinae: Only one species was recognised in the subtropical East Atlantic. *Selenoteuthis scintillans* (Fig. 7) is characterised by the early development of three photophores on the ventral periphery of each eye. The central photophore is markedly larger than the others and of a different structure and colour (even recognisable after preservation). On the posterior end of the mantle one large globular photophore is visible, that darkens in later developmental stages.

S. scintillans is a small-bodied squid (up to 4.5cm ML in adults), which is widely distributed in the tropical and subtropical Atlantic, with lower abundances in the eastern part.

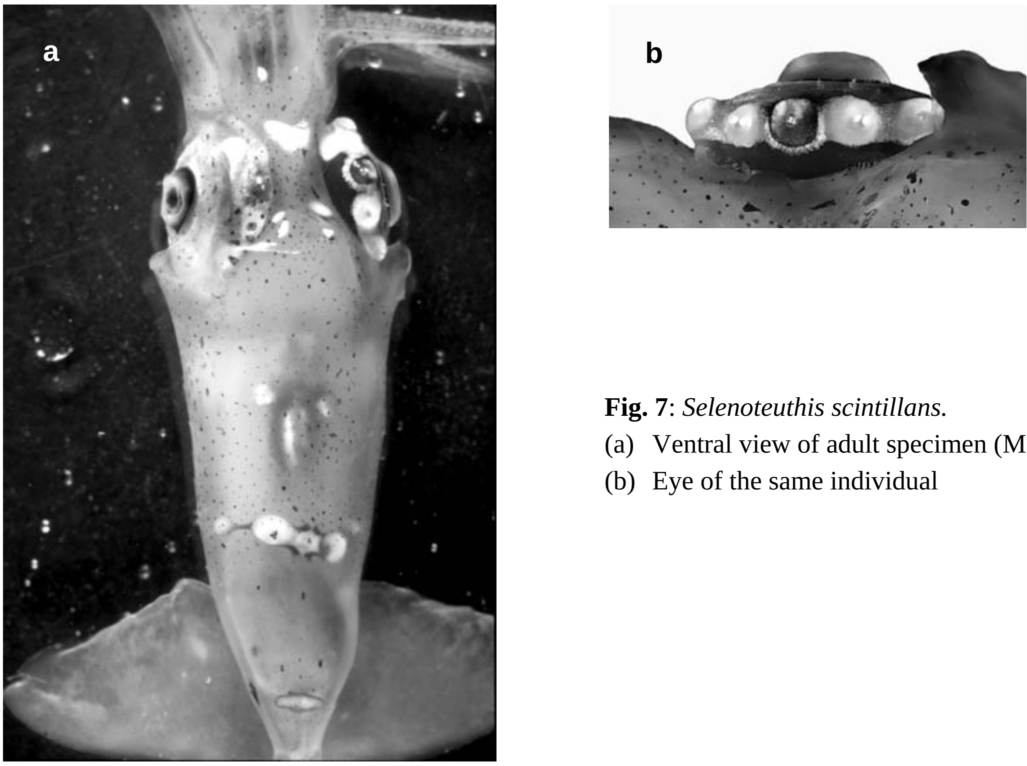


Fig. 7: *Selenoteuthis scintillans.*
(a) Ventral view of adult specimen (ML~30mm),
(b) Eye of the same individual

Family Histioteuthidae

Histioteuthidae are medium to large-bodied squids, that occur worldwide apart from the Arctic and Antarctic. They are meso- to bathypelagic and some species apparently show association with continental slopes, islands, and seamounts. The family is currently under revision (N. Voss, pers. comm.). 13 species in a single genus are recognised so far. Early life stages are problematic to distinguish on the species level. Generally juveniles may be identifiable at 10mm ML or above. The advanced literature should be consulted for detailed species characteristics (e.g. Voss, 1969; Voss et al., 1998). Nevertheless, the family can be easily separated from other oegopsid families at nearly all developmental stages.

Typical family characteristics are (see also Fig. 8):
Conical and short mantle; mantle tissue usually thick and firm; skin colour of juvenile to adult specimens brownish red; head large; in older specimens eyes large and asymmetrically developed with the left eye larger than the right one; numerous compound photophores, anteriorly directed, on mantle (often in diagonal rows), head and arms.

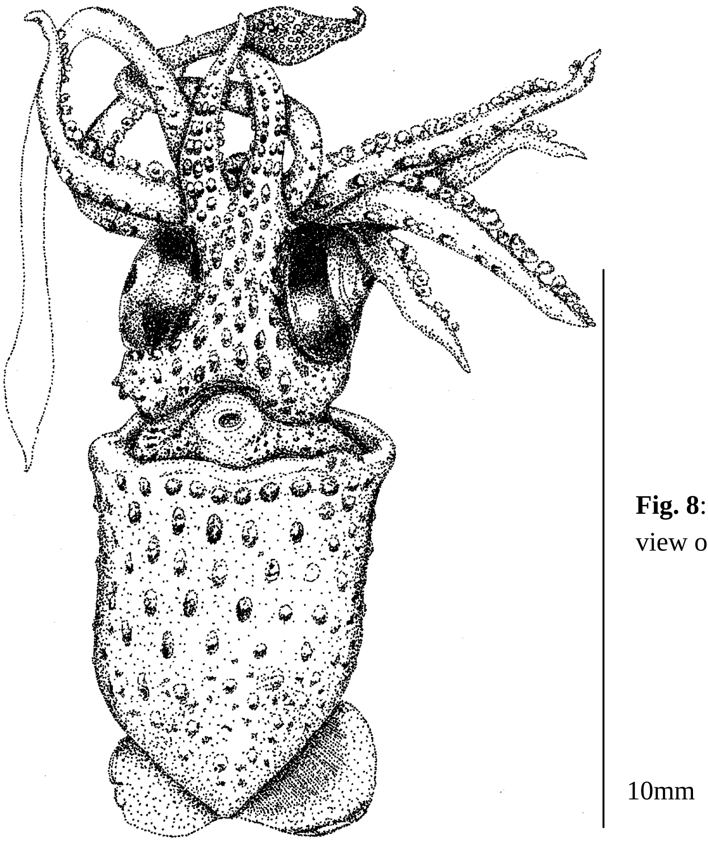


Fig. 8: *Histioteuthis celetaria celetaria*. Ventral view of juvenile specimen (ML=7.1mm).

Family Ommastrephidae

The Ommastrephidae or “Flying squids” are an oceanic and neritic family representing powerful swimmers. Six of the ten genera currently support a fishery and the family is supposed to be the most important commercial oceanic cephalopod group. The fertilised eggs are released and encapsulated in large gelatinous egg masses, which are probably pelagic. The hatchling is characterised by a distinctive paralarval form, the “rhynchoteuthion”. In this developmental stage the tentacles are fused into a trunk-like structure, the proboscis. As the squid grows, the proboscis begins to divide with a splitting groove forming at its base. The separation into the two tentacles is completed at a mantle length of 6-10mm, depending on species (Tab. 5).

Presumably four genera/ species of this family occur in the oceanic regions of the subtropical North Atlantic and around the investigated seamounts. The most common type in the samples was the rhynchoteuthion type A’ (c.f. *Ommastrephes bartramii*, Fig. 10). Specimens of type B’ represented three different morphological characters possibly assigned to *Hyaloteuthis pelagica* (Fig. 9), *Sthenoteuthis pteropus* and *Ornithoteuthis antillarum*. Paralarvae of type B’ were only found sporadically. Identification to species level is still tentative (Vecchione et al., 2001) and table 5 is only a first approach to distinguish between the four paralarval forms.

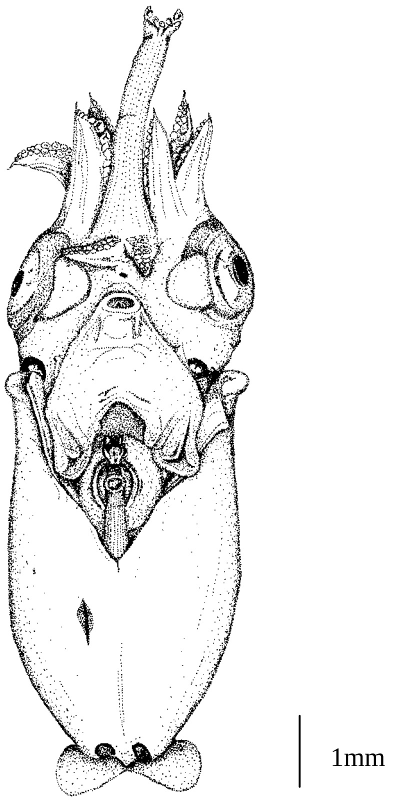


Fig. 9: *Hyaloteuthis pelagica*. Ventral view of rhynchoteuthion paralarva (ML=4.3mm); parts of mantle removed, to show the single round photophore centrally located on intestine.

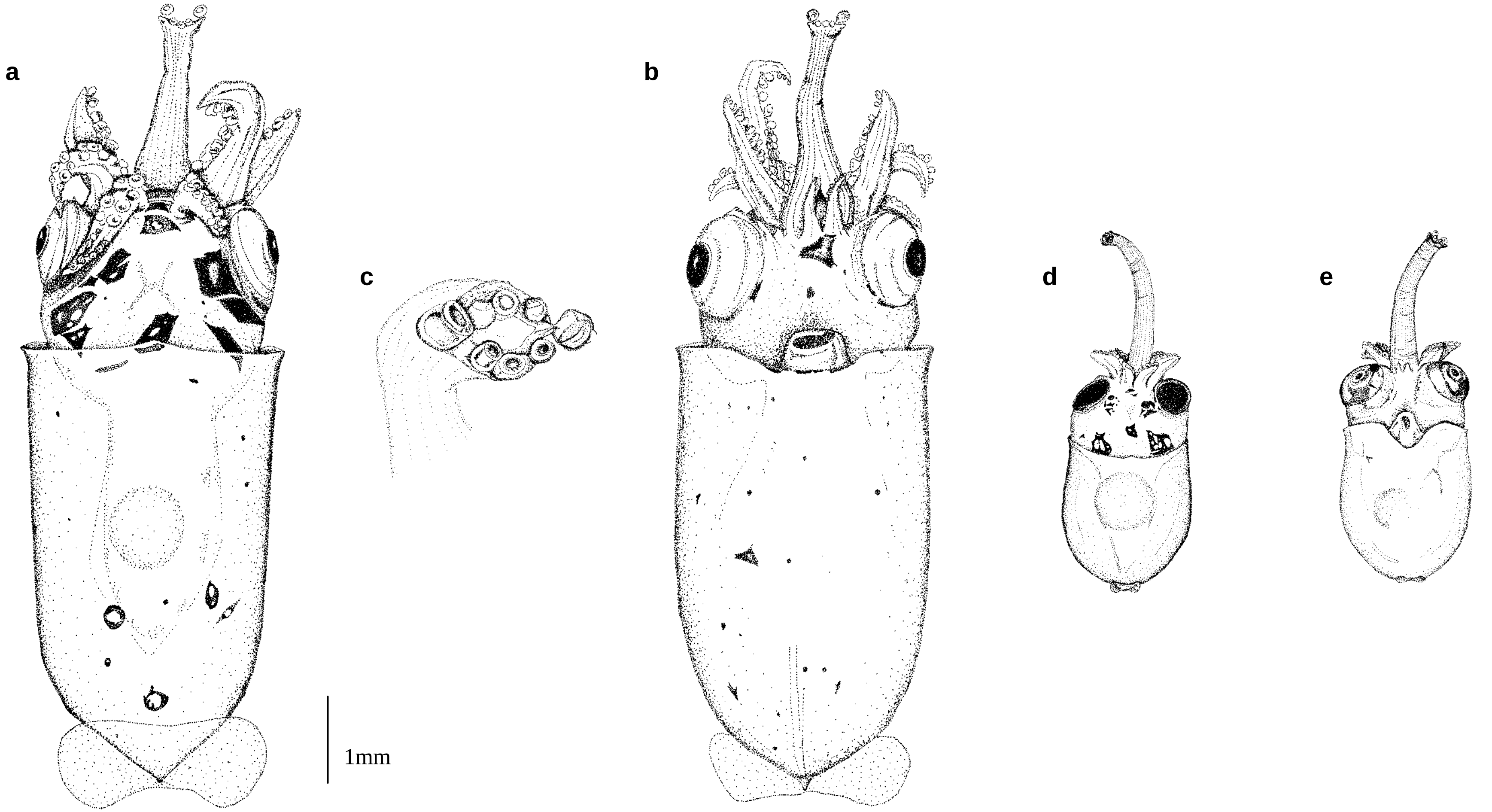


Fig. 10: Type A’ c.f. *Ommastrephes bartramii*. Dorsal (a) and ventral (b) view of rhychoteuthion paralava (ML=5.2mm), (c) end of proboscis of the same specimen; dorsal (d) and ventral (e) view of hatchling (ML=1.4mm).

Tab. 5: Summary of characters of early young stages of ommastrephids. Data are based upon own measurements and workshop studies as described in Wormuth et al. (1992).

	Type A'	**Type B'**		
	Ommastrephes bartramii	*Hyaloteuthis pelagica*	*Ornitoteuthis antillarum*	*Sthenoteuthis pteropus*
lateral suckers	enlarged approx. 200%	enlarged to >= 150%	enlarged up to 150%	slightly enlarged, sometimes invisible
Proboscis length *	approx. 100% ML	up to 80%	approx. 50%	up to 80 - 90%
Photophores on eyes	photogenic tissue	large, round photophore	round photogenic tissue	large round photophore
Photophores on intestine	absent	one large round photophore (ML >=1.5mm)	two photophores, posterior one larger than anterior (difficult to observe)	two photophores of similar size, development probably later than 3,0mm ML (difficult to observe)

* before beginning of the proboscis division

Family Onychoteuthidae

Two species, *Onychoteuthis banksii* and *Onykia carriboea*, occur in the eastern subtropical North Atlantic. Both are distributed worldwide.

Onykia carriboea (Fig. 11) is a small, broad-bodied squid, frequently found in surface collections from warm-water masses. The mantle is almost bullet-shaped and not as sharply pointed as in *Onychoteuthis* (see below). Photophores are absent. Mantle, head, tentacles, arms and funnel of paralarvae are densely covered with chromatophores (>3mm ML). Most striking are the characteristic dark chromatophores on the dorsal midline of the mantle, which increase in size from anterior to posterior and can be easily recognised also in preserved specimens. All cephalopods identified as *O. carriboea* so far have been immature. This suggests that the species may only represent an immature growth stage of another onychoteuthid species (Tsuchiya & Okutani, 1991; Kubodera et al., 1998).

Onychoteuthis banksii (Fig. 12) is probably a complex of several species (Young, 1972; Young & Harman, 1987). Specimens are muscular, fins are rhomboidal and the tail is pointed. Tentacular clubs of juveniles and adults bear 19 to 23 claw-like hooks in two rows. *Onychoteuthis* is considered to be a fast-growing squid. The paralarvae can be easily identified by their muscular body and their visible, sharply pointed gladius. One patch of photogenic tissue, a developing photophore, can be sometimes recognised on the ventral side of the eyes. In very young specimens hooks cannot be seen or are just partly developed. Two large round, bulbous light organs along the ventral midline on intestinal tract will develop in grown up specimens.

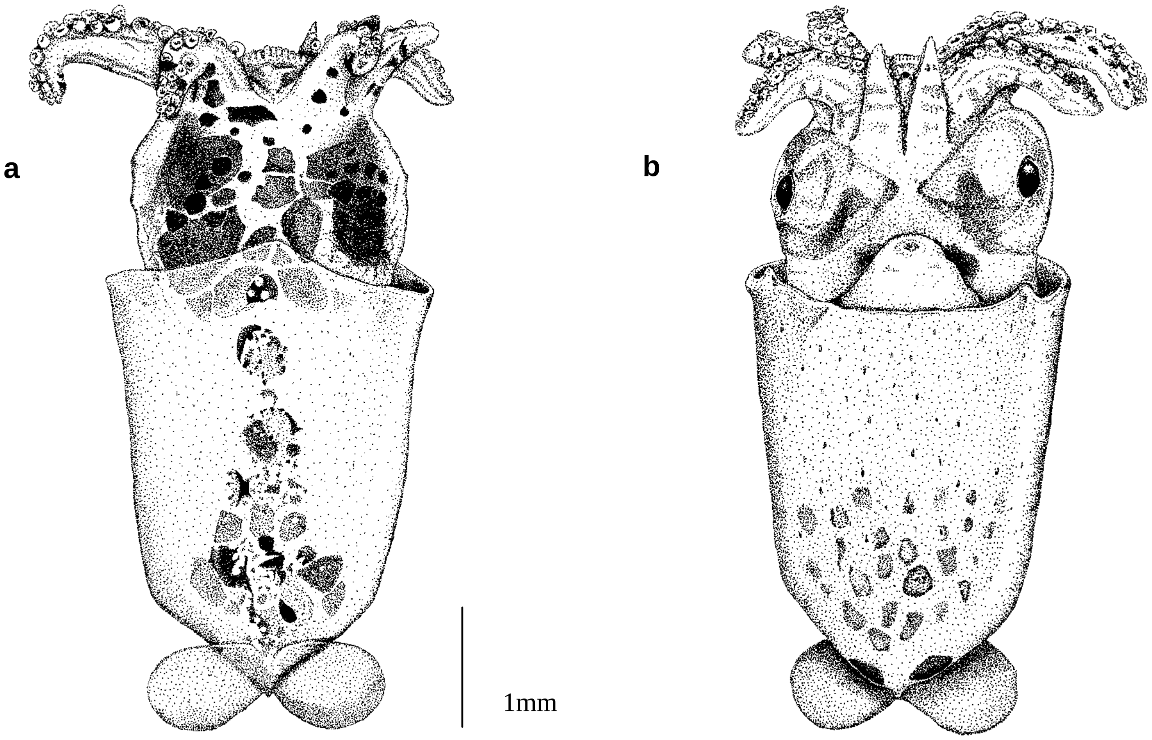


Fig. 11: *Onykia carriboea*. Dorsal (a) and ventral (b) view of early juvenile (ML=3.7mm).

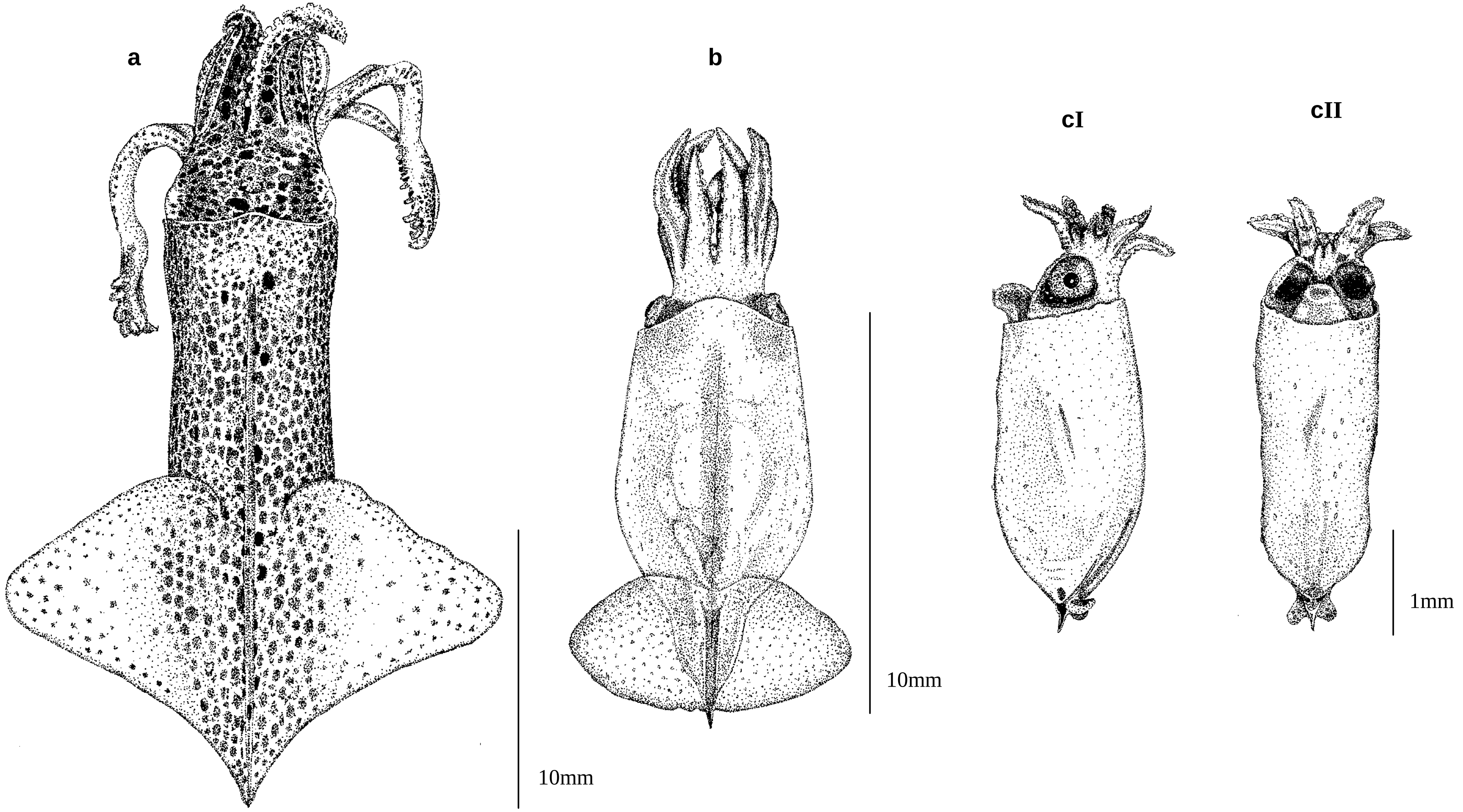


Fig. 12: *Onychoteuthis banksii* complex. (a) Dorsal view (ML=23mm); (b) dorsal view (ML=11.7mm); (cI) lateral and (cII) ventral view of early juvenile (ML=2.7mm).

Family Chtenopterygidae

The Chtenopterygidae are a monotypic family with the single species *Chtenopteryx sicula* (Fig. 13). The species is distributed worldwide and easily identifiable at all developmental stages. In young specimens fins are small and start to develop muscular ribs (transversely elongated outline). Tentacles are short and the club spatulate; club suckers form a distinct circular pad. The fin length increases with size and almost extends along the whole mantle in adults. Fins are “ribbed”: The muscular trabeculae are only joined by a membrane.

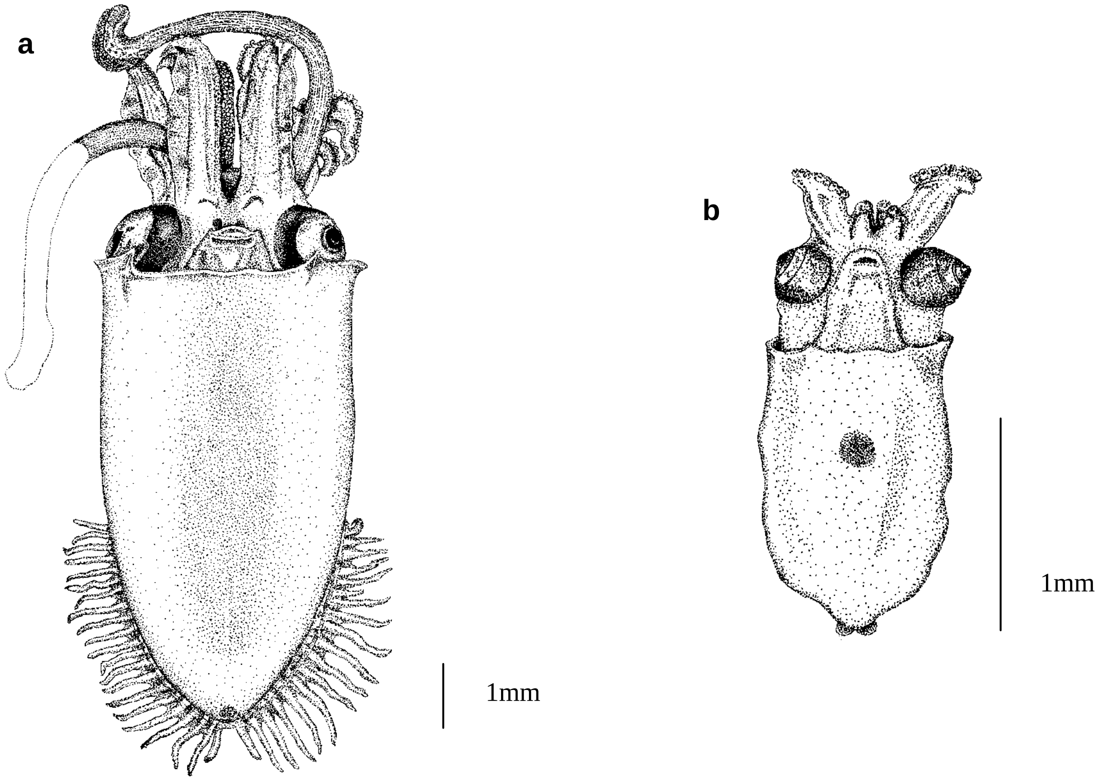


Fig. 13: *Chtenopteryx sicula*. Ventral view of (a) juvenile (ML=7.5mm) and (b) hatchling (ML=1.3mm).

Family Thysanoteuthidae

The family Thysanoteuthidae is presently considered to be monotypic. The only species *Thysanoteuthis rhombus* (Fig. 14) is distributed worldwide from warm to temperate seas. Young specimens are recognisable by their (90° rotated) T-shape funnel locking-cartilage and their dense concentration of chromatophores on mantle, head and arms. Eyes are comparably small and broadly separated. Fins are small and rounded but extend more and more to the length of the mantle in growing specimens. Adults are large nektonic, muscular squids with rhomboidal fins. The characteristic funnel locking-cartilage remains unchanged in adults.

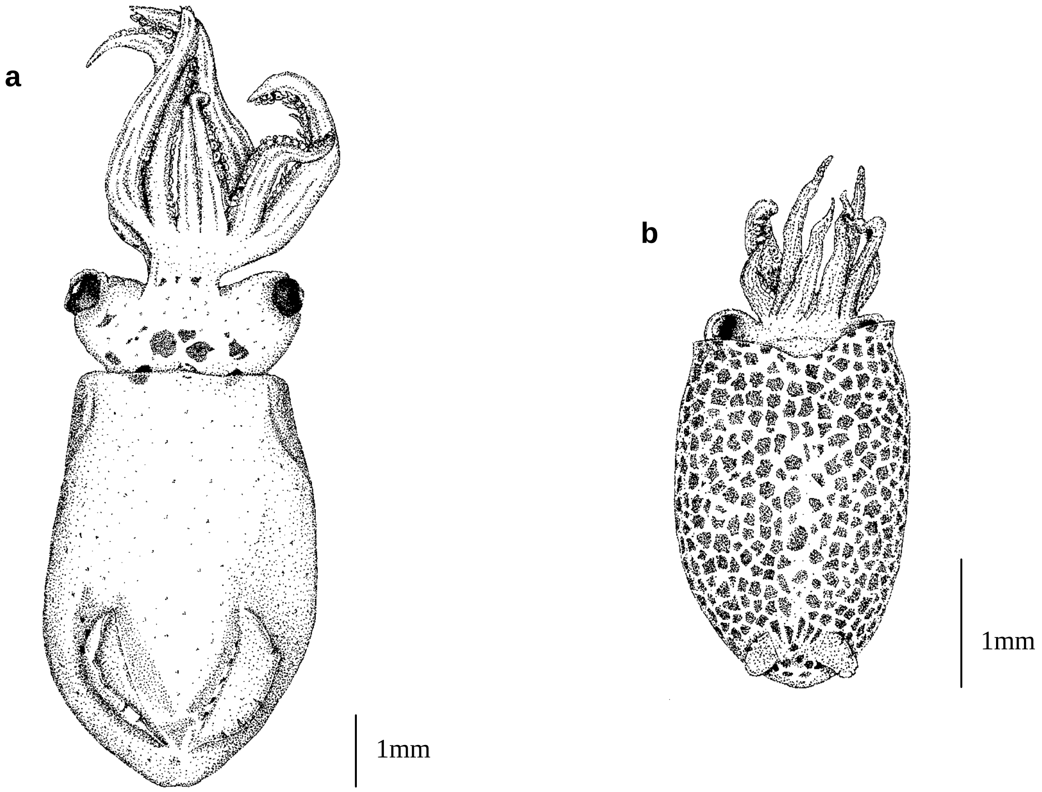


Fig. 14: *Thysanoteuthis rhombus.* Dorsal view of juveniles (a) ML=5.6mm, (b) ML=2.7mm.

Family Cycloteuthidae

Cycloteuthidae are distributed in the warm, subtropical to tropical waters of the oceans. Fins in adult specimens extend to more than 50% of mantle length. Early juveniles are characterised by a subtriangular funnel locking-cartilage and by eyes protruding on short stalks. Young Cycloteuthidae may be confused with young Octopoteuthidae because of similar fin size, tissue consistency and a few large suckers on the tentacular club. However, in Cycloteuthidae the fin musculature is separated by the gladius and suckers on the tentacular club exceed 12 in number.

Two genera are known within the family that can be distinguished by the characteristics given in Table 6.

Tab. 6: Key to the genera *Cycloteuthis* and *Discoteuthis.*

	Cycloteuthis sp.	*Discoteuthis* sp.
fins	short (≤25% ML at 8.5mm ML), never more than 75% ML	long (50% ML at 5mm ML), grow up to 100% ML
tail	present in larger specimens	no tail
suckers on manus	suckers of equal size	suckers unequal in size
arm formula	2 = 3 ≥ 4 > 1	2 ≥ 3 > 4 > 1

Discoteuthis discus was the only species recognised in the subtropical eastern North Atlantic. It can be distinguished from the related species *D. laciniosa* by the absence of papillae on the ventral side of the mantle margins.

Family Octopoteuthidae

The Octopoteuthidae are cosmopolitan medium to large squids with a gelatinous body and a conical mantle. Similar to the Cycloteuthidae fins are very large and almost extend along the entire length of the mantle, but the fin musculature is not separated by the gladius. The funnel locking-cartilage is straight and moderately broad. The head is characterised by gelatinous tissue. In adult specimens tentacles are absent, whereas early juveniles have tentacles with a short, spatulate club with eight, partly very large suckers. Some arm tips, if not missing, bear photophores. Two genera are known within the family that can be distinguished by the characteristics given in Table 7.

Tab. 7: Key to the genera *Octopoteuthis* and *Taningia.*

	Octopoteuthis sp.	*Taningia danae*
tentacular stalk	weak, gelatinous; tentacles lost at >12mm ML	robust; tentacles lost at >38mm ML
tentacular club	up to 8 large suckers	8 small suckers
arms	longer than tentacles, no hooks on arms before 2.5mm ML	short, robust; no hooks on arms before 5mm ML
photophores on ink sac	paired photophores by 15mm ML	large median photophore by 5mm ML

Although both genera are distributed worldwide the monotypic *Taningia danae* was the only species of this family that was identified in the samples of the subtropical eastern North Atlantic.

Family Bathyteuthidae

The Bathyteuthidae is a monogeneric family with currently three recognised species: *Bathyteuthis abyssicola*, *B. berryi*, *B. bacidifera*. Only one species (*B. abyssicola*) is distributed in the North Atlantic. It is a bathy- to mesopelagic squid and generally occurs between 700 to 2000m water depth. All known species are small-bodied (up to 7.5cm ML) and of a dark brown or maroon colour. Fins are small and paddle-shaped. At the base of each arm I-III a single photophore is imbedded into the tissue and all photophores are readily recognisable in early juveniles.

Family Brachioteuthidae

This family comprises small nektonic squids with a long neck and an elongated muscular mantle. Fins are paddle-shape and separated. Even young specimens show a distinctive swelling or hump on the dorsal surface of the head. Tentacles are large and relatively robust compared to the arms. There is no arm-crown stalk present. Brachioteuthidae are distributed circumglobally from the surface (young specimens) to the bathypelagial. The number of species in this family is not known and the family needs urgent revision.

Family Mastigoteuthidae

The Mastigoteuthidae are a monogeneric family. Two forms were recognised within the investigated area: *Mastigoteuthis* c.f. *atlantica* and *Idioteuthis* c.f. *hjorti* (formerly *Mastigopsis hjorti*).

Young specimens of this genus are identifiable by their elongated mantle, the long gladius, that is projecting posterior to the fins as a long pointed tail, the anteriorly protruding eyes and the thick (thicker than the arms) tentacular stalks. Tentacular clubs bear more than 4 rows of suckers. In juvenile to adult specimens the funnel locking-cartilage is recognisable as an oval structure with inward projecting knobs. Nevertheless, the posterior and the medial tragus are mostly poorly developed.

Family Chiroteuthidae

(incl. Grimalditeuthidae)

The family Chiroteuthidae is currently known to include four genera: *Chiroteuthis, Asperoteuthis, Grimalditeuthis* and *Planctoteuthis* (Young, 1991). Its most distinctive feature is the “doratopsis” paralarvae, which is defined by e.g. the following characteristics:

- elongated chambered neck
- a gladius that extends posteriorly beyond the fins
- vesiculate arms in advanced stage
- greatly elongated ventral arms in advanced stage

The genus ***Planctoteuthis*** is a synonym to ***Valbyteuthis***, which is now recognised as the early life stage of *Planctoteuthis*. *Chiroteuthis* (Fig. 15) and *Valbyteuthis* (*Planctoteuthis*) can be distinguished by the characteristics listed in Table 8.

The genus ***Grimalditeuthis*** was formerly put into the separate family Grimalditeuthidae and is treated like this in the identification key. Early life stages from this genus are not known so far, so that the doratopsis characteristics do not meet for subadult *Grimalditeuthis*. At this stage the tail is maintained and the gladius still extends well posterior to the fins. The funnel-mantle locking-cartilages fuse, similar to the Cranchiidae. Another distinguishing feature is the vesiculate region surrounding the posterior end of the mantle. The only species described so far is *Grimalditeuthis bonplandi*.

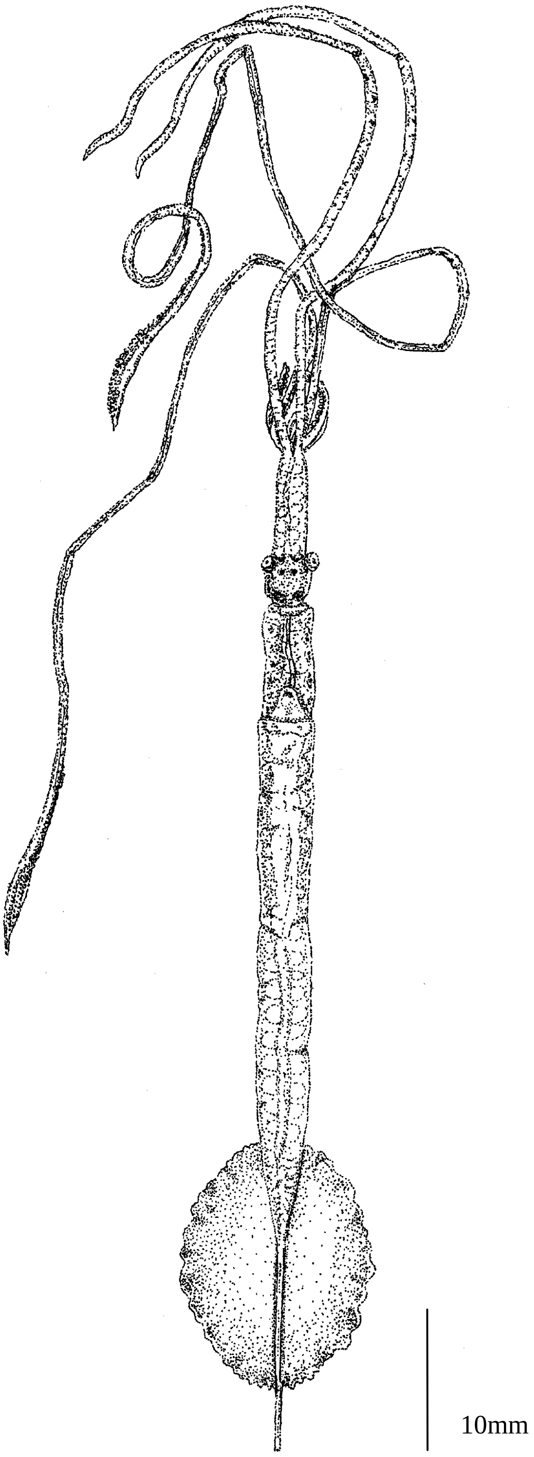


Fig. 15: *Chiroteuthis* sp. Ventral view, larval features still retained; (ML=56mm).

Tab. 8: Key to genera *Chiroteuthis* and *Valbteuthis*.

	Chiroteuthis sp.	*Valbyteuthis* sp.
Mantle	Long, slender, spindle shape	Relatively broad, bead-like shape
Arm-crown stalk	Short relative to neck length	As long or longer than neck
Tentacular stalkes	Suckers on oral surface (rarely naked)	naked

Family Cranchiidae

Cranchiids are distributed worldwide, from the Subarctic to the Antarctic. All species of this family exhibit an ontogenetic descent, as maturation occurs in deep waters down to 2000m water depth. Specimens are characterised by a thin walled mantle, often semigelatinous, and the permanently fusion of the mantle with the funnel locking-cartilage as well as with the head in the nuchal region. The family is currently under revision by N.Voss. Two subfamilies, 13 genera and more than 60 species are recognised so far.

Most of the cranchiid species display a special paralarval stage, that is characterised by stalked eyes and a short to long arm-crow stalk. Identification of early juveniles may be problematic and for details the relevant literature has to be consulted (Voss, 1980; Voss et al., 1992). An overview about an assortment of genera and species, occurring in the subtropical North Atlantic, and their respective characteristics is given in Table 9.

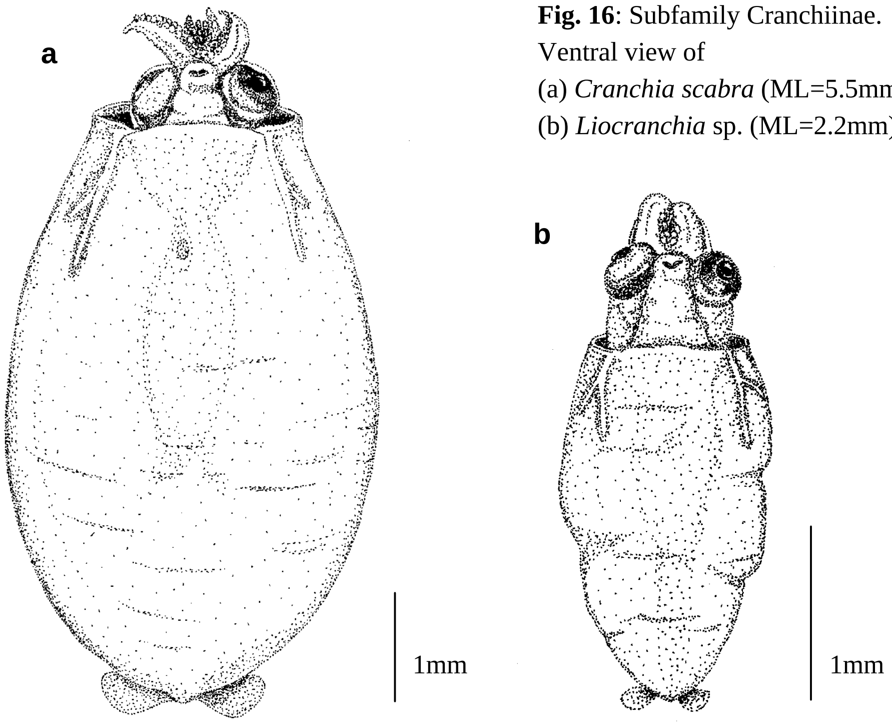
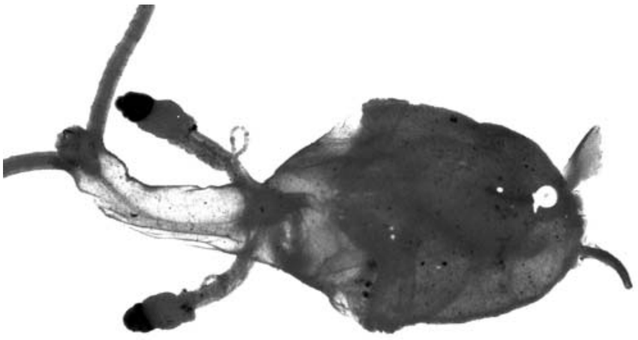


Fig. 16: Subfamily Cranchiinae.
Ventral view of
(a) *Cranchia scabra* (ML=5.5mm),
(b) *Liocranchia* sp. (ML=2.2mm).

Fig. 17: Subfamily Taoninae.
Bathothauma lyromma.
Early juvenile (ML=6.9mm).



Tab. 9: Key to the genera of the family Cranchiidae found in the subtropical eastern North Atlantic.

	mantle	gladius/ lanceola	fins	cartilaginous strips (on ventral surface of mantle)	arm crown stalk	eyes	other features
Sub-fam. Cranchiinae:							
Cranchia scabra (Fig. 16a)	stocky, often near-round	–	small, separated, paddle-shaped fins; unite dorsally with growth	inverted V-shape, non-tubercular (apparent not before 10-15mm ML)	no stalk	sessile, but protruding	scattered cross-shaped tubercles on mantle, few in early juveniles
Liocranchia (Fig. 16b)	stocky, spindle shaped	–	small, separated, paddle-shaped fins; fuse dorsally with growth	inverted V-shape, tubercular (extends from each funnel-mantle fusion)	no stalk	sessile, but protruding	arms very short
Leachia	moderately stout, spindle-shaped, but elongates with growth	gladial spine, projects between fins	transversely elliptical	single tubercular strip (extends from each funnel-mantel fusion)	long stalk	stalked	details of tubercu-lar strips important for species identification
Sub-fam. Taoninae:							
Helicocranchia (Fig. 18-20)	elongated, cylindrical, often with mucous outer layer	gladius projects dorsally free of mantle	small, paddle-shaped, insert on posterior tip of gladius	–	short stalk	oval, with pronounced ventral rostrum on short stalkes	very large funnel
Bathothauma (Fig. 17)	elongated, sac-shaped, rounded posteriorly	gladius expanded at right angle to mantle	small, paddle-shaped, widely set apart (on gladius)	–	long stalk	oval, on long stalkes, with ventral rostrum	tentacles short and robust in early juveniles
Liguriella	firm, spindle shaped	blunt-pointed, moderately broad, diamond-shaped lanceola	paddle-shaped, become oval with growth	–	medium to long stalk	oval, on long stalkes, with distinct short ventral rostrum	tentacles short and firm in early juveniles but elongate with growth
Taonius	elongated, narrow, cone-shaped	very elongated, narrow, diamond-shaped lanceola	short, lanceolate, but are extending along the lanceola with growth	–	moderately long stalk	oval, on very long stalks	specimens appear "stretched"
Megalocranchia	stocky, spindle-shaped, often with mucous outer layer	moderately narrow, diamond-shaped lanceola	small, become rounded with growth and extend to the mantle margins	–	long stalk	oval, on long stalkes, with short ventral rostrum	compound photo-phore on ventral surface of digestive gland (~25mm ML)

One of the most abundant cranchiids in the oceanic parts of the North Atlantic is the genus ***Helicocranchia***. It is probably composed of about 14 species (N.Voss, pers. comm.). In the subtropical eastern North Atlantic two species were identified, that can be distinguished by the following characteristics:

Tab. 10: Key to the species *Helicocranchia pfefferi* and *Helicocrancia papillata.*

	Helicocranchia pfefferi	*Helicocranchia papillata*
posterior end of gladius	long, narrow rostrum (Fig. 18, Ia, b)	short, broad based rostrum (Fig. 18, IIa, b)
fins (interspecies comparison)	larger	smaller
funnel organ	Ventral pads: L-shaped (Fig. 18, Ic)	Ventral pads: Curved club-shaped (Fig. 18, IIc)
arms	III: no suckers disproportionally enlarged	III: enlarged suckers on median portions (>7mm ML)
tentacles	moderately long and robust	long and delicate: >100% ML (>10mm ML)
tentacular club: Dactylus	Suckers gradually enlarged from dorsal to ventral margins	Suckers gradually enlarged from dorsal to ventral margins
tentacular club: Manus	Median two rows of suckers slightly enlarged	Five or more suckers of ventral row disproportionally enlarged

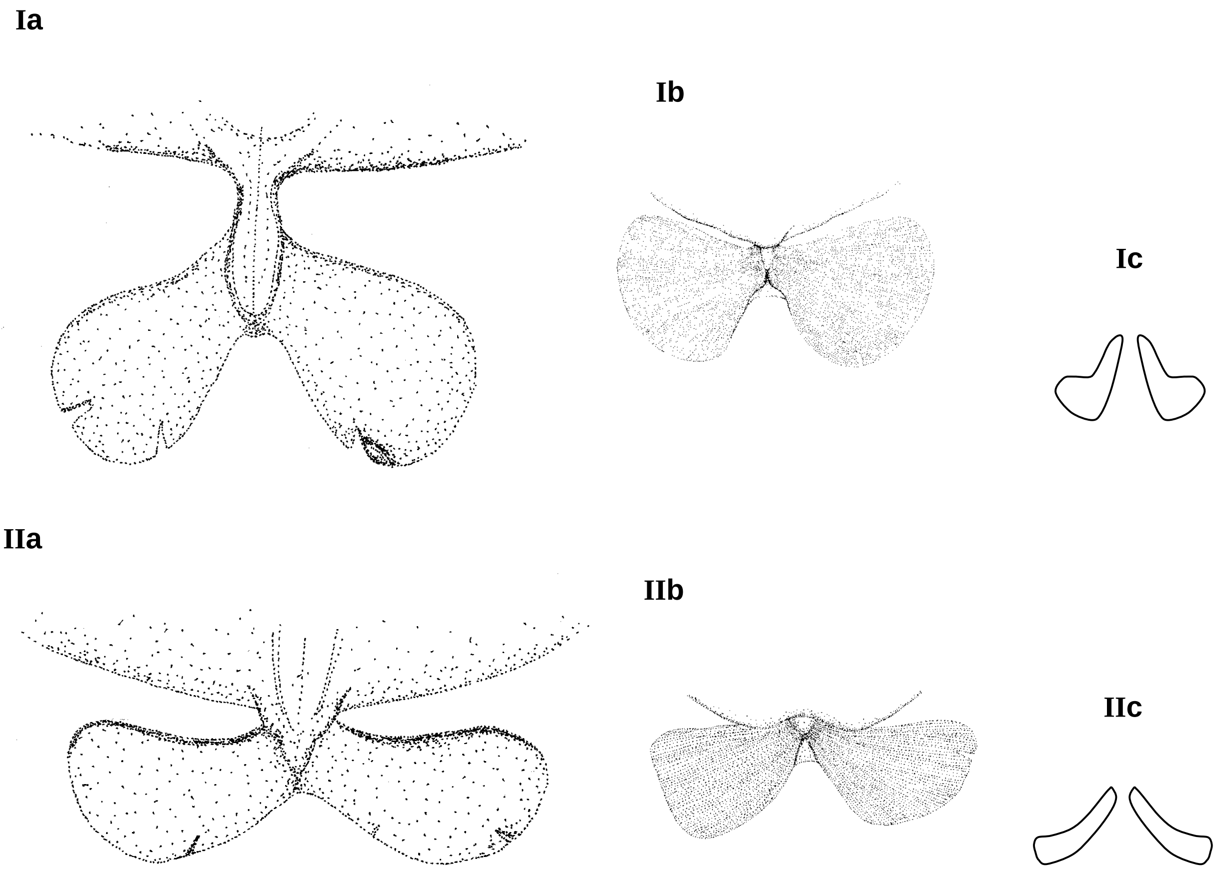


Fig. 18: Posterior end of (I) *Helicocranchia pfefferi* (ML=8.5mm) and (II) *Helicocranchia papillata* (ML=9mm). (a) Dorsal view, showing the projecting rostrum of the gladius; (b) ventral view of the same. (c) Ventral pads of the funnel organ.

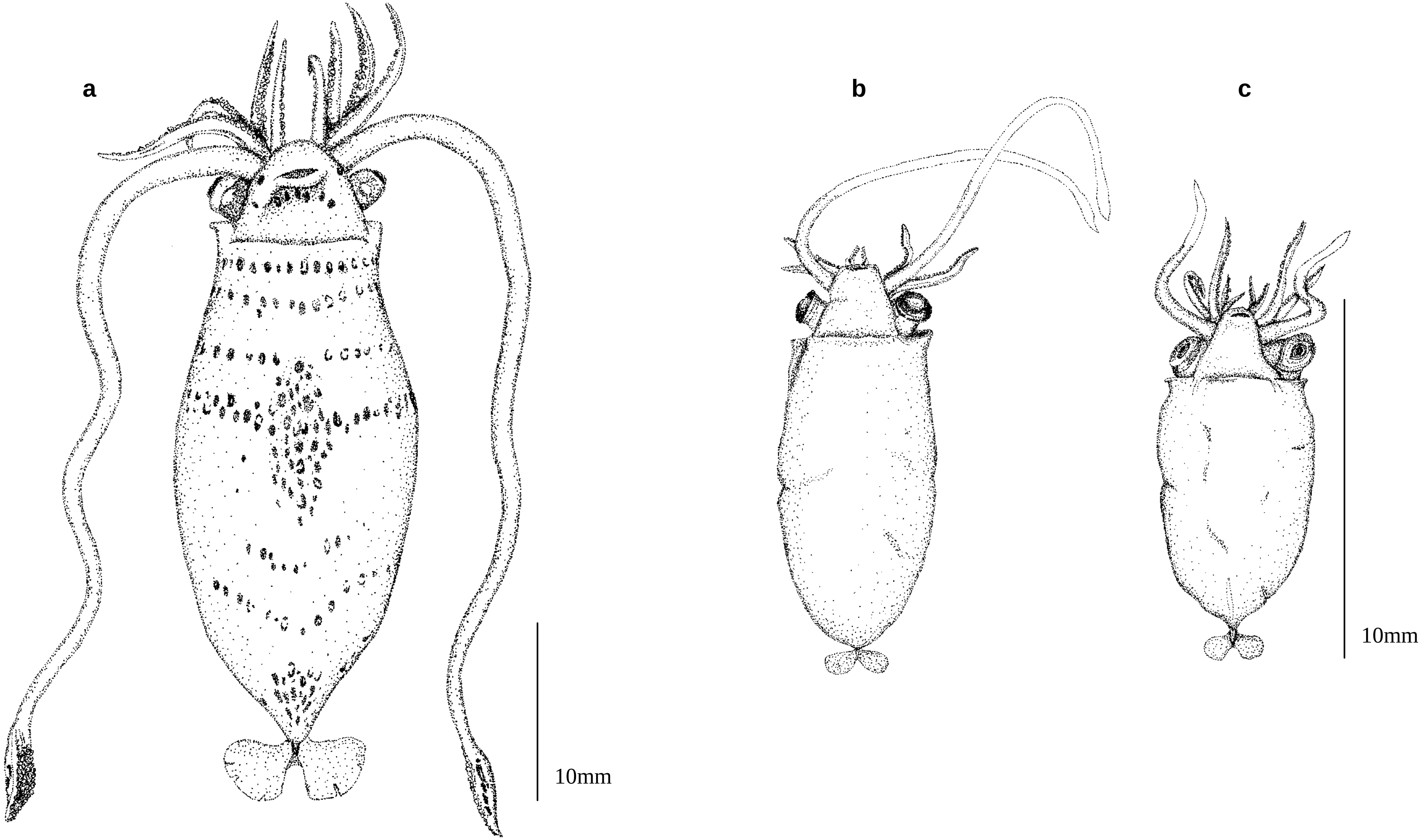


Fig. 19: *Helicocranchia pfefferi*. Ventral view: (a) ML=30mm, (b) ML=8.5mm, (c) ML=6.9mm.

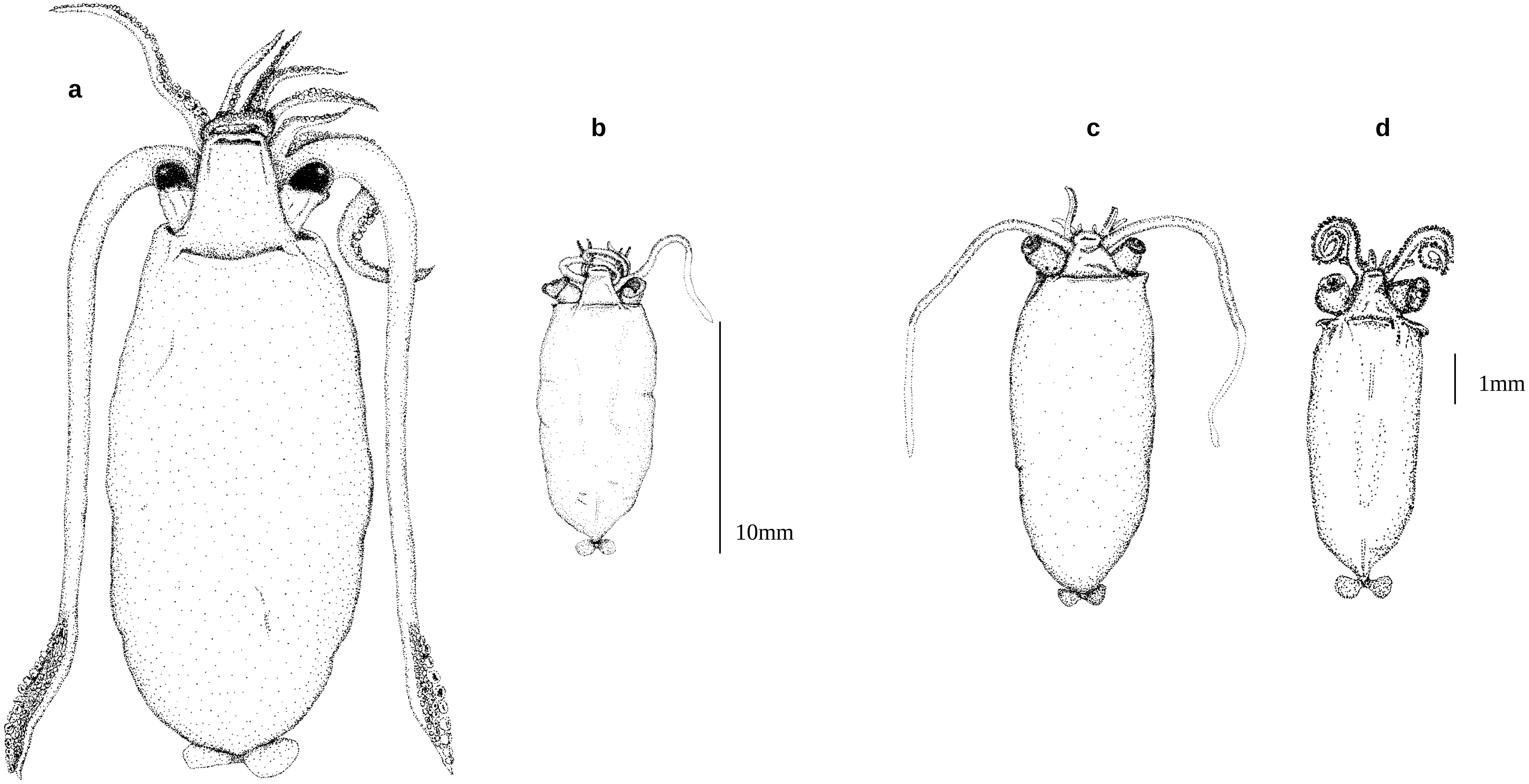


Fig. 20: *Helicocranchia papillata*. Ventral view: (a) ML=24mm, (b) ML=10.7mm, (c) ML=9mm, (d) ML=6.2mm.

Order Octopoda: Suborder Incirrina

All families within this octopod suborder have in common, that fins and arm cirri are absent. The skin of all specimens carries functional, chromatophores. The families identified in the subtropical eastern North Atlantic can be distinguished by the characteristics described below.

Tab. 11: Key to the families of the suborder Incirrinae, found near seamounts in the subtropical eastern North Atlantic

	mantle	arms	arm suckers	funnel locking-cartilage	eyes	male specimens	other features
Alloposidae (monotypic: *Alloposus mollis* / *Haliphron atlanticus*)	gelatinous, short, uniformly and densely pigmented	relatively short, connected by deep web	uniserial proximally, biserial distally (to edge of web)	hook like, only slightly developed	hemispherical, large, diameter about 40% ML	right arm III hectocotylized, develops in pouch	
Argonautidae (monogeneric: *Argonauta argo*), Fig. 25	muscular, firm	web weakly developed; hatchlings with brachial membrane	uniserial in hatchlings; biserial and small in growing specimens	specialised, knob-like	small, slightly anterolaterally directed	dwarfed; hectocotylized arm III in pouch; even visible in paralarvae	females with thin, calcareous shell; 1st arm longer, secreting the shell
Bolitaenidae (*Eldonella pygmaea*), Fig. 21	gelatinous, pigmented; jelly-like outer coating in young specimens	shorter than mantle; arms III slightly elongated	uniserial, generally small	absent	medium sized, elliptical, laterally directed	right or left arm III hectocotylized: enlarged suckers	elongated ovoid digestive gland
Octopodidae (c.f. *Scaeurgus unicirrhus*), Fig. 26	muscular; hatchlings with Koelliker´s bristles and	short, uneven; elongate slightly during growth; no web in larvae	uniserial (4 suckers) in hatchlings; biserial in growing	simple	small, anterolaterally directed	left arm III hectocotylized: mature males benthic	body of adults densely covered with rounded papillae; deep web
Ocythoidae (monotypic: *Ocythoe tuberculata*), Fig. 24	muscular; ventral side of females with tubercles and ridges (reticulate)	I and IV greatly elongated; no web; no brachial membrane in hatchlings	small suckers; biserial	specialised	medium sized, elliptical	dwarfed; hectocotylized arm III in stalked pouch	funnel very long; ventral pair of cephalic water pores
Tremoctopodidae (*Tremoctopus violaceus*), Fig. 22	muscular, thick, dorsally densely covered with chromatophores	I and II greatly elongated; web dorsally very deep, ventrally ± absent	small, numerous suckers; biserial; young: very large in dorsal arms	specialised	large, surrounded by gold iridophores	dwarfed; hectocotylized arm III develops in pouch below eye	cephalic water pores; in paralarvae: brachial membrane present
Vitreledonellidae (monotypic: *Vitreledonella richardi*), Fig. 23	semigelatinous, sac-like; jelly-like coating in young specimens	body to arm ratio 2:1; all arms connected by deep web	uniserial, widely spaced	absent	small, rectangular, laterally directed	tip of left arm III hectocotylized	long, slender digestiv gland, situated posterior to stomach

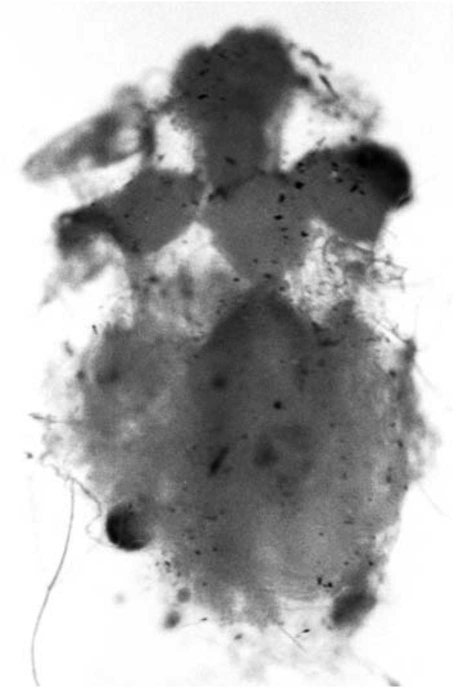


Fig. 21: *Eledonella pygmaea.*
Hatchling (ML=1.7mm);
cosmopolitan species, in tropical to temperate waters; meso- to bathypelagic.

Fig. 22: *Tremoctopus violaceus.*
Female juvenile (ML=2.2mm);
cosmopolitan species, in tropical to temperate waters; epi- to upper mesopelagic.

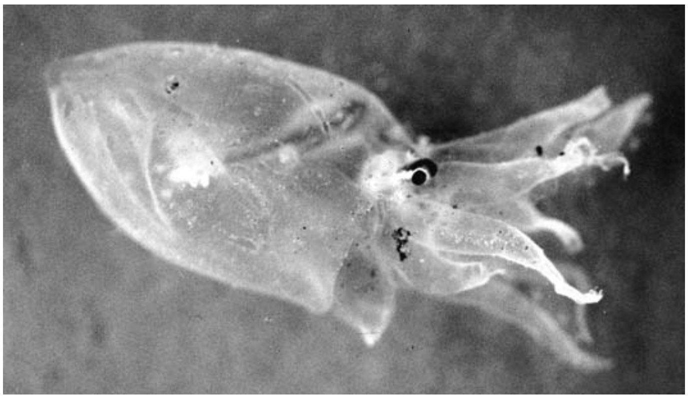
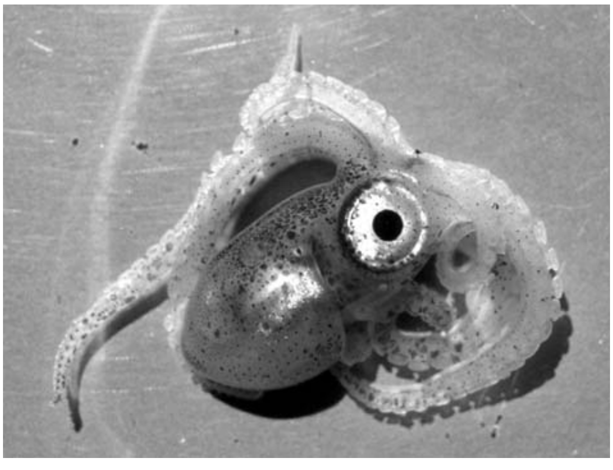


Fig. 23: *Vitreledonella richardi.*
Female juvenile (ML~30mm);
cosmopolitan species, in tropical to temperate waters; meso-to bathy-pelagic.

Fig. 24: *Ocythoe tuberculata.*
Female juvenile (ML~18mm);
cosmopolitan species, in tropical to temperate waters; epipelagic.



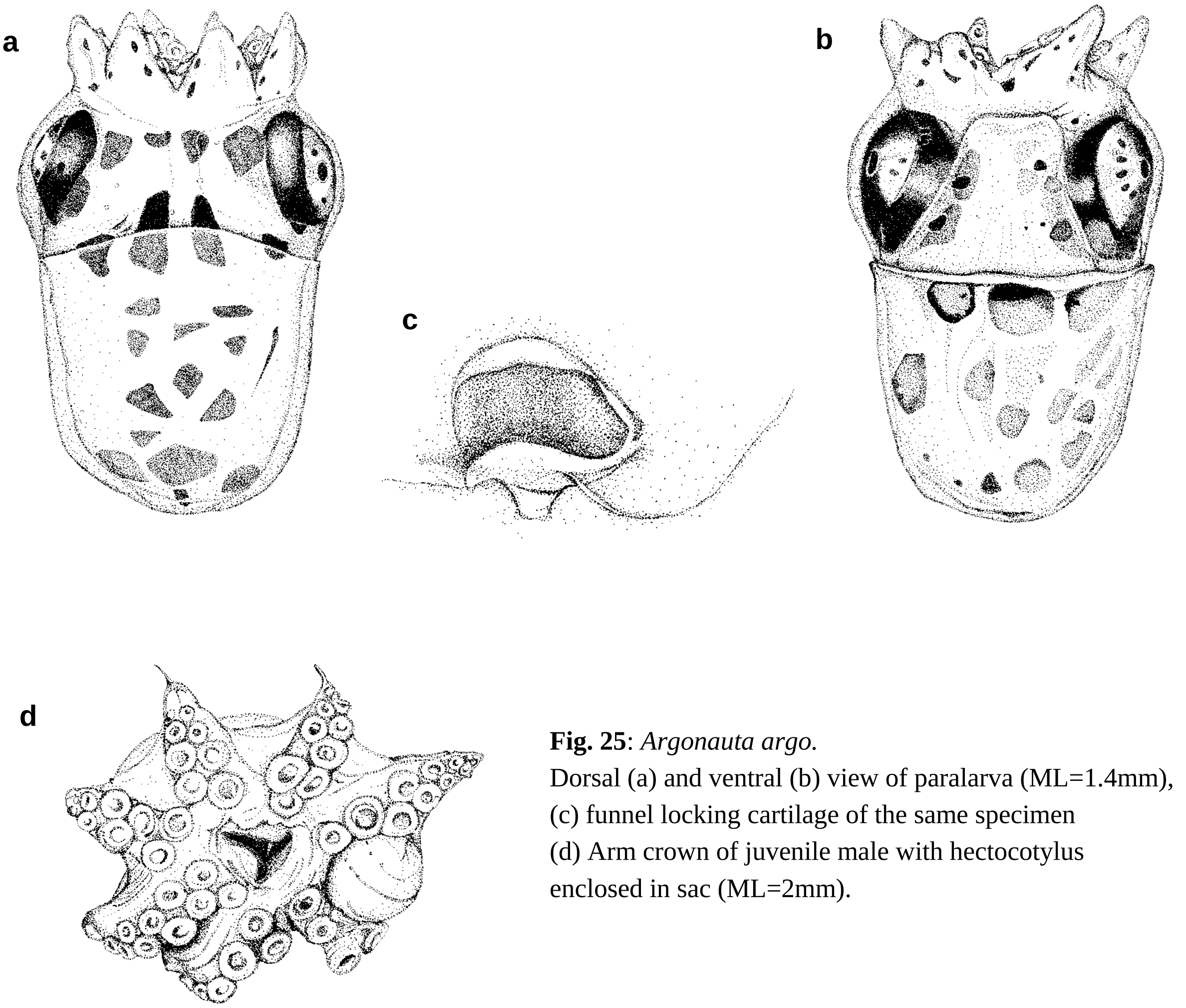


Fig. 25: *Argonauta argo.*
Dorsal (a) and ventral (b) view of paralarva (ML=1.4mm),
(c) funnel locking cartilage of the same specimen
(d) Arm crown of juvenile male with hectocotylus
enclosed in sac (ML=2mm).

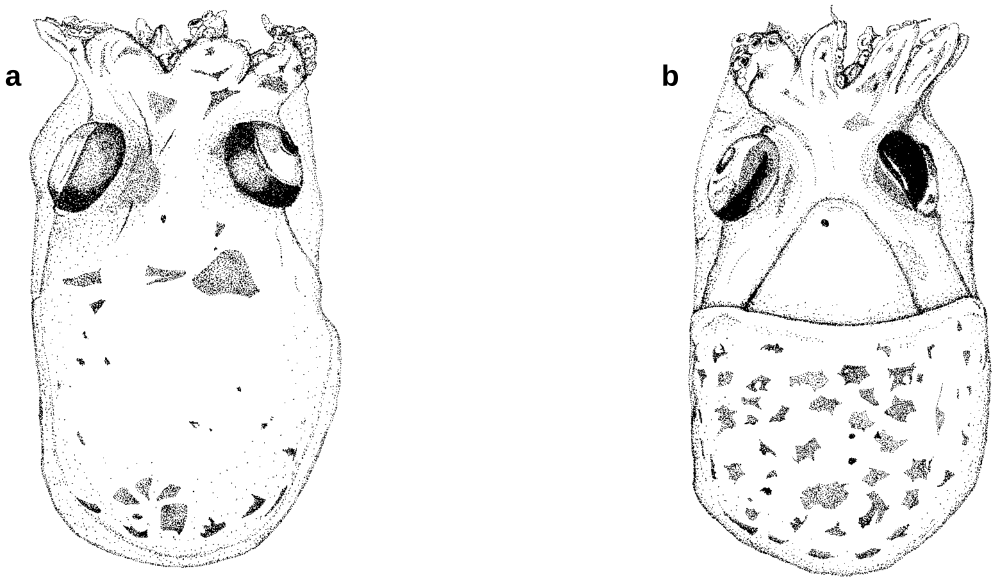


Fig. 26: Octopodinae c.f. *Scaeurgus unicirrhus.* Dorsal (a) and ventral view (b) of paralarva (ML=1.5mm)

Glossary

Arm crown = encompasses all circumoral appendages, i.e. arms and tentacles. In many juvenile squids and certain species (e.g. *Brachioteuthis*, *Chiroteuthis*) the arm crown is “stalked”, i.e. the arm crown is situated on an elongation of the head.

Arm formula = ratio between the length of the four arm pairs

Buccal mass = thickened tissue that encircles the mouth

Chromatophores = organs, located beneath or within the integument, and forming the colour patterns of cephalopods. Chromatophores are muscle- and nerve-innerved and, thus, provide the colour- and colour-pattern changes.

Cornea = thin, transparent membrane that covers the eyes of myopsid squids and Sepioidae. A cornea is missing in oegopsid squids, the eye has contact to the seawater.

Funnel locking-cartilage = a cartilaginous structure on each ventrolateral side of the funnel base. It locks the funnel and mantle together (see: mantle locking-cartilage) in order to close the anterior part of the mantle for locomotion (jet-propulsion). The funnel locking-cartilage may serve for species identification, as it is characterised by a species specific shape with grooves and pits.

Gladius = stabilising chitinous structure on the dorsal midline of the mantle in teuthoids and sepioids (not Sepiidae). It is homologous to the outer shell of ancestral forms (see also “Lanceola”).

Hectocotylus = modification of one (or more) arms of male cephalopods for transferring spermatophores to the females. A hectocotylus may be characterised by the arm shape, specialised suckers etc.. Not all cephalopod species show these modifications in males.

Lanceola = the posterior expanded portion of the gladius (see above), e.g. in the family Cranchiidae

Light organ = see: Photophores

Mantle locking-cartilage = the matching piece to the funnel locking-cartilage (see above). The cartilaginous structure can be found on the ventrolateral internal side of the mantle.

Nuchal region = dorsolateral area of the posterior part of the head, usually covered by the mantle. In the family Cranchiidae the mantle and head are fused in this area.

Paralarva = an introduced term by Young & Harman (1988) for early life stages of cephalopods that meet certain morphological and ecological criteria. Most cephalopods lack real “larval” modifications in their early life development. Early stages of cephalopods that differ in habit, habitat and/or often morphology from their adults are, thus, proposed to be defined as “paralarvae” to fill the gap in terminology. Most but not all pelagic cephalopods and octopods do fall in this category. For further information, refer to Young & Harman (1988).

Photophores = an organ that produces bioluminescence by means of a biochemical reaction (self-generated) or through luminescent bacteria. Photophores can be located within the integument but is also found on e.g. the intestinal tract (e.g. *Hyaloteuthis pelagica, Megalocranchia* sp.).

Proboscis = a trunk-like structure in the early life stages of Ommastrephidae (“Rhynchoteuthion”, see below). In the paralarvae development the proboscis divides into the two tentacles of the adults.

Rhynchoteuthion = a distinctive larval form of the family Ommastrephidae. It is characterised by the proboscis (see above), which is already present in hatchlings.

Rostrum = an extension of the gladius or cuttlebone which may project sharply out of the posterior part of the mantle.

Tragus = a small projection from the inner wall of the funnel locking-cartilage in certain families (e.g. Chiroteuthidae and Mastigoteuthidae).

Web = A fold of the skin that extends between the arms in some octopods (e.g. Vitreledonellidae) and a few squids (e.g. Histioteuthidae). This muscular skin fold connects all or only certain arm pairs and may extend to the arm tips as a deep web (e.g. Alloposidae).

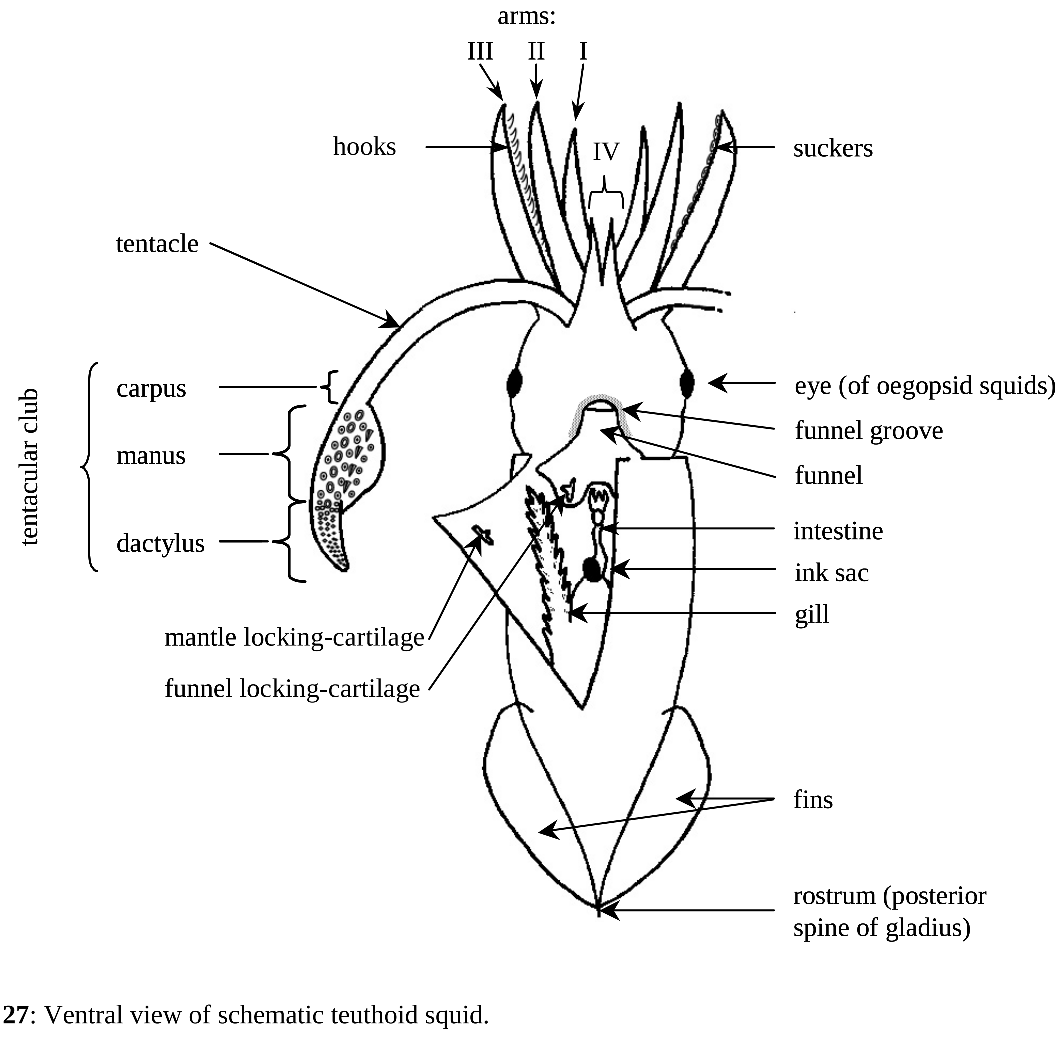


Fig. 27: Ventral view of schematic teuthoid squid.

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	Okt. 1999:	Beginn der Doktorarbeit am Institut für Meereskunde, Kiel in dem DFG-finanzierten Projekt: „Artenzusammensetzung und Verbreitung ozeanischer Tintenfische im Bereich der großen Meteorbank und bei Bermuda, Nordatlantik
	Okt. 2001-: Dez. 2003	Wissenschaftliche Angestellte in dem EU-Projekt LIFECO: „Linking hydrographic frontal activity to ecosystem dynamics in the North Sea and Skagerrak: Importance to fish stock recruitment"

Auslandsaufenthalte	Sept. 2002:	Gastaufenthalt an der Rosenstiel School of Marine and Atmospheric Sciences (RSMAS), Miami
Mitgliedschaft in wissenschaftlichen Arbeitsgruppen	seit 2002:	Working Group of Zooplankton Ecology (WGZE) des International Council for the Exploration of the Sea (ICES)

Kiel, 15.09.2004

Erklärung

Hiermit erkläre ich, daß die vorliegende Dissertation selbständig von mir angefertigt wurde. Die Dissertation ist nach Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel verwendet. Diese Arbeit wurde weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Fischereibiologie erfolgen. Des Weiteren erkläre ich, daß ich Zuhörer bei der Disputation zulasse.

Kiel, den 20.09.2004

Rabea Diekmann

Teilergebnisse dieser Dissertation die bereits vorab veröffentlicht worden sind:

Diekmann, R., and Piatkowski, U. (2000) Species composition and distribution of paralarval cephalopods in the subtropical North Atlantic Ocean with an emphasis on seamounts. Bull. Mar. Sci. **71**: 1118.

Diekmann, R., and Piatkowski, U. (2002) Early life stages of cephalopods in the Sargasso Sea: Distribution and diversity relative to hydrographic conditions. Mar. Biol. **141**: 123-130.

Diekmann, R., Piatkowski, U., and Schneider, M. (2002) Early life and juvenile cephalopods around seamounts of the subtropical North Atlantic: Illustrations and a key for their identification. Ber. Inst. f. Meeresk. **326**, 42pp.

Diekmann, R., and Piatkowski, U. (2004) Species composition and distribution patterns of early life stages of cephalopods at Great Meteor Seamount (subtropical NE Atlantic). Arch. Fish. Mar. Res. **51**: 115-131.