Zooplankton dynamics, fish zonation and trophic interactions at two seamounts in contrasting regimes of the Eastern Atlantic

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Summary

More than 125000 large seamounts >1000 m in height are predicted to occur on the ocean floor; most of them are active or extinct undersea volcanoes. Compared to the flat areas of the deep-sea plains, seamounts provide different habitats of hard substrata and soft bottom and have special geochemical and biological features. Recent seamount research has shown that seamount ecosystems may be highly variable, indicating that the classical picture of seamounts being areas of enhanced productivity cannot be generalised. The reasons why some seamounts appear to be much more productive than the surrounding ocean, while others do not show conspicuous differences, are still poorly understood. However, with regard to the sustainable exploitation and the management of natural resources at seamounts, such as fish and minerals, further knowledge of the driving forces and mechanisms in seamount ecosystems is absolutely necessary.

The present study compares the zooplankton communities and the benthopelagic fish fauna at two shallow seamounts, Ampère and Senghor, in relation to the large-scale and local current fields and hydrographic conditions of the contrasting regimes of the subtropical and tropical NE Atlantic gyres. Spatial and temporal distribution patterns of different zooplankton size fractions were elucidated in terms of biomass, abundance and taxonomic composition across the seamounts, which both reach into the euphotic zone. In order to detect possible seamount effects on the zooplankton due to, for example, current-topography interactions an unaffected open ocean reference site was always sampled for comparison. The study addressed several specific objectives. (1) The diel vertically migrating zooplankton was assessed to identify a possible influence of the topography, and how this affects the food supply to seamount residents. (2) Respiratory carbon demand was estimated for distinct zooplankton size fractions, in particular to assess the role of microzooplankton for the phytoplankton control and for the carbon conversion in subtropical *vs*. tropical areas. (3) Another question was, whether a seamount may be considered as larval source in the open ocean for benthic invertebrates. (4) Within the pelagic communities nutritional sources, trophic interactions and pathways were elucidated and linked to the benthopleagic fish fauna of the seamounts and the adjacent abyssal plains. (5) Furthermore these fish communities were characterised in a zoogeographical context in comparison with other NE Atlantic Seamounts.

Micro- (0.055-0.3 mm) and mesozooplankton (0.3-20 mm) standing stocks and respiratory carbon demand were three to six times higher at Senghor Seamount than at Ampère, respectively, indicating nutritional and productive differences between both seamount systems associated with the different trophic realms. While the zooplankton community at Ampère Seamount reflects the oligotrophic character of the NE Atlantic subtropical gyre, with microzooplankton attaining an important role for carbon conversion and the control on phytoplankton, the nutrient-rich waters of the cyclonic tropical gyre feature a higher zooplankton abundance of different composition at Senghor Seamount, with a lower contribution of microzooplankton to the total carbon demand. Surveys across Ampère show clear differences in the mesozooplankton distribution between day and night, reflecting the pattern of diel vertical migration, and a reduced biomass over the summit plateau. This gap formation over the plateau, associated with a general lower biomass, results from the blocked advection of vertically migrating zooplankton staying at depths greater than the summit. At Senghor Seamount no day-night related distribution patterns were observed, pointing to a high proportion of non-migrating zooplankton residing at the thermocline in the layer of the fluorescence maximum and a high food supply. Evidence for a general build-up of higher zooplankton biomass was not found as compared to the open ocean reference sites, neither at Ampère nor at Senghor. Topography-generated upwelling and trapping of passive particles can generally be assumed as an unlikely mechanism to affect secondary production at both seamounts. Only a higher abundance of dinoflagellates suggests possible interactions between current and topography over Senghor Seamount at times, such as upward displacement of isopleths and associated enhanced vertical mixing into the surface layer. Senghor Seamount was confirmed as a source for meroplanktonic larvae, with significantly enhanced larval abundance in the seamount surrounding flows as compared to the open ocean.

For the identification of food sources and trophic relationships a combination of stomach content and stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) analyses was used. Based on epipelagic particulate organic matter (POM), zooplankton usually occupied the 1st and 2nd trophic level and included herbivorous, omnivorous and carnivorous taxa. Feeding types of fish species comprised mainly zooplanktivores and mixed feeders, but also benthivores, piscivores, and predator-scavengers. They had trophic positions between the 2nd and 4th trophic level. Differences in stomach contents and stable isotope signatures indicate a resource partitioning among the benthopelagic fishes through distinct habitat choice, vertical feeding positions and prey selection. The lack of larger diel vertically migrating zooplankton over the summit plateau and the presence of non-migrating taxa in the stomach contents of the zooplanktivorous bottom associated fishes indicate that topographic trapping of diel vertical migrators on the summit plateau seemed to be of minor importance for the food supply at the seamounts. Rather, horizontal current-driven advection of the planktonic prey from the surrounding ocean was assumed as major food source for the benthopelagic fish fauna at Ampère and Senghor. The varying $\delta^{13}C$ and $\delta^{15}N$ signatures and correlations among the seamount systems and the reference sites indicate that the nutritional sources and the trophic structure of pelagic and benthopelagic communities may be highly variable not only at seamounts, but also over the uniform abyssal plains of the different regimes, pointing to a more complex food web in the tropics than in the subtropics. But, despite differences in production and trophic pathways in the surface layers, the remaining nutritional sources seem to be comparable in the deep-sea among all sampling sites, as were biomass, abundance and respiration.

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Zusammenfassung

Das Vorkommen großer Seeberge mit einer Höhe von mehr als 1000 m in den Ozeanbecken wird auf 125000 geschätzt. Hierbei handelt es sich in den meisten Fällen um aktive oder erloschene unterseeische Vulkane. Im Vergleich zu den umliegenden flachen Tiefseeebenen weisen Seeberge verschiedenartige Habitate von Hartsubstrat bis Weichböden auf und verfügen über spezielle geochemische und biologische Eigenschaften. Die aktuelle Forschung an Seebergen hat gezeigt, dass Seeberg-Ökosysteme sehr vielfältig sind und die klassische Vorstellung von Seebergen als Gebiete erhöhter Produktivität im Vergleich zum offenen Ozean nicht verallgemeinert werden kann. Die Ursachen, weswegen Ökosysteme einiger Seeberge deutlich produktiver erscheinen als der umgebende Ozean, während andere keine klaren Unterschiede aufweisen, sind weitgehend unbekannt. Ein fundiertes Verständnis der funktionalen Zusammenhänge und treibenden Kräfte innerhalb eines Seeberg-Ökosystems ist jedoch eine zentrale Vorraussetzung für die nachhaltige Nutzung natürlicher Seebergressourcen, wie Fisch und mineralische Rohstoffe.

Die vorliegende Arbeit vergleicht die Zooplanktongemeinschaften und die benthopelagische Fischfauna an zwei flachen Seebergen, Ampère und Senghor, im subtropischen und tropischen Nordostatlantik und setzt sie in Beziehung zu den vorherrschenden lokalen und großräumigen Strömungsverhältnissen und hydrographischen Bedingungen. An den Seebergen, die beide in die euphotische Zone reichen, wurden räumliche und zeitliche Verteilungsmuster verschiedener Zooplanktongrößenfraktionen bzgl. ihrer Biomasse, Abundanz und taxonomischen Zusammensetzung analysiert. Um einen möglichen Effekt des Seebergs auf das Zooplankton aufdecken zu können, wurde parallel jeweils eine unbeeinflusste Referenzstation im offenen Ozean beprobt. In diesem Zusammenhang beleuchtet die vorliegende Arbeit einige spezifische Aspekte. (1) Die Verteilung täglich vertikal wandernden Mesozooplanktons wurde dahingehend untersucht, ob sie durch die Topographie der Seeberge beeinflusst wird und wie sich dies auf den Nahrungseintrag der Seeberg assoziierten Fischfauna auswirkt. (2) Respirationsraten und respiratorischer Kohlenstoffbedarf wurden für verschiedene Größenfraktionen des Zooplanktons ermittelt, um bestimmen zu können, welche Rolle besonders das Mikrozooplankton in der Kontrolle des Phytoplanktons sowie im Stoffkreislauf in den unterschiedlichen Regionen einnimmt. (3) Eine weitere Frage war, ob Seeberge eine Quelle für Larven benthischer Invertebraten im offenen Ozean darstellen. (4) Innerhalb des Zooplanktons und Mikronektons wurden Nahrungsquellen und trophische Verbindungen beleuchtet, sowie deren Kopplung mit der benthopelagischen Fischfauna der Seeberge und der angrenzenden Tiefseeebenen.

(5) Die Fischgemeinschaften wurden zudem zoogeographisch eingeordnet und mit anderen nordostatlantischen Seebergen verglichen.

Die Bestände des Mikro- (0.055-0.3 mm) und Mesozooplanktons (0.3-20 mm) sowie der entsprechende respiratorische Kohlenstoffbedarf waren drei bis sechs mal höher am Senghor als am Ampère Seamount, was auf regional unterschiedliche Nährstoff- und Produktionsbedingungen in den umgebenden Gebieten zurückzuführen ist. Die Zooplanktongemeinschaft am Ampère spiegelt den oligotrophen Charakter des nordostatlantischen subtropischen Wirbels wider, wobei das Mikrozooplankton eine wichtige Rolle im Kohlenstoffumsatz einnimmt. Im Gegensatz zu den Gebieten um den Ampère Seamount, fördern die nährstoffreicheren Gewässer des zyklonischen tropischen Wirbels am Senghor eine höhere Planktondichte anderer Zusammensetzung und einem geringeren Anteil des Mikrozooplanktons am Kohlenstoffbedarf. Die Verteilung des Mesozooplanktons über dem Ampère Seamount weist typische, durch tägliche Vertikalwanderung bedingte Unterschiede zwischen Tag und Nacht auf, sowie eine generell reduzierte Biomasse über dem Gipfelplateau. Diese Lückenbildung über dem Plateau entsteht, wenn vertikal wanderndes Zooplankton in Tiefen unterhalb des Gipfels verbleibt und eine Advektion der Plankter auf das Plateau durch die Topographie des Seebergs verhindert wird. Am Senghor Seamount traten keine Tag-Nacht Unterschiede auf, was einen hohen Anteil nicht wandernden Zooplanktons andeutet, welches hauptsächlich an der Thermokline in der Schicht des Fluoreszenzmaximums und eines hohen Nahrungsangebots akkumuliert war. Hinweise für eine generell höhere Zooplanktonbiomasse im Vergleich zu den unbeeinflussten Referenzstationen gab es nicht, weder am Ampère noch am Senghor. Topographie induzierter Auftrieb und die Akkumulation passiver Partikel über dem Seeberg ließen sich als typische Mechanismen, welche die Sekundärproduktion beeinflussen können, an beiden Seebergen ausschließen. Lediglich eine höhere Abundanz an Dinoflagellaten über dem Senghor Seamount weist auf mögliche Interaktionen zwischen Topographie und Strömung hin und ist vermutlich die Folge von vertikaler Verlagerung der Isothermen und Isohalinen und damit einhergehender stärkerer Durchmischung der Oberflächenschicht. Senghor Seamount konnte als Quelle für meroplanktonische Larven durch signifikant erhöhte Abundanz der Invertebratenlarven in den Seeberg umgebenden Strömungsbändern im Vergleich zum offenen Ozean bestätigt werden.

Primäre Nahrungsquellen und trophische Beziehungen wurden mit Hilfe von Mageninhaltsanalysen und stabilen Isotopensignaturen (δ^{13}C and δ^{15}N) identifiziert. Basierend auf oberflächennahem partikulärem organischem Material gehörten Zooplanktonorganismen zumeist der 1. und 2. trophischen Ebene an und beinhalteten herbivore, omnivore und carnivore Taxa. Als Hauptnahrung der benthopelagischen Fische wurden Zooplankton und Mikronekton identifiziert, aber es gab auch Hinweise auf benthivore und piscivore Ernährungsweisen, sowie auf räuberische Aasfresser. Die trophischen Positionen der Fische erstreckten sich über die Ebenen zwei bis vier. Unterschiede in den Mageninhalten und Isotopensignaturen zeigen eine Ressourcenteilung durch Habitatwahl, vertikale

Fraßpositionen und Beutepräferenzen innerhalb der benthopelagischen Seebergfische an. Das Ausbleiben des größeren vertikal wandernden Zooplanktons über dem Gipfelplateau sowie die Präsenz nicht wandernder Taxa in den Mageninhalten der zooplanktivoren Boden assoziierten Fische deuten darauf hin, dass das Blockieren und Abfangen des abwärts wandernden Zooplanktons auf dem Gipfelplateau an beiden Bergen nicht zu einer erhöhten Nahrungsverfügbarkeit führt. Eher scheint horizontale Advektion der planktischen Beuteorganismen aus dem umgebenden Ozean der treibende Mechanismus der Nahrungsversorgung der benthopelagischen Fischfauna an Ampère und Senghor Seamount zu sein.

Die unterschiedlichen $\delta^{13}C$ und $\delta^{15}N$ Signaturen und Korrelationen zwischen den Seebergsystemen und den Referenzstationen deuten darauf hin, dass die Nahrungsbedingungen und die trophische Struktur pelagischer und benthopelagischer Gemeinschaften höchst variabel sein können. Diese Variabilität tritt nicht nur an den Seebergen auf, sondern auch über den gleichförmigen Tiefseeebenen beider Regionen, mit einem komplexeren Nahrungsnetz in den Tropen als in den Subtropen. In der Tiefsee scheinen an beiden Seebergen und Ebenen die verbleibenden Nahrungsressourcen, ebenso wie Biomasse, Abundanz und Respiration, vergleichbar zu sein, trotz der Unterschiede in der Produktion und den trophischen Vernetzungen an der Oberfläche.

3

General Introduction

3.1 Seamount ecosystems

The term seamount has been defined many times (e.g. Menard 1964; Schmidt & Schmincke 2000; Wessel et al. 2010) based on different aspects, such as the temporarily breach of the sea level, the tectonic setting of seamounts, their minimum size and their shape (see Staudiegel et al. 2010). But there is no explicit definition that is generally accepted, since distinct research disciplines define seamounts in quite different ways (Staudiegel et al. 2010). Staudiegel et al. (2010) combined all the diverse perspectives and features studied under one inclusive *umbrella definition* that describes seamounts as "*any geographically isolated topographic feature on the seafloor taller than 100 m, including ones whose summit regions may temporarily emerge above sea level, but not including features that are located on continental shelves or that are part of other major landmasses*". More than 125000 large undersea mountains >1000 m in height are predicted to occur on the ocean floor, many of them in linear seamount chains, and are classified as *shallow* if the summit lies within the photic layer (Genin 2004). Their abundance varies considerably among the ocean basins (Wessel 2007) and up to 30000-50000 large seamounts are located in the Pacific basin alone (Wessel 2007; Wessel et al. 2010).

In contrast to the general flat sediment-covered abyssal plains, the topography of seamounts provides special habitats of hard substrata and soft bottom for the benthic fauna as well as for associated pelagic and benthopelagic communities (Rogers 1994; Stocks & Hart 2007; Clark et al. 2010b; Morato et al. 2010), which form complex ecosystems within the surrounding current regime (Fig. 3-1). The abrupt seamount topography of varying shape and size interferes with ocean currents and affects local circulation patterns by the formation of seamount-associated eddies (Richardson 1980; Richardson 1981), Taylor caps/columns, tidal resonance and seamount-trapped waves (see Genin & Boehlert 1985; Dower et al. 1992; Lavelle & Mohn 2010) or increased vertical mixing (Erikson 1998). These hydrodynamic features generate advection, upwelling or local retention of water masses, including particles, phytoplankton and smaller zooplankton (Genin & Boehlert 1985; Roden 1994). The uplift of deeper nutrient-rich water into the euphotic zone through hydrodynamic processes may enhance local autochthonus production over a seamount, especially in oligotrophic regions (Genin & Boehlert 1985; Dower et al. 1992; Mouriño et al. 2001), and may cause changes in food sources and feeding conditions compared to allochthonus input from the surrounding open ocean (see Genin & Dower 2007). However, enhanced productivity is not a consistent feature at seamounts and may be highly variable dependent on the complex physical processes and the specific topographic characters (White et al. 2007). Evidence for enhanced primary production does exist at some seamounts (e.g. Genin & Boehlert 1985; Dower et al. 1992; Comeau et al. 1995), but as no subsequent increase in secondary production has been found, it is suggested that the retention time of the recirculating flow and therefore of the additional phytoplankton biomass over the seamount is too short to be locally transferred to higher trophic levels and to increase zooplankton or nekton biomass (Genin & Boehlert 1985; Dower & Mackas 1996; Genin & Dower 2007). In many cases the zooplankton biomass is even lower over the top of the seamount than in the surrounding waters, as observed at some NE Atlantic (Nellen 1973; Martin & Christiansen 2009; Denda & Christiansen 2014), Mediterranean (Denda & Christiansen 2011) and Pacific seamounts (Genin et al. 1988; Genin et al. 1994).

Fig. 3-1. Seamount ecosystem (Stefanowitsch 2015, modified after Mackay in Consalvey et al. 2010).

At several seamounts, especially in the Pacific, aggregations of demersal and benthopelagic fishes in high biomass concentrations have been reported (Koslow 1997; Parin et al. 1997; Koslow et al. 2000), supporting the assumption of seamounts being attractive locations of enhanced food supply in the open ocean for usually dispersed fish stocks as well as for typical shelf species. Most studies on the feeding ecology of seamount fishes suppose that large fish aggregations on seamounts are rather supported by advected pelagic food than by locally enhanced primary production (Porteiro & Sutton 2007), which is, as mentioned above, not a generalised phenomenon at seamounts. One important mechanism for the food supply to the benthopelagic community at shallow seamounts is the advection of diel vertically migrating zooplankton and micronekton over the summit and upper slopes, associated with topographic blockage and bottom trapping at dusk and day, when the blocked zooplankton can easily be consumed by seamount residents (Isaacs & Schwartzlose 1965; Genin et al. 1988; Genin et al. 1994; Haury et al. 2000; Wilson & Boehlert 2004). The concentration of pelagic prey appears to be an important factor for the specification of feeding strategies, habitat choice and resource partitioning in seamount associated fish assemblages (Fock et al. 2002a, b; Porteiro & Sutton 2007). However, the specific mechanisms driving trophic interactions between benthopelagic fishes and the pelagic community are not fully understood (Porteiro & Sutton 2007).

Seamounts have also been suggested to host species-rich benthic communities (Richer de Forges et al. 2000; Koslow et al. 2001; Samadi et al. 2006) different to those on the soft sediment-dominated abyssal plains (Rogers 2004). Especially sessile organisms, such as corals, hydroids, sponges and crinoids, which require hard substrate for attachment, are typical for seamounts (Rogers 2004). But also other organisms, such as crabs, lobsters, mobile echinoderms, polychaetes and molluscs settle on the diverse seamount substrates (Rogers 2004). Many of the sessile suspension feeders favour exposed areas near the peak or around the rim of the summit plateau, where strong currents supply them with food and disperse their eggs and larvae (Rogers 2004). It has been demonstrated by Mullineaux & Mills (1997) that current-topography interactions can retain larvae in seamount associated flows, which is likely to affect the recruitment to maintain the benthic populations. But only limited evidence exists that seamounts can support elevated biomass and abundance of the benthic invertebrate fauna (see Genin 2004; Clark et al. 2010b; Rowden et al. 2010).

Due to their habitat diversity, their vertical range and their geographical isolation seamounts are known for a high rate of speciation among their populations and some are considered as hotspots of endemic species (e.g. Shank 2010; Stocks et al. 2012). On the other hand, seamounts are also supposed to act as *stepping stones* for oceanic dispersal, particularly of typical shelf and slope species across large distances, for example, between continental margins and mid ocean ridges (Santos et al. 1995; Almada et al. 2001; Shank 2010), featuring faunal similarity among seamounts and within shelf and slope communities.

Since many seamounts host commercially valuable pelagic and demersal fish species, they have become important fishing grounds. Especially benthopelagic deep-sea fishes are associated with and often restricted to the isolated seamount habitats (e.g. Clark et al. 2010a; Morato et al. 2010), including many species of commercial interest. But overfishing and the destructive impact of bottom trawling on the benthic communities have led to rising concern about the vulnerability of seamount ecosystems in the past decades (e.g. Clark 2001; Clark & Koslow 2007; Clark et al. 2010b). For example, forming large aggregations over seamounts, deep-sea fishes are rapidly depleted in stock size by trawling (Clark et al. 2010b). Due to their longevity, low fecundity and slow growth rates they recover only slowly from fishing impacts, if at all, once they have been overexploited (Clark 2001; Morato et al. 2008; Clark et al. 2010b). Similarly, sessile organisms like corals and sponges grow extremely slowly, and their recovery after disturbance may take decades or even centuries. But the human impact on seamount communities may not be restricted to fishing. In recent years the interest for exploitation of mineral resources in the deep-sea has considerably increased, and the mining of ferromanganese crusts at seamounts possibly will have a greater impact on the highly vulnerable habitats in the future than trawling (Clark et al. 2010b). Further knowledge about the functioning of seamount ecosystems will be necessary for conservation strategies and the establishment of marine protected areas in order to prevent an unsustainable exploitation of seamount resources.

3.2 Microzooplankton *vs.* mesozooplankton

In a seamount ecosystem meroplanktonic larvae are an important factor for recruitment, food supply and production, but in most zooplankton studies invertebrate larvae, in particular larvae in the deep ocean, are not considered (e.g. Mullineaux & Mills 1997). Studies on zooplankton communities have often concentrated on larger mesozooplankton (>0.2 mm) (Pfaffenhöfer 1993; Gallienne & Robins 2001) with special focus on calanoid copepods as the generally most abundant and important taxa within this community (e.g. Roe 1988; Fabian et al. 2005; Koppelmann & Weikert 2007). Meroplanktonic larvae <0.2 mm and other small metazoans like copepods, copepodites and nauplii belong to the microzooplankton, usually defined as the size fraction 0.02-0.2 mm, including also protists like ciliates and flagellates. Especially the small copepods and nauplii are an important prey for fish larvae and other zooplanktivorous consumers (e.g. Turner 2004; Calbet 2008), and on the other hand exert an important grazing impact on phytoplankton communities of extremely small cells of nano- and picoplankton (Landry et al.1995; Böttjer & Morales 2005). However, due to the common usage of plankton nets with mesh sizes of >0.2 mm, the smaller sized zooplankton has usually been under sampled in the oceanic realm (Gallienne & Robins 2001; Turner 2004). There is also little knowledge of microzooplankton groups and developmental stages regarding their trophic position in the marine food web and their role in carbon conversion, as compared to, for example, larger calanoid copepod taxa, although their importance in the pelagic system as generally the most abundant metazoans in the ocean (e.g. Gallienne & Robins 2001; Turner 2004) has been widely recognized (Arístegui et al. 2001; Turner 2004; Schmoker et al. 2013).

3.3 Respiratory carbon demand

Respiration rates of zooplankton communities provide a useful assessment of the role of zooplankton in the consumption, secondary production, the energy flow and the carbon cycle in an oceanic realm. Respiration is an index of energy demand and represents the minimum requirements of organisms for organic carbon (Hernández-León & Ikeda 2005; Ikeda et al. 2006). Respiration rates reflect feeding and related swimming activity in zooplankton species (see Schmoker & Hernández-León 2003) and might therefore be an indication of increased food supply in a system. The assessment of respiration rates and the respiratory carbon demand of different sized zooplankton groups may elucidate geographical differences in their control of phytoplankton and their importance for carbon conversion in the biogeochemical cycle.

Direct determination of respiration involves the incubation of zooplankton under controlled environmental conditions, which is impractical in case of analysing large and diverse communities and nearly impossible for deep-living animals due to physical damage during capture and retrieval (Owens & King 1975) and the possible effects of decompression, unless pressurized experimental chambers or in situ incubation are available, which are highly demanding in terms of technical and financial effort (e.g. Smith 1982; Koyama et al. 2002). In the present study respiratory oxygen consumption rates of taxonomically mixed zooplankton size fractions were calculated from body mass (mean individual weight) and habitat temperature, using a general multiple regression model between those quantities from literature, and were converted to carbon equivalents (see Ikeda 1985; Ikeda et al. 2001; Ikeda et al. 2006). However, this is only an approach, since the model, which has been established in different temperate regimes, refers directly only to distinct taxonomic groups of epipelagic (<250 m) zooplankton (Ikeda 1985; Ikeda et al. 2001). For the respiration rates of deep-sea zooplankton a general reduction to about 30-60 % that of epipelagic respiration is assumed (Torres et al. 1994; Ikeda et al. 2006), maybe affected by hydrostatic pressure, oxygen concentrations, limited light and food supply (Childress 1995; Ikeda et al. 2006).

3.4 Stable isotopes in trophic analyses

Biochemical markers, such as stable isotopes, are effective and common tools for the identification of trophic interactions within marine food webs (e.g. Hobson & Welch 1992; Post 2002). Whereas stomach content analysis provides information of recently ingested prey, stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are a measure of assimilated diet integrated over time (e.g. Davenport & Bax 2002).

Ratios of heavier to lighter stable isotopes in organic matter change from prey to predator due to isotopic fractionation during feeding and metabolism (Peterson & Fry 1987). Usually the heavier isotope (^{13}C or ^{15}N) is retained and accumulated in the consumer tissue relative to its diet, mainly due to primary loss of the lighter isotope by respiration and excretion (Checkley & Entzeroth 1985; Peterson & Fry 1987). Along the food chain this isotopic fractionation is reflected in a stepwise enrichment of isotope ratios between consumers and their diets. The stable isotope signature of carbon ($\delta^{13}C$) changes little from prey to predator with usually small enrichment of about 0.4-1 ‰, and is used to track the diet and carbon source of an organism (DeNiro & Epstein 1978; Fry & Sherr 1984; Peterson & Fry 1987; Post 2002). The nitrogen isotope ratio ($\delta^{15}N$) is usually enriched by 1-5 ‰ for a single feeding step and allows for estimation of the trophic position of an organism in a food web with respect to the trophic signature of primary producers (DeNiro & Epstein 1981; Minagawa & Wada 1984; Michener & Schell 1994; Mill et al. 2007). In the ocean correlations between $\delta^{15}N$ and $\delta^{13}C$ values of producers and consumers may indicate whether a food web is mainly dependent on a single primary food source, or relies on several energy providers (e.g. Polunin et al. 2001; Drazen et al. 2008; Reid et al. 2012), pointing to differences in trophic structures and feeding conditions.

3.5 Objectives of the study

The present study compares the pelagic communities, for the first time, of a size range from microzooplankton to micronekton, and the nutritional links to the benthopelagic fish fauna at two shallow seamounts, Ampère and Senghor, in relation to the large-scale and local current fields and hydrographic conditions of the contrasting regimes of the subtropical and tropical Eastern Atlantic. At the subtropical Ampère plankton production and distribution are supposed to be affected by local seamount effects through, for example, tidal resonance, trapped waves and tidal rectification, since the seamount is located within the critical latitudes (>30° N) for the trapping of diurnal internal tides, which may induce vertical displacement of isotherms and isohalines over a seamount (Beckmann & Mohn 2002). The faunal composition at Ampère may be influenced by the dispersal of typical Mediterranean species via the Mediterranean outflow and the formation of meso-scale Mediterranean eddies, so-called meddies (O'Neil Baringer & Price 1999). In contrast, at Senghor Seamount the plankton community is expected to be rather influenced by large-scale flow features, such as seasonal filaments of the Mauritanian upwelling (e.g. Mittelstaedt 1991; Vangriesheim et al. 2003) and the Cape Verde frontal zone (e.g. Zenk et al. 1991), than by topography interaction with the local flow field. Since Senghor is located close to the equator, where the influence of the Coriolis force on the current regime is small, no tidal resonance exists and seamount trapped waves do not occur (Beckmann & Mohn 2002; Dumont et al. subm.), the retention potential of this seamount is supposed to be small, presumably not affecting the local plankton production and distribution.

Spatial and temporal distribution patterns of different zooplankton size fractions were elucidated in terms of biomass, abundance and taxonomic composition over the seamount summits, around the rim of the summit plateau and on the slopes. In order to detect possible seamount effects on the zooplankton due to, for example, current-topography interactions, an unaffected open ocean reference site (hereafter referred to as 'far field') was always sampled for comparison. The study addressed several specific objectives. The diel vertically migrating zooplankton was assessed to identify a possible influence of the topography, and how this affects the food supply to seamount residents. The role of microzooplankton was elucidated in the different regions, particularly for the control of phytoplankton and carbon conversion, in context of the estimated respiratory carbon demand of distinct zooplankton size fractions. Whether a seamount may be considered as larval source in the open ocean for benthic invertebrates, since the retention of meroplanktonic larvae in seamount surrounding flows could maintain the recruitment of the benthic population (Mullineaux & Mills 1997), was another question. Within the pelagic community trophic interactions of zooplankton and micronekton were elucidated, using stable isotope ratios as trophic marker, to detect possible differences between nutritional sources and pathways, for example, due to different shares of autochthonus and allochthonous food supply at the seamount compared to the open ocean. Nutritional links and potential pelagic food sources to the benthopelagic fish fauna on the shallow summits of the seamounts, the slopes and the adjacent abyssal plains were identified using a combination of stable isotope ratios and stomach content analyses. Furthermore the benthopelagic fish communities were characterized at different depths and locations at and around Ampère and Senghor seamounts in a zoogeographical context in comparison with other NE Atlantic seamounts.

Ampère Seamount belongs to the Horseshoe Seamounts Chain between the island of Madeira and the Portuguese mainland, and is located ~360 nm west of the Strait of Gibraltar within the sphere of the oligotrophic subtropical NE Atlantic gyre (see Longhurst 1995; Lathuiliere et al. 2008; Fig. 3-2). Ampère is a conical shaped seamount and rises from a base depth at 4500 m to a summit depth at 120 m with one peak of 55 m. Senghor Seamount is located near the equator in a mesotrophic tropical region (see Morel 1996; Bory et al. 2001; Vangriesheim et al. 2003) ~60 nm east of the Cape Verde islands. Water depth at the base of the nearly circular shaped seamount is ca. 3300 m with a minimum summit plateau depth of 90 m.

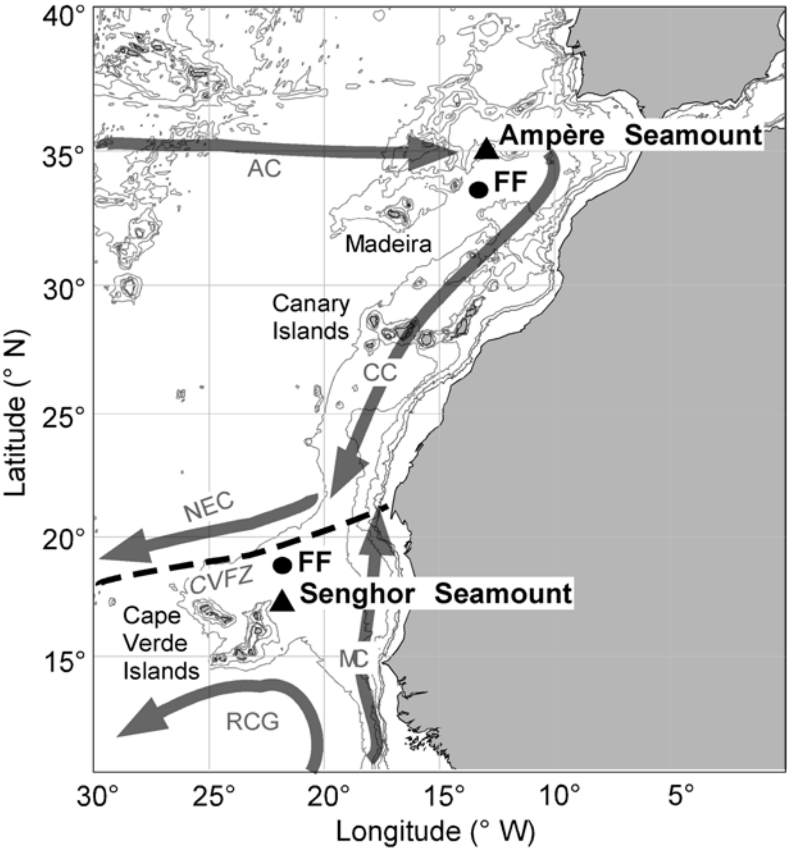

Fig. 3-2. Locations of Ampère and Senghor seamounts and the far field sites (FF) in the NE Atlantic with schematic surface circulation (after Lathuilière et al. 2008; Mason et al. 2011). AC, Azores Current; CC, Canary Current; MC, Mauritania Current; NEC, North Equatorial Current; CVFZ, Cape Verde Frontal Zone; RCG, Recirculation Gyre.

The following manuscripts focus on the distribution patterns of micro- and mesozooplankton and benthopelagic fishes, on the respiratory carbon demand for different zooplankton size fractions and on the trophic interactions of selected zooplankton, micronekton and fish species at each seamount compared to the open ocean.

Manuscript 1 - Zooplankton distribution patterns at two seamounts in the subtropical and tropical NE Atlantic focuses on the biomass distribution of mesozooplankton at Ampère and Senghor seamounts in relation to local and large-scale hydrodynamic features in a subtropical area as compared to a tropical region. Distribution patterns of distinct zooplankton size fractions were investigated for small-scale spatial patterns across each seamount with respect to diel vertical migration as well as their importance for carbon conversion. Evidence of higher primary and secondary production in the seamount ecosystems, expressed by high concentrations of zooplankton biomass as compared to the unaffected open ocean, was not detected.

In **Manuscript 2 - Microzooplankton and the dispersal of meroplanktonic larvae at two seamounts in the subtropical and tropical NE Atlantic** the importance of microzooplankton within the pelagic community at the subtropical Ampère Seamount and the tropical Senghor Seamount was investigated, and whether spatial distribution patterns of microzooplankton in terms of biomass and abundance exist due to local current-topography interactions and hydrographic conditions. The contribution of the microzooplankton community to the total zooplankton respiratory carbon demand was evaluated with respect to the distinct trophic regions in which each seamount is located. Furthermore the potential of the two seamounts as source for benthic invertebrate larvae in the open ocean was assessed.

The aim of **Manuscript 3 - From the epipelagic zone to the abyssal plain: Trophic interactions of zooplankton and benthopelagic fishes at two seamounts in the tropic-subtropical NE Atlantic** was to identify possible differences in feeding conditions and trophic structures at Ampère and Senghor seamounts compared to the open ocean as well as between the oligotrophic subtropical and the mesotrophic tropical region. Spatial differences in the composition of organic matter and in the diets and trophic positions of selected zooplankton and micronekton species were assessed from stable isotope analyses. The diets and trophic positions of benthopelagic fishes were investigated using a combination of stomach content and stable isotope ratios and were compared to the trophic signatures of the potential pelagic food sources sampled from the epipelagic to the abyssal zone.

In **Manuscript 4 - The fish fauna of Ampère Seamount (NE Atlantic) and the adjacent abyssal plain** an inventory of benthic and benthopelagic fishes and their vertical zonation is presented and compared to other NE Atlantic seamounts.

Manuscript 5 - Demersal fishes from Senghor Seamount and the adjacent abyssal plain (Central Eastern Atlantic) focuses on the deep-water biodiversity of the Cape Verde fish fauna in a zoogeographical context.

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Zooplankton distribution patterns at two seamounts in the subtropical and tropical NE Atlantic

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4.1 Abstract

Spatial distribution patterns of zooplankton biomass in relation to local and large-scale hydrographical and biological driving forces were studied at Ampère and Senghor, two shallow seamounts in the subtropical and tropical NE Atlantic, respectively. The study includes a first assessment of the taxonomic composition and an estimation of the respiratory carbon demand of the zooplankton community. Zooplankton was sampled during three cruises at the seamount and open ocean reference sites in May and September/October 2009 and in November/December 2010. Zooplankton standing stocks and the corresponding respiratory carbon demand were about 6 times higher at Senghor than at Ampère, with mean stocks of 24.7 and 4.6 g m^{-2}, respectively, in the upper 1000 m. Mean respiratory carbon demand in the epipelagic zone was calculated as 61.4 mg m^{-2} day^{-1} for Senghor and 9.6 mg m^{-2} day^{-1} for Ampère. At neither site were differences between seamount and open ocean sites significant. However, horizontal surveys across Ampère Seamount show clear differences between day and night distributions and a reduced biomass above the summit. Across Senghor, zooplankton biomass increased from the SW to the NE flank, with the highest concentrations in the subsurface layer of the chlorophyll maximum and just above a strong oxycline. The zooplankton community at Ampère Seamount reflects the oligotrophic character of the NE Atlantic subtropical gyre whereas the nutrient-rich waters of the cyclonic tropical gyre at Senghor support a higher biomass. This difference in the zooplankton biomass between the two seamounts can be attributed to the large-scale hydrographical features governing the productivity regimes rather than to regional seamount effects.

Keywords: carbon demand; composition; distribution patterns; seamount; subtropical-tropical NE Atlantic; zooplankton

4.2 Introduction

Seamounts are widespread elevations of usually volcanic or tectonic origin, which rise at least 1000 m above the ocean bottom (Rogers 1994). Through the interaction of their abrupt topography and the surrounding current regime, seamounts may affect the large-scale flow of the ocean and generate meso-scale variability in the water column (Roden 1994). In contrast to the surrounding flat sediment-covered abyssal plains, seamounts feature different habitats of hard substrata and soft bottom and have special geochemical and biological features.

For several seamounts, especially in the Pacific, aggregations of demersal and benthopelagic fish in high biomass concentrations have been reported (Rogers 1994; Koslow 1997; Parin et al. 1997; Koslow et al. 2000), leading to the assumption of higher primary and secondary production in the seamount ecosystem. A local increase in the chlorophyll *a* concentration has been observed over some seamounts shallower than ~300 m such as Minami-Kasuga (Genin & Boehlert 1985), Cobb (Dower et al. 1992) and Great Meteor (Mouriño et al. 2001), but this persisted only for short periods of days to 3 weeks. The chlorophyll *a* enhancement has been related to the occurrence of a Taylor column, an anticyclonic circulation cell trapped over the seamount summit (e.g. Freeland 1994; Beckmann & Mohn 2002), producing an uplift of deeper nutrient-rich water associated with particle retention (Genin & Boehlert 1985; Dower et al. 1992). But as there has been no evidence of any subsequent increase in secondary production, it is suggested that the retention time of the recirculating flow and therefore of the additional phytoplankton biomass above the summit is too short to be transferred to higher trophic levels and to increase zooplankton or nekton biomass (Genin & Boehlert 1985; Dower & Mackas 1996; Genin & Dower 2007). In many cases the zooplankton biomass is even lower above the seamount summit than in the surrounding waters, as observed at Great Meteor (Nellen 1973) and Seine and Sedlo seamounts in the NE Atlantic (Martin & Christiansen 2009). Advection of diel vertically migrating zooplankton associated with bottom trapping at dusk may be an important process for supplying the benthopelagic community over shallow seamounts with food, as the blocked zooplankton can easily be consumed by fish (Isaacs & Schwartzlose 1965; Genin et al. 1988, 1994; Haury et al. 2000; Wilson & Boehlert 2004). Over intermediate and deep seamounts an enhanced horizontal flux of plankton and organic particles due to strong interactions between amplified currents, internal waves and the seamount topography (Genin & Dower 2007; Clark et al. 2010) may be the major mechanism supporting high consumer biomass (Genin & Dower 2007).

Most studies suggest that the interaction between the flow field and the topography in combination with the general productivity regime is the key driver for shaping the pelagic communities at seamounts. The present study compares the biomass distribution of zooplankton at two seamounts in different hydrographical settings and different seasons. Ampère Seamount in the subtropical NE Atlantic lies within the sphere of the subtropical gyre, where the Azores frontal system as well as the seasonal variability of the NW African upwelling system (e.g. Mittelstaedt 1991; Van Camp et al. 1991) may influence the production at the seamount. At depths below 800 m, Ampère is reached by the Mediterranean outflow, which may affect the faunal composition of the seamount. In addition, the formation of meso-scale Mediterranean eddies, so called meddies (O'Neil Baringer & Price 1999), contribute to the dispersal of Mediterranean fauna in the NE Atlantic. Besides these large-scale hydrodynamic features, local seamount effects such as tidal resonance may influence the plankton biomass and production as well.

Senghor Seamount near the Cape Verde islands is located close to the equator (e.g. Morel 1996; Bory et al. 2001; Vangriesheim et al. 2003), where the influence of the Coriolis force on the current regime is small and no tidal resonance exists, which might be an important process for the biological retention potential of seamounts. The lack of seamount-trapped waves close to the equator could play an important role in the production at the seamount if this is not compensated by other local mechanisms such as Taylor caps, topographic trapping or trophic subsidy. Apart from these local seamount effects, the production at Senghor may be affected by the episodic input of Saharan dust (e.g. Chester et al. 1979; Kremling & Streu 1993; Prospero 1996; Bory et al. 2001) and seasonally by filaments of the Mauritanian upwelling (e.g. Mittelstaedt 1991; Vangriesheim et al. 2003). The ocean dynamics around Senghor Seamount is mainly characterized by the north equatorial current system which drives the north Atlantic tropical gyre (e.g. Mittelstaedt 1991; Lathuilière et al. 2008), and by the Cape Verde frontal zone (CVFZ) between North (NACW) and South Atlantic central water (SACW) (Zenk et al. 1991). The following main questions are addressed with respect to the biomass of meso- and macrozooplankton:

(1) Does the zooplankton biomass differ between the seamounts and the unaffected open ocean reference stations in terms of standing stock and vertical distribution?
(2) Does the zooplankton biomass show a spatial variability between distinct regions of the seamount (summit plateau, rim, slope, upstream, downstream) in terms of standing stock, vertical and size distribution patterns?
(3) Does the zooplankton biomass show a temporal variability between day and night in terms of vertical and size distribution patterns?
(4) Does the zooplankton community differ between a tropical and a subtropical seamount in the effects of the local and large-scale hydrodynamic features and the effects of different sampling seasons?

Zooplankton distribution above NE Atlantic seamounts has rarely been investigated before (e.g. Nellen 1973; Martin & Christiansen 2009). Processes such as particle retention or plankton advection and topographic blockage were more frequently observed at seamounts in the Pacific. Our study presents basic knowledge on spatial distribution patterns in relation to latitudinal and seasonal differences in terms of the local and large-scale current regime, compared for the first time between a subtropical and a tropical seamount.

4.2.1 Study sites

4.2.1.1 Ampère Seamount

Ampère Seamount is located in the subtropical NE Atlantic ~360 nm west of the Strait of Gibraltar and belongs to the Horseshoe Seamounts Chain between the island of Madeira and the Portuguese mainland (Fig. 4-1). The seamount rises from a base depth at 4500 m to a summit depth at 120 m, with one small peak rising to 55 m, partially overgrown with macroalgae in the photic zone (Christiansen unpubl. data). The seamount has a conical shape with a small, rough summit plateau and steep rocky slopes and canyons (Halbach et al. 1993; Kuhn et al. 1996; Hatzky 2005) as well as sediment-covered flat areas. For comparison, one open ocean reference station (hereafter referred to as 'far field') ca. 70 nm southwest of Ampère Seamount, located at 33° 48' N, 013° 00' W was also sampled. Water depth was about 4400 m above a flat sedimentary plain.

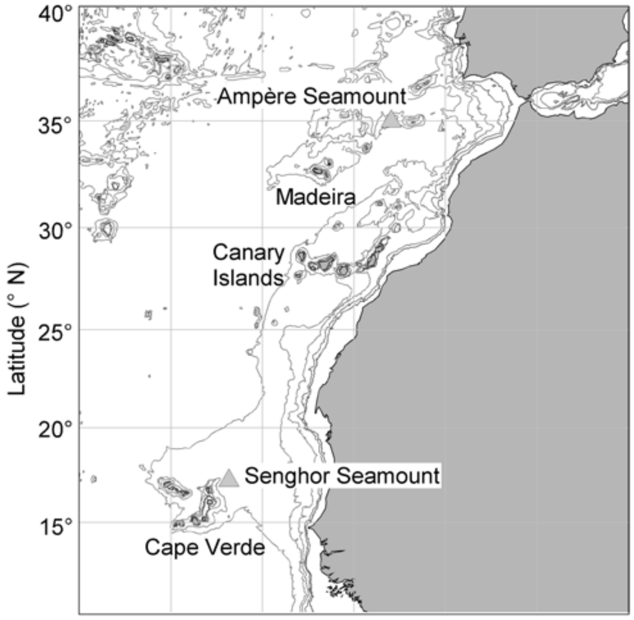

Fig. 4-1. Locations of Ampère and Senghor Seamount.

4.2.1.2 Senghor Seamount

Senghor Seamount is located in a tropical region ca. 60 nm east of the Cape Verde islands (e.g. Morel 1996; Bory et al. 2001; Vangriesheim et al. 2003) (Fig. 4-1). Water depth at the base of Senghor Seamount is ca. 3300 m; the minimum summit depth is 90 m. Senghor Seamount has a nearly circular shape with a small summit plateau, and features a heterogeneous surface structure, as shown by several ROV dives during cruise M79/3 of RV Meteor in September/October 2009 (Christiansen &

Koppelmann 2011). The summit plateau is covered with sediment in most parts but also shows rocky areas in the center, and ripple marks indicate strong currents at a water depth of 100 m. At the edge of the summit plateau at a depth of 320 m the sea floor is also sediment-covered, but without ripple marks. Along the slopes down to the deep sea floor, soft bottom alternates with rocky areas. For comparison, a far field station ca. 60 nm north of Senghor Seamount, located at 18° 05’ N, 022° 00’ W, was sampled. Water depth was about 3300 m above a flat sedimentary plain.

4.3 Materials and Methods

4.3.1 Zooplankton sampling

Zooplankton was caught by oblique and horizontal hauls with a 1 m²-Double-MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System; Wiebe et al. 1985) and by vertical hauls with a 0.25 m²-Hydro-Bios-MultiNet® (MSN, Weikert & John 1981). The MOCNESS carried 20 nets of 333 µm mesh size and sensors for temperature and salinity. Environmental data (temperature, salinity) were recorded simultaneously during sampling. The towing speed was 2 knots. The Multi-Net® was equipped with five 300 µm nets. MOCNESS and MultiNet® casts were generally performed during both day and night, to allow the study of diel vertical migration. The sampling took place in different seasons, not as part of the sampling design but due to logistics. Thus biomass concentrations of zooplankton will generally be affected by seasonal variability and will differ in spring, autumn and early winter besides the seamount correlated and latitudinal effects we want to assess in the present study.

Ampère Seamount was sampled during cruise P384 of RV Poseidon in May 2009 and during cruise M83/2 of RV Meteor in November/December 2010. On cruise P384, two oblique hauls were taken at the eastern mid slope with the MOCNESS and four horizontal hauls were taken above the summit of Ampère Seamount at 50 m depth and close to the bottom depth of the summit plateau (Fig. 4-2). During M83/2 the MOCNESS was used for four oblique hauls at the far field site and for 10 hauls at the eastern and western mid and deep slopes of the seamount. Sampling took place from close to the bottom to the surface. The sampling design with the smaller MultiNet® comprised four vertical profiles at the southern far field station and two orthogonal transects, one in a north-south and one in an east-west direction, across Ampère Seamount, with stations above the mid slopes down to 1000 m depth, above the rim of the plateau and above the summit. The water column was subdivided into following sampling intervals for MOCNESS and MultiNet® hauls, depending on the maximum water depth: 3000-2500-2000-1500-1000-750-500-400-300-200-100-50-25-0 m.

Zooplankton was sampled at Senghor Seamount during cruise M79/3 of RV Meteor in September/October 2009. Four oblique MOCNESS hauls were taken at the far field site and six hauls above the northwestern (NW) and southeastern (SE) slopes of Senghor Seamount (Fig. 4-2). The whole water column, subdivided into smaller sampling intervals, was sampled from a few meters above the bottom to the surface. Additionally, four horizontal hauls were taken above the seamount summit at 50 m depth and close to the bottom depth of the summit plateau. The sampling strategy with the MultiNet® and the sampling intervals were the same as at Ampère Seamount.

Upon recovery of the MOCNESS and the MultiNet®, the nets were rinsed with seawater. The material was preserved in a 4 % formaldehyde-seawater solution buffered with borax for biomass determination and taxonomic identifications.

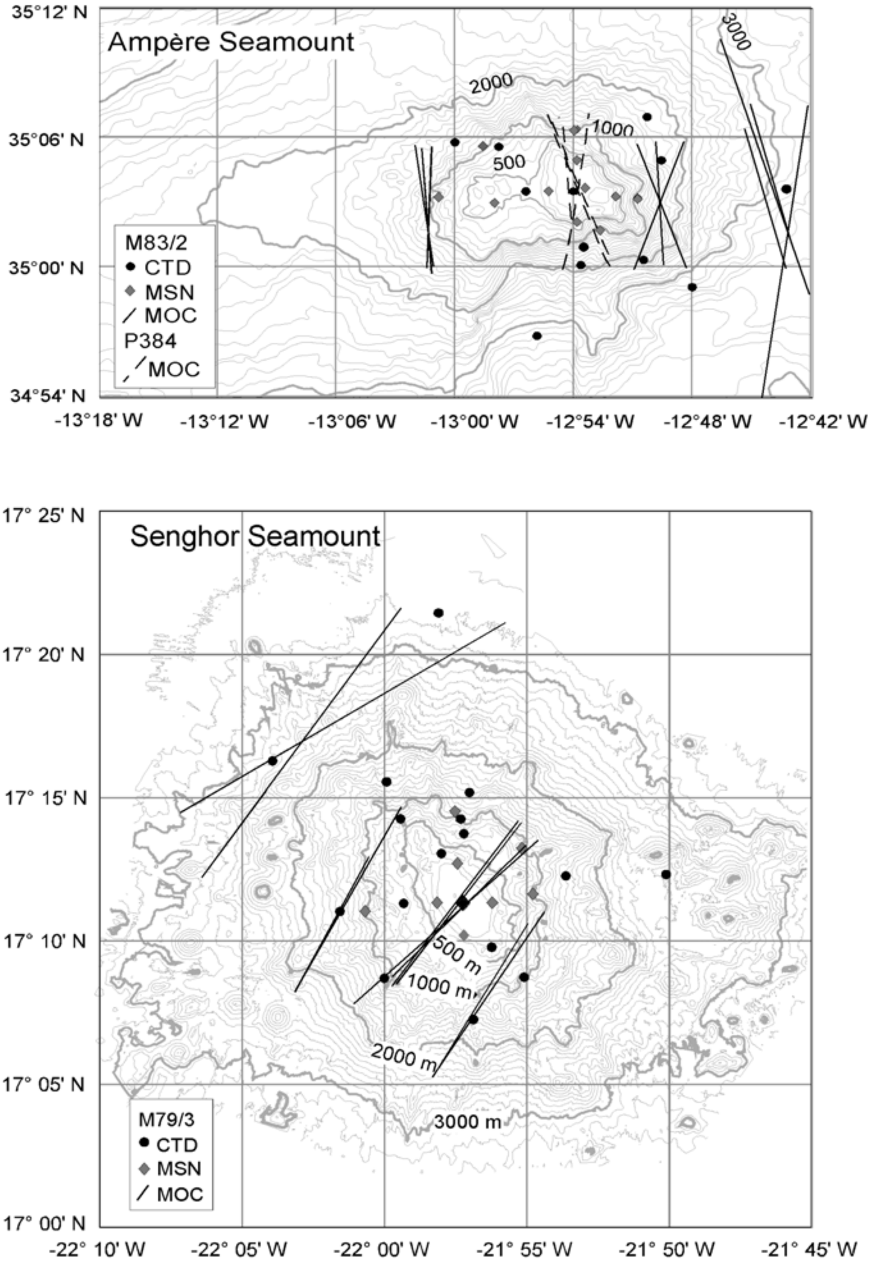

Fig. 4-2. Bathymetry and sampling locations at Ampère and Senghor seamounts. The locations of the MOCNESS, MSN and CTD hauls are shown for Ampère Seamount in May 2009 on cruise P384 and in November/December 2010 on cruise M83/2 and for Senghor Seamount in September/October 2009 on cruise M79/3.

4.3.2 Biomass analyses

In the laboratory, the zooplankton samples were fractionated by sieving into the size classes <0.5, 0.5-1, 1-2, 2-5, 5-20 and >20 mm and gelatinous organisms >20 mm. The wet weight of each size fraction was measured after removal of the interstitial water with 70 % alcohol according to the method of Tranter (1962). Wet weights were used instead of more accurate quantities of biomass, like dry weights, in order to preserve samples for subsequent taxonomic identification. Biomass (wet weight) was standardized to milligrams per 1 m^3 (mg m^{-3}). Standing stocks in terms of biomass for the whole water column or a given depth range were calculated as g m^{-2}, respectively.

4.3.3 Statistical analyses

For the statistical analyses, data were log-transformed [$Y' = \log(Y+1)$] to achieve approximate normal distributions and homogeneity of variances. One- and two-way analyses of variance (ANOVA; Clarke 1993; Lozán & Kausch 2004) were used to test for differences between zooplankton standing stocks and between vertical zooplankton distributions of the far field and the seamount stations as well as for differences between up- and downstream sites of a seamount.

4.3.4 Calculation of respiratory carbon demand

After wet weight determination, the size fractions of the integrated nets, which were not used for taxonomic analyses, were dried at 60 °C for 48-72 h until the sample reached a stable weight. The mean percentage of dry weight per size class was used to convert wet weights to dry weights. Size-specific respiration rates were calculated from body mass (dry weight) and temperature using a multiple-regression model after Ikeda et al. (2001):

$$\ln(\mu l\ O_2\ Ind^{-1}\ h^{-1}) = -0.399 + 0.801 \ln(\text{dry weight Ind}^{-1}) + 0.069\ \text{temp}$$

with temp = mean temperature of sampling intervals. The respiratory oxygen consumption rates were converted to carbon equivalents by the equation:

$$\mu g\ C\ Ind^{-1}\ h^{-1} = \mu l\ O_2\ Ind^{-1}\ h^{-1} * RQ * 12/22.4$$

using a respiratory quotient (RQ) of 0.97 (Omori & Ikeda 1984; Ikeda et al. 2000) and the atomic ratio of 12/22.4, where 12 g is the weight of carbon in 1 mol of 22.4 l carbon dioxide (Ikeda et al. 2000). The carbon respiration rates per individual (µg Ind^{-1} h^{-1}) were divided by individual dry weight (mg Ind^{-1}) to estimate the biomass-specific respiration rates (mg mg^{-1} h^{-1}). Community rates (mg m^{-3} day^{-1}) were calculated as the product of the biomass-specific respiration rates at the sampled depth layers and the corresponding biomass (mg dry weight m^{-3}). Respiratory carbon demands for distinct depth layers were calculated as mg m^{-2} day^{-1}. Since Ikeda's regression model refers only to epipelagic zooplankton, calculated respiration rates of zooplankton for the meso/bathypelagic zone (200-3000 m) were reduced by 50 %, following Ikeda et al. (2006), who concluded that meso/bathypelagic respiration rates were in the order of one-half to one-third that of epipelagic respiration.

4.3.5 Taxonomic analyses

Since this study is focused on biomass, only an overview of the taxonomic composition of zooplankton at the deep slopes of Ampère and Senghor seamounts will be presented here. For taxonomic analyses the fractionated zooplankton were sorted into higher taxonomic groups. Copepoda were identified to family or genus level, abundant taxa to species level. Carcasses, according to Wheeler (1967) and Weikert (1977), were counted separately, as were fragments of gelatinous organisms such as Siphonophora.

4.4 Results

4.4.1 Hydrography

At Ampère Seamount in spring 2009 the hydrographic profiles indicate a shallow, warm, surface layer with temperature of 18.0 °C and a salinity of 36.6 PSU in the upper 20-30 m (Fig. 4-3). A gradual decrease in temperature followed down to 800 m and in salinity to 600 m. Down to 1200 m, temperature remained rather constant, but salinity increased with some variability. Below this depth, both temperature and salinity decreased to minimum values of 2.9 °C and 35.0 PSU, respectively, at 3000 m.

In winter 2010, a warm surface layer of uniform temperature and salinity extended in the upper 60-80 m at all sampling locations (Fig. 4-3). Temperature varied between 18.8 °C at the seamount and 20.4 °C in the far field. Salinity was about 36.6 PSU. Below the mixed layer a steep gradient in temperature and salinity extended over 20 m, followed by a gradual decrease to 600 m depth at all stations. Down to 1200 m the temperature remained rather constant, whereas salinity increased, more pronounced at the slopes than at the far field site, followed by a decrease below 1200 m. At the greatest depth of 4500 m in the far field, temperature was 2.4 °C and salinity 34.9 PSU.

Surface water temperature at the far field site and at the slopes of Senghor was about 27.8 °C, building a warm mixed surface layer in the upper 20-30 m with salinity values about 36.2 PSU (Fig. 4-3). Down to 50 m, a steep gradient occurred with temperature and salinity decreasing. Between 100 and 1000 m temperature gradually decreased at all locations. The minimum temperature of 2.6 °C was observed in the far field, close to the bottom at 3300 m depth. Salinity generally decreased down to 800 m but showed some higher variability between 150 and 400 m at the slopes and in 500 m depth at the far field site. Below 800 m, salinity remained rather constant (34.9 PSU) with a slight increase between 900 and 1200 m.

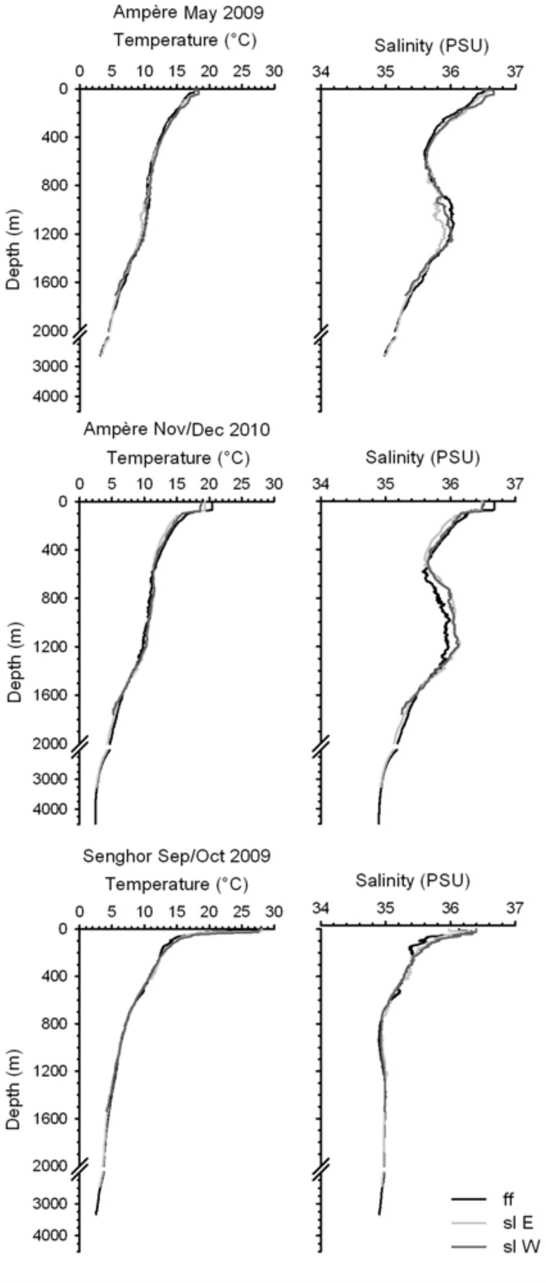

Fig. 4-3. Vertical profiles of temperature (°C) and salinity (PSU) at Ampère and Senghor seamounts and in the far field. Data are shown for Ampère Seamount in May 2009 and November/December 2010 and for Senghor Seamount in September/October 2009. ff, far field; sl, slope.

4.4.2 Zooplankton composition

Zooplankton were sorted into the following major groups: Cnidaria, Mollusca, Polychaeta, Cladocera, Harpacticoida, Cyclopoida, Calanoida, Ostracoda, Malacostraca, Chaetognatha, Tunicata, Crustacea-, fish- and other larvae, Stomiiformes (dragonfishes) and Myctophidae (laternfishes). At both seamounts, Calanoida were generally the most numerous organisms in the whole water column (Fig. 4-4).

At Ampère Seamount, Calanoida made up 44-77 % of the total zooplankton, with generally lower shares above 200 m as compared with the deeper layers. By contrast, Cyclopoida (16-26 %) and Mollusca (2-11 %) had the highest relative abundances in the upper 100 m. Ostracoda were rarely observed in the upper 25 m, whereas Chaetognatha (2-11 %) tended to be the most important in the bathypelagic layers. All other groups contributed less than 5 % to the total zooplankton at all depths. At Senghor Seamount, Calanoida contributed 49-85 % to the total zooplankton and had markedly higher shares below 500 m than above. No clear patterns were observed for Cyclopoida (4-37 %), Ostracoda (1-12 %) and Chaetognatha (1-12 %). All other groups contributed less than 5 % to the total zooplankton at all depths.

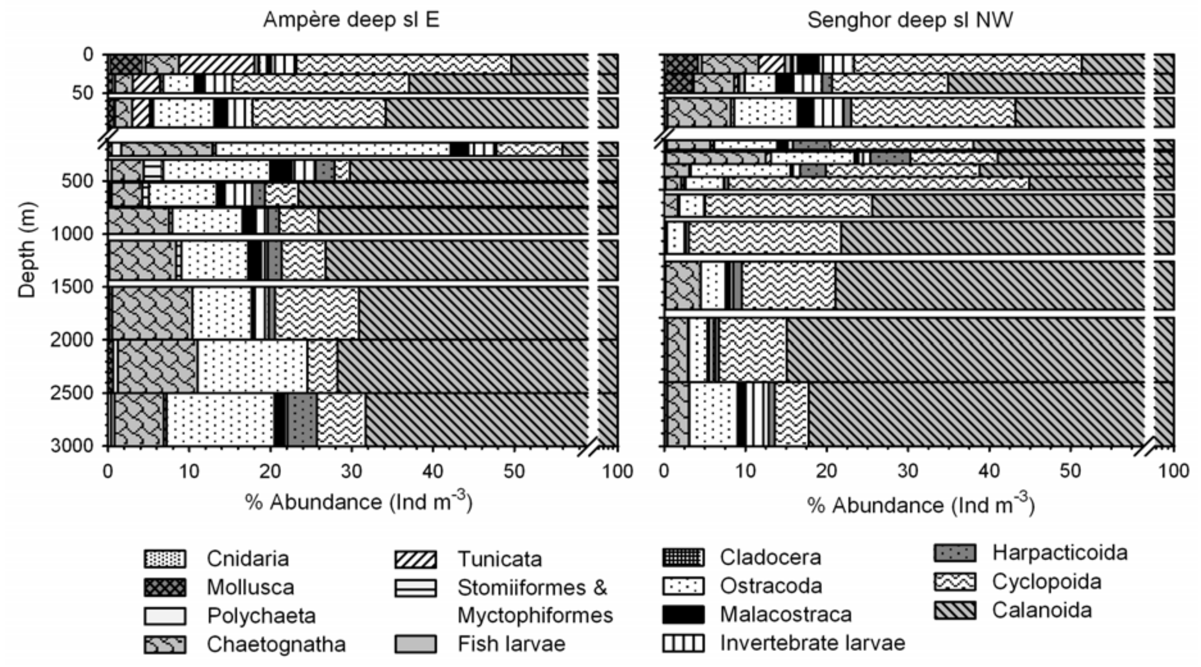

Fig. 4-4. Relative composition (%) of the major zooplankton groups (Ind m^{-3}) during night at the E slope of Ampère Seamount in December 2010 and at the NW slope of Senghor Seamount in October 2009.

4.4.3 Distribution of standing stocks and size classes

The standing stocks of zooplankton in the upper 1000 m were compared between slope and far field stations. In November/December 2010, mean stocks at Ampère differed little between stations, but were twice as high at the mid-eastern slope in May 2009 (Fig. 4-5). For the bathypelagic zone, data are only available for the far field site and the deep slope from the winter 2010 period. Here, standing stocks were about half as high as in the upper 1000 m.

The difference between the epi/mesopelagic and the bathypelagic zones was much more pronounced at Senghor Seamount than at Ampère, the standing stocks being nearly one order of magnitude lower in the layer 1000-2500 m (Fig. 4-5). Standing stocks in the upper 1000 m were slightly higher at the seamount stations than in the far field, but the reverse was found in the bathypelagic zone.

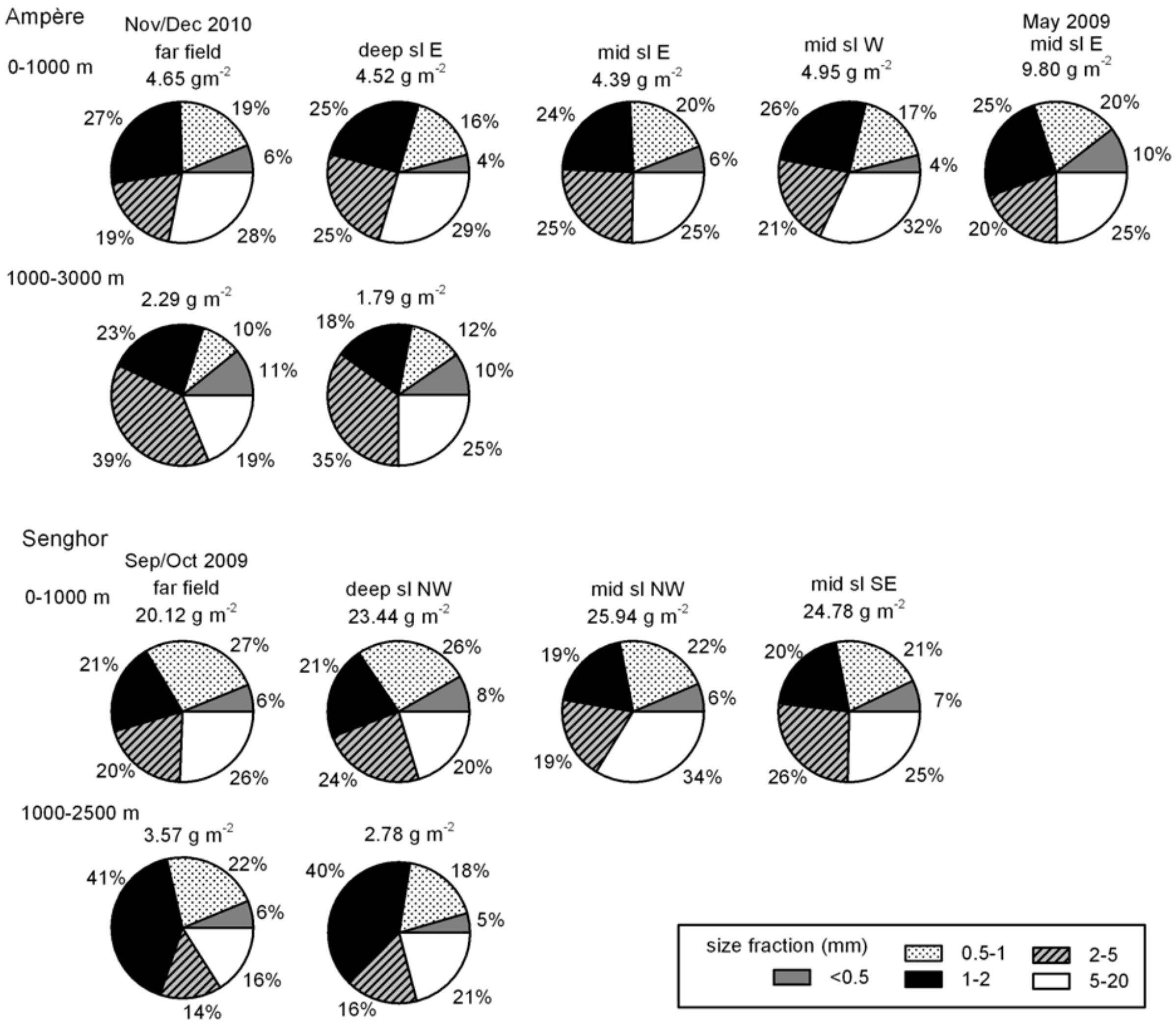

Fig. 4-5. Standing stock of zooplankton (<20 mm) biomass (g m^{-2}) and size composition (%) at the slopes of Ampère and Senghor seamounts and in the far field. Data are shown for Ampère Seamount in May 2009 and November/December 2010 and for Senghor Seamount in September/October 2009 (mean values of day and night MOCNESS hauls). sl, slope.

Differences between the far field and the pooled slope stations, for each seamount respectively, were not statistically significant for either Senghor or Ampère (Table 4-1). However, the zooplankton standing stock in the upper 1000 m (slope stations pooled) was significantly higher at Senghor than at Ampère, whereas below 1000 m the standing stocks did not differ significantly (Table 4-1).

Table 4-1. One-way ANOVA for differences in biomass standing stocks between seamount slopes and the far field.

depth (m)	**fixed effect location**	**n**	**df**	**F-ratio**	**p**
0-1000	Ampère slope	10			
	far field	4	1,12	0.018	0.897
0-1000	Senghor slope	6			
	far field	4	1,8	3.535	0.097
0-1000	Ampère slope	10			
	Senghor slope	6	1,14	368.791	<0.001
1000-3000	Ampère slope	2			
	Senghor slope	2	1,2	2.355	0.265

df, degrees of freedom; F, F-ratio of mean squares; p, probability of error.

The size composition of zooplankton in terms of biomass in the upper 1000 m was similar at all Ampère Seamount sampling sites (Fig. 4-5). The size classes 0.5-20 mm contributed nearly equally to the total biomass, whereas the size class <0.5 mm contributed a markedly lower share. A slightly higher contribution of the smaller size classes was observed in spring 2009. Below 1000 m, the size distribution shifted to a predominance of size class 2-5 mm, but the 0.5-1 mm fraction reached only 10-12 %.

At Senghor Seamount the size composition of zooplankton in the upper 1000 m was similar to Ampère and differed little between sampling sites (Fig. 4-5). However, in the bathypelagic zone the size composition changed in favor of the size fraction 1-2 mm, contributing 40 % of the total biomass, whereas the share of the larger fraction 2-5 mm decreased.

4.4.4 Small-scale distribution of standing stocks in the upper 100 m: orthogonal transects

At Ampère Seamount, stocks of mesozooplankton showed some variability between stations, but no clear spatial pattern or day-night differences were detected in the upper 100 m (Fig. 4-6).

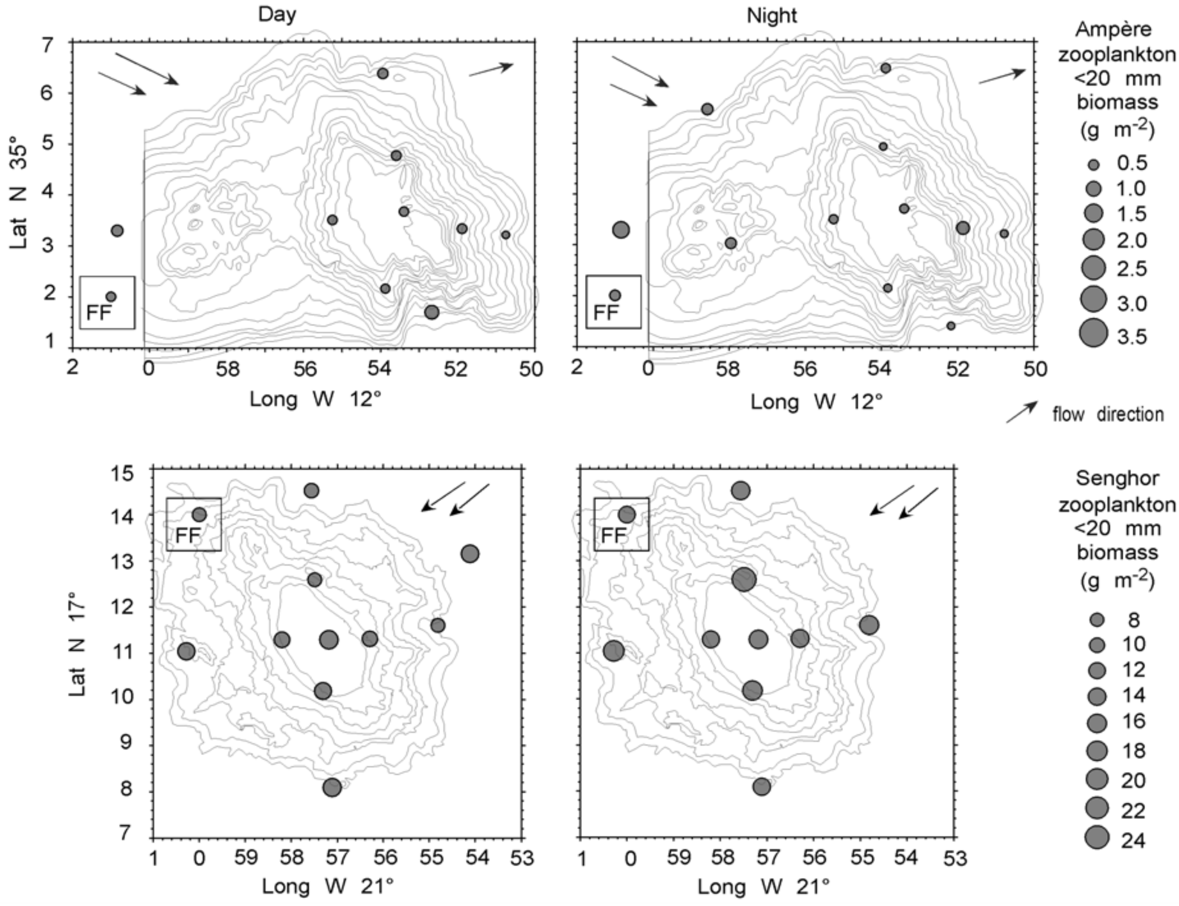

Fig. 4-6. Small-scale distribution of zooplankton (<20 mm) biomass (g m^{-2}) during the day and at night in the upper 100 m above Ampère Seamount in November/December 2010 and Senghor Seamount in September/October 2009. FF, far field.

Spatial differences in biomass standing stocks in the upper 100 m were slightly more pronounced at Senghor Seamount (Fig. 4-6). During the day, the standing stocks above the NE, S and W slopes and the summit were higher than at the N and E slopes and the rim stations. At night, the biomass in the upper 100 m was generally higher than during the day. The highest standing stocks were observed at the N and S rim stations, and at the E and W slope locations.

4.4.5 Biomass concentrations and size class distributions from horizontal surveys

Horizontal surveys at depths of 50 and 90 m from Ampère are available only from spring 2009. Biomass concentrations of zooplankton <20 mm along the horizontal surveys were at 50 m twice as high at night as during the day. At 90 m depth, the concentrations above the slopes were also higher during the night but in the center, concentrations were in the same range as the daytime biomass. All transects showed similar distribution patterns, with the highest concentrations above the slope on each side, a decrease towards the rim of the summit plateau and medium concentrations above the plateau (Fig. 4-7).

During the day the biomass concentration at 50 m decreased from the SE slope towards the summit and increased again along the NW slope to 35 mg m^{-3}. Similarly, at 90 m depth, the lowest values were observed above 200 m (2-3 mg m^{-3}), a higher concentration above the summit and increasing concentrations along the NW slope. To test for differences between the upstream (NW) and downstream (SE) sides of the seamount, slope data for each side were pooled, but differences were not significant in either 50 m or 90 m (Table 4-2).

At night biomass concentrations at 50 m showed the same pattern as during the day and decreased from the SE slope towards the summit rim. On the summit plateau, biomass was 25-30 mg m^{-3} and increased along the NW slope to 65 mg m^{-3}. Pooled concentrations on the NW site were significantly higher than on the SE side. The 90 m transect was sampled in a SW-NE direction. The biomass along both sides decreased from the outer slope towards the summit rim. The pooled data of each slope show a significant higher biomass on the SW site than on the NE side (Table 4-2).

Table 4-2. One-way ANOVA for differences in horizontal biomass distribution between up- and downstream sides of Ampère Seamount.

Ampère	fixed effect side	n	df	F-ratio	p
50 m day	upstream	6			
	downstream	6	1,10	0.648	0.439
90 m day	upstream	6			
	downstream	6	1,10	2.291	0.161
50 m night	upstream	6			
	downstream	6	1,10	38.467	<0.001
90 m night	upstream	6			
	downstream	7	1,11	5.020	0.047

df, degrees of freedom; F, F ratio of mean squares; p, probability of error.

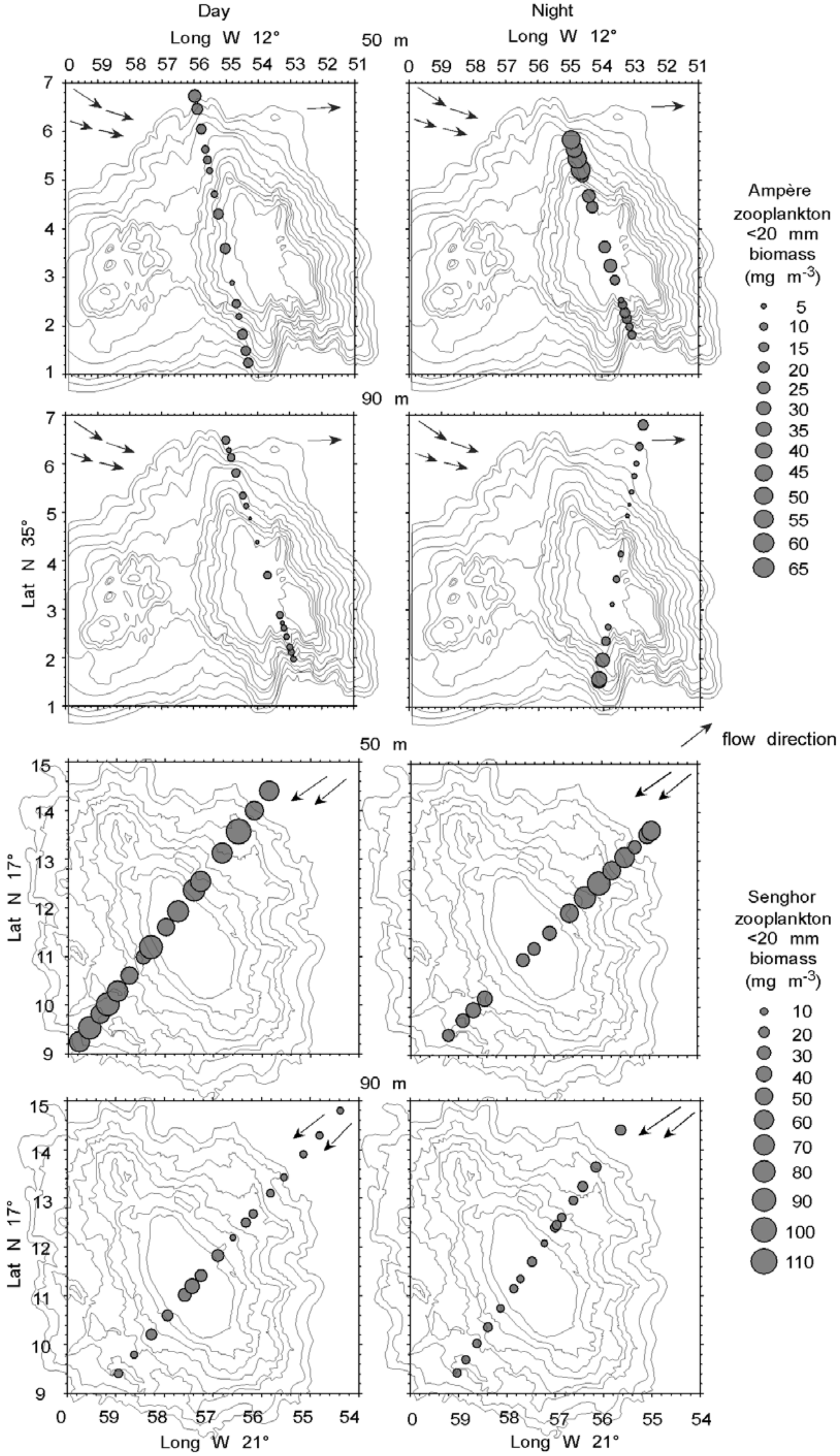

Fig. 4-7. Horizontal distribution of zooplankton (<20 mm) biomass (mg m^{-3}) during the day and at night in 50 and 90 m depth above Ampère Seamount in May 2009 and Senghor Seamount in October 2009.

The biomass concentrations of zooplankton above Senghor Seamount along horizontal surveys between the 1000 m isobaths were up to four times higher in 50 m than in 90 m depth, both during the day and at night (Fig. 4-7). At 50 m depth, differences between the daytime biomass concentrations along the survey were small and showed no clear spatial pattern. Along the 90 m depth transect, highest daytime biomass concentrations of 21-38 mg m^{-3} were observed above the plateau and rim, whereas the concentrations were markedly lower above the SW and NE slopes, ranging from 9 to 15 mg m^{-3}. For statistical analysis, slope data of each side were pooled and showed a significant higher biomass for the NE upstream side of Senghor at 90 m, but not at 50 m (Table 4-3).

During the night, higher biomass concentrations were observed above the NE slope than at the summit plateau and the SW slope. At 50 m depth, concentrations increased from 26 to 92 mg m^{-3} along the SW-NE transect. At 90 m, the range was smaller, from 11 to 20 mg m^{-3}. In both depths a higher biomass on the NE upstream side of Senghor was confirmed statistically (Table 4-3).

Table 4-3. One-way ANOVA for differences in horizontal biomass distribution between up- and downstream sides of Senghor Seamount.

Senghor	**fixed effect side**	**n**	**df**	**F-ratio**	**p**
50 m day	upstream	4			
	downstream	7	1,9	0.429	0.529
90 m day	upstream	5			
	downstream	6	1,9	9.434	0.013
50 m night	upstream	5			
	downstream	5	1,8	6.517	0.034
90 m night	upstream	5			
	downstream	6	1,9	8.695	0.016

df, degrees of freedom; F, F ratio of mean squares; p, probability of error.

The size composition along the horizontal transects above Ampère Seamount indicates different patterns in the two depth layers (Fig. 4-8). Generally, most of the biomass along transects was made up of the size classes 0.5-1 and 1-2 mm, each contributing 18-52 % to the total biomass. At 50 m, no clear spatial pattern was observed, but the importance of the smallest size group <0.5 mm was reduced during the night, whereas there were smaller proportions of the two largest size classes 2-5 and 5-20 mm during the day.

At 90 m, a clear horizontal pattern could be observed for the size group 5-20 mm during the night. Above the summit their contribution to the total biomass was negligible at 3 %, but increased to a maximum of 42 % above the 1000 m contour at the SW slope and to 27 % at the end of the transect above the NE slope. Similarly, the share of the size group 2-5 mm had a minimum above the summit and increased towards the outer parts of the survey above the slopes.

The relative distribution of zooplankton size classes along the horizontal transects above Senghor Seamount indicates differences between 50 and 90 m depth as well as between the SW and NE sides of the seamount (Fig. 4-8). Generally, zooplankton <0.5 mm contributed very little (<10 %) to the total biomass. Most of the biomass (38-87 %) at 50 m was made up of the size fraction 2-5 mm along the whole survey area. Whereas no spatial pattern was observed during the day, size class 1-2 mm had higher shares on the SW slope at night, and zooplankton of 5-20 mm had enhanced relative proportions above the NE rim and upper slope.

In 90 m depth, most of the biomass was made up of the two large size groups 2-5 and 5-20 mm during the day, with a trend for increasing shares of size group 5-20 mm towards the SW side. A similar spatial trend for this size group was observed during the night, but with generally lower shares along the whole track as compared with the daytime. On the other hand, size group 1-2 mm had markedly higher shares during the night along the transect and slightly higher shares were observed for size group 0.5-1 mm on the SW side.

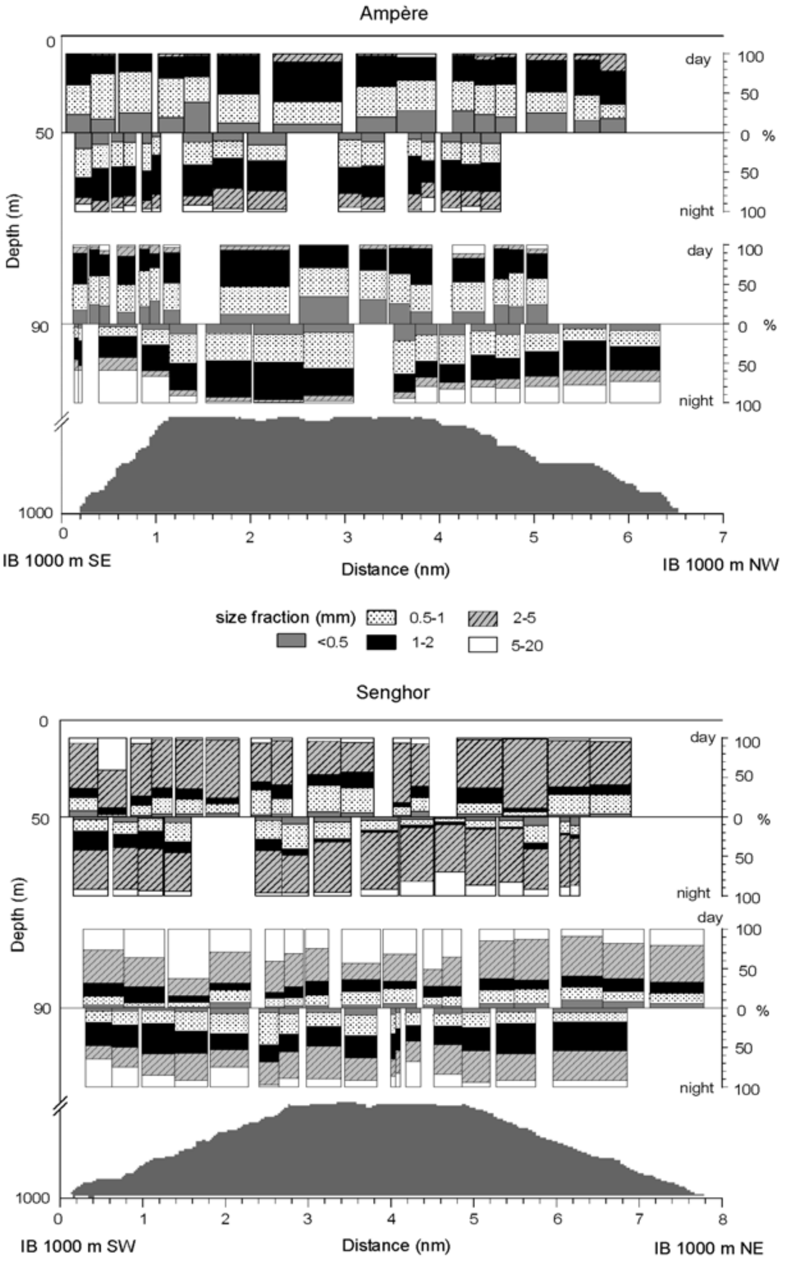

Fig. 4-8. Horizontal distribution of zooplankton size composition (%) in terms of biomass (mg m^{-3}) during the day and at night in 50 and 90 m depth above Ampère Seamount in May 2009 and Senghor Seamount in October 2009. IB, isobath.

4.4.6 Vertical distribution patterns of biomass concentrations

The biomass concentrations showed similar vertical patterns at all stations for both areas. Highest concentrations were always found in the upper 50 m, below which they declined rapidly down to 200 m depth and then gradually to 1000 m. A further strong decline was observed below 1000 m. A small second biomass peak between 200 and 400 m occurred at all Senghor stations, but only above the W mid slope in 2010 and the E mid slope in 2009 at Ampère (Fig. 4-9).

Day/night differences were small at Ampère, but the far field, NW deep slope and SE mid slope stations at Senghor featured enhanced biomass concentrations at night between 200 and 400 m. The winter 2010 data from Ampère (day and night data pooled) showed neither a significant interaction between location and depth, nor significant differences between the far field and the three slope stations in the upper 1000 m (Table 4-4). However, differences in biomass between the six depth layers were significant. The general decrease below 100 m in the vertical distribution was confirmed by subsequent Bonferroni comparisons of the distinct depths.

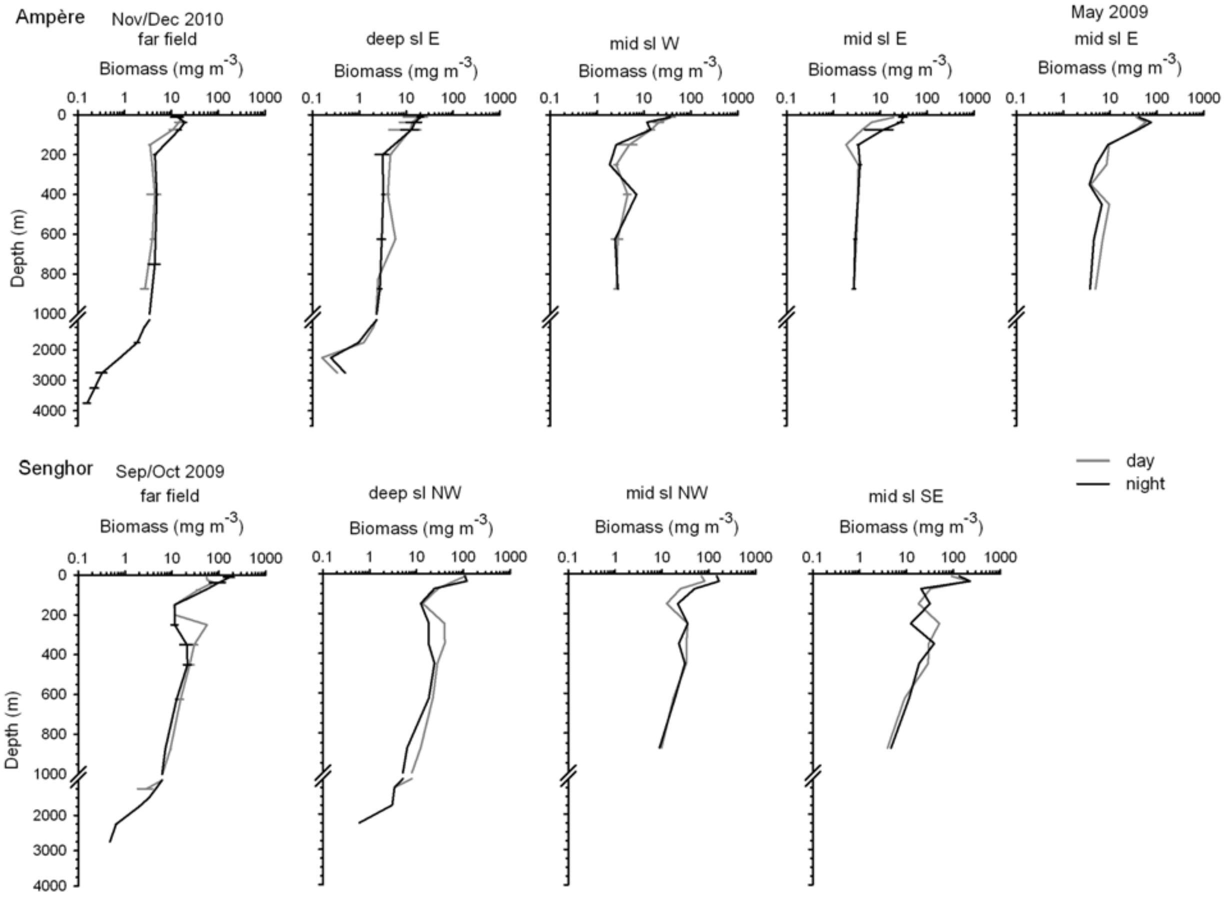

Fig. 4-9. Vertical distribution of zooplankton (<20 mm) biomass (mg m^{-3}) on a logarithmical scale at the slopes of Ampère and Senghor seamounts and in the far field during the day and at night. Data are shown for Ampère Seamount in May 2009 and November/December 2010 and for Senghor Seamount in September/October 2009. sl, slope; horizontal lines, range between minimal and maximal values.

Similarly, for pooled day and night data from Senghor, the interaction between location and depth was not significant nor were differences between the three slope stations and the far field (Table 4-4). However, biomass differed significantly between the nine depth layers in the upper 1000 m. Subsequent Bonferroni comparisons of different depths confirm the strong decrease below 50 m as well as changes in the mesopelagic depth and below 750 m.

Table 4-4. Two-way ANOVA for differences in vertical biomass distribution above Ampère and Senghor seamounts and in the far field.

				fixed effects		
location	**depth (m)**	**n**		**location*depth**	**location**	**depth**
Ampère mid slope W	0-25-50-100-300-500-1000	3	df	15,59	3,79	5,77
Ampère mid slope E		3	F-ratio	1.196	0.581	35.047
Ampère deep slope E		4	p	0.300	0.629	<0.001
far field		4				
Senghor mid slope SE	0-25-50-100-200-300-400-500-750-1000	2	df	24,49	3,81	8,76
Senghor mid slope NW		2	F-ratio	1.144	0.211	44.051
Senghor deep slope NW		2	p	0.337	0.889	<0.001
far field		4				

df, degrees of freedom; F, F-ratio of mean squares; p, probability of error.

4.4.7 Carbon demand

The depth-integrated respiratory carbon demand of the total zooplankton stock, subdivided into the epi-, meso- and bathypelagic zone, was compared between Ampère Seamount in November/December 2010 and Senghor Seamount in September/October 2009. In the epi- and mesopelagic zones, the overall carbon demand of mesozooplankton was about 6 times higher at Senghor (16.4-61.4 mg m^{-2} day^{-1}) than at Ampère (2.7-9.6 mg m^{-2} day^{-1}), whereas in the bathypelagic zone it was nearly in the same range (1.5.1.8 mg m^{-2} day^{-1}) (Fig. 4-10).

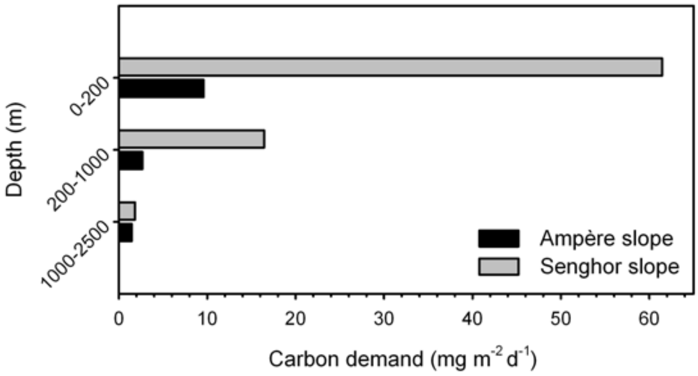

Fig. 4-10. Depth integrated respiratory carbon demand (mg m^{-2} d^{-1}) of the zooplankton standing stocks (<20 mm) at night at the slopes of Ampère Seamount in November/December 2010 and Senghor Seamount in September/October 2009.

The contribution of the single size groups to the total respiratory carbon demand varied with different depth. In the epipelagic zone (0-200 m) of Ampère Seamount, the carbon demand was dominated by smaller zooplankton (mainly size classes 0.5-1 mm and 1-2 mm), being responsible for up to 75 % of the total carbon demand (Fig. 4-11). Below 200 m, the two larger size groups, 2-5 and 5-20 mm, gained importance; their share increased up to 50 %.

At Senghor, a clear break between the epi- and mesopelagic zone and the bathypelagic zone was observed (Fig. 4-11). Between the surface and 1000 m, size group 0.5-1 mm predominated, its share increasing with depth to 50 % of the total respiratory carbon demand. Below 1000 m the 1-2 mm fraction became the predominant group, constituting up to 71 % of the carbon demand. The other size classes contributed less than 30 % each to the total carbon demand.

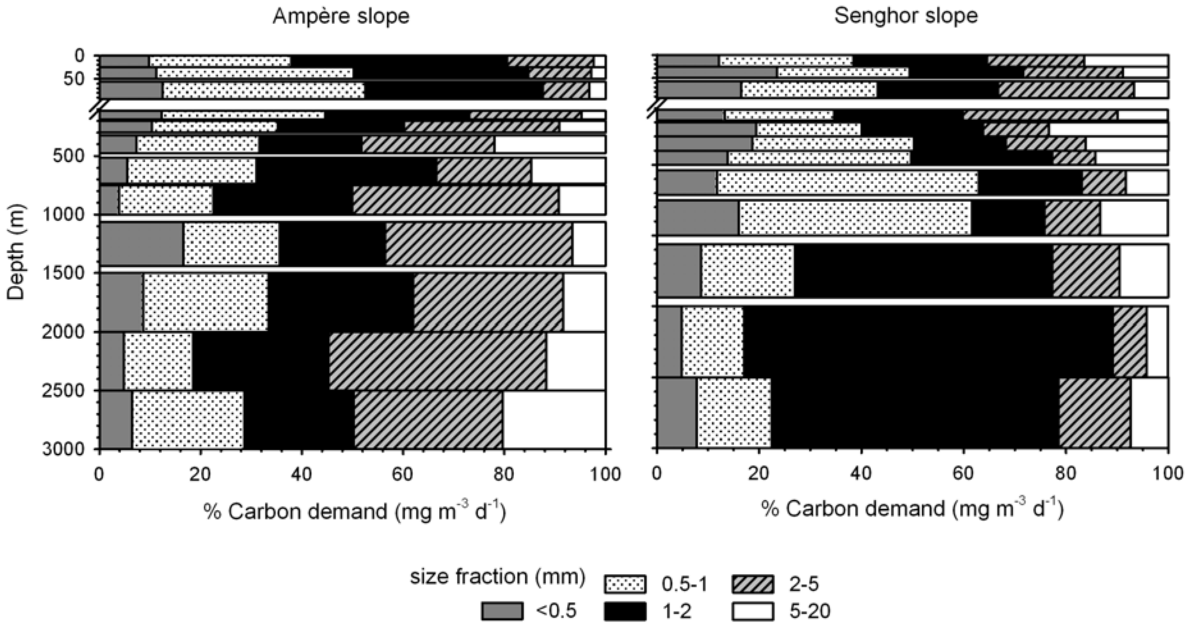

Fig. 4-11. Percentage contribution of size-specific respiratory carbon demand (mg m^{-3} d^{-1}) at night at the slopes of Ampère Seamount in November/December 2010 and Senghor Seamount in September/October 2009.

4.5 Discussion

The principal objective of this study was to investigate whether spatial and temporal distribution patterns of zooplankton exist at two latitudinal distinct seamounts in the NE Atlantic, Senghor and Ampère, and how distribution patterns and composition may differ between a tropical and a subtropical region depending on local and large-scale hydrodynamic features and between different seasons.

4.5.1 Latitudinal and seasonal variability of zooplankton biomass

In general, the zooplankton biomass standing stock in the upper 1000 m was about 6 times higher at Senghor Seamount in autumn 2009 than at Ampère in winter 2010 and about 2.5 times higher than at Ampère in spring 2009. Ampère Seamount is enclosed by the anticyclonic subtropical gyre which extends between 37° and 24° N (Longhurst 1995; Lathuilière et al. 2008). The eastern branch of this gyre is driven by the Azores and Canary current. Separated from the subtropical gyre by the CVFZ (e.g. Zenk et al. 1991), Senghor Seamount is located within the sphere of the cyclonic tropical gyre (19°-10° N), which is influenced by the equatorial current system and the Mauritanian upwelling (e.g.

Mittelstaedt 1991; Pelegrí et al. 2006; Pastor et al. 2008; Mason et al. 2011). The difference in the zooplankton biomass between the two seamounts can be attributed to the large-scale hydrographical features governing the productivity regimes rather than to regional seamount effects, as explained below.

4.5.1.1 Ampère Seamount and sphere of the subtropical gyre

The hydrographical profiles at Ampère Seamount show a strong thermocline persisting in November/December 2010 at a depth of 70-100 m, whereas in May 2009 the water column was mixed, with a weak indication of a developing thermocline at around 30 m. In spring, the deep chlorophyll maximum (DCM) occurred at a depth of 60-75 m, similar to previous observations at Seine and Sedlo seamounts in the NE Atlantic (Kiriakoulakis et al. 2006; Kaufmann unpubl. data). In winter, the DCM was observed at a slightly deeper depth of around 80 m (Kaufmann & Diniz 2012). The peak of the zooplankton biomass lay above the weak thermocline in spring, but nearly within the thermocline in winter. In comparison with the OASIS seamounts, the concentration of chlorophyll *a* was generally higher above Ampère (0.5-0.8 µg l^{-1}) in spring than above Seine in spring and autumn (0.2-0.5 µg l^{-1}) and above Sedlo in autumn (0.28-0.42 µg l^{-1}). Processed chlorophyll data of the Ampère winter season are not yet available. The chlorophyll concentrations in the area reflect the typical conditions in oligotrophic waters as described by Barton et al. (1998) for the NW area of the Canary Islands, with chlorophyll concentrations <0.5 µg l^{-1} in the surface mixed layer and ~0.1 µg l^{-1} in the DCM.

Differences in vertical zooplankton biomass profiles and in total standing stocks were small between seamount and far field stations in winter 2010 and did not indicate any local seamount effect on zooplankton distribution. The zooplankton biomass at Ampère in spring 2009 was twice as high as at Seine in May 2009 and in March-April 2003 and 2004, at least in the upper 200 m (Denda unpubl. data; Hirch et al. 2009; Martin & Christiansen 2009), in agreement with the observed higher concentrations of chlorophyll *a*. In November/December 2010, the water column was still stratified, leading to nearly exhausted nutrients, which explains the reduced zooplankton biomass as compared with May after nutrient replenishment during winter mixing and the onset of the phytoplankton bloom. The subtropical gyre is generally characterized by an additional late winter phytoplankton bloom (Arístegui et al. 2001), which is a feature of the winter convection and typical of oligotrophic regimes (Lathuilière et al. 2008). As a reaction to the enhanced food availability, an increase in zooplankton biomass can be expected after our sampling period, as observed by Hernández-León et al. (2004) in waters north of the Canary Islands.

The advection by the Azores current may be a reason for the higher biomass in phyto- and zooplankton at Ampère as compared with Seine Seamount. However, two small corridors north and south of the Azores front (33°-38° N) feature long-lived westward propagating cyclonic and anticyclonic eddies (Sangrà et al. 2009), which also affect the local current regime and produce regional and temporal variability in the area of both adjacent seamounts.

4.5.1.2 Senghor Seamount and sphere of the tropical gyre

In the tropical region around Senghor Seamount, a strong thermocline below 30 m inhibited mixing between surface and deep waters in autumn 2009. While nutrients were depleted in the surface mixed layer, the concentrations were relatively high just below the thermocline at 30 m, comparable to Ampère at 250 m, and increased rapidly with depth (Kaufmann et al. 2011). Pelegrí et al. (2006) proposed a connection between the seasonal coastal upwelling south of the CVFZ, pumping nutrients into the surface layers, and the high nutrient levels in subsurface waters off Cape Verde. In general, the SACW, which determines the waters south of the CVFZ, is considered as nutrient-rich (Pastor et al. 2008). Chlorophyll data are not yet available for the sampling period in autumn 2009 but preliminary results indicate that the DCM coincided with the nutricline (Kaufmann et al. 2011). A slightly deeper DCM between 25 and 50 m with lower chlorophyll *a* concentrations at the bottom of the thermocline was observed in December 2011 (Springer unpubl. data) and in April 2005 (Meyer-Klaeden 2007).

The shallow DCM at Senghor might be a response to positive wind stress curl and upward Ekman pumping within the cyclonic tropical gyre, which together create a shallow nutricline and increase the nutrient concentrations in the subsurface waters (Lathuilière et al. 2008). During the coastal upwelling season from October to May along the southern part of the NW African coast, surface chlorophyll concentration increases from 1 to 10 µg l^{-1} and extends up to 300-400 km from the shore (Lathuilière et al. 2008) into the area of Senghor Seamount. The lower chlorophyll *a* concentration of April 2005 might be due to the beginning of relaxation of the coastal upwelling that is reflected by a drop of the surface chlorophyll and a much smaller offshore extension (Lathuilière et al. 2008). In contrast, negative wind stress and downward Ekman pumping within the anticyclonic subtropical gyre force a deep nutricline and lower nutrient concentrations of waters brought by coastal upwelling than further south (Lathuilière et al. 2008) and result in significant lower biomass concentrations at Ampère compared with Senghor Seamount.

Vertical profiles of biomass concentrations and total standing stocks of zooplankton differed only little in the upper 1000 m between far field and seamount stations, giving no indication of a local effect of the interaction between seamount and current field on the zooplankton distribution. Similarly, no influence of coastal upwelling filaments or the position of the CVFZ could be observed. Temperature and salinity between 150 and 600 m indicate the influence of SACW both at Senghor and in the far field. The SACW is characterized by temperatures between 15.2 and 9.7 °C and a salinity of 35.7-35.2 PSU (Tomczak 1981). The salinity of 34.9 PSU between 800 and 1000 m corresponds to the Antarctic intermediate water (AAIW) (e.g. Pierre et al. 1994). This water mass distribution indicates that both locations, the seamount and the far field, lie within the so called ‘shadow zone’, south of the CVFZ (Tomczak 1981; Zenk et al. 1991).

4.5.2 Latitudinal differences in zooplankton composition

An analysis of the zooplankton composition at a lower taxonomic level will be necessary for a detailed assessment of possible taxonomic differences at a regional and at a local scale with respect to water masses and current fields. However, some differences between the two seamounts were observed in higher taxonomic groups.

Latitudinal differences between Ampère and Senghor seamounts show up in a higher proportion of smaller sized copepods at Senghor, as can be expected in a tropical region (Angel & de Baker 1982; Weikert & Trinkhaus 1990). In the whole water column the importance of copepods seems to be greater at Senghor than at Ampère. The general shift within copepods towards cyclopoids and harpacticoids in warm waters (Schneider 2002) is reflected by relatively high proportions of both groups at Senghor Seamount. Due to smaller average size of particles and faster bacterial degradation in warm surface waters (Angel & de Baker 1982), the abundance of fine-filter feeders such as salps and pteropods usually increases from boreal to tropical waters (Schneider 2002), as visible in the epipelagic zone above Ampère. However, at Senghor, salps and pteropods were almost absent. Instead, small herbivorous calanoids and cyclopoids were prevalent in the upper 100 m (Denda unpubl. data). Of the eastern tropical Pacific it is known that salps and small herbivorous copepods have species-specific depths of maximum abundance on the upper side of the shallow and steep thermocline (Longhurst & Harrison 1989).

Differences between Ampère and Senghor were also observed in the relative abundances of chaetognaths and ostracods. The higher proportion of chaetognaths in the upper 100 m at Senghor as compared with Ampère may be a result of the higher abundance of small copepods, their favorite prey. The contributions of chaetognaths and ostracods to the total community at Ampère were higher in the meso- and bathypelagic zones.

4.5.3 Small-scale spatial variability and size distribution patterns of zooplankton biomass

The biomass standing stocks of total zooplankton showed some variability, but without a clear spatial pattern for the upper 100 m of both seamounts. However, along the horizontal transects, part of the variability of biomass concentrations and size composition can be attributed to the interaction of the local current field with the seamount topography, the proportion of migrating and non-migrating organisms, and predation pressure, as pointed out below.

4.5.3.1 Sphere of Ampère Seamount

Differences of standing stock between stations along the orthogonal transects at Ampère Seamount were small and did not indicate any relationship with the topography or to the flow field. Phytoplankton (Kaufmann pers. com.) and zooplankton biomass were both slightly higher at the seamount than in the far field, which could be an indication of an effect of the seamount on the plankton community in surface waters. Day-night differences in the upper 100 m were generally small.

The horizontal surveys across Ampère Seamount show clear differences between day and night distributions, indicating diel vertical migrations. The pattern of the zooplankton distribution across the seamount seems to correspond to the mechanism of topographic blockage and gap formation, as described by several authors, particularly for seamounts with summit depths of 100-300 m (Isaacs & Schwartzlose 1965; Genin et al. 1988, 1994; Haury et al. 2000). The daily migrating zooplankton would be blocked by the shallow summit of Ampère during its descent at dawn, trapped during the day and eaten by (benthopelagic) resident visual predators such as planktivorous fish and invertebrates, as reported by Genin et al. (1994) for the Sixtymile Bank in the NE Pacific, or mesopelagic micronekton, as supposed by De Forest & Drazen (2009) for Cross Seamount south of Hawaii. The general decrease in biomass from the slopes towards the summit area of Ampère points to a decreasing predation pressure in surface waters with distance from the summit. This is reflected by the size distribution patterns above Ampère as well. There were almost no larger size classes (2-20 mm), which include most of the migrators, above the summit in the daytime, while their relative biomass increased towards the slopes. A similar distribution pattern with larger zooplankton missing above the summits of Seine and Ampère was observed by Martin & Christiansen (2009); however, a trophic analysis of the benthopelagic fish populations at Seine Seamount did not show a high proportion of diel vertical migrators in their diet (Christiansen et al. 2009; Hirch & Christiansen 2010).

The observation that zooplankton of 2-20 mm rarely occurred above the summit but increased towards the slopes above deeper waters during night, as indicated in the horizontal distribution pattern at the 90 m depth level, could also support the hypothesis that the advection of the vertically migrating zooplankton to the summit area is blocked during the day when the deep migrating taxa stay at depths below that of the summit (Genin et al. 1994; Rogers 1994), resulting in a generally lower biomass above the summit, both during the day and at night.

The present results corroborate previous studies, which describe, at least for strong vertical migrators, a reduction in zooplankton biomass above topographic structures such as found in the NE Pacific (Genin et al. 1988, 1994) and the NE Atlantic (Nellen 1973; Martin & Christiansen 2009). Similarly, Dower & Mackas (1996) found no evidence of locally enhanced zooplankton and micronekton biomass above the shallow Cobb Seamount in the NE Pacific, nor did De Forest & Drazen (2009) above the summit of Cross Seamount. However, the distribution of the zooplankton biomass may be decoupled from phytoplankton production and stocks. For example, the reduced zooplankton biomass above Seine summit (Martin & Christiansen 2009) was in contrast to the temporarily increased chlorophyll *a* concentrations found by Arístegui et al. (2009) and Kiriakoulakis et al. (2009). Dower et al. (1992) and Comeau et al. (1995) also reported enhanced chlorophyll *a* concentrations from Cobb Seamount, but no increased zooplankton biomass. Locally enhanced primary production at seamounts has often been attributed to Taylor columns or Taylor caps (e.g. Genin & Boehlert 1985) but these features are usually not persistent enough to allow for the transfer of the increased primary production to higher trophic levels, which would require time spans of weeks to months (Boehlert & Genin 1987; Dower et al. 1992).

4.5.3.2 Sphere of Senghor Seamount

Although day-night differences in the upper 100 m of the vertical profiles at the summit, rim and slopes of Senghor Seamount, suggest the presence of daily migrating zooplankton, the horizontal surveys do not show a strong pattern of diel vertical migration. In contrast to Ampère, a reduction in biomass above the summit was not observed. Both the horizontal surveys and the vertical profiles show a persistent higher biomass at 50 than at 90 m across the seamount, which points to a high proportion of non-migrating zooplankton residing in the layer of the chlorophyll *a* maximum and just above the oxycline. Below this layer, oxygen concentrations dropped sharply between 55 and 85 m from 4.4 ml l^{-1} to 2.2 ml l^{-1}, as shown by preliminary results from December 2011 (Fig. 4-12).

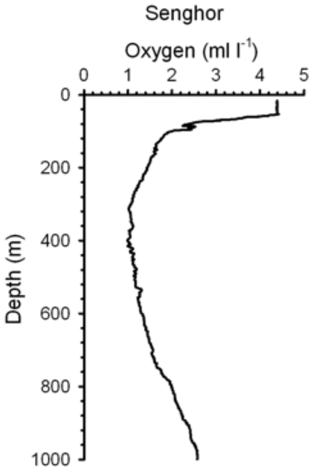

Fig. 4-12. Vertical profile of oxygen (ml l^{-1}) at Senghor Seamount in December 2011.

Since oxygen is a key factor for efficient metabolism, the low oxygen concentrations affect the vertical distribution of zooplankton and exclude most zooplankton from the core of the oxygen minimum layer below the thermocline (Saltzmann & Wishner 1997). This becomes obvious in the vertical zooplankton profiles at Senghor with a minimum biomass between 50 and 100 m. In contrast to Ampère, the distribution of the larger zooplankton size classes across the seamount without an explicit reduction above the summit, and the generally low relative abundances of strong vertical migrators such as euphausiids and the copepod *Pleuromamma* (Denda unpubl. data), suggest that topographic blockage is not an important feature of the pelagic community at the tropical Senghor.

The small-scale distribution of zooplankton shows higher biomass concentration at the NE slope of the seamount, as compared with the summit and the SW slope, but only at night, whereas during the day the biomass was more evenly distributed, with a trend towards an enhanced biomass above the summit at 90 m. During the study period, acoustic Doppler current profile (ADCP) recordings at Senghor showed a flow in a southwestward direction with current velocities of 5-10 cm s^{-1} in the upper 100 m on the east side of the seamount, whereas above the summit and on the west side, the flow was more variable (Mohn unpubl. data). This flow could cause the accumulation of advecting zooplankton at the upstream side of the seamount, but it is not clear why this occurs only at night. Although Senghor is generally located in the ‘shadow zone’ of the CVFZ, flows to the SW are prevailing in the surface layers, driven by the northeasterly trade winds (e.g. Mittelstaedt 1991; Pelegrí et al. 2006) and the Mauritania current, which turns to the SW south of the CVFZ (e.g. Mason et al. 2011). Similar accumulations of zooplankton biomass on the upstream side of a seamount have been reported by Martin & Nellen (2004) from Great Meteor.

The observed vertical and horizontal patterns of zooplankton biomass were mainly determined by the size fraction 2-5 mm. This was, in terms of biomass, the predominating size class at 50 m depth and, less pronounced, also at 90 m. Here, an increasing proportion of the largest class (5-20 mm) from NE to SW was observed, indicating an accumulation of larger zooplankton on the downstream side of the seamount, for example through displacement by currents, as reported by Wilson & Boehlert (2004) for SE Hancock Seamount in the Central North Pacific, but only by the end of the night. The mechanism behind this is far from clear.

4.5.4 Latitudinal and vertical variability of zooplankton respiratory carbon demand

The community respiratory carbon demand was estimated from the biomass using a multiple-regression model after Ikeda et al. (2001), which considers ambient temperature and size distribution, but not the effect of pressure. However, the influence of depth on respiration is mentioned by several authors (e.g. Childress 1975, 1977; Torres et al. 1979; Torres & Childress 1983; Ikeda 1988), and meso- and bathypelagic values can be assumed as one-half to one-third that of epipelagic respiration (Ikeda et al. 2006). Torres et al. (1994) observed a similar relation for pelagic crustaceans with respiration rates of a species living at 1000 m being 30-60 % that of a species living at the surface, whereas Thuesen et al. (1998) showed that respiration rates of megacalanid copepods were relatively unaffected by hydrostatic pressure. To account for pressure effects, we reduced the modeled respiration rates below the epipelagic zone by 50 %. This is only an approach and should be interpreted with some caution.

Compared with data from areas close to seamounts in the upper 1000 m of the subtropical NW Atlantic (Longhurst et al. 1990), the carbon demand at Ampère was lower by about one order of magnitude. The results from Senghor were in the lower range of the Longhurst et al. (1990) data and comparable to values from the oligotrophic Sargasso Sea (55.7-75.5 mg m^{-2} day^{-1}, Longhurst et al. 1990). Differences in respiration rates between the western and the eastern Atlantic can be attributed to deeper mixing in winter in the west, which recharges the upper ocean with nutrients and drives a general higher production in the west, whereas a comparable surface recharging of nutrients followed by phytoplankton growth is less strong in the east (Longhurst 1995).

Ampère is located in the North Atlantic subtropical gyre East (NASE), which is characterized by an oligotrophic regime (Longhurst 1995; Harrison et al. 2001; Robinson et al. 2002) and generally supports only low mesozooplankton biomass and respiratory carbon demand. Even lower rates were reported for the upper 150 m of the slopes of the adjacent Seine Seamount in spring (1.1-3.1 mg m^{-2} day^{-1}) and summer (4.8-6.3 mg m^{-2} day^{-1}) (Hirch et al. 2009), whereas the depth integrated (0-700 m) respiratory carbon demand at the western slope of Sedlo Seamount north of the Azores (12.0 mg m^{-2} day^{-1}, Hirch et al. 2009) in November was similar to Ampère. For the epipelagic zone (0-200 m) of the NE Atlantic between 40° and 30° N, Hernández-León & Ikeda (2005) estimated an average community respiration rate for mesozooplankton of ~19 mg m^{-2} day^{-1}. All these data confirm the generally low zooplankton respiration in the subtropical NE Atlantic; however, the observed regional differences in this area should be interpreted with caution, as part of the variability may be attributed to differences in methodology.

At Senghor, the respiratory carbon demand was six times higher than at Ampère. Both the higher biomass at Senghor and the higher specific respiration rates for tropical zooplankton, which Hernández-León & Ikeda (2005) attributed to the combined effects of higher temperature and smaller body size of individuals, are responsible for this difference. At Senghor Seamount, the small-sized zooplankton contributed most to the total respiratory carbon demand in the upper 1000 m, emphasizing the importance of this group for the conversion of carbon in tropical areas, whereas at Ampère larger size groups became more important already below 200 m. A similar latitudinal difference was shown in respiration measurements by Robinson et al. (2002) with 1.1 mmol m^{-3} day^{-1} in the NASE province (30°-35° N) and 6.5 mmol m^{-3} day^{-1} in the NW African upwelling (14.9°-21.2° N).

Hernández-León & Ikeda (2005) calculated respiration rates for the area 15°-22° N in the NE Atlantic and discriminated between the epi-, meso- and bathypelagic zones. The respiration at Senghor matched their calculated rates of 97.5 $\pm$ 39.7 mg m^{-2} day^{-1} in the epipelagic zone and of 20.6 $\pm$ 3.4 mg m^{-2} day^{-1} in the mesopelagic zone, respectively. In the bathypelagic zone the carbon demands at Senghor and Ampère were similar (1.5-1.8 mg m^{-2} day^{-1}) and also close to the average value calculated by Hernández-León & Ikeda (2005) for the tropical NE Atlantic (3.8 ± 1.4 mg m^{-2} day^{-1}). This suggests that the latitudinal difference in mesozooplankton biomass and their respiration rates become smaller below 1000 m water depth and that, despite different production in surface layers, the food availability in the deep sea is comparable, pointing to differences in the vertical carbon flux, with lower recycling rates in the oligotrophic subtropical gyre as compared with the more productive tropical areas. However, the influence of different water masses, such as the Mediterranean outflow water at Ampère and AAIW at Senghor, on the zooplankton carbon demand in the bathypelagic zones of Ampère and Senghor above the North Atlantic deep water (NADW) at 2500 m (Zenk et al. 1991; Vangriesheim et al. 1993) appears to be low, but may be more important for differences in the taxonomic composition of the deep communities.

4.6 Conclusions

The zooplankton distribution across Ampère Seamount seems to be driven by the mechanism of topographic blockage on diel vertical migrators, whereas at Senghor the distribution pattern indicates a strong correlation to the oxygen minimum layer. However, clear evidence of higher primary and secondary production in the seamount ecosystem, expressed by high concentrations of zooplankton biomass as compared with the unaffected open ocean reference station, was not detected. The differences in zooplankton standing stock between both seamounts are driven by the large-scale current systems and distinct water masses in relation to seasonal and latitudinal variability in general, rather than by local seamount effects. The zooplankton community in the region of Ampère Seamount reflects the oligotrophic character of the NE Atlantic subtropical gyre whereas, in the vicinity of Senghor, the nutrient-rich waters of the cyclonic tropical gyre south of the CVFZ feature a significant higher biomass. The differences in respiratory carbon demand between the two seamounts mirror this pattern, but show also the increasing importance of the smaller-sized zooplankton for carbon conversion at lower latitudes.

4.7 Acknowledgements

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Microzooplankton and the dispersal of meroplanktonic larvae at two seamounts in the subtropical and tropical NE Atlantic

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5.1 Abstract

Spatial distribution patterns of microzooplankton (0.055-0.3 mm) biomass and abundance were studied in relation to the hydrographical situation and the local flow field in the waters off Ampère and Senghor, two shallow seamounts in the subtropical and tropical NE Atlantic, in comparison with unaffected open ocean reference sites. Ampère was sampled during November/December 2010 and Senghor during December 2011 and February 2013. The study includes taxonomic composition, dispersal of meroplanktonic larvae and an estimation of the respiratory carbon demand. Biomass (dry weight) standing stocks of microzooplankton in the upper 100 m ranged between 0.03-0.12 g m^{-2} over Ampère and 0.14-0.26 g m^{-2} over Senghor, corresponding up to 33 % and 24 % of the total zooplankton (0.055-20 mm). Highest total abundance was always found in the upper 50 m with numbers of 1070-5060 Ind m^{-3} at Ampère and 5050-20000 Ind m^{-3} at Senghor whereof microzooplankton made up 70-95 %. Zooplankton accumulated mainly at the thermocline coincident with the deep chlorophyll maximum and was rather ascertained by food supply than by oxygen limitation. The microzooplankton contribution to the total respiratory carbon demand was about 50 % in the subtropical waters off Ampère and 30 % at Senghor, reflecting the important role of microzooplankton in the waters of the NE Atlantic subtropical gyre. Clear evidence of local seamount effects resulting in enhanced microzooplankton biomass compared with the unaffected reference sites were not detected. But, at least we confirmed Senghor as a source for meroplanktonic larvae, with a retention potential resulting in significantly enhanced larval abundance in the seamount waters compared to the open ocean.

Keywords: microzooplankton; respiratory carbon demand; seamount; spatial distribution patterns; tropic-subtropical NE Atlantic

5.2 Introduction

The abrupt topography of seamounts in all oceans provides special habitats of hard substrata and soft bottom for the benthic fauna as well as for associated pelagic communities, in contrast to the general flat and sediment-covered deep-sea plains (Rogers 1994; Stocks & Hart 2007). In the water column, current-topography interaction between seamount and the surrounding oceanic flows may generate meso-scale variability and affect the local retention time of water masses, including particles, phytoplankton and smaller zooplankton (Genin & Boehlert 1985; Roden 1994; Lavelle & Mohn 2010). The uplift of deeper nutrient-rich water associated with the biological retention potential of seamounts may be increased by hydrodynamic processes such as seamount associated eddies (Richardson 1980; Richardson 1981), Taylor caps/columns or tidal resonance and seamount-trapped waves (see White et al. 2007; Lavelle & Mohn 2010).

Despite the hypothesis of seamounts as places of enhanced biomass and production (Rogers 1994), only limited evidence suggests that seamounts can support elevated biomass and abundance of the benthic invertebrate fauna (see Genin 2004; Clark et al. 2010; Rowden et al. 2010). However, it has been demonstrated by Mullineaux & Mills (1997) that current-topography interaction can retain larvae in seamount associated flows, which is likely to effect the recruitment of the benthic population. Boehlert & Mundy (1993) assumed seamounts as sources of eggs and larvae leading to assemblages of ichthyoplankton. Though over a seamount small meroplanktonic larvae, belonging to the microzooplankton community, are an important factor for recruitment, food supply and production in a seamount ecosystem, related studies are sparse (e.g. Mullineaux & Mills 1997; Metaxas 2011).

The microzooplankton community, usually defined as the size fraction 0.02-0.2 mm, includes protists like ciliates, dinoflagellates (Sherr & Sherr 2007), foraminiferans, but also metazoan larvae and small metazoans like small copepods, nauplius and copepodite stages of copepods. Especially the small copepods and nauplii are an important prey for fish larvae and other zooplanktivorous consumers (Turner 2004), and on the other hand exert an important grazing impact on phytoplankton communities, which are seasonally dominated in low latitudes by extremely small cells of nano- and picoplankton (Landry et al.1995). However, there is still little knowledge on the small zooplankton groups and their trophic position in the marine food web as compared with, for example, larger copepod taxa, because the small-sized zooplankton has usually been undersampled in the oceanic realm due to the common usage of nets with mesh sizes >0.2 mm (Gallienne & Robins 2001; Turner 2004).

Using multiple opening and closing nets with a mesh size of 0.055 mm, the present study assesses the spatial distribution of microzooplankton in relation to the mesozooplankton fraction at Ampère and Senghor, two shallow seamounts in the subtropical and tropical NE Atlantic, with special attention to the abundance of invertebrate larvae.

In particular we were interested whether and where microzooplankton is accumulated over Ampère and Senghor. The study further addresses the question whether meroplanktonic larvae are retained in seamount surrounding waters as proposed by Mullineaux & Mills (1997) and whether the seamounts may be considered as larval source in the open ocean for benthic invertebrates, as corals, polychaetes and echinoderms, which have been sampled during a cruise to Senghor in September/October 2009 and to Ampère in November/December 2010 (Christiansen & Koppelmann 2011; Molodtsova & Vargas 2012; Chivers et al. 2013). Complementary to our previous study on mesozooplankton (Denda & Christiansen 2014), we give an assessment of the respiratory carbon demand and the taxonomic composition in order to better understand the trophic position of the microzooplankton and their impact on the phytoplankton community in the oligotrophic system of the NE Atlantic subtropical gyre compared to the mesotrophic system of the tropical gyre. In this context we addressed the following questions:

(1) How do the local current regime and the hydrographic conditions affect the microzooplankton distribution in distinct seamount regions (summit plateau, rim, slope, up- and downstream sides) compared to the open ocean reference site in terms of biomass and abundance?
(2) How does the large-scale current regime of the subtropical and tropical gyre affect the microzooplankton distribution at Ampère and Senghor seamounts, respectively, in terms of biomass, abundance and respiratory carbon demand?
(3) Are Ampère and Senghor seamounts a larval source for benthic invertebrates, featuring enhanced larval abundance compared to the open ocean?

5.3 Materials and Methods

5.3.1 Study sites

5.3.1.1 Ampère Seamount

Ampère Seamount was sampled during cruise M83/2 of RV Meteor in November/December 2010. Ampère, within the sphere of the NE Atlantic subtropical gyre, belongs to the Horseshoe Seamounts Chain, which is located between the island of Madeira and the Portuguese mainland ~360 nm west of the Strait of Gibraltar at 35° 02’ N, 012° 54’ W (Fig. 5-1). The current regime around Ampère is mainly driven by the Azores current and the Mediterranean outflow. The seamount rises from a base depth at 4500 m to a summit depth at 120 m with one small peak rising to 55 m (Fig. 5-2a), partially overgrown with macroalgae in the photic zone (Christiansen unpubl. data). The seamount has a conical shape with a small, rough summit plateau and steep rocky slopes and canyons (Halbach et al. 1993; Kuhn et al. 1996; Hatzky 2005) as well as sediment-covered areas. For comparison, one open ocean reference station (hereafter referred to as ‘far field’) ca. 70 nm southwest of Ampère Seamount, located at 33° 48’ N, 013° 00’ W, was also sampled. Water depth was about 4400 m over a flat sedimentary plain.

5.3.1.2 Senghor Seamount

Senghor Seamount was sampled during the cruises P423 and P446 of RV Poseidon in December 2011 and February 2013. Senghor is located ca. 60 nm east of the island of Sal, Cape Verde at 17° 12’ N, 021° 57’ W (Fig. 5-1). The ocean dynamics around Senghor are mainly characterized by the north equatorial current system which drives the NE Atlantic tropical gyre (see Mittelstaedt 1991; Lathuilière et al. 2008) and by the Cape Verde frontal zone between North and South Atlantic central water (Zenk et al. 1991). Water depth at the base of the seamount is about 3300 m; the minimum summit depth is 90 m (Fig. 5-2b). Senghor Seamount has a nearly circular shape with a small summit plateau and features a heterogeneous surface structure, which was shown by several ROV dives during cruise M79/3 of RV Meteor in September/October 2009 (Christiansen & Koppelmann 2011). The summit plateau is covered with sediment in most parts but also shows rocky areas in the centre, and ripple marks indicate strong currents at a water depth of 100 m. At the edge of the summit plateau at a depth of 320 m the seafloor is also sediment-covered, but without ripple marks. Along the slopes down to the deep sea floor soft bottom alternates with rocky areas. For comparison, an unaffected open ocean reference station (hereafter referred to as ‘far field’) ca. 60 nm north of Senghor Seamount, located at 18° 05’ N, 022° 00’ W, was sampled. Water depth was about 3300 m over the flat sedimentary plain.

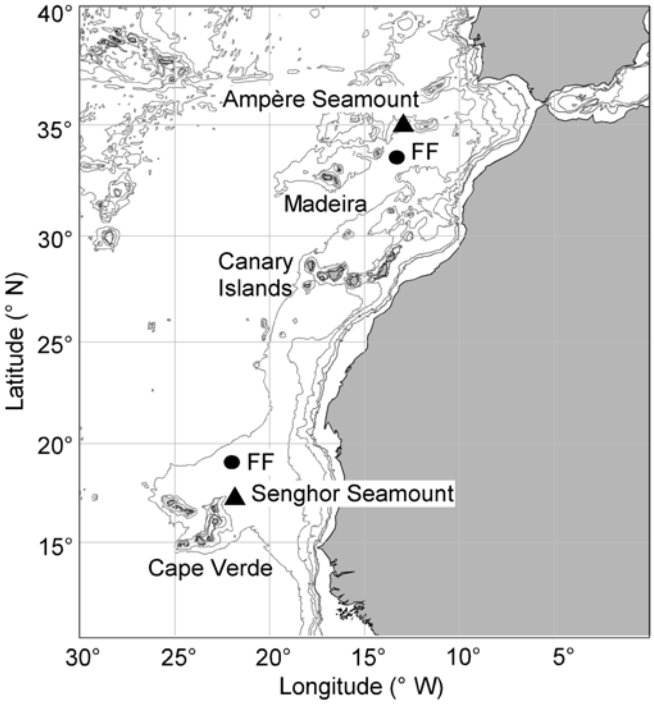

Fig. 5-1.Locationsof Ampère and Senghor seamounts and the far field sites (FF) in the NE Atlantic.

5.3.2 Hydrographic data collection

CTD (Conductivity-Temperature-Depth) casts were performed around Ampère and Senghor seamounts and in the far field, using a Seabird CTD equipped with sensors for temperature, conductivity, oxygen and fluorescence. In our study we examined CTD stations in the proximity of the zooplankton sampling stations, covering the upper 100 m of the water column over the summit plateau and rim and the upper 1000 m of the water column over the mid slopes and at the far field sites (Fig. 5-2a, b; Table 5-1).

Direct current velocities were obtained from vessel-mounted ADCP (Acoustic Doppler Current Profiler) data collected during the surveys M83/2 to Ampère Seamount and P446 to Senghor Seamount, but not on cruise P423 to Senghor due to technical problems. ADCP measurements were conducted with 38 kHz (M83/2) and 75 kHz (P446) Teledyne RDI Ocean Surveyor systems. Single ping velocity profiles were recorded along with corresponding records of position, heading and time. Depth bin size settings varied between 16 m (depth range 27-651 m, Ampère Seamount) and 8 m (depth range 22-814 m, Senghor Seamount). Two minute ensemble velocity averages were created from all single ping ADCP velocity profiles. Further processing was carried out using the Common Oceanographic Data Access System (CODAS) developed by the University of Hawaii (Firing et al. 1995; http://currents.soest.hawaii.edu/docs/ adcp_doc/index.html). Individual processing steps are described in detail in Mohn et al. (2013) and included evaluation and correction (if applicable) of transducer misalignment, transducer orientation, velocity amplitude scale factor and navigation. Depth bins with percent good values less than 80 % of the return signal were discarded. ADCP velocities were not de-tided to retain the full spectrum of motion. Finally, along ship-track velocity profiles were spatially interpolated over a uniform grid using the DIVA software (Data Interpolating Variational Analysis; Troupin et al. 2012) following the procedure and settings described in Mohn et al. (2013). The grid size was 0.02 degrees in latitude and longitude.

5.3.3 Zooplankton sampling

Zooplankton was collected using vertical hauls with a Hydro-Bios 0.25 m²-MultiNet® (MSN; Weikert & John 1981) equipped with five nets. The mesh aperture was 0.055 mm. The sampling design comprised a vertical profile at the far field station and two orthogonal transects across the seamounts, one in north-south and one in east-west direction, with stations at the mid slopes down to 1000 m depth, at the rim of the plateau and at the summit centre (Fig. 5-2a, b; Table 5-1). The water column was subdivided into the following sampling intervals, depending on the maximum water depth: 1000-750-500-400-300-200-100-50-25-0 m. In order to get this vertical resolution with a five nets MultiNet® sampler at the slope stations, the 1000 m profiles were split into two casts, one from 1000 to 300 m and a 2nd one from 300 m to the surface. During the Senghor surveys each cast was usually performed twice, for two complete vertical profiles at each station, to allow for statistical analyses.

Due to lack of ship time casts were performed independent of daytime. Due to technical problems of the ship, the sampling design could not be completed as planned, and some stations are missing from each cruise. At Ampère Seamount casts were performed only once during day or night due to lack of ship time.

Upon recovery of the MultiNet®, the nets were rinsed with seawater and the catch transferred into PE bottles. The material was preserved in a 4 % formaldehyde-seawater solution buffered with borax for biomass determination and taxonomic identifications.

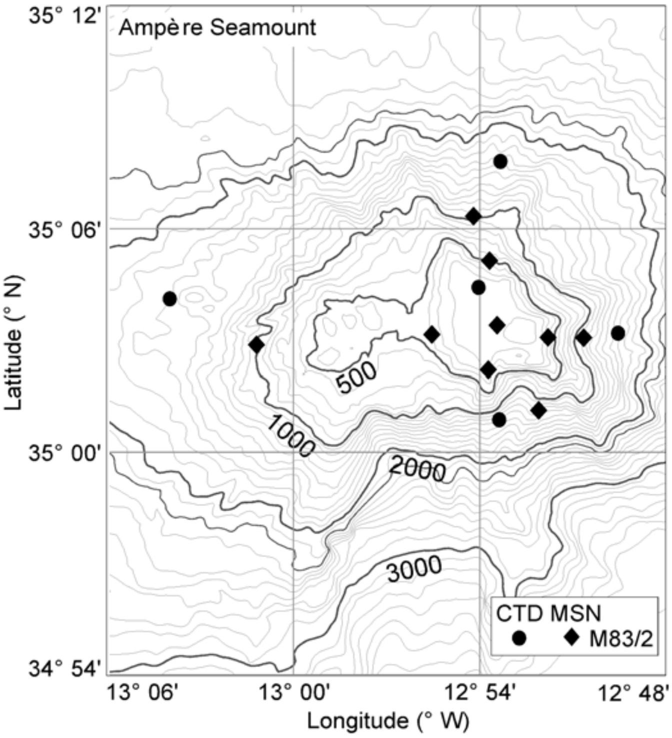

Fig. 5-2a. Bathymetry and sampling locations of CTD and MSN at Ampère Seamount on cruise M83/2 in November/December 2010.

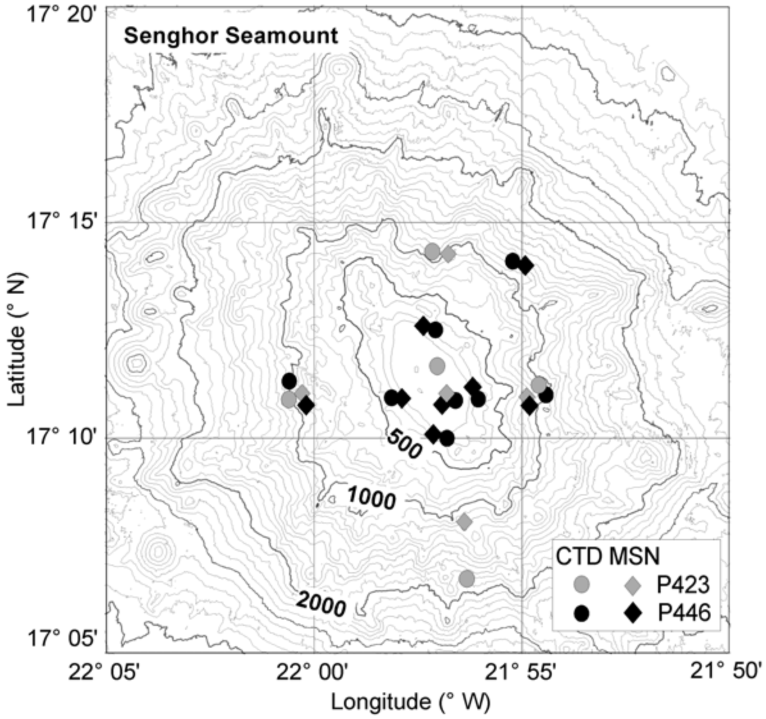

Fig. 5-2b. Bathymetry and sampling locations of CTD and MSN at Senghor Seamount on cruise P423 in December 2011 and P446 in February 2013.

Table 5-1. Haul data for CTD and MSN during expeditions in November/December 2010 to Ampère Seamount and in December 2011 and February 2013 to Senghor Seamount.

Station				Position		Water	Sampling	
No	Gear	Date	Time	Lat N	Long W	depth (m)	depth (m)	Location
M83/2		**2010**						**Ampère**
946	CTD	22.11.	night	33° 47.96'	13° 00.05'	4413	0-1000	far field
1178	CTD	08.12.	night	35° 03.03'	12° 49.63'	1751	0-1000	slope E
1194	CTD	09.12.	day	35° 00.99'	12° 53.45'	1270	0-1000	slope S
1245	CTD	12.12.	night	35° 08.00'	12° 53.60'	1694	0-1000	slope N
1267	CTD	14.12.	night	35° 03.63'	13° 04.94'	1740	0-1000	slope W
1330	CTD	18.12.	day	35° 04.47'	12° 54.27'	106	0-100	summit
969-970	MSN	25.11.	night	33° 48.03'	13° 59.98'	4418	1000-0	far field
1279-1280	MSN	14.12.	night	35° 01.69'	12° 52.66'	1055	1000-0	slope S
1282-1283	MSN	15.12.	night	35° 03.20'	12° 50.75'	1094	1000-0	slope E
1284	MSN	15.12.	night	35° 03.30'	12° 51.87'	307	250-0	rim E
1285	MSN	15.12.	night	35° 02.13'	12° 53.82'	223	200-0	rim S
1298-1299	MSN	15.12.	night	35° 03.29'	13° 00.83'	1044	1000-0	slope W
1316-1317	MSN	17.12.	night	35° 06.40'	12° 53.95'	1037	1000-0	slope N
1326	MSN	18.12.	day	35° 04.99'	12° 53.80'	376	300-0	rim N
1328	MSN	18.12.	day	35° 03.52'	12° 55.29'	268	250-0	rim W
1329	MSN	18.12.	day	35° 03.72'	12° 53.41'	127	100-0	summit
P423		**2011**						**Senghor**
729	CTD	11.12.	night	18° 05.03'	22° 00.02'	3294	0-1000	far field
739	CTD	13.12.	night	17° 12.39'	21° 57.80'	133	0-100	summit
744	CTD	13.12.	day	17° 14.49'	21° 57.42'	1059	0-1000	slope N
753	CTD	14.12.	night	17° 06.86'	21° 56.15'	1652	0-1000	slope S
771	CTD	15.12.	day	17° 11.03'	22° 00.77'	1079	0-1000	slope W
780	CTD	16.12.	day	17° 11.68'	21° 54.78'	1031	0-1000	slope E
731-734	MSN	12.12.	night	18° 05.00'	22° 00.00'	3294	1000-0	far field
737-738	MSN	13.12.	day	17° 14.48'	21° 57.39'	1088	1000-0	slope N
745-746	MSN	13.12.	night	17° 14.48'	21° 57.39'	1088	1000-0	slope N
751-752	MSN	14.12.	night	17° 11.62'	21° 54.78	1039	1000-0	slope E
756-757	MSN	14.12.	day	17° 11.62'	21° 54.78	1039	1000-0	slope E
766-767	MSN	15.12.	night	17° 08.10'	21° 56.76'	1079	1000-0	slope S
764-765	MSN	15.12.	night	17° 11.05'	22° 00.77'	1044	1000-0	slope W
784	MSN	17.12.	day	17° 11.29'	21° 57.26'	100	90-0	summit
785-786	MSN	17.12.	day	17° 11.05'	22° 00.77'	1044	1000-0	slope W
P446		**2013**						**Senghor**
499.1	CTD	08.02.	night	17° 14.10'	21° 55.50'	1190	0-1000	slope NE
500.3	CTD	08.02.	day	17° 11.34'	21° 56.37'	232	0-180	rim E
501.1	CTD	08.02.	day	17° 11.26'	21° 57.24'	102	0-100	summit
502.3	CTD	08.02.	day	17° 11.29'	21° 58.20'	253	0-250	rim W
518.5	CTD	13.02.	night	17° 11.07'	22° 00.75'	1077	0-1000	slope W
524.1	CTD	14.02.	night	17° 11.60'	21° 54.77'	1049	0-1000	slope E
525.3	CTD	14.02.	day	17° 10.18'	21° 57.23'	227	0-240	rim S
526.1	CTD	14.02.	day	17° 12.62'	21° 57.49'	231	0-180	rim N
529.1	CTD	15.02.	day	18° 04.99'	22° 00.02'	3295	0-1000	far field
499.2-5	MSN	08.02.	day	17° 14.10'	21° 55.50'	1179	1000-0	slope NE
500.1-2	MSN	08.02.	day	17° 11.34'	21° 56.31'	253	240-0	rim E
501.2-3	MSN	08.02.	day	17° 11.23'	21° 57.21'	102	95-0	summit
502.1-2	MSN	08.02.	day	17° 11.29'	21° 58.16'	233	225-0	rim W
509.1-4	MSN	11.02.	night	17° 14.10'	21° 55.50'	1179	1000-0	slope NE
514.1-4	MSN	11.02	night	17° 14.10'	21° 55.50'	1179	1000-0	slope NE
518.1-4	MSN	13.02.	day	17° 11.03'	22° 00.75'	1072	1000-0	slope W
520.1-4	MSN	13.02.	night	17° 14.10'	21° 55.50'	1179	1000-0	slope NE
524.2-5	MSN	14.02.	day	17° 11.60'	21° 54.78'	1038	1000-0	slope E
525.1-2	MSN	14.02.	day	17° 10.17'	21° 57.25'	251	240-0	rim S
526.2-3	MSN	14.02.	day	17° 12.63'	21° 57.51'	216	200-0	rim N
528.2-5	MSN	14.02.	day	17° 14.10'	21° 55.50'	1179	1000-0	slope NE
529.2-5	MSN	15.02.	day	18° 04.97'	21° 59.97'	3286	1000-0	far field

5.3.4 Biomass analyses and carbon demand

In the laboratory, the zooplankton samples were fractionated by sieving into the size classes 0.055-0.3 mm and 0.3-20 mm (hereafter referred to as 'microzooplankton' and 'mesozooplankton'). The size fractionating through a 0.3 mm sieve allowed for estimating the importance of the microzooplankton in comparison with the commonly used 0.3 mm net samples. The wet weight of each size fraction was measured after removal of the interstitial water with 70 % alcohol according to the method of Tranter (Tranter 1962). After wet weight determination the size fractions were split into two sub-samples by a modified Folsom plankton splitter (McEwen et al. 1954). One half was transferred into sorting fluid (0.5 % propylenphenoxetol, 5 % propylenglykol and 94.5 % H_2O; Steedmann 1976) for counts and taxonomic analyses. For dry weight determination the other half was filtrated in a volume of 250 ml distilled water on a pre-combusted (at 500 °C for 0.5 h) and pre-weighed fibre glass filter (Whatman GF/C, ø 45 mm), and oven-dried at 60 °C for 24 h until the sample reached a stable weight. The volume of the filtered water for each net was calculated by multiplying the net opening (0.25 m^2) with the sampling interval as measured by the pressure sensor, assuming a filtration efficiency of 100 %. Biomass (dry weight) was standardized to milligrams per 1 m^3 (mg m^{-3}). Standing stocks in terms of biomass integrated over the whole water column or a given depth range were calculated as g m^{-2}.

For the calculation of the respiratory carbon demand mean individual dry weight (mg Ind^{-1}) was determined by dividing the dry weight of the sample by the number of individuals in the parallel sample. Individual respiration rates were calculated from mean individual dry weight and temperature for each sample, respectively, using a multiple-regression model after Ikeda (Ikeda et al. 2001):

$$\ln R = -0.399 + 0.801 \ln W + 0.069\ T$$

with R = individual O_2 respiration rate (µl Ind^{-1} h^{-1}); W = mean individual body dry weight (mg Ind^{-1}); T = mean temperature in sampling intervals (°C). The respiratory oxygen consumption rates were converted to carbon equivalents RC (µg Ind^{-1} h^{-1}) by the equation:

$$RC = R * RQ * 12/22.4$$

where RQ is a respiratory quotient of 0.97 (Omori & Ikeda 1984; Ikeda et al. 2000) and 12/22.4 is the weight (12 g) of carbon in 1 mole (22.4 l) of carbon dioxide (Ikeda et al. 2000). The carbon respiration rates per individual (µg Ind^{-1} h^{-1}) were divided by individual dry weight (mg Ind^{-1}) to estimate the biomass-specific respiration rates (mg mg^{-1} h^{-1}). Community rates (mg m^{-3} d^{-1}) were calculated as the product of the biomass-specific respiration rates at the sampled depth layers and the corresponding biomass in terms of dry weight (mg m^{-3}). Respiratory carbon demands for distinct depth layers were calculated as mg m^{-2} d^{-1}. Since Ikeda's regression model refers only to epipelagic zooplankton, calculated respiration rates of zooplankton for the mesopelagic zone (300-1000 m) were reduced by 50 % to consider the effect of pressure, following Ikeda et al. (2006), who concluded that mesopelagic respiration rates were in the order of one-half that of epipelagic respiration.

5.3.5 Taxonomic analyses

Microzooplankton samples of M83/2 were split by a plankton splitter after Wiborg (Wiborg 1951), using a sub-sample of 1/5, 1/10, 1/20 or 1/25. Microzooplankton samples of P423 and P446 were split using a Stempel pipette. Depending on the total number of individuals, an aliquot of 2.5, 5 or 10 ml was removed by the pipette from the sample diluted in a conical flask of 250 ml. Mesozooplankton samples were split using a modified Folsom plankton splitter (McEwen et al. 1954) to a sub-sample of 1/2, 1/4, 1/8 or 1/16.

Protistan and metazoan zooplankton was sorted and counted under a dissecting microscope, identified at phylum, class or order level or at developmental stage and grouped as follows: Dinoflagellata, other Protista (Foraminifera and Tintinnina), Appendicularia, other non-Crustacea (Cnidaria, Mollusca, Polychaeta, Chaetognatha, Thaliacea), nauplii (including mainly Copepoda, but also Euphausiacea and Decapoda), other invertebrate larvae and other Crustacea (Ostracoda, Cladocera, Hyperiidea, other Amphipoda, Decapoda, Euphausiacea, Mysidacea, other Harpacticoida). Copepoda were identified at the family, genus or species level, such as the most abundant *Micro-/Macrosetella* spp., *Oithona* spp., *Oncaea* spp., Paracalanidae and Clausocalanidae. Other less abundant or juvenile copepod taxa were grouped and presented in the graphic results as other Cyclopoida and other Calanoida. A particular focus was on the identification of invertebrate larvae of Cnidaria, Gastropoda, Polychaeta, Cirripedia and Echinodermata. Exoskeletons, according to Wheeler (1967) and Weikert (1977), and fragments of gelatinous organisms like Siphonophora were not considered in this study.

Counts were multiplied by the division factor of the sub-sample, and abundance was standardized to individuals per 1 m^3 (Ind m^{-3}). Standing stocks integrated over the whole water column or a given depth range were calculated as Ind m^{-2}.

5.3.6 Data analyses

Prior to the statistical analyses, data were log transformed [$Y' = \log (Y+1)$] in order to reach approximate normal distribution and homogeneity of variances. Standing stocks of microzooplankton biomass (g m^{-2}) and abundance standing stocks of meroplanktonic larvae (Ind m^{-2}) were calculated for two depth layers: 0-100 m and 100-1000 m, roughly corresponding to the epipelagic zone above the summit depths and the mesopelagic zone including the lower epipelagic. Within each layer differences in standing stocks of biomass and abundance between distinct seamount regions and the far field were tested for hauls with two parallels available. One-way analyses of variance (ANOVA) were used (Lozán & Kausch 2004; Sokal & Rohlf 2009), followed by *a priori* hypothesis tests using contrasts to test for differences between distinct pairs of samples (summit *vs.* rim, summit *vs.* slope, rim *vs.* slope, up- *vs.* downstream, seamount *vs.* far field). Differences between both seamounts (Ampère *vs.* Senghor) of all stations pooled, respectively, were analysed by *t*-test in terms of biomass and abundance standing stocks and carbon demand (mg m^{-2} d^{-1}).

All statistical tests were performed using the SYSTAT 8.0 statistical package (SPSS Inc. 1998). For clarity, only significant results of *t*-tests and ANOVAs/ *a priori* tests are given in the text in form of t and F values, respectively, together with degrees of freedom and significance levels of $p < 0.05$, $p < 0.01$ and $p < 0.001$. Full statistic results are available in the supplementary results (Table 5-A1, 2, 3).

In order to investigate similarities between distinct seamount regions and the far field in terms of zooplankton abundance standing stocks, multivariate analyses were performed by group-average linked cluster analysis and non-metric multi-dimensional scaling (MDS) using PRIMER 6 v. 6.1.6 (PRIMER-E Ltd. 2006). For Ampère 24 taxa were included, for Senghor 44 taxa for 2011 and 50 taxa for 2013. Abundance (Ind m^{-3}) of each taxon was integrated over 0-100 m and 100-1000 m depth, calculated as Ind m^{-2}. Abundance standing stocks of the respective depth layer were square-root transformed and Bray-Curtis similarity matrices were calculated to generate clusters, which were described by non-metric MDS plots with ten restarts to determine lowest stress giving a good ordination of similarities into the corresponding distance matrix. Statistically significant differences ($p < 0.05$) among groups of locations in the cluster analyses were determined by similarity profile tests (SIMPROF) (Clarke & Warwick 2001; Clarke & Gorley 2006).

Linkage between the physical and biological data was determined by the BEST (Biota and/or Environment matching) procedure using the BIO-ENV method (PRIMER 6 v. 6.1.6). For each cruise physical and biological data were used of each slope station, the summit and the far field, respectively. The rim stations were included only for Senghor 2013, since biological data are not available for Senghor 2011, and physical not for Ampère. Physical variables included depth, temperature, salinity, oxygen and fluorescence from the CTD casts. Mean values were calculated for each MSN sampling interval. Physical variables except depth were log transformed [$Y' = \log (Y+1)$] according to Clarke & Warwick (2001). All variables were normalised. Dissimilarity matrices of the physical variables were calculated by Euclidean distance. Biological data, zooplankton abundance of the distinct taxa (Ind m^{-3}), respective micro- and mesozooplankton biomass (mg m^{-3}) (mean values of parallel hauls) were square-root transformed and Bray-Curtis similarity matrices were calculated. The BIO-ENV procedure then measures the matching entries of the physical and biological matrices by a Spearman rank correlation and selects the combination of physical variables which maximises the correlation coefficient (Clarke et al. 2008).

5.4 Results

5.4.1 Hydrography

Hydrographic conditions at Ampère Seamount and the far field site indicate a strong stratification of the water column during November/December 2010 (Fig. 5-3). A homogenous warm mixed surface layer extended over the upper 60-80 m with temperature about 18.6 °C and salinity about 36.4 PSU above the seamount. In the far field, temperature and salinity of the mixed layer were higher with 20.4 °C and 36.7 PSU, respectively.

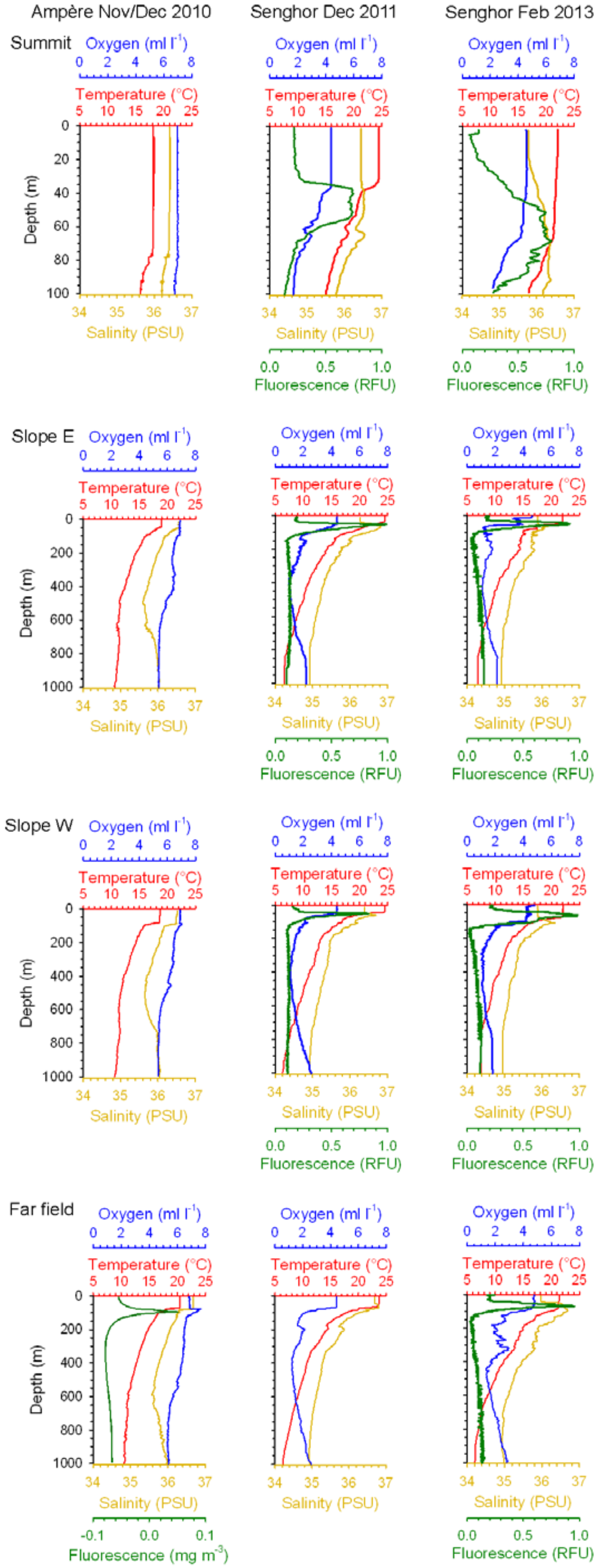

Fig. 5-3. Vertical profiles of temperature (°C), salinity (PSU), oxygen (ml l^{-1}) and fluorescence (Ampère: mg m^{-3}; Senghor: RFU = relative fluorescence unit) for the summit, E and W slope and the far field of Ampère Seamount in November/December 2010 and Senghor Seamount in December 2011 and February 2013.

An oxygen maximum occurred between 80 and 100 m in the far field with values of 7.5 ml l^{-1}. Over the seamount slopes, oxygen concentrations reached 6.7-7.0 ml l^{-1} but without showing a distinct maximum. Over the shallow summit no oxygen increase was obvious. Coincident with the oxygen maximum, the relative fluorescence data in the far field showed a maximum at around 80 m. Due to technical failure fluorescence data are not available for the seamount. Below the mixed layer a steep gradient in temperature, salinity and oxygen extended over 20 m, followed by a gradual decrease of temperature and oxygen to 1000 m depth at all deep stations. In contrast, salinity increased below 600 m depth reaching maximum values of ≥36 PSU at 1000 m depth. This deep salinity increase was more pronounced over the slopes than in the far field.

Over Senghor Seamount and at the corresponding far field site hydrograhpic conditions indicate a well stratified water column during both sampling seasons (Fig. 5-3). Surface water temperature was about 24.5 °C in December 2011 and 22.1 °C in February 2013, building a warm mixed surface layer in the upper 50-75 m with salinity values of 36.4 and 35.8 PSU, respectively. This layer was characterized by a distinct oxygen maximum of 4.6 ml l^{-1} and was markedly thinner above the summit and the eastern slope compared to the western slope and far field site in 2013. At the bottom of the mixed layer of the deep stations the relative fluorescence data (not available for far field 2011) show a deep maximum, and salinity reached a peak of 36.8 PSU. A steep gradient in all parameters extended down to 150 m, marking the thermocline. Below 150 m, temperature decreased gradually to 6.3 °C at 1000 m, and salinity to 34.9 PSU. Oxygen had a minimum of 1.3 ml l^{-1} at 400-500 m and increased gradually below this depth, reaching concentrations of >2 ml l^{-1} at 1000 m.

Water current estimates from ADCP measurements at Ampère Seamount indicate generally southeastward flow in the upper 100 m with maximum currents of 35 cm s^{-1} to the south of the seamount and 15-25 cm s^{-1} directly impinging at the seamount. Weaker currents (5-10 cm s^{-1}) were observed downstream of the seamount at the eastern and southeastern slopes (Fig. 5-4a). At 251 m and 395 m depth the flow was approximately 10-15 cm s^{-1} to the east. At the northern slope of the seamount a deflection to the north/northeast was apparent at all depths, reaching magnitudes of 30-40 cm s^{-1} in the upper 100 m and 20 cm s^{-1} in deeper waters. Between 400 m and 600 m a flow field was observed similar to the layers above (data not shown).

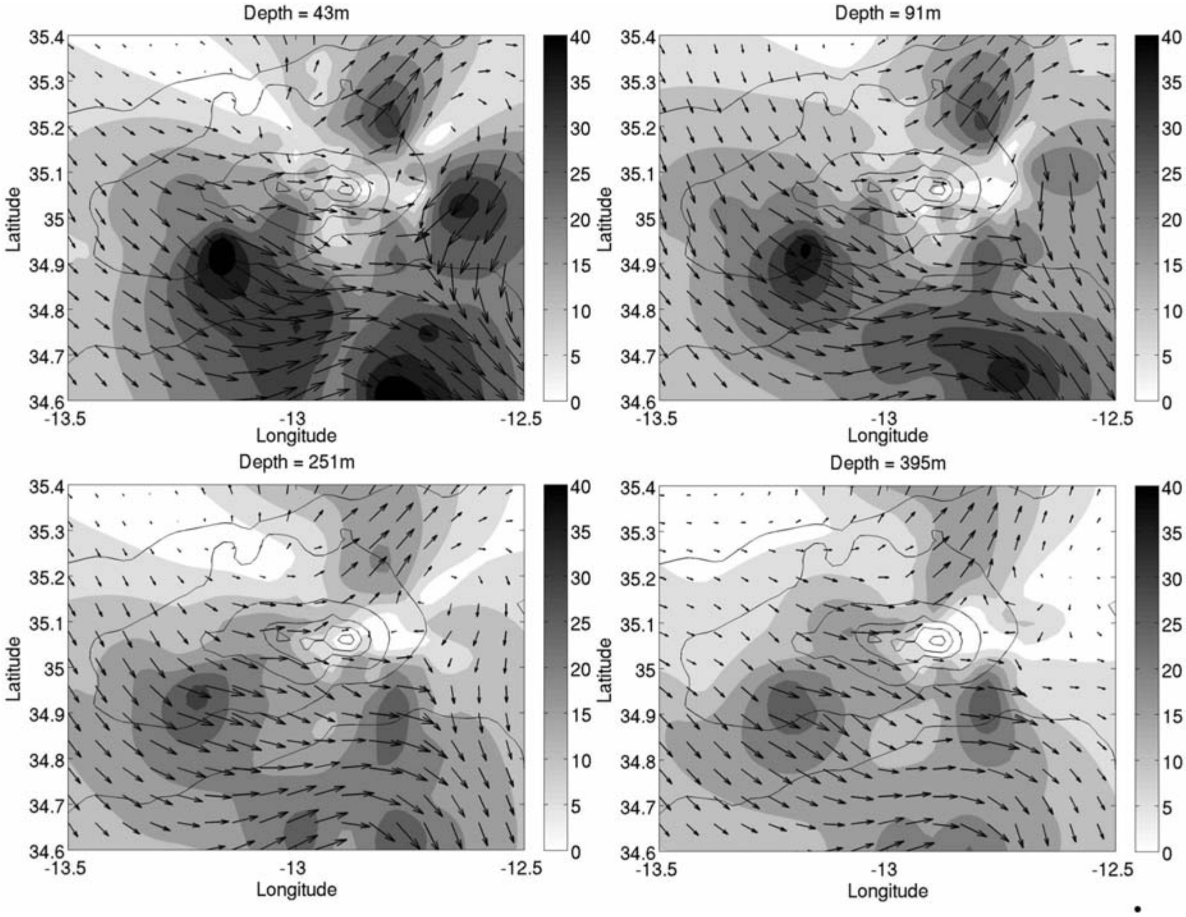

Fig. 5-4a. Gridded current velocities (cm s^{-1}) at Ampère Seamount in November/December 2010 derived from two minute ensemble averaged 38 kHz ADCP data from the M83/2 cruise using DIVA objective analysis. Flow vectors and current speeds are presented at four discrete depth levels (43 m, 91 m, 251 m, 395 m) and every third flow vector is shown. Filled contours denote current speed magnitudes. The contour interval is 5 cm s^{-1}. Solid depth contours represent the 200 m, 500 m, 1000 m, 2000 m, 3000 m and 4000 m isobaths (shallowest water depths at the seamount centre).

Senghor Seamount was dominated by southwestward flow with magnitudes up to 15 cm s^{-1} in the upper 100 m during the cruise in February 2013 (Fig. 5-4b). At 246 m and 398 m depths the flow was approximately 5-10 cm s^{-1} to the south/southwest and steady on the east side of the seamount at all depths. At the southwest and western slopes flow direction was more variable. Down to 600 m the flow field did not change around Senghor (data not shown) ADCP data are not available for the survey in 2011.

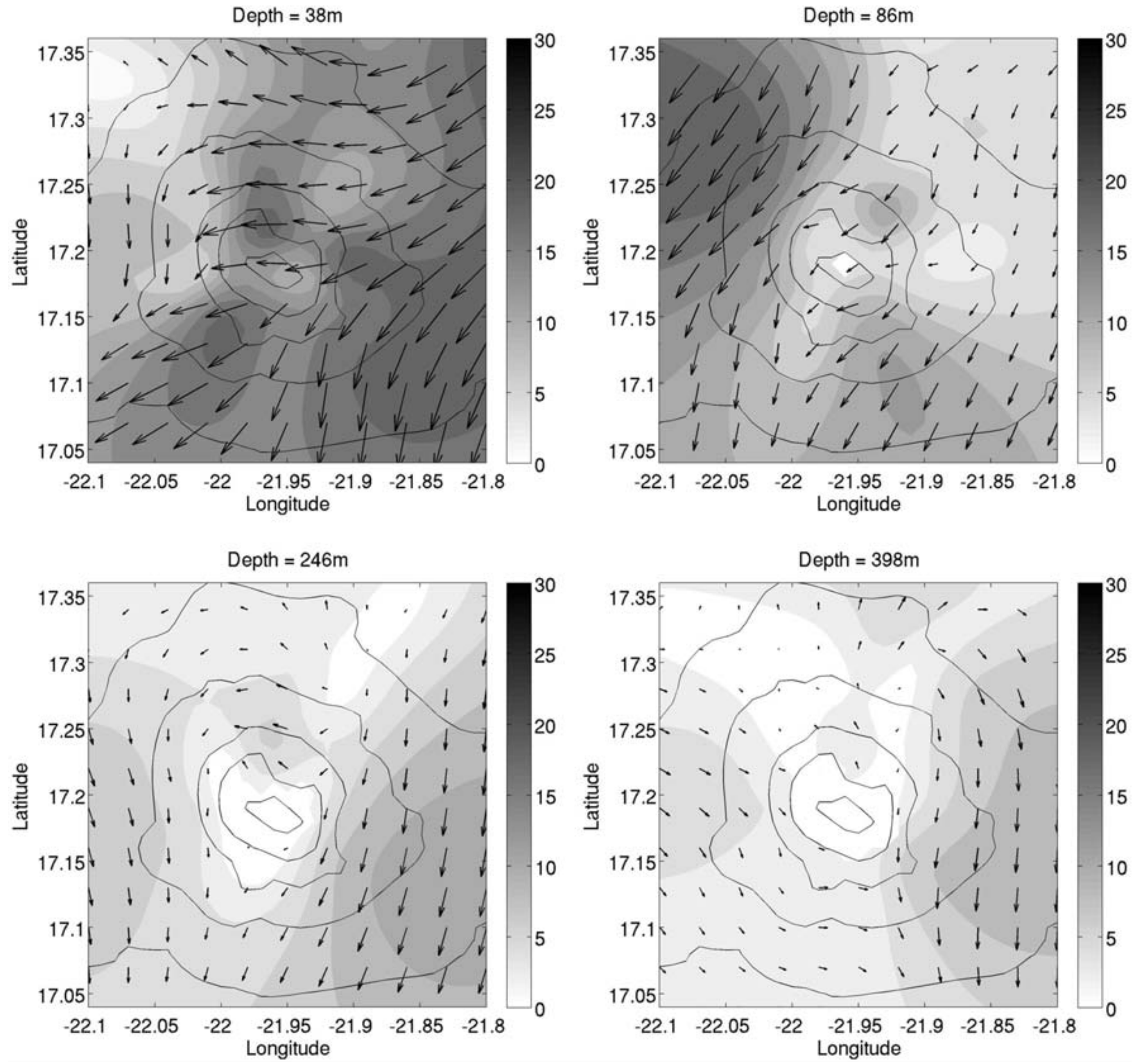

Fig. 5-4b. Gridded current velocities (cm s^{-1}) at Senghor Seamount in February 2013 derived from two minute ensemble averaged 75 kHz ADCP data from the P446 cruise using DIVA objective analysis. Flow vectors and current speeds are presented at four discrete depth levels (38 m, 86 m, 246 m, 398 m) and every third flow vector is shown. Filled contours denote current speed magnitudes. Colour scale is different from Fig. 5-4a. The contour interval is 2 cm s^{-1}. Solid depth contours represent the 200 m, 500 m, 1000 m, 2000 m and 3000 m isobaths (shallowest water depths at the seamount centre).

5.4.2 Abundance and composition

5.4.2.1 Total zooplankton

In terms of abundance, microzooplankton made up 65-95 % of the total zooplankton over each seamount, and highest abundance was always found in the upper 50 m. Within the microzooplankton community at the slopes of Ampère Seamount and the far field nauplii, *Oncaea* spp. and Clausocalanidae occurred in equal parts of 100-440 Ind m^{-3} in the upper 100 m, contributing to 10-25 % of the total microzooplankton (Fig. 5-5a). Over the rim and especially the summit numbers of nauplii (230-1460 Ind m^{-3}) and other calanoid copepods (240-1400 Ind m^{-3}) were markedly enhanced as compared to the slope and the far field. Below 100 m *Oncaea* spp. remained the most numerous organism (10-130 Ind m^{-3}), making up 30-40 % of all individuals.

At Senghor Seamount the microzooplankton composition was similar during both sampling seasons (Fig. 5-5a). In the upper 25 m dinoflagellates showed up in high numbers over the seamount (1120-3950 Ind m^{-3}), especially over the summit in 2011, as compared to the far field (200-800 Ind m^{-3}). Nauplii were overall the most numerous organisms in the upper 100 m, reaching abundances of 2460-4700 Ind m^{-3} (40-55 % of the total microzooplankton). Calanoid copepods in the upper layer made up 450-1790 Ind m^{-3}, contributing to 15-25 % of the abundance, and were dominated by species of the families Para- and Clausocalanidae. Below 100 m the number of cyclopoid copepods increased and exceeded calanoids. *Oncaea* spp. contributed 25-45 % to the total zooplankton between 100-300 m with 420-950 Ind m^{-3} and remained the most abundant organism in the mesopelagic zone beside nauplii.

Within the mesozooplankton Clausocalanidae (55-170 Ind m^{-3}) and other calanoid copepods (66-338 Ind m^{-3}) were the most abundant organisms in the upper 100 m over Ampère Seamount, making up10-20 % and 30-45 % of all mesozooplankton (Fig. 5-5b). Below 100 m numbers of mesozooplankton decreased from 75 to 12 Ind m^{-3} down to 1000 m, whereof calanoids made up 35-55 % and *Oncaea* spp. and *Micro-/Macrosetella* spp. 10-20 % each. At the far field site mesozooplankton abundance of the upper 100 m was markedly lower than at the seamount, reaching in total 230-340 Ind m^{-3}. Especially Clausocalanidae (30-42 Ind m^{-3}) and other calanoid copepods (75-84 Ind m^{-3}) occurred in comparably low numbers.

Over Senghor Seamount highest mesozooplankton abundance was found in the upper 50 m during December 2011 (1230 Ind m^{-3}) (Fig. 5-5b). The composition was similar during both years with Clausocalanidae (30-530 Ind m^{-3}) and other calanoid copepods (60-310 Ind m^{-3}) as the most abundant organisms in the upper 100 m, making up 10-50 % and 15-35 %, respectively, of the mesozooplankton. Below 100 m *Oncaea* spp. was the most numerous organism (18-38 Ind m^{-3}), beside calanoid copepods, contributing 20-50 % to the total mesozooplankton. The mesozooplankton composition at the far field site was comparable to Senghor slope.

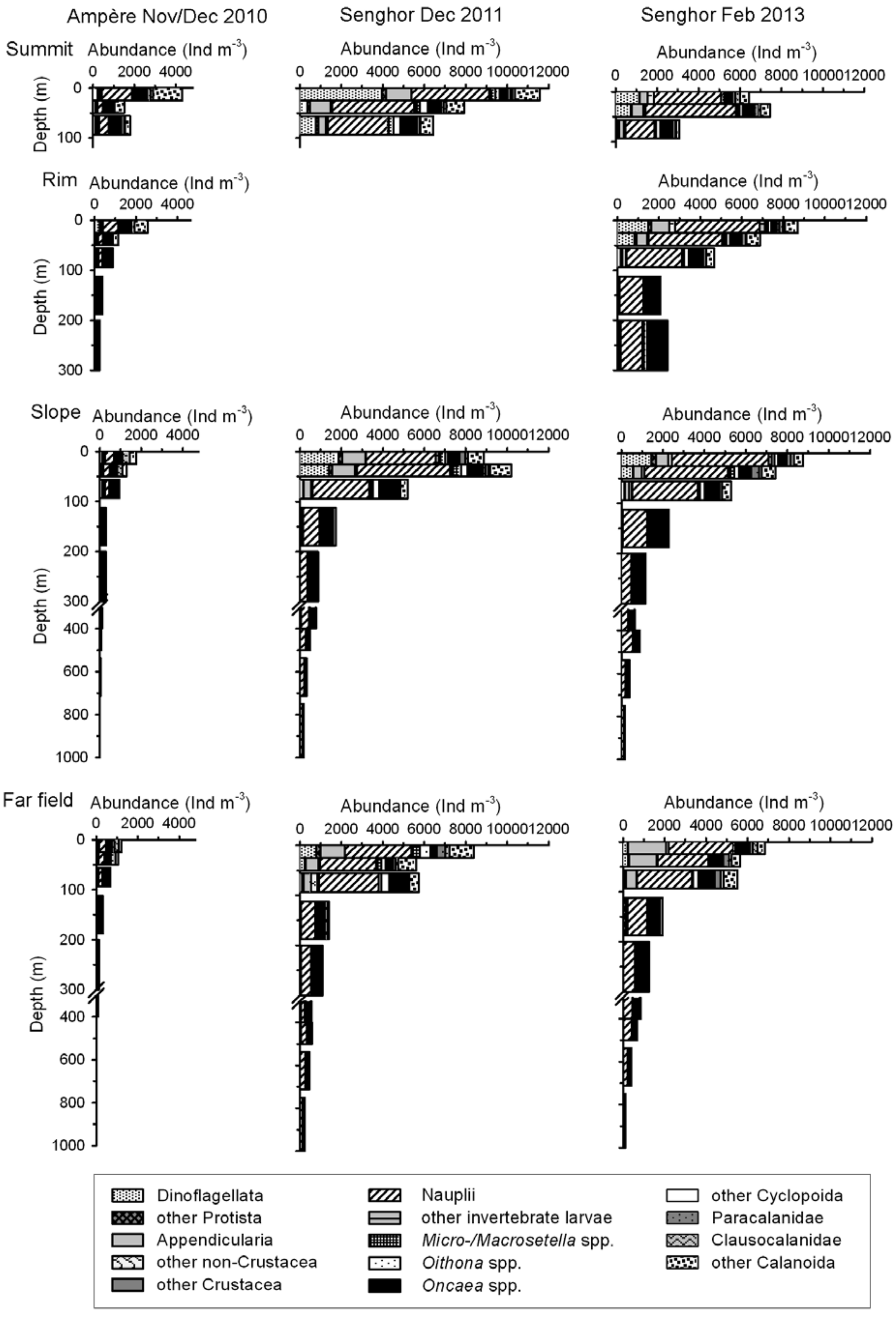

Fig. 5-5a. Vertical distribution of microzooplankton (0.055-0.3 mm) abundance (Ind m^{-3}) with taxonomic composition at summit, rim, slope and far field of Ampère Seamount in November/December 2010 and of Senghor Seamount in December 2011 and February 2013.

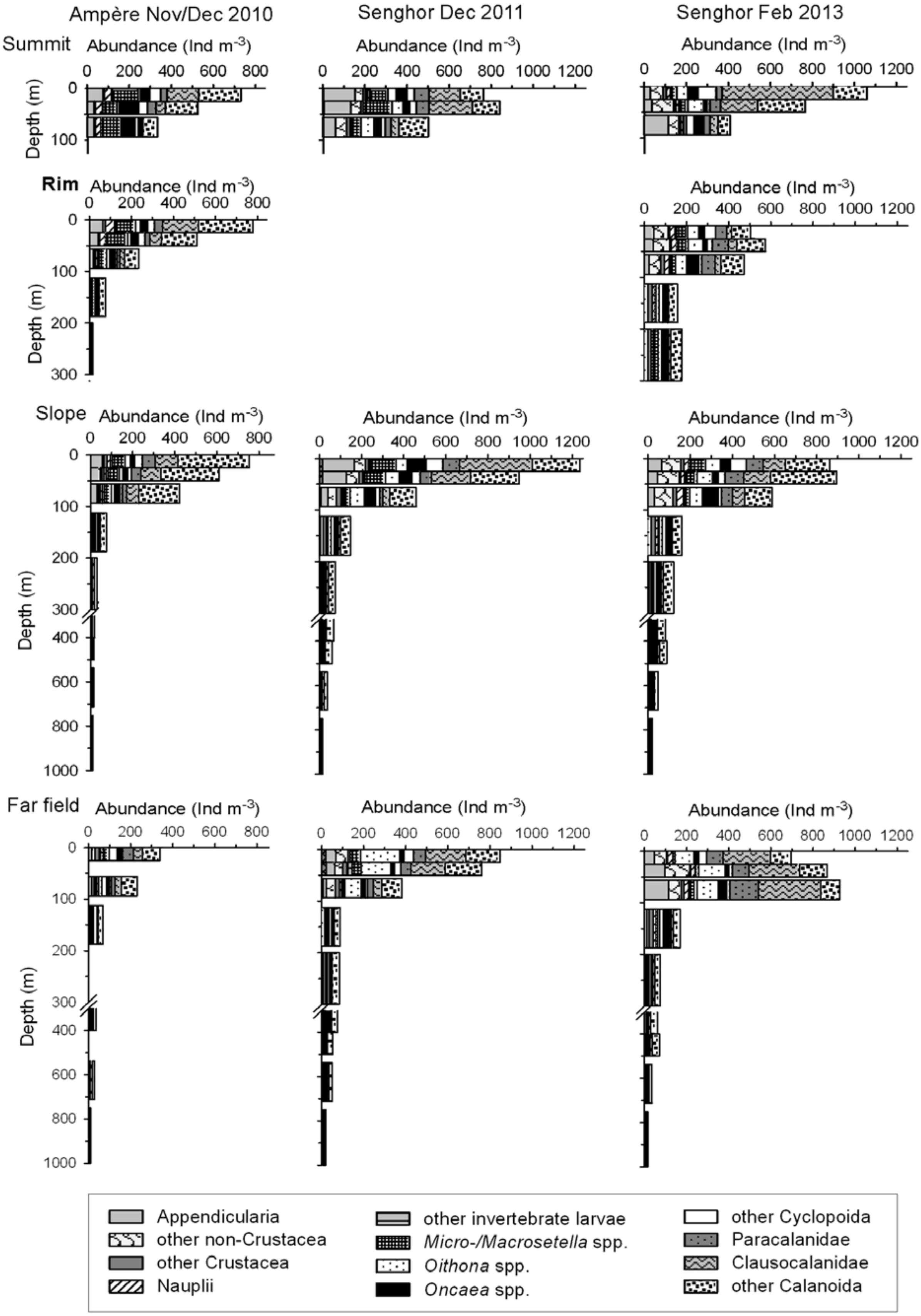

Fig. 5-5b. Vertical distribution of mesozooplankton (0.3-20 mm) abundance (Ind m^{-3}) with taxonomic composition at summit, rim, slope and far field of Ampère Seamount in November/December 2010 and of Senghor Seamount in December 2011 and February 2013.

5.4.2.2 Associations between zooplankton and location

The group-average linked cluster analyses and the SIMPROF permutation test showed in general a high level of 80-94 % similarity between locations in terms of zooplankton abundance standing stocks (Ind m^{-2}) in depths of 0-100 m and 100-1000 m, respectively. For the upper 100 m of Ampère Seamount and the far field site two clusters of locations were defined with average internal similarity of 88 % and dissimilarity between clusters of 18 %. One group was formed by the northern and southern slope and the far field. The 2nd group included the summit, all rim stations and the eastern and western slope (Fig. 5-6). In the deeper waters no clustering was detected.

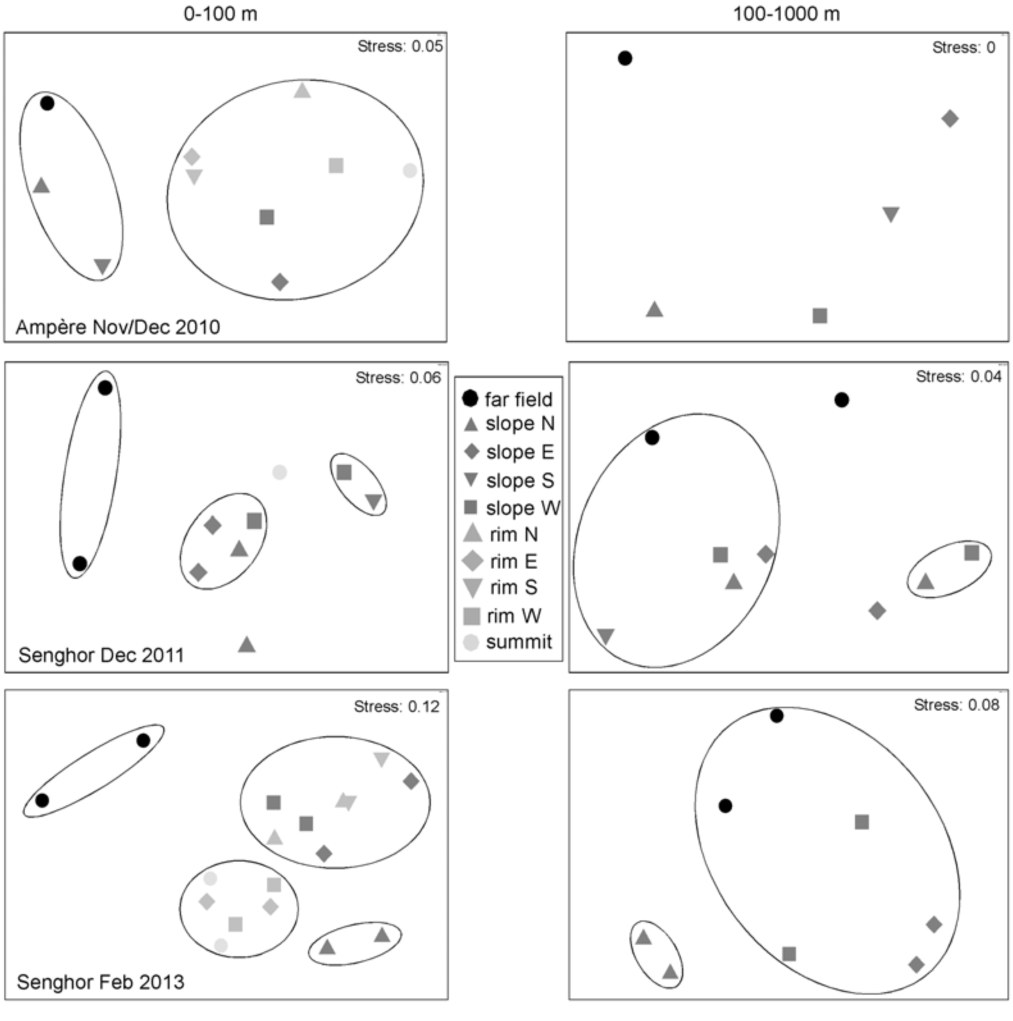

Fig. 5-6. Non-metric multi-dimensional scaling (MDS) plots, based on cluster analyses of depth integrated zooplankton abundance standing stocks within locations of Ampère Seamount in November/December 2010 and Senghor Seamount in December 2011 and February 2013 and the far field sites. Significant location cluster groups are circled, defined by % similarity between samples (SIMPROF-test).

In the upper 100 m of Senghor Seamount and the far field in 2011 the internal similarity was about 90 % and dissimilarity about 12 % between three distinct groups. The far field was separated from the seamount ($p < 0.05$), but no clear distributional pattern was defined within the seamount locations, neither in the shallow nor in the deeper waters. In 2013 four significantly separate clusters of locations ($p < 0.05$) were defined at Senghor with average internal similarity of 88 % and 15 % dissimilarity between clusters. Both far field casts formed one group, separated from the seamount locations. Within the seamount one group comprised the summit and the eastern and western rim. The 2nd group was formed by the northern slope and the 3rd one by the eastern and western slope and the northern and southern rim. Below 100 m two clusters of locations were defined: the northern slope was separated from all other slope stations and the far field.

The BIO-ENV analyses showed that in the waters off Ampère Seamount temperature best explains the structure of the zooplankton abundance data (Ind m^{-3}) (Spearman rank correlation coefficient $r_s = 0.757$; $p < 0.01$). For Senghor in 2011 the best match between matrices of physical data and zooplankton abundance was given by four physical variables, depth, temperature, salinity and oxygen ($r_s = 0.849$; $p < 0.01$), while for Senghor in 2013 it was given by temperature only ($r_s = 0.921$; $p < 0.01$).

5.4.2.3 Meroplanktonic larvae

Invertebrate larvae, excluding nauplii, of both size fractions were pooled and the abundance was analysed separately for each station. Cnidarians, gastropods and polychaetes were the dominant meroplanktonic larvae; other taxa as echinoderms, tunicates or other molluscs were rarely observed. In general, meroplanktonic larvae were concentrated in the upper 50 m; below 200 m larval abundance was generally low (Fig. 5-7a, b, c). Small differences in composition could be detected between the seamount locations: In the upper 100 m over Ampère larvae of gastropods were most abundant over the summit, the southern and eastern rim and at the far field site (12-46 Ind m^{-3}), whereas cnidarians (16-52 Ind m^{-3}) were more abundant over the seamount slopes (Fig. 5-7a). Polychaete larvae appeared frequently in the bottom near water layers of summit and rim (13-27 Ind m^{-3}) and were the most abundant group in deeper waters.

At Senghor Seamount in December 2011 larvae of polychaetes were the dominating group of meroplankton in nearly all samples (12-193 Ind m^{-3}) (Fig. 5-7b). Gastropod larvae occurred in numbers of 16-96 Ind m^{-3} in the upper 100 m of the slope stations. Cnidarians reached relatively high abundances in some samples particularly in the upper 25 m during both sampling times at Senghor with 16-64 Ind m^{-3}. At the far field site meroplanktonic larvae were rarely found in the whole water column (1-13 Ind m^{-3}).

In February 2013, larvae of polychaetes were also the most abundant group (16-267 Ind m^{-3}) making up 55-95 % of the meroplankton (Fig. 5-7c). Especially at the rim stations they showed up in high numbers in the bottom-near water layers between 100 and 240 m. Relatively high numbers of gastropod larvae were observed at the northeastern slope and at the northern and southern rim (41-160 Ind m^{-3}). Like in 2011 meroplanktonic larvae were scarce at the far field site in all depth layers (1-32 Ind m^{-3}).

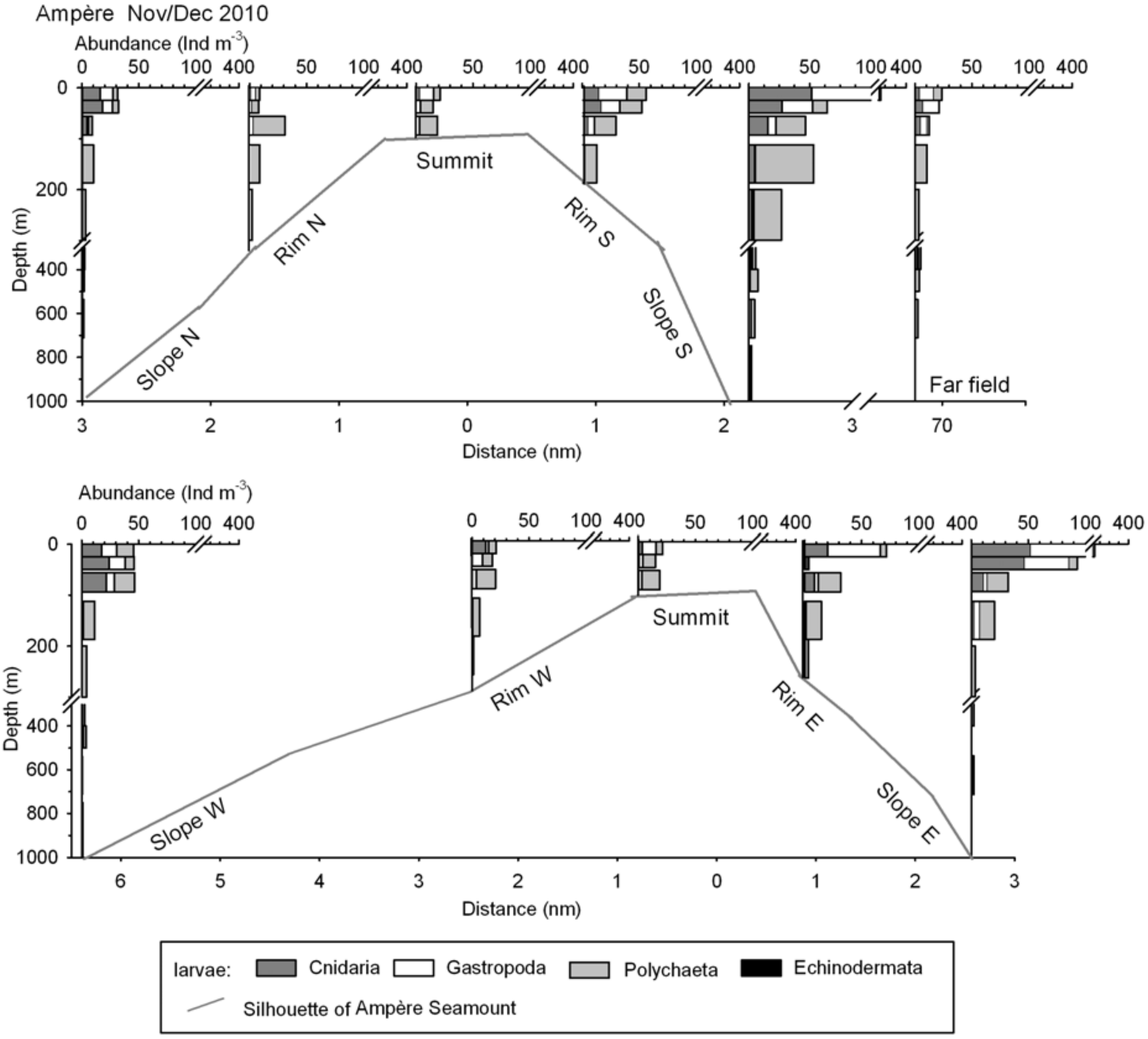

Fig. 5-7a. Vertical distribution of meroplanktonic larvae abundance (Ind m^{-3}) and composition at summit, rim, slope and far field of Ampère Seamount in November/December 2010.

The distribution of total meroplanktonic larvae was statistically compared between distinct seamount regions and the far field in terms of abundance standing stocks integrated over 0-100 m and 100-1000 m depth (see Table 5-A1 for full statistic results). Over Ampère Seamount standing stocks ranged between 1960 and 7360 Ind m^{-2} in the upper 100 m and from 2480 to 4570 Ind m^{-2} between 100 and 1000 m. In the upper 100 m over Senghor in December 2011 mean standing stocks of meroplanktonic larvae reached 3720-14600 Ind m^{-2} and between 100 and 1000 m 5310-9250 Ind m^{-2}. In February 2013 standing stocks ranged from 4660 to 12800 Ind m^{-2} in the upper 100 m and from 2890 to 11600 Ind m^{-2} in the deeper layer. In both years the standing stocks were significantly higher at the seamount than at the far field site in the upper 100 m (far field$_{2011}$ = 630 Ind m^{-2}; ANOVA$_{2011}$: $F_{3,4} = 13.11$, $p < 0.05$; *a priori*: $F_{1,4} = 34.95$, $p < 0.01$; far field$_{2013}$ = 952 Ind m^{-2}; ANOVA$_{2013}$: $F_{8,9} = 3.51$, $p < 0.05$; *a priori*: $F_{1,9} = 22.30$, $p < 0.01$).

Between both sampling periods at Senghor the abundance of meroplanktonic larvae was similar in the whole water column. In general standing stocks of meroplankton were higher by a factor of 1.5-2.5 at Senghor than at Ampère and differed significantly in the upper 100 m (ANOVA: $F_{2,30} = 7.07$, $p < 0.01$; *a priori*$_{2011}$: $F_{1,30} = 10.23$, $p < 0.01$; *a priori*$_{2013}$: $F_{1,30} = 11.62$, $p < 0.01$).

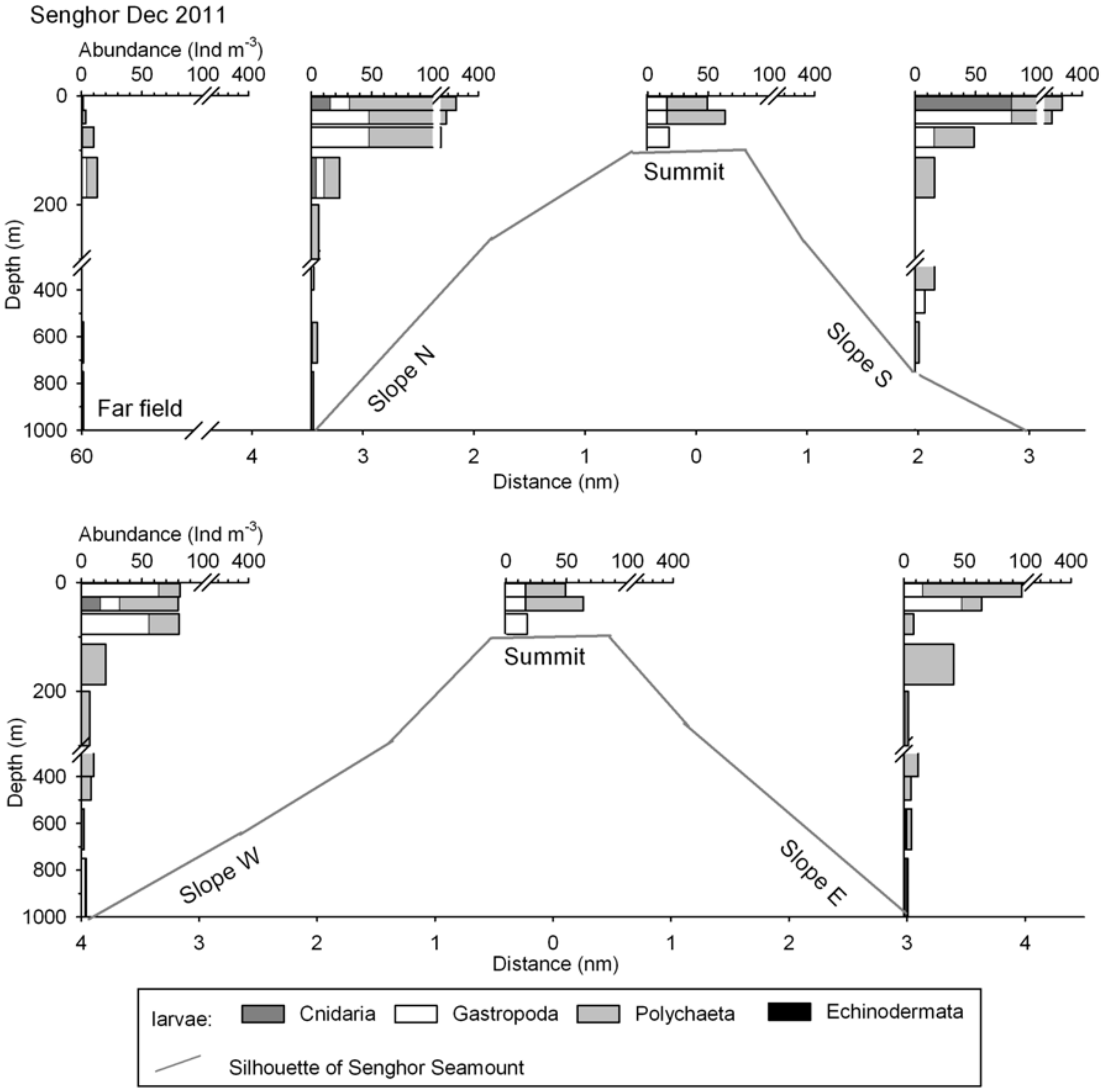

Fig. 5-7b. Vertical distribution of meroplanktonic larvae abundance (Ind m^{-3}) and composition at summit, slope and far field of Senghor Seamount in December 2011.

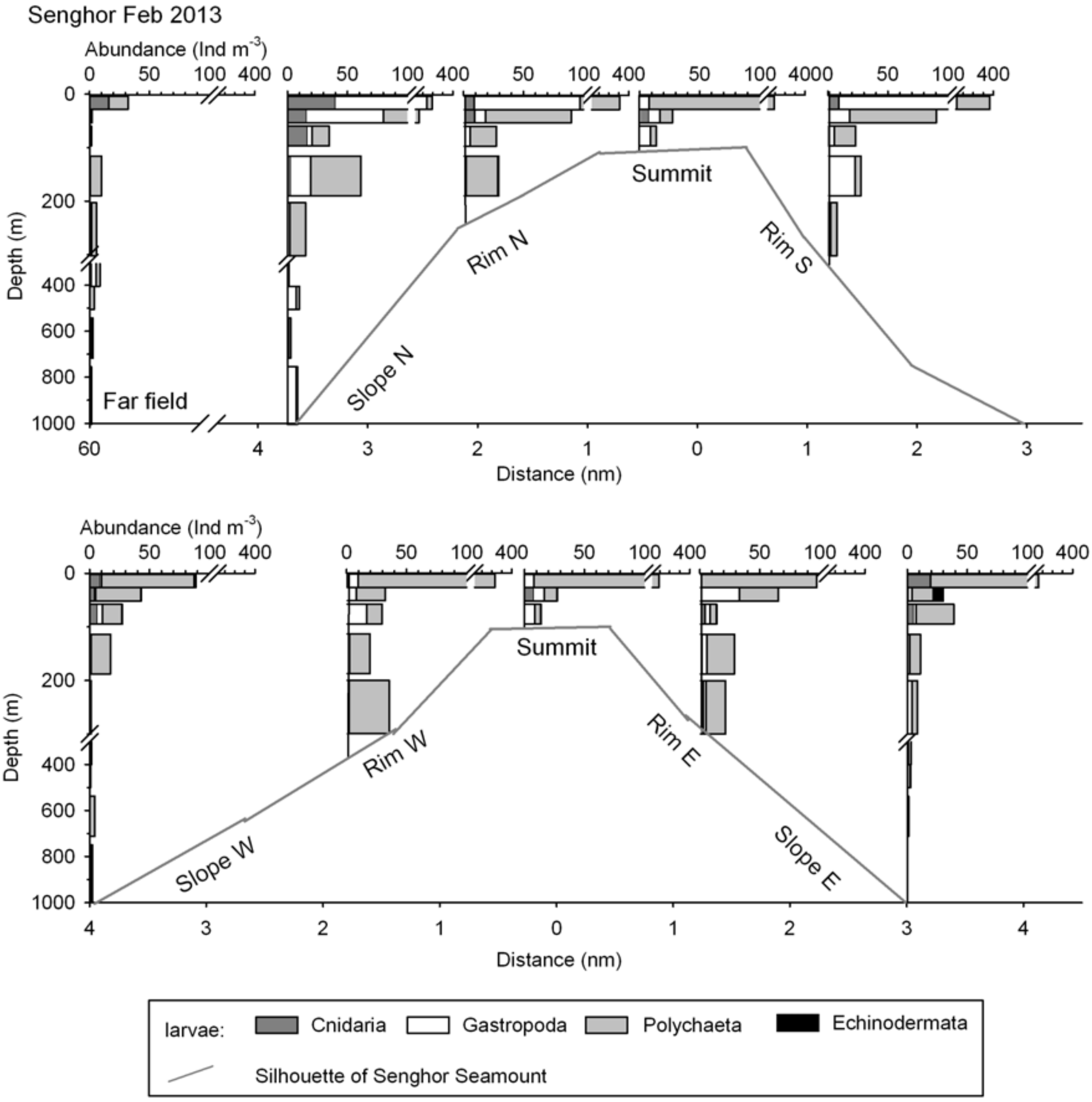

Fig. 5-7c. Vertical distribution of meroplanktonic larvae abundance (Ind m^{-3}) and composition at summit, rim, slope and far field of Senghor Seamount in February 2013.

5.4.3 Spatial distribution of biomass standing stocks

For each seamount comparisons in terms of biomass standing stocks were made between all stations for the upper 100 m, corresponding roughly to the mixed layer and the minimum depth (95-120 m) of the summit topography, and between slope and far field stations for the water column of 100-1000 m (Fig. 5-8a, b). At Ampère Seamount microzooplankton biomass ranged between 0.03 g m^{-2} and 0.12 g m^{-2} in the upper 100 m, corresponding to 33 % of the total zooplankton (0.055-20 mm; hereafter means micro- and mesozooplankton), with the highest concentration over the northern slope (Fig. 5-8a). The area of the lowest biomass extended over the summit and the northern and western rim. The mesopelagic biomass (100-1000 m) reached 0.09-0.15 g m^{-2}. No significant differences between rim and slope stations or between northwest up- and southeast downstream side were detected (see Table

5-A2 for full statistic results). The microzooplankton biomass of the far field site was in the same range than the seamount values.

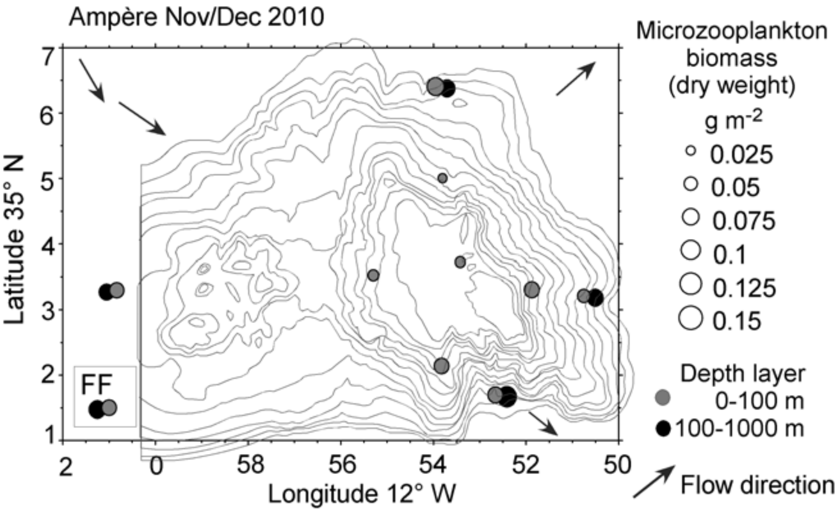

Fig. 5-8a. Depth integrated standing stocks of microzooplankton (0.055-0.3 mm) biomass (dry weight, g m^{-2}) at Ampère Seamount in November/December 2010. FF, far field.

Over Senghor Seamount in December 2011, the mean biomass of the microzooplankton in the upper 100 m was about 0.18 g m^{-2}, corresponding to 24 % of the total zooplankton (Fig. 5-8b). A mean stock of 0.20 g m^{-2} was measured for the deep stations in 100-1000 m. Biomass standing stocks at the far field site (~0.50 g m^{-2}) were twice as high than at the seamount in both depth layers, with a significant difference in the mesopelagic zone (ANOVA: $F_{3,4} = 3.14$, $p > 0.05$; *a priori*: $F_{1,4} = 9.09$, $p < 0.05$; see Table 5-A2 for full statistic results). The flow direction is assumed to be the same than in 2013, as it was also in September/October 2009 (see Denda & Christiansen 2014; Dumont et al. subm.).

In February 2013 mean biomass standing stock in the upper 100 m was about 0.22 g m^{-2}, and in mid water about 0.26 g m^{-2} (Fig. 5-8b). Mean standing stocks over the summit (ANOVA: $F_{8,9} = 4.09$, $p < 0.05$; *a priori*: $F_{1,9} = 5.34$, $p < 0.05$) and the rim stations (*a priori*: $F_{1,9} = 9.62$, $p < 0.05$) were significantly higher than over the slopes in the upper 100 m (see Table 5-A2 for full statistic results). Between northeast up- and southwest downstream side no significant differences were detected, neither between all seamount stations and the far field. Comparisons among standing stocks of both seamounts indicate significant differences in the upper 100 m ($t_{29} = 7.16$, $p < 0.001$) and in the deeper waters ($t_{14} = 4.06$, $p < 0.01$), showing a 2.5 times higher microzooplankton biomass at Senghor than at Ampère.

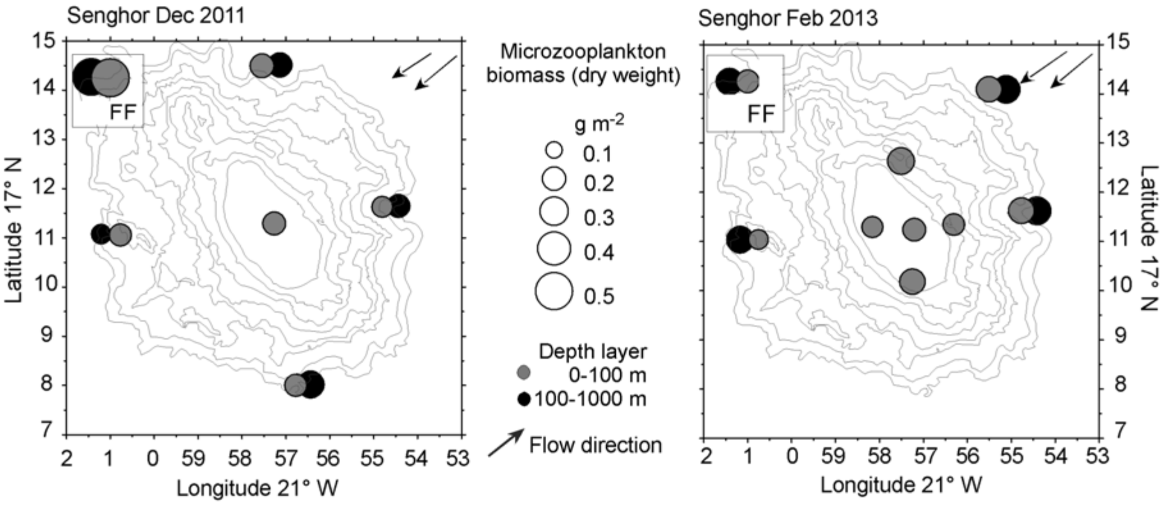

Fig. 5-8b. Depth integrated standing stocks of microzooplankton (0.055-0.3 mm) biomass (dry weight, g m^{-2}) at Senghor Seamount December 2011 and February 2013. FF, far field. Flow direction measured in 2013 is considered to be representative of the circulation on the seamount for both years.

5.4.4 Vertical biomass distribution

Vertical distribution of micro- and mesozooplankton biomass was analysed separately for each seamount and far field station, showing similar profiles for both seamounts (Fig. 5-9a, b, c). Around the summit plateau of Ampère Seamount mean microzooplankton biomass was 1.11 mg m^{-3} at the surface and declined to 0.14 mg m^{-3} in the bottom near water layer (Fig. 5-9a). At the surface over the slopes mean biomass was 1.37 mg m^{-3}, decreasing to 0.27 mg m^{-3} at 150 m. Around 300 m a slight increase followed before concentrations declined to 0.06 mg m^{-3} at 1000 m. Biomass concentration of mesozooplankton was about twice as high than of microzooplankton and ranged between 1.91 mg m^{-3} and 0.45 mg m^{-3} around the summit and between 2.54 mg m^{-3} and 0.14 mg m^{-3} at the slopes. In the far field micro- and mesozooplankton biomass was in the same range as in the seamount waters.

Over Senghor summit in 2011 microzooplankton biomass was 2.68 mg m^{-3} at the surface and 1.98 mg m^{-3} close to the bottom (Fig. 5-9b). Mean concentrations over the slopes declined gradually from 2.79 mg m^{-3} at the surface to 0.12 mg m^{-3} at 1000 m. At the far field site mean microzooplankton biomass (11.34-0.32 mg m^{-3}) was two to four times higher than over Senghor slope. Mesozooplankton concentrations were in the same order of magnitude at both locations and ranged between 7.87 mg m^{-3} and 0.26 mg m^{-3}. In general biomass concentration of mesozooplankton was about four times higher than of microzooplankton at Senghor Seamount.

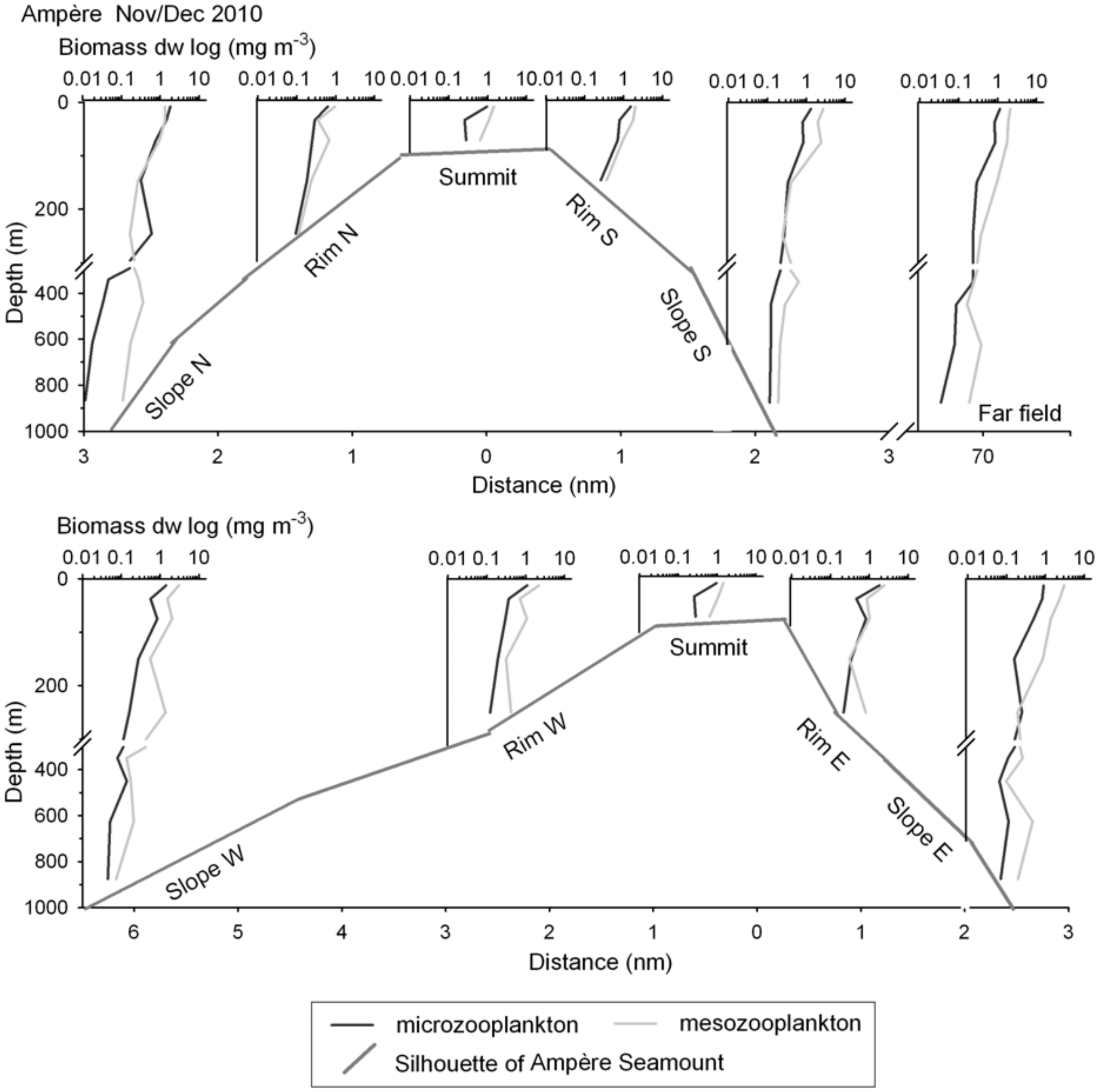

Fig. 5-9a. Vertical distribution of micro- (0.055-0.3 mm) and mesozooplankton (0.3-20 mm) biomass (dw, dry weight; mg m^{-3}) on a logarithmical scale at summit, rim, slope and far field of Ampère Seamount in November/December 2010.

At Senghor in 2013 mean microzooplankton biomass ranged between 3.21 mg m^{-3} and 0.79 mg m^{-3} over the summit plateau (Fig. 5-9c). Over the slopes biomass was 3.38 mg m^{-3} at the surface and declined towards 1000 m to 0.17 mg m^{-3}. At the far field concentrations ranged from 2.06 mg m^{-3} to 0.13 mg m^{-3}. Mesozooplankton biomass was between 9.87 mg m^{-3} and 2.08 mg m^{-3} at the shallow stations. Over the slopes highest concentration of 14.42 mg m^{-3} occurred between 25 and 50 m. Below, biomass declined towards 1000 m (0.42 mg m^{-3}) with a slight peak around 450 m (2.56 mg m^{-3}). At the far field site concentrations ranged between 8.23 mg m^{-3} and 0.35 mg m^{-3} and showed a similar vertical profile than Senghor slope.

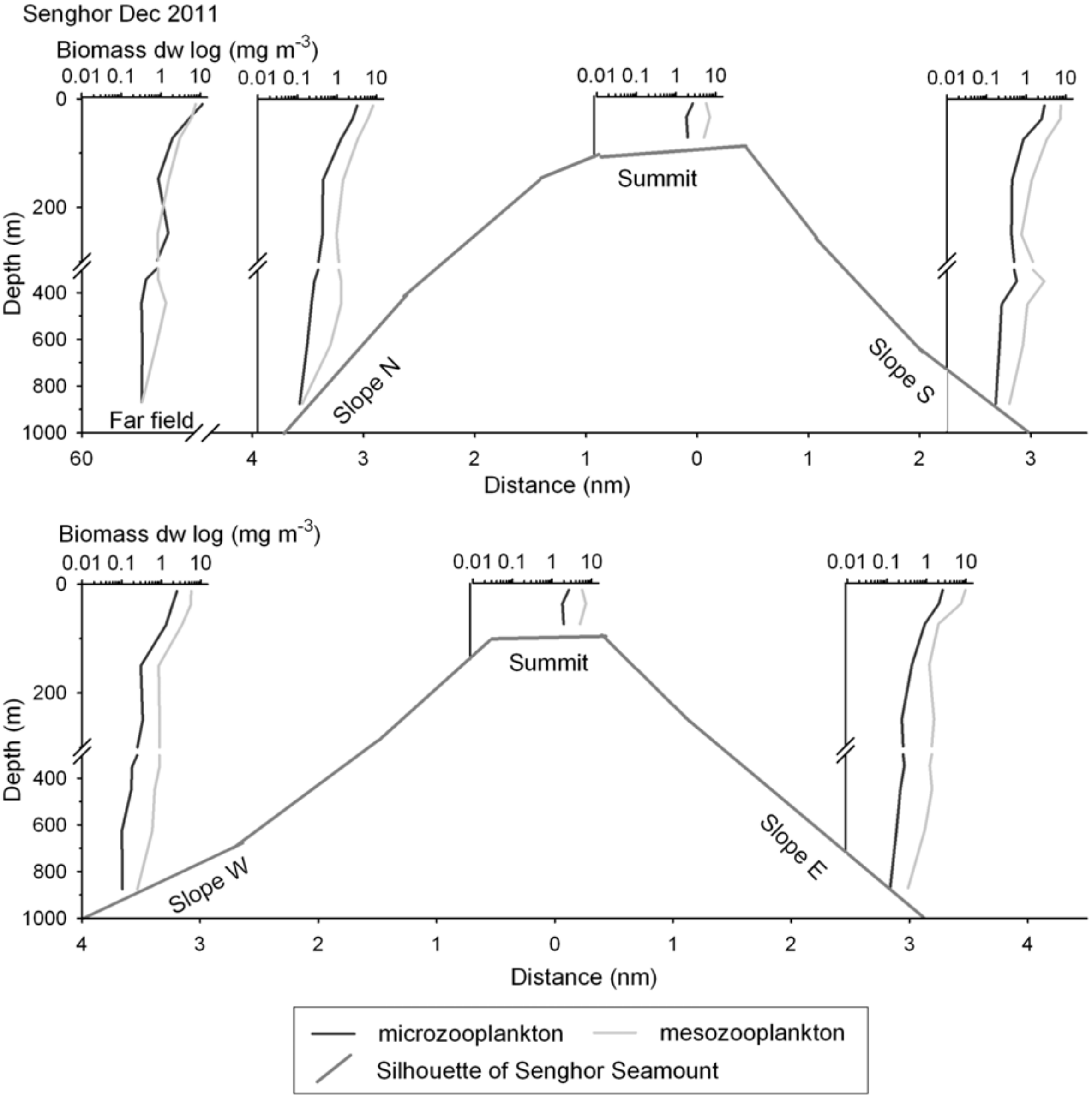

Fig. 5-9b. Vertical distribution of micro- (0.055-0.3 mm) and mesozooplankton (0.3-20 mm) biomass (dw, dry weight; mg m^{-3}) on a logarithmical scale at summit, slope and far field of Senghor Seamount in December 2011.

The BIO-ENV analyses showed that in the waters off Ampère Seamount temperature best explains the structure of the biomass (mg m^{-3}) data between locations (Spearman rank correlation coefficient $r_s = 0.810$; $p < 0.01$). For Senghor in 2011 the best match between matrices of physical data and zooplankton biomass required two variables, temperature and oxygen ($r_s = 0.849$; $p < 0.01$), while for Senghor in 2013 it was given by temperature only ($r_s = 0.820$; $p < 0.01$).

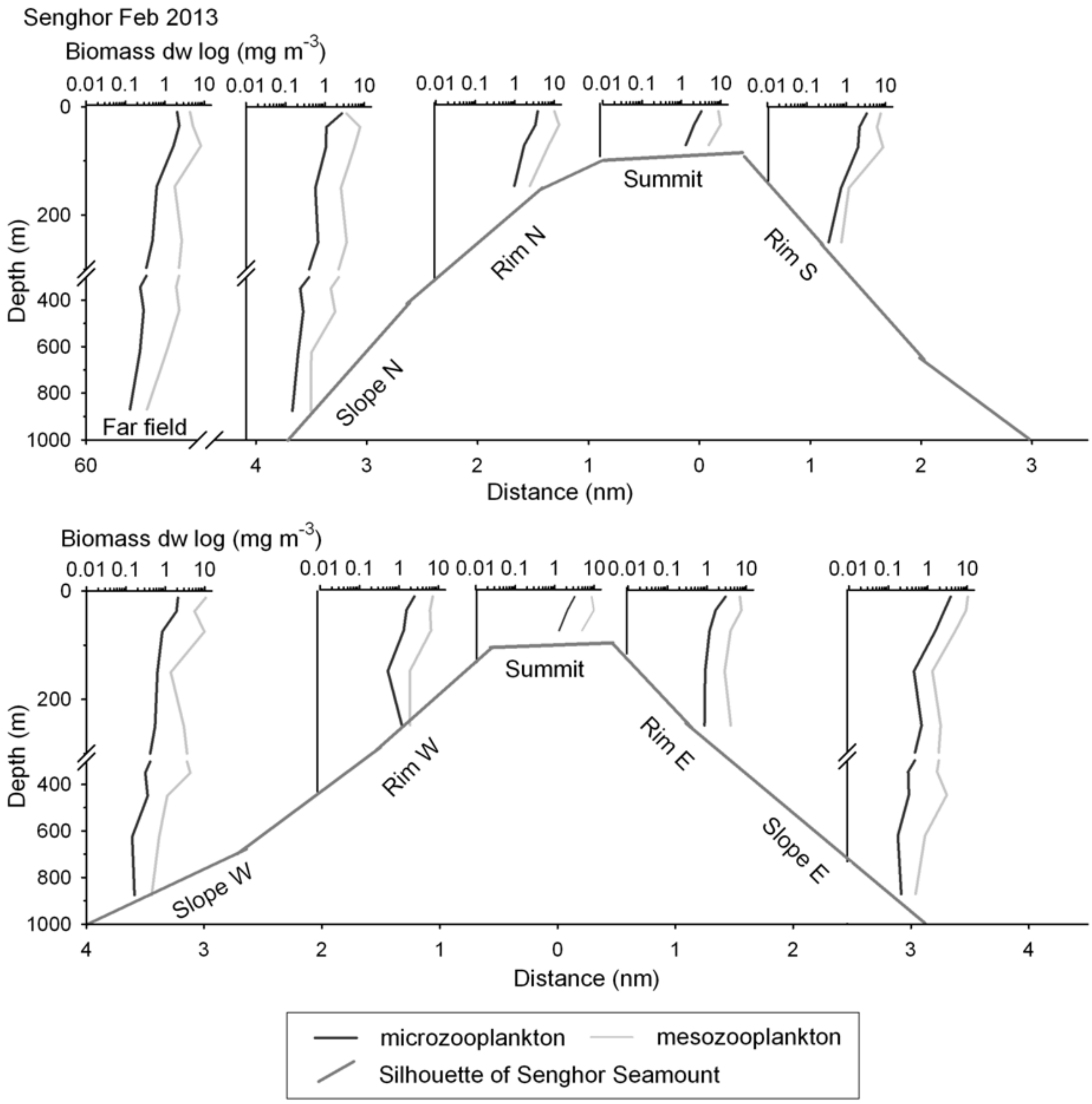

Fig. 5-9c. Vertical distribution of micro- (0.055-0.3 mm) and mesozooplankton (0.3-20 mm) biomass (dw, dry weight; mg m^{-3}) on a logarithmical scale at summit, rim, slope and far field of Senghor Seamount in February 2013.

5.4.5 Carbon demand

The respiratory carbon demand of the zooplankton standing stock was compared between summit, rim and slope of each seamount, and the far field site in 0-100 m and 100-1000 m depth, separated for micro- and mesozooplankton (Fig. 5-10). In the waters of Ampère Seamount and at the far field site the contribution of each size fraction to the total respiratory carbon demand was about 50 % in the whole water column. In the upper 100 m the mean total carbon demand ranged from 16.5 mg m^{-2} d^{-1} over the summit to 29.1 mg m^{-2} d^{-1} over the slope. Between 100 and 1000 m a mean ratio of 13.1 mg m^{-2} d^{-1} was calculated for the slope and of 15.0 mg m^{-2} d^{-1} for the far field site.

At Senghor Seamount the contribution of microzooplankton to the total carbon demand was 30-40 % in the whole water column during both years (Fig. 5-10). In December 2011 mean total respiratory carbon demand in the upper 100 m was 93.5 mg m^{-2} d^{-1} over the summit and 96.6 mg m^{-2} d^{-1} over the slope, while at the far field site it was 132.4 mg m^{-2} d^{-1}, in which the microzooplankton made up 60 %. Between 100 and 1000 m mean carbon demand ranged from 29.9 mg m^{-2} d^{-1} at Senghor slope to 41.3 mg m^{-2} d^{-1} at the far field site, where the smaller fraction contributed 54 %.

In February 2013 the respiratory carbon demand of the upper 100 m over Senghor was in the same range as in December 2011 (Fig. 5-10). During this sampling time the mean ratio of 95.6 mg m^{-2} d^{-1} at the far field site was similar to the seamount values with a contribution of 35 % for the microzooplankton to the total carbon demand. In the deeper waters mean total carbon demand was 43.1 mg m^{-2} d^{-1} at Senghor slope and 46.7 mg m^{-2} d^{-1} at the far field site.

In comparison of both seamounts the respiratory carbon demand of each size fraction in both layers was 3-4 times higher at Senghor than at Ampère, the difference being significant in the upper 100 m (microzooplankton: $t_{32} = 13.51$, $p < 0.001$; mesozooplankton: $t_{32} = 14.14$, $p < 0.001$) as well as in the deeper waters (microzooplankton: $t_{15} = 4.80$, $p < 0.001$; mesozooplankton: $t_{15} = 6.97$, $p < 0.001$) (see Table 5-A3 for full statistic results).

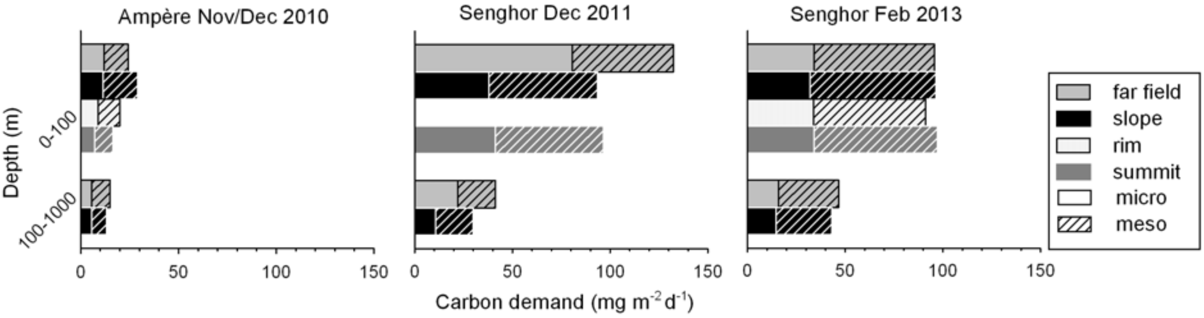

Fig. 5-10. Depth integrated respiratory carbon demand (mg $m^{-2}d^{-1}$) of micro- (0.055-0.3 mm) and mesozooplankton (0.3-20 mm) standing stocks at summit, rim, slope and far field of Ampère Seamount in December 2010 and of Senghor Seamount in December 2011 and February 2013.

5.5 Discussion

The principal objective of this study was to investigate the importance of microzooplankton within a tropical and a subtropical seamount pelagic community in the NE Atlantic, and whether spatial distribution patterns of microzooplankton in terms of biomass and abundance exist due to local and large-scale current-topography interactions and hydrographic conditions. The carbon demand of the micro- and mesozooplankton community was evaluated with respect to the distinct trophic regions which enclose each seamount. Furthermore we assessed the potential of the two seamounts studied as source for benthic invertebrate larvae in the open ocean.

5.5.1 The influence of the large-scale current regime and the local flow field on biomass and abundance

Ampère Seamount belongs to the sphere of the NE Atlantic subtropical gyre (37°-24° N), whereas Senghor Seamount is located in the adjacent cyclonic tropical gyre (19°-10° N). Both gyres are separated by the Cape Verde frontal zone (CVFZ; e.g. Zenk et al. 1991). The larger biomass standing stocks of microzooplankton at Senghor as compared to Ampère can be attributed to differences in productivity in the two areas: Whereas the subtropical gyre to the north of the CVFZ is oligotrophic (Robinson et al. 2002), the waters south of the CVFZ are considered as nutrient-rich (Pastor et al. 2008) with a strong influence of the Mauretanian upwelling (e.g. Pastor et al. 2008; Mason et al. 2011) and enhanced chlorophyll concentrations which may extend up to 300-400 km from the shore (Lathuilière et al. 2008) into the area of Senghor Seamount.

Some seamounts are known as locations of enhanced plankton production, at least for short periods, as compared to the surrounding ocean (Genin & Boehlert 1985; Dower et al. 1992; Mouriño et al. 2001). In the waters off Ampère a tendency of a general higher abundance of the respective micro- and mesozooplankton around the summit plateau was observed as compared to the far field. But, since we cannot confirm this observation statistically and no clear associated pattern can be seen in the cluster analyses, we rather assume common patchiness as the main reason for differences in distribution of the small data sets than possible seamount effects on the zooplankton. At Senghor Seamount in 2011 the total abundance of microzooplankton was in the same order of magnitude as in the far field, but the biomass standing stock was even significantly lower at the seamount. Temperature and salinity at both sampling locations were characteristic for the water masses south of the CVFZ (e.g. Tomczak 1981; Pierre et al. 1994), but we cannot exclude an influence of the frontal zone by filaments or associated eddies at the far field station at times, generating meso-scale variability (Onken & Klein 1991; Zenk et al. 1991), and possibly affecting composition and densities of phyto- and zooplankton. However, in 2013 the concentrations and vertical profiles of biomass did not differ between far field and Senghor Seamount, suggesting that the far field station is not affected by extensions of the CVFZ, featuring enhanced plankton biomass, and current-topography interaction does not lead to a general build-up of higher biomass at Senghor, as explained below.

Microzooplankton biomass showed some small-scale spatial variability at each seamount, which might be attributed to the interaction of the local flow field with the seamount topography to some extent. ADCP measurements across Ampère indicate strong impinging currents of 15-25 cm s^{-1} from the northwest in the upper 250 m, probably causing the low biomass over the summit plateau and the northern and western rim stations by the advection of plankton. On the eastern and southern side enhanced accumulations of microzooplankton occurred in an area of lower current velocities. We generally assumed depleted biomass on the upstream side of the seamount, but biomass was enhanced also over the northern slope, where a calm area was generated above the 1000 m isobaths, before currents turned to the north/northeast with velocities of 30-40 cm s^{-1}. Thus, we cannot verify a clear pattern of depleted biomass on the upstream and enhanced biomass on the downstream side for the microzooplankton distribution at Ampère, coincident with observations on the meso- and macrozooplankton (>0.3 mm) during the same cruise (Denda & Christiansen 2014).

ADCP measurements across Senghor in 2013 showed steady impinging currents of 10-15 cm s^{-1} from the north/northeast, which could cause the generation of a recirculation cell on the top of the seamount affecting the local retention time of water masses and passive particles at the seamount summit (see Roden 1987; Beckmann & Mohn 2002; Genin 2004; Lavelle & Mohn 2010). But for Senghor it seems generally unlikely that a Taylor column could persist above the seamount for longer periods due to the high, primarily tide- and trade wind-driven, spatio-temporal current variability in the region (Müller & Siedler 1992; Vangriesheim et al. 2003; Dumont et al. subm.). Consistently, observations of currents did not detect any evidence for a recirculating flow in the upper 200 m during the cruises, neither in September/October 2009 (Dumont et al. subm.) nor during this study in February 2013. This supports previous observations on larger meso- and macrozooplankton (>0.3 mm) at Senghor in 2009 (Denda & Christiansen 2014), and also at other seamounts in the NE Atlantic (Nellen 1973; Hirch et al. 2009; Martin & Christiansen 2009), where no evidence of higher production, expressed as high concentrations of zooplankton biomass, was found in the seamount system. Rather, the impinging currents were deflected by the seamount generating a calm area with low current velocities in lee at the south/southwestern side. But a substantial accumulation of microzooplankton in this potential calm area was not observed. Microzooplankton biomass was significantly enhanced around the summit plateau compared to the slopes of Senghor, but did not indicate any clear connection to the flow field; no significant differences were detected between northeast up- and southwest downstream side and no corresponding clustering occurred between the respective stations based on zooplankton abundance. By contrast, Huskin et al. (2001), for example, observed a significantly higher zooplankton biomass at the downstream side of Great Meteor Tablemount, which is located between two southwestward currents (Siedler & Onken 1996; Mohn & Beckmann 2002). Thus, although local effects of current-topography interaction can influence the zooplankton distribution at a seamount at times, this cannot be generalized.

5.5.2 The influence of oxygen concentration and food supply on the vertical distribution

The vertical zooplankton distribution reflected the hydrographical situation of the stratified water column around each seamount, particularly profiles of oxygen and fluorescence. The distribution between distinct seamount locations and the far field site was best explained by temperature. The hydrographical situation over Ampère and at the far field site was characterized by a strong stratification of the water column, typical for a subtropical ocean in winter, with a thermo- and halocline at 60-80 m. Zooplankton were accumulated right below the thermocline in the zone of the oxygen and the deep fluorescence maximum, which were at least clearly present at the far field site. During December the 6th and 7th of the cruise a cyclonic depression passed over the region with strong southwesterly winds (7-8 Bft) mixing the upper layer so that the oxygen maximum layer almost completely disappeared over Ampère Seamount as well as the deep chlorophyll maximum (Kaufmann & Diniz 2012), but without any effect on the zooplankton distribution. Thermal stratification was still present and presumably phytoplankton and particles were still attached to the thermocline followed by zooplankton accumulations due to sufficient food availability.

Over Senghor Seamount maximum densities of zooplankton occurred in the surface mixed layer and were coincident with the distinct deep fluorescence and oxygen maximum, featuring also higher respiration rates within this zone. Oxygen is a key factor for efficient metabolism, and in areas with a strong oxygen minimum zone (OMZ) the gradient in oxygen concentrations below the thermocline affects the vertical distribution of zooplankton biomass and abundance, as described by Saltzmann & Wishner (1997a) for a seamount in the eastern tropical Pacific with most mid-water zooplankton excluded from the core of the oxygen minimum layer (OMZ; <0.1 ml l^{-1}). But, oxygen was not as restrictive to copepods as expected, and many speciemens such as *Clausocalanus* spp., *Oncaea* spp., *Euchaeta* spp., *Oithona* spp., and *Corycaeus* spp., were present throughout the OMZ (<0.2 ml l^{-1}; Saltzmann & Wishner 1997b). Experiments on hypoxia tolerance by Stadler & Marcus (1997) showed that nauplii and adults of three calanoid species avoided neither severely hypoxic (<0.5 ml l^{-1}) nor moderately hypoxic (1.0 ml l^{-1}) layers. Although oxygen concentrations above Senghor decreased strongly below the thermocline, they were always >1.0 ml l^{-1} and therefore not critically low for most zooplankton. Instead we assume that the zooplankton distribution over Senghor is mainly determined by the food supply, showing a typical decline in biomass and abundance with depth. Small peaks in microzooplankton abundance occur at ~400 m, representing a food source for larger omni- and carnivorous plankter in the mesopelagic zone, which is reflected in a slight biomass increase of the mesozooplankton in the respective depth.

5.5.3 The composition of the zooplankton community

In the past, most studies of oceanic zooplankton have concentrated on larger meso- and macrozooplankton (Pfaffenhöfer 1993; Gallienne & Robins 2001), using a medium mesh size (0.2-0.3 mm) and consequently undersampling, among others, the smaller copepod species and developmental stages, as copepodites and nauplii (Greene 1990; Calbet et al. 2001; Gallienne & Robins 2001). However, their important role in the pelagic system (Arístegui et al. 2001; Turner 2004; Schmoker et al. 2013) as generally the most abundant metazoans in the ocean (e.g. Gallienne & Robins 2001; Turner 2004) has been widely recognized.

In the tropical waters off Senghor Seamount nauplii were the most abundant microzooplankton and made up 35-55 % of the total abundance, whereas in the winter condition of the subtropical waters off Ampère, the relative abundance of nauplii was lower and in the same order of magnitude as that of copepodites and adults. Copepodites and adults of the cyclopoid family Oncaeidae were present in high densities throughout the whole water column at both seamounts. This family is generally known as widespread in all parts of the oceans and at all depths (Pfaffenhöfer 1993). Individuals of the genus *Oithona* occurred also in high numbers, as well as individuals of the small calanoid families Para- and Clausocalanidae and of the harpacticoid *Microsetella*. All these small copepod species, which reach an adult length <0.6 mm, were much more abundant in the fine-meshed nets (0.055 mm) than the larger taxa, emphasizing the important role of small copepods in the pelagic food web. The strong grazing impact of microzooplankton, primarily on phytoplankton <20 µm, can produce a significant removal of the primary production (>100 %) (Böttjer & Morales 2005). For mesozooplankton, larval fish and other planktivorous consumers, microzooplankton are important prey items (e.g. Turner 2004; Calbet 2008). Even the distribution of fish larvae and other predators can in turn be affected by microzooplankton distribution patterns (Sánchez-Velasco & Shirasago 1999). In the diet of seamount associated fish species especially oncaeid copepods play a key role and were found at Seine Seamount in the NE Atlantic as the main prey in the snipefish *Macroramphosus* spp. and the boarfish *Capros aper* (Christiansen et al. 2009) and at Ampère Seamount in the parrot seaperch *Callanthias ruber* (Denda unpubl. data; Manuscript 3).

The taxonomic variability at the levels studied was highest in the upper mixed layer, which is typical for a tropical region as reported by Saltzmann & Wishner (1997b) for the eastern Pacific. The vertical differences in taxonomic composition of small copepods over Ampère and Senghor seamounts seemed to be mainly determined by food availability and feeding ecology. The omnivorous Clauso- and Paracalanidae were concentrated in the mixed layer, where, at least over Senghor, a high amount of dinoflagellates occurred. Both copepods are known as important grazers of phytoplankton and protozoans, especially dinoflagellates and ciliates (Kleppel 1993; Calbet & Landry 1999; Suzuki et al. 1999). *Microsetella* spp., the most common harpacticoid copepod in our study, was present in all depth layers, where it is often found in association with marine snow aggregates as food source (Uye et al. 2002; Koski et al. 2005), but with main concentration in the epipelagic zone, as reported also for the Arabian Sea (Böttger-Schnack 1996).

Below the thermocline *Oncaea* spp. made up 35-45 % of the total abundance. This genus is known for an opportunistic omnivorous to carnivorous feeding behaviour (Pfaffenhöfer 1993; Kattner et al. 2003). *Oncaea* spp. is suggested to utilize a variety of prey organisms and to feed on particles and organisms attached to marine snow and houses or body walls of salps, appendicularians or chaetognaths, using them as physical substrate and food source (Ohtsuka & Kubo 1991; Ohtsuka et al. 1993; Go et al. 1998). Böttger-Schnack (1994) also found higher relative abundance of *Oncaea* spp. in

deeper layers than in the epipelagic zone in the Eastern Mediterranean and the Arabian Sea and regarded this copepod as common down to meso- and bathypelagic zones for wide areas.
The taxonomic composition at Senghor showed in general a high level of similarity between the different seamount sites based on the abundance of distinct taxa. The separation of the far field from the seamount stations in the cluster analyses of the upper 100 m can be attributed to the much higher abundance of dinoflagellates over Senghor, especially around the summit. Passive particles may be accumulated at the seamount summit by current-topography interaction (Roden 1987; Beckmann & Mohn 2002; Genin 2004; Lavelle & Mohn 2010), but since a closed recirculation cell can be excluded to persist above Senghor for longer periods, topography-generated upwelling and particle trapping seem to be unlikely mechanisms to affect the secondary production (see Genin 2004; Genin & Dower 2007). Rather, enhanced vertical mixing of the waters near the summit, indicated by vertical displacement of the isotherms- and isohalines in the upper 100 m due to variable tidal flow (Dumont et al. subm.), might induce nutrients and detritus to the surface mixed layer and increase dinoflagellate abundance at times. Since the abundance of other taxonomic groups than dinoflagellates was not higher over Senghor as compared to the far field, it seems unlikely that the nutritional input lasted long enough for a transfer to higher trophic levels, which would require several weeks to months according to the typical zooplankton generation times (Genin & Boehlert 1985; Dower & Mackas 1996; Genin & Dower 2007).

5.5.4 The distribution of meroplanktonic larvae

Seamounts can host diverse and abundant communities of benthic invertebrates, but the mechanisms of their recruitment and their dispersal as well as larval traveling between isolated habitats, such as seamounts, are not fully understood (Clark et al. 2010; Shank 2010). In near shore areas or around isolated islands, where fronts, internal waves or tidal cycles might affect the plankton communities, knowledge of the dispersal of invertebrate and especially fish larvae is much better (e.g. Boehlert et al. 1992; Pineda 1994; Rodríguez et al. 2001; Shanks et al. 2003; Landeira et al. 2009). But would current-topography interaction at seamounts, creating Taylor caps, rectified flows or eddies, result in similar larval dispersal and distribution patterns in the different habitat?

Since seamounts provide special habitats for benthic deep-sea and shallow-water organisms and host diverse and abundant communities (Rogers 1994; Shank 2010), we expected and indeed confirmed Senghor Seamount to be a source for invertebrate larvae in the open ocean, with significantly enhanced larval abundance in the seamount waters as compared to the far field site. This supports the hypothesis by Mullineaux & Mills (1997) that larvae of benthic invertebrates are retained in flows near the seamount, although direct evidence of such flow features like Taylor caps, eddies formed in lee of the seamount, or a rectified flow generated by seamount-trapped waves (see Mullineaux & Mills 1997 and references therein) was rarely found at Senghor. In the upper 200 m the steady southwestward flow across Senghor did not result in the generation of a recirculating flow (see also

Dumont et al. subm.), as mentioned above. Only in deeper waters from 250 to 400 m and down to 600 m the observations suggest weak recirculating near-bottom flows around Senghor (see also Dumont et al. subm.; Mohn unpubl. data), potentially retaining larvae close to the seamount, as indicated by small larval accumulations in the waters around the lower edge of the summit plateau and on the upper slopes. But since it is unlikely that this recirculating water extended into the surface layers because of high current variability (Dumont et al. subm.), the observed enhanced vertical mixing induced by tidal flow seems to be the major mechanism also for the high larval abundance in the upper mixed layer over Senghor. Trapped waves can generally be excluded as retention mechanism because Senghor is located equatorwards of 30° N, where trapped waves are not assumed to occur (Beckmann & Mohn 2002; Dumont et al. subm). On the other hand, the expected higher abundance of meroplanktonic larvae, as compared to the far field, was not found over Ampère Seamount, suggesting that larvae were not retained as result of the local flow field and thus did not accumulate at the seamount, or that larval release was low during the four days of sampling. Neither for Senghor nor for Ampère it is known, whether a retention time could last long enough for meroplanktonic larvae to complete their planktonic stages (~30 days) and settle at the seamount, or whether larvae are transported away from the seamount by lateral advection.

In general larval abundance was highest in the upper mixed surface waters over the thermocline. But no significant indication for local differences between summit, rim or slope stations was observed, beside the slight trend of larval accumulation around the edge of the plateau of Senghor Seamount. At Fieberling Guyot in the eastern North Pacific Mullineaux & Mills (1997) reported highest absolute larval numbers on the summit at roughly 500 m and lower values above the flank with cnidarians, polychaets and gastropods as the dominant larval taxa. In our study polychaete larvae were overall most abundant, especially around the summit plateau and also between 100-300 m over the slopes. This agrees well with studies on the macroinfauna on Senghor Seamount by Chivers et al. (2013) during a previous cruise, which showed a high polychaete abundance with highest biomass levels on the seamount summit (~130 m) and lower standing stocks on the upper northern mid slope (~800 m) in the presence of the oxygen minimum zone, however, not all producing planktonic larvae. Similarly, polychaetes were the most abundant component of the Ampère macrofauna with highest individual numbers on the eastern mid slope (~1700 m) (Lamont & Chivers 2012). Cnidarian larvae were rarely found in the deep zones over Senghor and Ampère and were more abundant in the surface layers. Information about megafauna on both seamounts is sparse. Molodtsova & Vargas (2012) found corals as the most common megafauna on the plateau and the upper slope of Ampère during our cruise, representing a potential larval source. Already on previous cruises to Ampère in 2005 and 2009 high densities of soft corals were observed in places on the summit and rim by an altimeter-controlled camera sled (Christiansen unpubl. data). Bivalves were collected on the abyssal plain of the far field site, but not at the seamount (Molodtsova & Vargas 2012), presumably due to the rocky substrate. In general the longer larval stages of more than two weeks for bivalves suggest enhanced ability of larval dispersal, which includes the enhanced possibility of lateral advection off the seamount, than of settlement on the seamount, resulting in rare abundance of bivalves, as observed at Cobb Seamount (Parker & Tunnicliffe 1994). ROV dives on a previous cruise to Senghor Seamount in 2009 showed diverse habitats with high numbers of corals in places on the plateau and on the upper slope, but also areas with high densities of sponges, brittle stars, sea urchins, holothurians or small crustaceans (Christiansen & Koppelmann 2011). Regarding the relatively high amount of echinoderms observed on the summit and slopes, we expected also comparable abundances of larvae in the plankton samples, but we found ophio- and echinopluteus larvae only sporadically in the waters over Senghor.

5.5.5 The variability of zooplankton respiratory carbon demand

The community respiratory carbon demand was estimated from individual respiration rates based on the mean individual weight (dry weight, mg Ind^{-1}) for each sample. Since the mean individual weight is strongly influenced by the occurrence of even a few very small or large organisms, the respiration rate might be over- or underestimated, depending on the size distribution within each sample, and the presented respiratory carbon demand can only be an approach.

Respiratory carbon demand of microzooplankton in the epi- and mesopelagic zones was about one half of the total zooplankton demand in the waters off Ampère Seamount and about one third over Senghor, emphasizing the importance of the small-sized zooplankton for the conversion of carbon in the biogeochemical cycle in subtropical and tropical areas, as indicated in previous studies (e.g. King et al. 1978; Hernández-León et al. 1999; Calbet 2008). In absolute terms, the carbon demand of the microzooplankton community at Senghor was three to four times higher than at Ampère, which can be attributed to the higher biomass at Senghor on the one hand, and to the higher weight-specific respiration rates due to higher temperatures and smaller mean body size in the tropical realm (Hernández-León & Ikeda 2005) on the other hand.

Differences in the contribution of the microzooplankton to the total carbon demand between the two trophic regions may be attributed to the size structure of the phytoplankton community and the corresponding availability as prey for the microzooplankton. Usually larger phytoplankton cells dominate in areas of higher productivity, and numbers of extremely small cells are depressed (Landry et al. 1995; Edwards et al. 1999), resulting in favourable conditions for larger zooplankton.

At Ampère and other NE Atlantic seamounts in higher latitudes with a deep nutrient depletion, e.g. Great Meteor Tablemount, the phytoplankton community comprises mainly nano- and picoplankton, which are specialised in low nutrient levels (Kaufmann 2004; Kaufmann et al. 2011). For example, nano- and picoplankton contributed 56-95 % to total chlorophyll *a* in the waters off Ampère Seamount in May 1996 (Kaufmann 2004), and within the adjacent Azores current, Fernández & Pingree (1996) measured a share of picoplankton of more than 90 %. The low ingestion rates of copepods (>0.2 mm) on chlorophyll *a* as described by Huskin et al. (2001) for the waters off the Azores indicate that larger copepods belonging to the mesozooplankton do not exploit the abundant picoalgae to a large extent. Hence, microzooplankton is considered to be more important than larger copepods for the control of phytoplankton in a subtropical oligotrophic region (Jackson 1980; Huskin et al. 2001), as confirmed by the size specific respiratory carbon demand estimated for the Ampère Seamount area. In Canarian waters Arístegui et al. (2001) regarded microzooplankton (protozoans and smallest metazoans) even as key component of the trophic web, controlling more than 80 % of the primary production.

In tropical waters we would generally also expect low nutrient concentrations and a phytoplankton community dominated by picoplankton. However, the tropical waters south of the CVFZ, including the area of Senghor Seamount, are characterized as mesotrophic (Pierre et al. 1994; Morel 1996) due to occasional influence of the frontal system. Rapidly increasing nutrient concentrations below the thermocline (25-30 m) were measured over Senghor in 2009 by Kaufmann et al. (2011), being as high there as at Ampère only at 250 m depth. Accordingly, Kaufmann et al. (2011) assumed diatoms and dinoflagellates to be more abundant than nano- and picoplankton in the waters off Senghor. Diatoms and dinoflagellates show higher growth rates at high nutrient concentrations and are primarily grazed by larger copepods resulting in a higher biomass and carbon demand of mesozooplankton compared to microzooplankton as observed over Senghor in 2011 and 2013 contrary to Ampère in the oligitrophic region.

5.6 Conclusions

This study confirms that microzooplankton forms a considerable fraction of the zooplankton community at seamounts and is an important link between small phytoplankton cells and planktivorous consumers. The percentage contribution of microzooplankton to the total zooplankton biomass and to the respiratory carbon demand depends on the overall productivity, with lower productivity favouring smaller phytoplankton and subsequently also smaller zooplankton, as reflected in the two trophic regimes around Ampère and Senghor seamounts.

Clear evidence of local seamount effects resulting in higher primary and secondary production in the seamount ecosystems and expressed by high concentrations of microzooplankton biomass as compared to the unaffected open ocean, was not detected. In contrast the chosen far field site off Senghor might be influenced towards higher production by the CVFZ at times. The horizontal distribution of total microzooplankton biomass and abundance across each seamount did not indicate any correlations to the topography or the local flow field, neither at Ampère nor at Senghor. However, we can confirm Senghor as an example for the expected higher retention potential for meroplanktonic larvae in seamount surrounding waters, and as a larval source for benthic invertebrates in the open ocean.

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5.9 Supplementary Results

Table 5-A1. One-way ANOVA, *a priori* hypothesis tests and *t*-test for differences in depth integrated abundance standing stocks (Ind m^{-2}) of meroplanktonic larvae at Ampère Seamount in November/December 2010 and Senghor Seamount in December 2011 and February 2013.

Location	**Test**	**N**	**Source**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**
0-100 m								
Ampère: rim NW, SE; sl NW, SE	ANOVA	8	Location	0.139	3	0.046	1.273	>0.05
			Error	0.145	4	0.036		
	a priori		rim *vs.* slope	0.034	1	0.034	0.939	>0.05
	a priori		NW (up-) *vs.* SE (downstream)	0.092	1	0.092	2.523	>0.05
Senghor$_{2011}$: sl N, E, W; ff	ANOVA	8	Location	2.502	3	0.834	13.108	<0.05
			Error	0.255	4	0.064		
	a priori		NE (up-) *vs.* W (downstream)	0.061	1	0.061	0.962	>0.05
	a priori		seamount *vs.* far field	2.223	1	2.223	34.945	<0.01
Senghor$_{2013}$: sum; rim N, E, S, W; sl NE, E, W; ff	ANOVA	18	Location	2.966	8	0.371	3.514	<0.05
			Error	0.950	9	0.106		
	a priori	10	sum *vs.* rim	0.177	1	0.177	1.679	>0.05
	a priori	8	sum *vs.* sl	0.280	1	0.280	2.658	>0.05
	a priori	14	rim *vs.* sl	0.004	1	0.004	0.034	>0.05
	a priori	14	NE (up-) *vs.* W (downstream)	0.006	1	0.006	0.060	>0.05
	a priori	18	seamount *vs.* far field	2.352	1	2.352	22.297	<0.01
Ampère & Senghor$_{2011\&2013}$	*t*	32	Ampère *vs.* Senghor$_{2011\&2013}$		30	0.345	3.674	<0.01
100-1000 m								
Ampère: sl NW, SE	*t*	4	slope NW *vs.* slope SE		2	0.188	3.088	>0.05
Senghor$_{2011}$: sl N, E, W; ff	ANOVA	8	Location	0.451	3	0.150	3.281	>0.05
			Error	0.006	4	0.001		
	a priori	6	NE (up-) *vs.* SW (downstream)	0.024	1	0.024	0.528	>0.05
	a priori	8	seamount *vs.* far field	0.398	1	0.398	8.681	<0.05
Senghor$_{2013}$: sl NE, E, W; ff	ANOVA	8	Location	0.385	3	0.128	5.328	>0.05
			Error	0.096	4	0.024		
	a priori	6	NE (up-) *vs.* W (downstream)	0.045	1	0.045	1.857	>0.05
	a priori	8	seamount *vs.* far field	0.010	1	0.010	0.420	>0.05
Ampère & Senghor$_{2011\&2013}$	*t*	16	Ampère *vs.* Senghor$_{2011\&2013}$		14	0.250	2.056	>0.05

Location: sum, summit; sl, slope; ff, far field.
***ANOVA/ a priori*:** SQ, Sum-of-squares; df, degrees of freedom; MQ, Mean-square; F, F-ratio; p, probability of correlation.
***t*-test:** df, degrees of freedom; DM, Difference in Means; t, Pooled Variance t; p, probability of correlation.

Table 5-A2. One-way ANOVA, *a priori* hypothesis tests and *t*-test for differences in depth integrated microzooplankton biomass standing stocks (g m^{-2}) at Ampère Seamount in November/December 2010 and Senghor Seamount in December 2011 and February 2013.

Location	**Test**	**N**	**Source**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**
0-100 m								
Ampère: rim NW, SE; sl NW, SE	ANOVA	8	Location	0.001	3	0.000	7.079	<0.05
			Error	0.000	4	0.000		
	a priori		rim *vs.* slope	0.000	1	0.000	5.753	>0.05
	a priori		NW (up-) *vs.* SE (downstream)	0.000	1	0.000	1.856	>0.05
Senghor$_{2011}$: sl N, E, W; ff	ANOVA	8	Location	0.015	3	0.005	0.971	>0.05
			Error	0.020	4	0.005		
	a priori		NE (up-) *vs.* W (downstream)	0.000	1	0.000	0.063	>0.05
	a priori		seamount *vs.* far field	0.014	1	0.014	2.863	>0.05
Senghor$_{2013}$: sum; rim N, E, S, W; sl NE, E, W; ff	ANOVA	18	Location	0.004	8	0.000	4.085	<0.05
			Error	0.001	9	0.000		
	a priori	10	sum *vs.* rim	0.000	1	0.000	3.580	>0.05
	a priori	8	sum *vs.* sl	0.001	1	0.001	5.339	<0.05
	a priori	14	rim *vs.* sl	0.001	1	0.001	9.621	<0.05
	a priori	14	NE (up-) *vs.* W (downstream)	0.001	1	0.001	4.809	>0.05
	a priori	18	seamount *vs.* far field	0.000	1	0.000	0.010	>0.05
Ampère & Senghor$_{2011\&2013}$	*t*	32	Ampère *vs.* Senghor$_{2011\&2013}$		30	0.044	7.159	<0.001
100-1000 m								
Ampère: sl NW, SE	*t*	4	slope NW *vs.* slope SE		2	0.011	1.157	>0.05
Senghor$_{2011}$: sl N, E, W; ff	ANOVA	8	Location	0.014	3	0.005	3.137	>0.05
			Error	0.006	4	0.001		
	a priori	6	NE (up-) *vs.* SW (downstream)	0.000	1	0.000	0.000	>0.05
	a priori	8	seamount *vs.* far field	0.014	1	0.014	9.088	<0.05
Senghor$_{2013}$: sl NE, E, W; ff	ANOVA	8	Location	0.000	3	0.000	0.364	>0.05
			Error	0.000	4	0.000		
	a priori	6	NE (up-) *vs.* W (downstream)	0.000	1	0.000	0.369	>0.05
	a priori	8	seamount *vs.* far field	0.000	1	0.000	0.652	>0.05
Ampère & Senghor$_{2011\&2013}$	*t*	16	Ampère *vs.* Senghor$_{2011\&2013}$		14	0.042	4.058	<0.01

See Table 5-A1 for explanations.

Table 5-A3. *T*-tests for differences in depth integrated respiratory carbon demand (mg $m^{-2}d^{-1}$) of micro- and mesozooplankton between Ampère Seamount and Senghor Seamount$_{2011\&2013}$.

Depth (m)	**Size fraction**	**N**	**df**	**DM**	**t**	**p**
0-100	microzooplankton	34	32	0.569	13.518	<0.001
	mesozooplankton	34	32	0.660	14.140	<0.001
100-1000	microzooplankton	17	15	0.337	4.808	<0.001
	mesozooplankton	17	15	0.496	6.974	<0.001

See Table 5-A1 for explanations.

From the epipelagic zone to the abyssal plain: Trophic interactions of zooplankton and benthopelagic fishes at two seamounts in the tropic-subtropical NE Atlantic

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6.1 Abstract

Specific mechanisms, driving trophic interactions between seamount associated fishes and the pelagic community may be highly variable in different seamount systems. This study investigates the trophic structure of zooplankton and micronekton as well as the main prey of benthopelagic fishes from the summit and slope regions of Ampère and Senghor, two shallow seamounts in the subtropical and tropical NE Atlantic, and the adjacent abyssal plains. For the identification of food sources and trophic relationships a combination of stomach content and stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) analyses was used. $\delta^{13}C$ ranged from -26.9 ‰ to -14.0 ‰ and $\delta^{15}N$ covered a total range of 0.8-15.8 ‰. Based on epipelagic particulate organic matter (POM), zooplankton usually occupied the 1st and 2nd trophic level and included herbivorous, omnivorous and carnivorous taxa. Feeding types of fish species comprised mainly zooplanktivores and mixed feeders, but also benthivores, piscivores, and predator-scavengers. They had trophic positions between the 2nd and 4th trophic level. Differences in stomach contents and stable isotope signatures indicate a resource partitioning among the benthopelagic fishes through distinct habitat choice, vertical feeding positions and prey selection. Topographic trapping of vertically migrating zooplankton on the summit seemed to be of minor importance for food supply, rather horizontal current-driven advection of the planktonic prey was assumed as major factor. Correlations between $\delta^{15}N$ and $\delta^{13}C$ values of POM, zooplankton and fish suggest a linear food chain based on a single energy source from primary production for Ampère Seamount, but indicate varying nutritional sources and trophic pathways for the open ocean reference site. Significant differences in the $\delta^{13}C$ values support the assumption of food sources of different origin between Senghor Seamount and the open ocean, although correlations between $\delta^{15}N$ and $\delta^{13}C$ values did not indicate altered feeding conditions. Among both seamounts isotope ratios point to different feeding conditions and trophic structures in a more complex food web in the tropics than in the subtropics.

Keywords: benthopelagic fish; seamount; stable isotope; trophic interaction; tropic-subtropical NE Atlantic; zooplankton

6.2 Introduction

On the seafloor of the world ocean any geographically isolated topographic feature taller than 100 m are described as seamounts, which are active or extinct undersea volcanoes (Staudiegel et al. 2010; Wessel et al. 2010). Over 100000 large seamounts >1 km in height are predicted to occur on the ocean floor and are often found in linear seamount chains (Wessel et al. 2010). The abrupt topography of the undersea mountains provides special habitats of hard substrata and soft bottom for the benthic fauna in contrast to the general flat sediment-covered abyssal plains. In the water column hydrodynamic processes such as seamount-associated eddies (Richardson 1980; Richardson 1981), Taylor caps/columns or tidal resonance and seamount-trapped waves (see Genin & Boehlert 1985; Dower et al. 1992; Lavelle & Mohn 2010) affect the associated pelagic community. Current-topography interaction between seamount and the surrounding oceanic flows generates advection or local retention of water masses, including particles, phytoplankton and smaller zooplankton over the seamount (Genin & Boehlert 1985; Roden 1994). The uplift of deeper nutrient-rich water and a stabilization of the water column may feature enhanced primary production correlated with aggregations of zooplankton, micronekton and fish at the seamount (Genin & Boehlert 1985; Dower et al. 1992; Genin 2004) and may cause changes in food sources and trophic interactions. The trapping of diel vertically migrating zooplankton may be an important food supply at shallow seamounts since the blocked zooplankton becomes available as prey for benthopelagic consumers (Isaacs & Schwartzlose 1965; Genin et al. 1988; Wilson & Boehlert 2004). Enhanced horizontal flux of pelagic prey organisms past the seamount is likely to sustain fish aggregations (Tseytlin 1985; Dower & Mackas 1996; Koslow 1997). Benthopelagic fishes in high biomass concentration have been reported for several seamounts especially in the Pacific (Koslow 1997; Parin et al. 1997; Koslow et al. 2000), verifying the assumption of seamounts as attractive sources with enhanced food supply in the open ocean for usually dispersed fish stocks as well as for typical shelf species. Most studies on the feeding ecology of seamount fishes suppose that large fish aggregations on seamounts are rather supported by imported pelagic food supplies than by locally enhanced primary production (Porteiro & Sutton 2007). For the fish fauna at Seine Seamount a close nutritional link to pelagic food sources was indicated by stomach content and stable isotope analyses, while benthic contributions to the diet were less important (Hirch & Christiansen 2010). The concentration of pelagic prey appears to be an important factor for the specification of feeding strategies, habitat choice and resource partitioning in seamount associated fish assemblages (Fock et al. 2002a, b; Porteiro & Sutton 2007). However, the specific mechanisms driving trophic interactions between benthopelagic fishes and the pelagic community are not fully understood (Porteiro & Sutton 2007).

For the identification of food sources and trophic relationships the combination of stomach contents and biochemical markers, such as stable isotopes, is an effective and common method (e.g. Hirch & Christiansen 2010). A stomach content of recently ingested prey provides information on consumers' feeding behaviour and the preferred prey type. Stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) change from prey to predator during metabolism and are a measure of already digested and assimilated diet (Peterson & Fry 1987). This isotopic fractionation during feeding, assimilation and respiration processes allows for estimation of the diet carbon source as well as of the trophic level of an organism and the food web structure (e.g. Minagawa & Wada 1984; Peterson & Fry 1987; Post 2002).

The coupling between pelagic food sources and benthopelagic fishes at Ampère and Senghor seamounts in the subtropical and tropical NE Atlantic is the focus of the present study. The aim was to elucidate trophic interactions within the pelagic community of zooplankton and micronekton and to identify main food sources of benthopelagic fishes from the shallow summits of the seamounts, the slopes and the adjacent abyssal plains in two different trophic regimes. In particular we were interested in the following questions using stomach content analyses in combination with stable isotope ratios of carbon and nitrogen:

(1) What are the dietary sources within the zooplankton community at the two seamounts and the unaffected open ocean reference stations?
(2) What are the main food sources for benthopelagic fishes at the distinct seamount regions and the abyssal plains?
(3) What are the nutritional links between the pelagic and benthopelagic communities?
(4) How do trophic structure and interactions differ between the oligotrophic subtropical and the mesotrophic tropical seamount?

6.3 Materials and Methods

6.3.1 Study sites

6.3.1.1 Ampère Seamount

Ampère Seamount, within the sphere of the oligotrophic NE Atlantic subtropical gyre, belongs to the Horseshoe Seamounts Chain, which is located between the island of Madeira and the Portuguese mainland ~360 nm west of the Strait of Gibraltar at 35° 02' N, 012° 54' W (Fig. 6-1). The current regime around Ampère is mainly driven by the Azores current and the Mediterranean outflow. The seamount rises from a base depth at 4500 m to a summit depth at 120 m with one peak of 55 m (Fig. 6-2), partial overgrown with macroalgae in the photic zone (Christiansen unpubl. data). Ampère Seamount has a conical shape with a small rough summit plateau and steep rocky slopes and canyons (Halbach et al. 1993; Kuhn et al. 1996; Hatzky 2005) as well as sediment-covered flat areas. For comparison, an unaffected open ocean reference site (hereafter referred to as 'far field') ca. 70 nm southeast of Ampère Seamount located at 33° 48' N, 013° 00' W was sampled. Water depth was about 4400 m above the flat sedimentary plain.

6.3.1.2 Senghor Seamount

Senghor Seamount is located in a mesotrophic tropical region ca. 60 nm east of the island of Sal, Cape Verde at 17° 12' N, 021° 57' W (Fig. 6-1). The ocean dynamics around Senghor are mainly characterized by the north equatorial current system which drives the NE Atlantic tropical gyre (see Mittelstaedt 1991; Lathuilière et al. 2008) and by the Cape Verde frontal zone (CVFZ) between North (NCAW) and South Atlantic central water (SACW) (Zenk et al. 1991). Water depth at the base of the seamount is ca. 3300 m; the minimum summit depth is 90 m (Fig. 6-3). Senghor Seamount has a nearly circular shape with a small summit plateau and features a heterogeneous surface structure, which was shown by several ROV dives during the cruise (Christiansen & Koppelmann 2011). The summit plateau is covered with sediment in most parts but also shows rocky areas in the centre, and ripple marks indicate strong currents at a water depth of 100 m. At the edge of the summit plateau at a depth of 320 m the seafloor is also sediment-covered, but without ripple marks. Along the slopes down to the deep sea floor soft bottom alternates with rocky areas. For comparison, a reference station (hereafter referred to as 'far field') ca. 60 nm north of Senghor, located at 18° 05' N, 022° 00' W, was sampled. Water depth was about 3300 m above the flat sedimentary plain.

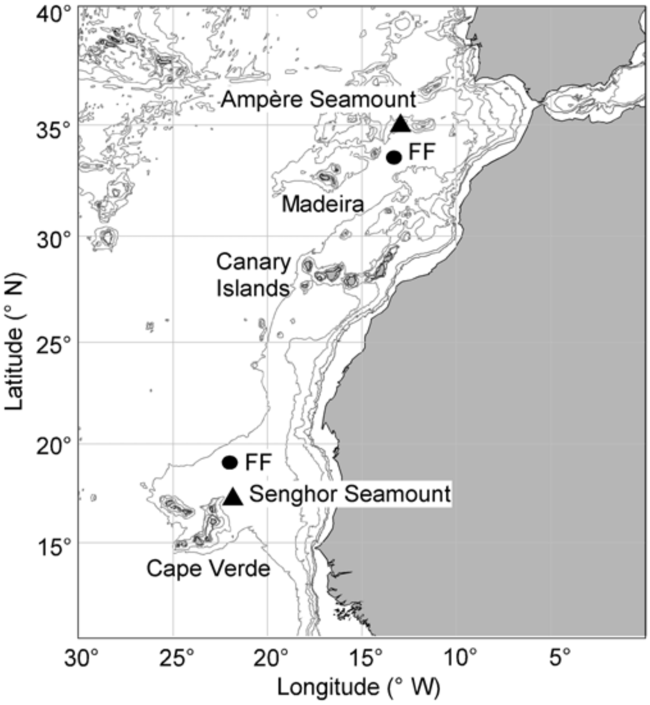

Fig. 6-1. Locations of Ampère and Senghor seamounts and the far field sites (FF) in the NE Atlantic.

6.3.2 Sampling and sample processing

For the analyses of stable carbon and nitrogen isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of the pelagic and benthopelagic communities, samples for suspended particulate organic matter (POM), zooplankton and benthopelagic fishes were collected at the summit, the slopes and the far field site off Ampère and Senghor seamounts. Ampère was sampled during cruise P384 of RV Poseidon in May 2009 and M83/2 of RV Meteor in November/December 2010 (Fig. 6-2; Table 6-1); Senghor was sampled during cruise M79/3 of RV Meteor in September/October 2009 (Fig. 6-3; Table 6-1).

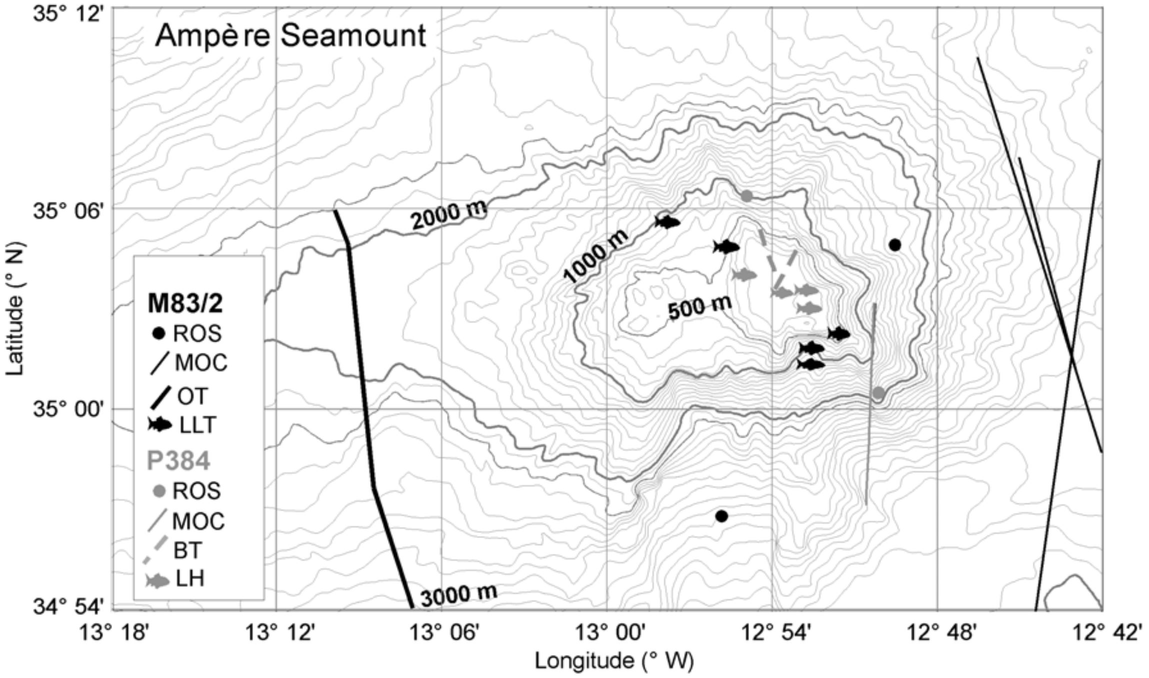

Fig. 6-2. Bathymetry and sampling locations at Ampère Seamount on cruise P384 in May 2009 and M83/2 in November/December 2010. Gear abbreviations: ROS: CTD-Rosette; MOC: MOCNESS; BT: beam trawl; OT: otter trawl; LH: line-and-hook; LLT: longline with trap.

6.3.2.1 Particulate Organic Matter

Water samples for POM were taken in surface layers, mid waters and bottom-near depths using Niskin bottles mounted on a Seabird CTD (Conductivity Temperature Depth)-Rosette (Fig. 6-2, 6-3; Table 6-1). For our study we choose CTD stations in the proximity of the zooplankton sampling locations. After recovery of the CTD-Rosette, water samples were vacuum filtered at low pressure on pre-combusted (500 °C; 0.5 h) and pre-weighed fibre glass filters (Whatman GF/F, ø 2.5 cm, pore size 0.7 µm), rinsed with Milli-Q water and frozen at -20 °C until further analyses. Three parallels were run per sampling depth using a sample volume of 5 l per filter. On M79/3 no water samples could be taken deeper than 1000 m at Senghor Seamount due to technical failure of the CTD.

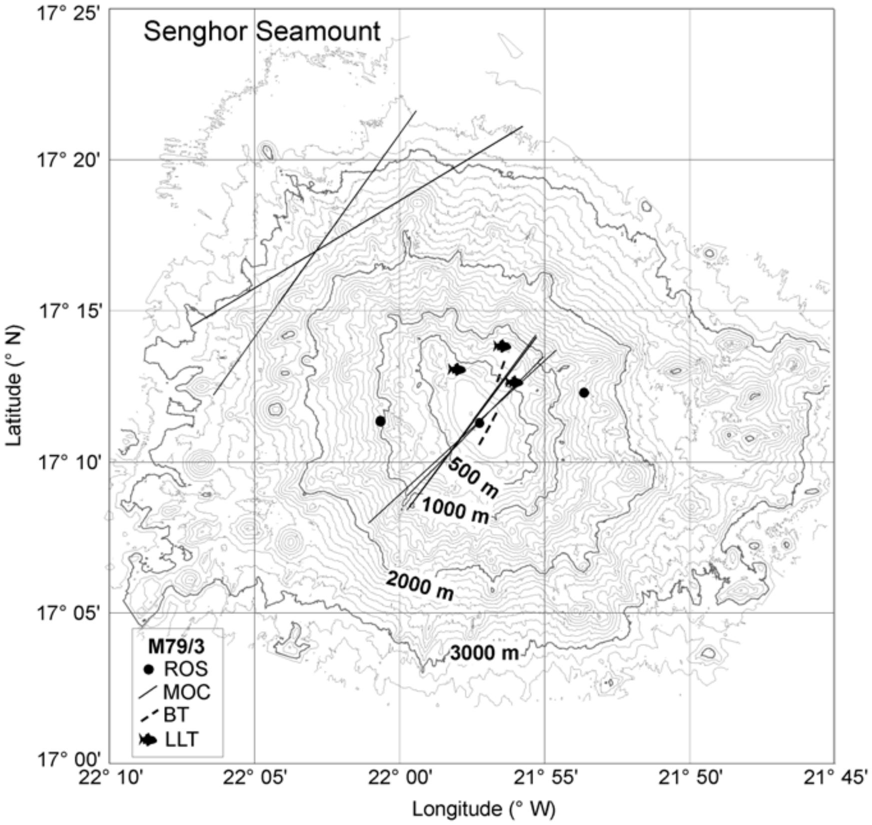

Fig. 6-3. Bathymetry and sampling locations at Senghor Seamount on cruise M79/3 in September/October 2009. Gear abbreviations: see Fig. 6-2.

6.3.2.2 Zooplankton

Zooplankton and mesopelagic fishes were caught by oblique and horizontal hauls with a 1 m²-Double-MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System; Wiebe et al. 1985) equipped with 20 nets of 333 µm mesh size and sensors for pressure, temperature and salinity. Sensor data were recorded simultaneously during sampling. The towing speed was 2 knots. At all sites stratified sampling took place from bottom-near water layers to the surface. The water column was subdivided into following sampling intervals depending on the maximum water depth, respectively: 4000-3000-2000-1000-500-300-100-50-0 m. Across Senghor summit horizontal hauls were taken in 50 m depth and close to the plateau bottom in 90 m. In general each cast was performed twice to allow for statistical analyses. The isotopic signatures presented in this study include samples from the far field sites, from one slope per seamount and from Senghor summit (Fig. 6-2, 6-3; Table 6-1). On P384 no samples could be taken at the far field site of Ampère Seamount due to technical failure of the MOCNESS.

Upon recovery of the MOCNESS, the nets were rinsed with seawater. One half of the zooplankton samples were preserved in a 4 % formaldehyde-seawater solution buffered with borax for further biomass determination and taxonomic identification. The other half of the material was rinsed with freshwater and specimen for stable isotope analyses were directly withdrawn on board using a dissecting microscope in a temperature controlled laboratory at 4 °C. Specimens were identified using several taxonomic keys and descriptions (Rose 1970; Judkins 1978; Ambler 1980; Fenner 1986; Whitehead et al. 1986; Boltovskoy 1999; Galil 2000; Judkins & Kensley 2008; Ahyong 2009; MacPherson & Segonzac 2005; Cardoso 2013). Depending on the organism size, each sample consisted of 1-100 individuals (Table 6-2). All samples were frozen at -20 °C until further analyses. The selected zooplankton should reflect abundant taxa over the whole sampling depth include different feeding types and cover a range of trophic levels.

Table 6-1. Haul data for CTD-Rosette (water for POM), MOCNESS (zooplankton), trawls and line fisheries (benthopelagic fish) during expeditions in May 2009 and November/December 2010 to Ampère Seamount and in September/October 2009 to Senghor Seamount.

Station No	Gear	Date	Time	Position Lat N	Position Long W	Water depth (m)	Sampling depth (m)	Location
P384		**2009**						**Ampère**
256	ROS	18.05.	day	35° 1.82’	12° 50.26’	964	947, 400, 90, 25	mid slope SE
257	ROS	18.05.	day	35° 6.66’	12° 55.30’	1067	1000, 400, 25	mid slope N
247	MOC	17.05.	day	34° 57.26’	12° 50.54’	1695	1000-200	mid slope E
258	MOC	19.05.	day	35° 3.08’	12° 50.15’	1197	200-0	mid slope E
245	BT	17.05.	day	35° 4.18’	12° 54.47’	134-177	134-177	summit
266	BT	20.05.	day	35° 3.57’	12° 53.93’	137-145	137-145	summit
243	LH	16.05.	day	35° 4.70’	12° 55.50’	213-118	213-118	summit
245	LH	16.05.	day	35° 3.23’	12° 52.71’	110	110	summit
265	LH	20.05.	day	35° 3.49’	12° 53.69’	110	110	summit
267	LH	20.05.	day	35° 4.36’	12° 53.23’	100	100	summit
M79/3		**2009**						**Senghor**
812	ROS	29.09.	day	18° 4.92’	22° 0.09’	3294	2500, 750, 200, 25	far field
844	ROS	03.10.	day	17° 11.31’	21° 57.20’	101	90, 25	summit
902	ROS	03.10.	day	17° 14.30’	21° 57.40’	1043	750, 200, 25	mid slope W
1029	ROS	17.10.	day	17° 12.28’	21° 53.68’	1503	700, 200, 25	mid slope E
809	MOC	28.09.	night	18° 5.01’	21° 59.88’	3260	2670-0	far field
811	MOC	29.09.	day	18° 5.32’	21° 59.80’	3270	1500-0	far field
883	MOC	05.10.	night	17° 8.88’	21° 59.76’	97	50	summit
887	MOC	06.10.	day	17° 8.00’	22° 1.08’	98	50	summit
892	MOC	06.10.	night	17° 8.47’	21° 59.73’	98	90	summit
897	MOC	07.10.	day	17° 8.55’	21° 59.67’	100	90	summit
992	MOC	13.10.	day	17° 2.24’	22° 6.45’	2590	2500-0	deep slope NW
1000	MOC	14.10.	night	17° 4.49’	22° 7.18’	2618	2500-0	deep slope NW
820	OT	30.09.	day	17° 51.98'	22° 14.64'	3310	3310-0	far field
863	BT	04.10.	day	17° 10.63'	21° 57.13'	103	103-0	summit
886	LLT	06.10.	day	17° 12.99'	21° 58.00'	356	356	upper slope N
926	LLT	09.10.	day	17° 12.56'	21° 56.10'	533	533	upper slope NE
961	LLT	11.10.	day	17° 13.69'	21° 56.41'	734	734	mid slope NE
M83/2		**2010**						**Ampère**
946	ROS	22.11.	night	33° 47.96’	13° 0.05’	4410	4000, 750, 200, 25	far field
1089	ROS	02.12.	night	34° 56.83’	12° 55.84’	3191	3000, 750, 200, 25	deep slope S
1180	ROS	08.12.	day	35° 4.96’	12° 49.70’	1722	750, 200, 25	mid slope E
945	MOC	21.11.	night	33° 48.30’	13° 0.29’	4415	4000-0	far field
952	MOC	22.11.	night	34° 4.74’	13° 5.34’	4414	4135-0	far field
1191	MOC	08.12.	night	34° 57.72’	12° 39.33’	2018	3000-0	deep slope E
1217	MOC	12.12.	day	35° 8.63’	12° 44.92’	2938	1000-0	deep slope E
1248	MOC	12.12.	day	35° 8.83’	12° 40.56’	3410	3000-1000	deep slope E
963	OT	24.11.	day	33° 51.59'	13° 8.70'	4413-4419	4419-4413	far field
1315	OT	16.12.	day	34° 58.96'	13° 8.33'	2446-2467	2467-2446	deep slope W
1094	LLT	02.12.	day	35° 2.20'	12° 51.67'	313	313	upper slope SE
1112	LLT	03.12.	day	35° 4.85'	12° 54.83'	489-164	489-164	upper slope NW
1216	LLT	10.12.	day	35° 1.86'	12° 52.68'	938	938	mid slope S
1228	LLT	11.12.	day	35° 5.91'	12° 57.67'	992	992	mid slope NW
1288	LLT	15.12.	day	35° 1.39'	12° 52.90'	1200	1200	mid slope S

Gear abbreviations: ROS: CTD-Rosette; MOC: MOCNESS; BT: beam trawl; OT: otter trawl; LH: line-and-hook; LLT: longline with trap.

Table 6-2. Sampling depth (m) and number of stable isotope samples (n_{SI}) for POM and per specimen for zooplankton. Number of pooled individuals per sample in brackets.

		Ampère n_{SI}			**Senghor n_{SI}**		
		May 2009	**Nov/Dec 2010**		**Sep/Oct 2009**		
Specimen	**Sampling depth (m)**	**slope**	**slope**	**far field**	**summit**	**slope**	**far field**
POM	25-50	9	6	3	4	3	3
	200-1000	6	6	6		6	3
	2500-4000		3	2			2
Ostracoda (30)	0-100	1	2	2	3	4	3
	2000-3000			1			
Oncaea spp. (100)	0-100	1	2	2	4	2	1
	1000-2000			2			2
Corycaeus spp. (100)	0-100	1	2	3	4	3	2
Megacalanus princeps (5)	1000-3000		2			4	
Calanoides carinatus (30)	500-2000		3	2		3	6
Subeucalanus monachus (30)	500-1000		3	2		2	3
Rhincalanus cornutus (30)	1000-2000					2	6
Rhincalanus nasutus (30)	1000-3000	1	5	14			
Clausocalanus spp. (100)	0-100	1	3	1	3	2	2
Aetedeidae (20)	100-300			2			
Gaetanus pileatus (5)	1000-2000		3				2
Euchaeta spp. (10)	0-100	2	1	6	4	3	
	100-1000		6	3		5	2
	1000-2000		1	1		3	4
Scolecithrix spp. (10)	0-50		3				
Pleuromamma spp. (20)	0-100	2	5	3	3	3	4
Lucicutia flavicornis (50)	0-100	1		2	2	2	1
Lucicutia maxima (5)	1000-3000		4	5		3	5
Disseta palumbii (10)	500-2000		8	6			
Haloptilus spp. (20)	100-300			1			
Candacia spp. (30)	0-100		4	4	5	2	1
Labidocera spp. (10)	0-50				2	3	2
Exoskeletons (30)	2000-4000		4	4			
Amphipoda (10)	1000-2000					3	4
Hyperiidea (10)	0-50			2		2	1
Euphausiacea (10)	0-100	1	7	3	2	5	4
Sergestes spp. (1-2)	500-1000		5	6		1	2
Acanthephyra spp. (1-2)	500-1000	1	5	7		3	6
Munidopsis aries (1)	3300						2
Willemoesia leptodactyla (1)	3300						8
Siphonophora (10)	0-100	2			5	2	7
Scyphozoa (3)	1000-3000		1	2		3	
Heteropoda (1)	0-25	1					
Chaetognatha (10)	0-50	2	1		4	3	2
	300-1000		6	2			2
	1000-3000		3	6			
Cephalopoda (1-2)	0-100					2	
	3300						2
Leptocephalus larvae (3)	0-50				5	1	2
Myctophidae (1-2)	0-100		4	9	2	3	6
Cyclothone alba/braueri (1-2)	300-1000	2	5	4		3	8
Argyropelecus hemigymnus (1-2)	300-500		1			1	
	500-1000						2
Astronesthes neopogon (1)	1000-2000		1	2			
Photonectes braueri (1)	1000-2000			2			

6.3.2.3 Benthopelagic fishes

Demersal fishes were collected by a variety of sampling methods, using hooks-and-line, longline, baited trap, beam trawl and otter trawl (Fig. 6-2, 6-3; Table 6-1) in order to broader the range of feeding types. A 2 m-beam trawl with 6 mm mesh (see Christiansen et al. 2009 for details) was towed on the summits. At Ampère summit fishes were collected also by hooks-and-line in 100-213 m depth. For fishes on the upper and mid slopes down to 1200 m demersal baited longline sets and traps were deployed. A 15 m-semiballoon otter trawl was towed at 2-3 knots at the deep slopes below 2000 m and on the abyssal plains of the far field sites (see Christiansen et al. 2015 and Vieira et al. subm. for detailed sampling design).

Directly after recovery of the catch, specimens were identified to the lowest taxonomic level possible using a variety of taxonomic keys and descriptions (Sulak 1977; Whitehead et al. 1986; Sulak & Shcherbachev 1997; Nielsen et al. 1999; Franco et al. 2009; Froese & Pauly 2015).Total (TL) and standard lengths (SL) and weights of all specimens were measured and, where possible, stomachs were dissected and preserved in a 4 % formaldehyde-seawater solution buffered with borax for diet analyses. Dorsal muscle tissue was taken for stable isotope analyses and frozen at -20 °C.

In the home laboratory stomach contents were analysed using a dissecting microscope. All food items were measured in length and identified to the lowest taxonomic level possible using the above mentioned keys. Cephalopod beakers were identified after Clarke (1986), Lu & Ickeringill (2002) and Xavier & Cherel (2009). However, depending on the digestion state, many items could not be identified to species or genus level or allocated to any prey category. Fish diets were characterized by the percentage contribution of distinct prey groups to the total number of prey items.

6.3.2.4 Stable isotope analysis

All frozen material was oven dried at 60 °C for at least 48-72 h. Filters were cut into halves, folded and put into tin capsules. Zooplankton organisms and fish tissue were ground to a homogeneous powder using pestle and mortar. 1-3 mg pulverised material were weighed into tin capsules. Depending on the amount of material 1-5 replicates per sample were created. Samples were measured without any additional treatment.

The analyses of the stable isotope ratios of carbon and nitrogen were performed at Biozentrum Klein Flottbek, Universität Hamburg, Hamburg, Germany. The $\delta^{13}C$ and $\delta^{15}N$ values of the pulverised samples were determined simultaneously in an Euro EA-3000 Elemental Analyser connected to a NU-Horizon stable isotope ratio mass spectrometer. The reference gas used for nitrogen stable isotope determination was atmospheric N_2 and for carbon pure CO_2 from a cylinder calibrated against the standard Peedee Belemnite (PDB). Standard deviation of this method was <0.05 ‰ for carbon and <0.1 ‰ for nitrogen for replicates of Leucin used as running standard. Stable isotope values were expressed in δ notations as parts per thousand (‰):

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = [(R_{sample}/R_{standard}) - 1] * 1000$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

$\delta^{13}C$ values are used to track the diet and carbon source of organisms since the enrichment is usually small about 0.4-1 ‰ from prey to predator (e.g. DeNiro & Epstein 1978; Fry & Sherr 1984; Post 2002). $\delta^{15}N$ is usually enriched by 1-5 ‰ for a single feeding step and is used to determine the trophic position of an organism (e.g. DeNiro & Epstein 1981; Minagawa & Wada 1984; Michener & Schell 1994; Mill et al. 2007). In this study we used values of epipelagic POM as baseline for a trophic cascade through the whole water column and for estimation of consumer levels assuming an average enrichment of 3.4 ‰ per trophic level (DeNiro & Epstein 1981; Minagawa & Wada 1984; Post 2002).

6.3.3 Data analyses

Data from the distinct sampling intervals were grouped into three depth layers: 0-100 m, 100-1000 m, 1000-4000 m, roughly corresponding to the epipelagic zone above the summit depths, the mesopelagic zone including the lower epipelagic, and the bathypelagic zone. Within each layer differences in stable isotope ratios between seasons and locations were tested for taxa with more than two replicates available. *t*-tests were employed if two samples were available. For more than two samples 1-way analyses of variance (ANOVA) were used (Lozán & Kausch 2004; Sokal & Rohlf 2009), followed, if significant, by *a priori* hypothesis tests using contrasts to test for differences between distinct pairs of samples (Ampère$_{2009}$ *vs.* Ampère$_{2010}$, Ampère$_{2010}$ *vs.* Ampère FF, Senghor *vs.* Senghor FF, Ampère$_{2009\&2010}$ *vs.* Senghor).

For POM and some zooplankton taxa stable isotope differences between each of the three depth layers were tested separately for each location (Ampère$_{2010}$, Ampère FF, Senghor, Senghor FF) using 1-way ANOVA followed by a *post-hoc* Bonferroni test for pairwise comparison of all three depth layers. Spatial differences of stable isotope signatures between sampling sites at Ampère and Senghor Seamount, respectively, were tested by *t*-tests or 1-way ANOVA and *post-hoc* Bonferroni tests for some fish species. In order to assess the association between δ^{15}N and δ^{13}C, *Pearson product-moment correlation coefficients* (Sokal & Rohlf 2009) were estimated across all taxa for each location, both for the whole water column and for each pelagic layer separately.

All statistical tests were performed using the SYSTAT 8.0 statistical package (SPSS Inc. 1998). For clarity, only significant results of *t*-tests and ANOVAs/*a priori* tests are given in the text in form of *t* and F values, respectively, together with degrees of freedom and significance levels of $p < 0.05$, $p < 0.01$ and $p < 0.001$. For *post-hoc* tests, only significance levels are given. Full statistic results are available in the supplementary results (Table 6-A1, 2, 3).

6.4 Results

6.4.1 Association of δ^{15}N and δ^{13}C

Overall the organisms and the organic matter of the trophic communities covered a δ^{15}N range of ~14 ‰ (0.8-14.8 ‰) in the subtropical waters and of ~13 ‰ (2.4-15.8 ‰) in the tropical region, which correspond to 3-4 trophic levels. The δ^{13}C range was about 10 ‰ in both areas. There was a positive correlation between δ^{15}N and δ^{13}C values across all taxa from the epi- to the bathypelagic zone for each location. Correlation coefficients ranged from $r = 0.577$ for the Senghor far field site to $r = 0.693$ for Ampère Seamount.

The trophic assemblages of the pelagic zones showed some variability in associations between δ^{15}N and δ^{13}C. Over Ampère Seamount δ^{15}N and δ^{13}C values were highly correlated in the epipelagic zone ($n = 119$, $r = 0.876$, $p < 0.01$). A positive correlation was also calculated for the meso- ($n = 66$, $r = 0.423$, $p < 0.01$) and bathypelagic zone ($n = 89$, $r = 0.589$, $p < 0.01$). At the far field site there was no correlation for the epi- ($n = 40$, $r = 0.020$, $p = 0.899$) and mesopelagic values ($n = 31$, $r = -0.152$, $p = 0.414$), but for the bathypelagic ($n = 106$, $r = 0.700$, $p < 0.01$). At Senghor Seamount association was positive between δ^{15}N and δ^{13}C in all pelagic zones (epi: $n = 98$, $r = 0.649$, $p < 0.01$; meso: $n = 45$, $r = 0.506$, $p < 0.01$; bathy: $n = 17$, $r = 0.487$, $p < 0.05$) as well as in the far field (epi: $n = 55$, $r = 0.601$, $p < 0.01$; meso: $n = 30$, $r = 0.451$, $p < 0.05$; bathy: $n = 35$, $r = 0.625$, $p < 0.01$).

6.4.2 Stable isotope ratios of POM and zooplankton

6.4.2.1 Vertical variability in isotope signatures

Depth related trends of stable isotope signatures in the water column were assessed for POM and selected zooplankton taxa from the epi- (0-100 m), meso- (100-1000 m) and bathypelagic (1000-4000 m) zones of Ampère Seamount in November/December 2010, Senghor Seamount, and both far field (FF) sites (Fig. 6-4; see Table 6-A1 for full statistic results).

Mean δ^{13}C values of surface POM were enriched compared to the mid waters at each location but differences were not significant. Bathypelagic POM showed a high variability, and at Ampère it was significantly depleted in δ^{13}C (-25.5 ‰) as compared to the surface POM (-24.5 ‰) (ANOVA: $F_{2,16} = 7.46$, $p < 0.01$; *post-hoc*: $p < 0.01$), while at the far field site (-22.0 ‰) it was enriched (ANOVA: $F_{2,10} = 15.23$, $p < 0.01$; *post-hoc*: $p < 0.05$). No deep water values were available for Senghor Seamount. The zooplankton δ^{13}C values did not indicate any general trend in the vertical distribution (Fig. 6-4a). At Ampère Seamount and the far field site the δ^{13}C signatures of the zooplankton specimen were slightly enriched in the bathypelagic compared to the epi- or mesopelagic zone, except for the copepod *Oncaea* spp., but did not differ significantly between depths. At Senghor Seamount epipelagic *Euchaeta* spp. (-21.2 ‰) had significantly lower mean δ^{13}C ratios than individuals from the mid waters (ANOVA: $F_{2,12} = 5.86$, $p < 0.05$; *post-hoc*: $p < 0.05$). δ^{13}C of the epipelagic *Lucicutia flavicornis* (-24.0 ‰) was significantly lower than for the deep water species *Lucicutia maxima* (-20.0 ‰) (*t*-test: $t_3 = 15.16$, $p < 0.01$). Epipelagic chaetognaths from the far field site had a significantly lower mean δ^{13}C (-19.8 ‰) than mesopelagic individuals (-18.4 ‰) (*t*-test: $t_2 = 13.47$, $p < 0.01$).

The δ^{15}N of mesopelagic POM with means of 8.6-9.7 ‰ was always significantly enriched compared to the epi- and bathypelagic ratios ($\text{ANOVA}_{\text{Ampère}}$: $F_{2,16} = 81.61$, $p < 0.001$; $\text{ANOVA}_{\text{AmpèreFF}}$: $F_{2,10} =$

23.78, $p < 0.001$; *t*-test$_{Senghor}$: $t_{11} = 11.89$, $p < 0.001$; ANOVA$_{SenghorFF}$: $F_{2,7} = 14.85$, $p < 0.01$; *post-hoc*: $p < 0.01$) (Fig. 6-4b). At Ampère Seamount mean $\delta^{15}N$ of surface POM (4.4 ‰) was significantly enhanced compared to the deep water POM (1.9 ‰; *post-hoc*: $p < 0.01$), while at the far field site epipelagic POM (3.8-4.9 ‰) covered similar $\delta^{15}N$ ranges than bathypelagic POM (0.8-4.7 ‰), as well as at the Senghor far field site (4.2-5.8 ‰ and 3.0-5.5 ‰).

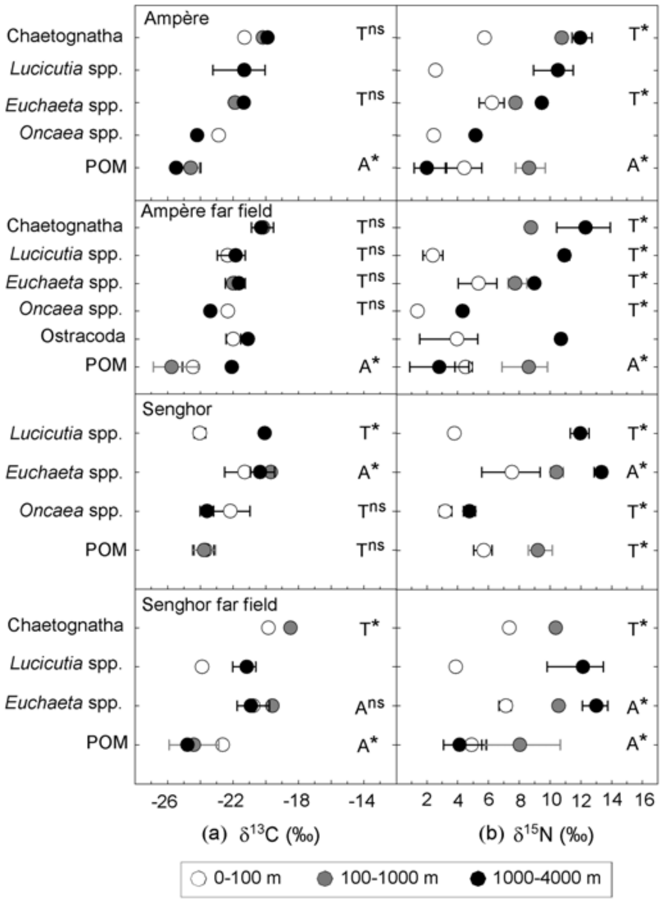

Fig. 6-4. Mean (a) $\delta^{13}C$ and (b) $\delta^{15}N$ signatures of epi- (0-100 m), meso- (100-1000 m) and bathypelagic (1000-4000 m) POM and some zooplankton taxa at Ampère Seamount in November/December 2010, Senghor Seamount in September/October 2009 and at the far field sites. Error bars representing minimum and maximum values. Vertical differences between depth layers were tested using either 2-sample *t*-test (T) or 1-way ANOVA (A). Significance of tests: *, significant ($p < 0.05$); ns, not significant ($p > 0.05$). See text and Table 6-A1 for full statistic results.

The zooplankton taxa analysed showed a general trend of enhanced $\delta^{15}N$ signatures with increasing depth (Fig. 6-4b). Significant differences between epi- and bathypelagic individuals were found for the copepods *Oncaea* spp. (*t*-test$_{AmpèreFF}$: $t_2 = 15.34$, $p < 0.01$; *t*-test$_{Senghor}$: $t_4 = 4.31$, $p < 0.05$) and *Lucicutia* spp. (*t*-test$_{AmpèreFF}$: $t_5 = 21.58$, $p < 0.001$; *t*-test$_{Senghor}$: $t_3 = 16.92$, $p < 0.001$) from the far field site of Ampère and from Senghor Seamount. At Ampère and the far field, bathypelagic chaetognaths had significantly higher values (~12.1 ‰) than the mesopelagic specimens (~8.7 ‰) (*t*-test$_{Ampère}$: $t_6 = 3.65$, $p < 0.05$; *t*-test$_{AmpèreFF}$: $t_6 = 3.69$, $p < 0.05$). At Senghor Seamount and the far field mean $\delta^{15}N$ values of *Euchaeta* spp. were lowest in the upper layer (7.5 ‰ and 7.1 ‰) and significantly enhanced in the mid waters (10.4 ‰ and 10.5 ‰) and in the deep zone (13.3 ‰ and 13.0 ‰) ($\text{ANOVA}_{\text{Senghor}}$: $F_{2,12} = 34.43$, $p < 0.001$; *post-hoc*: $p < 0.01$; $\text{ANOVA}_{\text{SenghorFF}}$: $F_{2,6} = 69.09$, $p < 0.001$; *post-hoc*: $p < 0.01$).

6.4.2.2 The epipelagic zone (0-100 m)

In the waters off Ampère Seamount mean $\delta^{13}C$ of surface POM was significantly higher in May 2009 than in November/December 2010 (-23.8 ‰ *vs.* -24.5 ‰; ANOVA: $F_{4,25} = 15.62$, $p < 0.001$; *a priori*: $F_{1,25} = 8.81$, $p < 0.01$) (Fig. 6-5a; see Table 6-A2 for full statistic results). $\delta^{13}C$ values at Senghor with a mean of -23.6 ‰ were significantly higher as compared to Ampère (*a priori*: $F_{1,25} = 10.18$, $p < 0.01$) and lower than at the far field site (-22.6 ‰; *a priori*: $F_{1,25} = 14.02$, $p < 0.01$).

No distinction is made in the following between zooplankton specimens collected at Ampère Seamount in May 2009 and November/December 2010, either because ratios did not differ significantly between seasons, or only single values per taxon were available for May 2009.Within the epipelagic zooplankton community at Ampère Seamount lowest mean $\delta^{13}C$ values were measured for *Oncaea* spp. (-22.8 ‰) and *Candacia* spp. (-22.8 ‰). Siphonophores had the highest mean signature of -19.3 ‰ (Fig. 6-5a). All seamount signatures agreed fairly with the far field. At Senghor Seamount *Lucicutia flavicornis* (-24.0 ‰) had the lowest average $\delta^{13}C$ ratio. The most enriched $\delta^{13}C$ signatures were found for chaetognaths (-19.4 ‰) and myctophids (-19.6 ‰). At the far field site isotope ratios were similar, where only ostracods (-23.1 ‰ *vs.* -20.5 ‰; ANOVA: $F_{3,12} = 6.77$, $p < 0.01$; *a priori*: $F_{1,12} = 18.70$, $p < 0.01$) and the copepod *Labidocera* spp. (-20.5 ‰ *vs.* -20.0 ‰; *t*-test: $t_5 = 4.02$, $p < 0.05$) had significantly lower $\delta^{13}C$ values as compared to the seamount. Mean $\delta^{13}C$ values were significantly higher at Senghor than at Ampère for ostracods (-20.5 ‰ *vs.* -21.9 ‰; *a priori*: $F_{1,12} = 6.56$, $p < 0.05$) and myctophids (-19.6 ‰ *vs.* -21.3 ‰; ANOVA: $F_{3,20} = 3.39$, $p < 0.05$; *a priori*: $F_{1,20} = 4.80$, $p < 0.05$). Mean $\delta^{13}C$ signatures of the flying fishes from the far field ranged from -16.9 ‰ to -16.6 ‰.

At Ampère Seamount mean $\delta^{15}N$ of POM was significantly higher in November/December 2010 (4.4 ‰) than in May 2009 (3.2 ‰; ANOVA: $F_{4,25} = 10.23$, $p < 0.001$; *a priori*: $F_{1,25} = 10.27$, $p < 0.01$). Far field ratios were within the range of values from Ampère_{2010} with a mean of 4.5 ‰ (Fig. 6-5b; see Table 6-A2 for full statistic results). Mean $\delta^{15}N$ values of POM from Senghor Seamount (5.6 ‰) were significantly higher than from Ampère in both seasons (4.0 ‰; *a priori*: $F_{1,25} = 35.70$, $p < 0.001$), but were not higher than values from the far field site (4.9 ‰).

Within the epipelagic specimens at Ampère Seamount *Oncaea* spp. had the lowest mean $\delta^{15}N$ of 2.4 ‰ and myctophids the highest of 8.0 ‰ (Fig. 6-5b). At the far field site isotope ratios of most taxa were similar to those from the seamount, but *Pleuromamma* spp. (5.3 ‰ *vs.* 3.2 ‰) had significant lower $\delta^{15}N$ values compared to seamount specimens (ANOVA: $F_{4,15} = 14.11$, $p < 0.001$; *a priori*: $F_{1,15} = 13.08$, $p < 0.01$). In the surface waters off Senghor Seamount *Oncaea* spp. (3.1 ‰) and myctophids

(9.8 ‰) also marked the extremes of mean δ^{15}N values. At the far field site siphonophores had significantly higher δ^{15}N values as compared to Senghor (6.8 ‰ *vs.* 6.2 ‰) (ANOVA: $F_{2,15} = 3.55$, $p > 0.05$; *a priori*: $F_{1,12} = 7.07$, $p < 0.05$) as well as myctophids (11.8 ‰ *vs.* 9.8 ‰; ANOVA: $F_{3,20} = 13.60$, $p < 0.001$; *a priori*: $F_{1,20} = 6.20$, $p < 0.05$). Significant differences between both seamounts with higher δ^{15}N ratios at Senghor were detected for the two cyclopoid copepods *Oncaea* spp. (2.4 ‰ *vs.* 3.1 ‰; ANOVA: $F_{2,5} = 25.54$, $p < 0.05$; *a priori*: $F_{1,5} = 15.66$, $p < 0.05$) and *Corycaeus* spp. (4.0 ‰ *vs.* 5.7 ‰; ANOVA: $F_{3,9} = 14.00$, $p < 0.01$; *a priori*: $F_{1,9} = 12.07$, $p < 0.01$). In addition, three flying fish species at the surface of the far field site were analysed, which covered a range of mean δ^{15}N from 7.6 ‰ for *Exocoetus obtusirostris* to 10.0 ‰ for *Hirundichthys speculiger*.

For each location we assumed the mean δ^{15}N of epipelagic POM as the basic food source and 1st trophic level of the pelagic food chain, and an average increase of 3.4 ‰ per feeding step. Since POM values were partly higher than ratios of zooplankton, the calculated trophic level was negative for *Oncaea* spp., *Clausocalanus* spp. and *L. flavicornis*. *Corycaeus* spp., ostracods, hyperiids and leptocephalus larvae occupied the lowest position at the base of the 1st trophic level (Fig. 6-5b). Euphausiids and chaetognaths had a position in the upper range of level 1, whereas small myctophids and the flying fishes ranked on the 2nd level.

6.4.2.3 The mesopelagic zone (100-1000 m)

At Ampère Seamount mesopelagic δ^{13}C values of POM ranged from -26.9 ‰ to -26.4 ‰ in May 2009 and from -24.8 ‰ to -24.0 ‰ in November/December 2010 with a significant difference between the seasons (ANOVA: $F_{4,22} = 12.78$, $p < 0.001$; *a priori*: $F_{1,22} = 21.45$, $p < 0.001$) (Fig. 6-5a; see Table 6-A2 for full statistic results). POM from the far field in 2010 covered the total δ^{13}C range of both seamount seasons (-26.8 ‰ to -24.1 ‰) with a mean of -25.5 ‰ and was significantly depleted in δ^{13}C compared to Ampère during the same sampling period (*a priori*: $F_{1,22} = 7.61$, $p < 0.05$). At Senghor Seamount δ^{13}C ranged from -23.0 ‰ to -24.0 ‰ with a mean of -23.7 ‰ and for the far field of -24.3 ‰. δ^{13}C signatures differed significantly between both seamounts (*a priori*: $F_{1,22} = 20.47$, $p < 0.001$).

δ^{13}C values of mesopelagic species from Ampère Seamount covered a narrow range (Fig. 6-5a). The lowest mean δ^{13}C was measured for *Euchaeta* spp. (-21.9 ‰) and highest for *Subeucalanus monachus* (-19.3 ‰). Decapods, chaetognaths and fishes varied between -20.5 ‰ and -19.7 ‰. Signatures from the far field site covered the same ranges and means without any significant difference. The δ^{13}C ratios at Senghor ranged between -20.1 ‰ in *Calanoides carinatus* and -18.0 ‰ in *Acanthephyra* spp.. δ^{13}C signatures agreed well between Senghor Seamount and the far field and tended to be about 1-2 ‰ enriched compared to Ampère, except for *C. carinatus* and *S. monachus*, which had similar ratios at both seamounts. Differences were significant for *Euchaeta* spp. (ANOVA: $F_{4,11} = 42.31$, $p < 0.001$; *a priori*: $F_{1,11} = 110.97$, $p < 0.001$), *Sergestes* spp. (ANOVA: $F_{2,8} = 142.19$, $p < 0.001$; *a priori*: $F_{1,8} =$

232.92, $p < 0.001$), *Acanthephyra* spp. (ANOVA: $F_{3,16} = 12.14$, $p < 0.001$; *a priori*: $F_{1,16} = 15.00$, $p < 0.01$) and the sternoptychid fish *Argyropelecus hemigymnus* (ANOVA: $F_{2,3} = 19.17$, $p < 0.05$; *a priori*: $F_{1,3} = 32.36$, $p < 0.05$).

$\delta^{15}N$ values of POM from Ampère Seamount covered the same range in May 2009 than in November/December 2010 with means of 8.7 ‰ and 8.6 ‰, respectively (Fig. 6-5b; see Table 6-A2 for full statistic results). The same mean $\delta^{15}N$ of 8.6 ‰ as at Ampère in 2010 was measured for POM from the far field. $\delta^{15}N$ values from Senghor Seamount covered a range from 8.6-10.1 ‰ with a mean of 9.2 ‰. Isotope signatures from the far field (9.7 ‰) did not differ significantly from Senghor, nor did the values between both seamounts.

Ampère zooplankton covered a narrow $\delta^{15}N$ range. The lowest mean value was 7.4 ‰ for *Euchaeta* spp. (Fig. 6-5b). The other copepods, *C. carinatus* and *S. monachus*, had values with mean of 8.2 ‰, respectively. The highest average $\delta^{15}N$ was found in chaetognaths with 9.6 ‰. The copepods from the far field covered almost the same $\delta^{15}N$ range as at the seamount. The decapod *Acanthephyra* spp. had a significantly higher mean $\delta^{15}N$ at the far field (8.8 ‰ *vs.* 8.0 ‰; ANOVA: $F_{3,16} = 55.05$, $p < 0.001$; *a priori*: $F_{1,16} = 6.78$, $p < 0.05$), whereas $\delta^{15}N$ ratios of chaethognaths (8.7 ‰ vs. 9.6 ‰; ANOVA: $F_{2,7} = 6.76$, $p < 0.05$; *a priori*: $F_{1,7} = 13.08$, $p < 0.01$) were significantly lower at the far field. Mean $\delta^{15}N$ at Senghor ranged from 8.0 ‰ in *C. carinatus* to 11.5 ‰ in the gonostomatid fish *Cyclothone alba/braueri*. The values of isotope ratios were quiet similar between Senghor and the far field site. Only *Acanthephyra* spp. had a significantly enhanced $\delta^{15}N$ of 12.1 ‰ as compared to 9.7 ‰ at the seamount (*a priori*: $F_{1,16} = 36.28$, $p < 0.001$). The mesopelagic species from Senghor Seamount and the far field tended to 1-3 ‰ higher $\delta^{15}N$ ratios as compared to Ampère, except for *C. carinatus* which had the same mean $\delta^{15}N$ at both seamounts. Significant differences were found in *Euchaeta* spp. (ANOVA: $F_{4,11} = 58.79$, $p < 0.001$; *a priori*: $F_{1,11} = 165.00$, $p < 0.001$), both decapods *Sergestes* spp. (ANOVA: $F_{2,8} = 7.09$, $p < 0.05$; *a priori*: $F_{1,8} = 13.30$, $p < 0.01$) and *Acanthephyra* spp. (*a priori*: $F_{1,16} = 19.00$, $p < 0.001$), and *C. alba/braueri* (ANOVA: $F_{4,16} = 19.76$, $p < 0.001$; *a priori*: $F_{1,16} = 33.61$, $p < 0.001$).

Zooplankton and fishes at both seamounts ranked on the 2nd trophic level, based on the epipelagic POM (Fig. 6-5b). At Ampère Seamount *Euchaeta* spp. had the lowest trophic position at the base of level 2, while at Senghor it was *C. carinatus*. The highest trophic position in the upper range of the 2nd level was occupied by chaetognaths at Ampère Seamount. In the waters off Senghor *C. alba/braueri* almost reached the 3rd level.

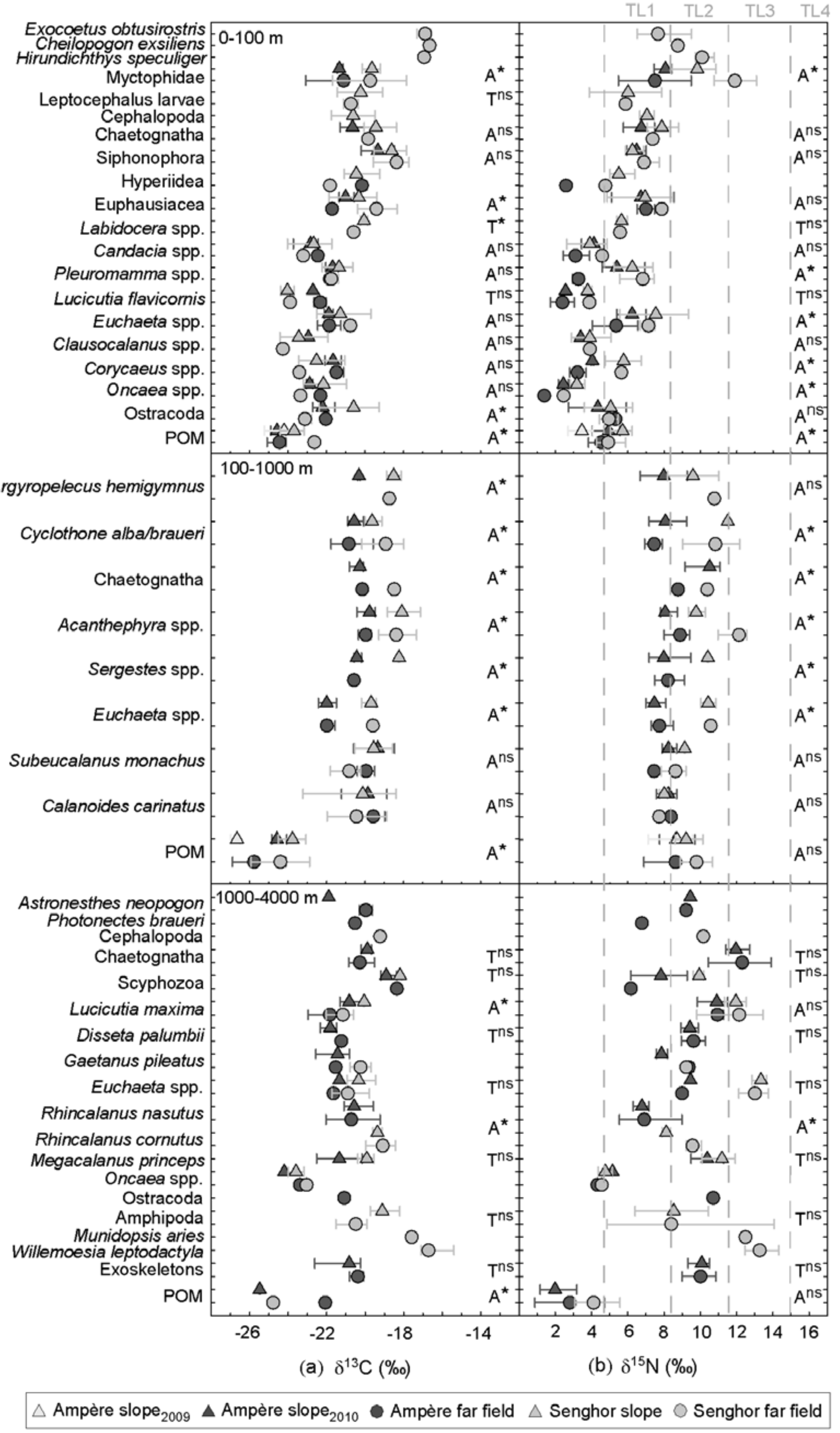

Fig. 6-5. Mean (a) $\delta^{13}C$ and (b) $\delta^{15}N$ signatures of epi- (0-100 m), meso- (100-1000 m) and bathypelagic (1000-4000 m) POM and zooplankton at Ampère Seamount in May 2009 and November/December 2010, Senghor Seamount in September/October 2009 and at the far field sites. Error bars representing minimum and maximum values. Trophic levels (TL) were estimated using mean $\delta^{15}N$ of epipelagic POM as baseline (TL1) and an increase of 3.4 ‰ per trophic level. Spatial differences between sampling locations were tested using either 2-sample *t*-test (T) or 1-way ANOVA (A). Significance of tests: *, significant ($p < 0.05$); ns, not significant ($p > 0.05$). See text and Table 6-A2 for full statistic results.

6.4.2.4 Bathypelagic zone (1000-4000 m)

At Ampère Seamount δ^{13}C values of bathypelagic POM covered a narrow range with a mean of -25.4 ‰ (Fig. 6-5a). The mean ratio at the far field (-22.0 ‰) site was significantly lower (ANOVA: $F_{2,4}$ = 776.44, $p < 0.001$; *a priori*: $F_{1,4}$ = 1486.02, $p < 0.001$). The mean δ^{13}C ratio of POM from the Senghor far field site was -24.7 ‰.

The mean δ^{13}C ratios of the bathypelagic zooplankton at Ampère Seamount ranged from -24.2 ‰ in *Oncaea* spp. to -18.9 ‰ in scyphozoans (Fig. 6-5a; see Table 6-A2 for full statistic results). Exoskeletons had an averge δ^{13}C of -20.8 ‰. In general differences between δ^{13}C signatures from Ampère and the far field site were small. Only *Disseta palumbii* had values significantly higher at the far field site compared to Ampère (-21.3 ‰ *vs.* -21.7 ‰; *t*-test: t_{10} = 2.85, $p < 0.05$), whereas δ^{13}C ratios of *Lucicutia maxima* were significantly lower (-21.8 ‰ *vs.* -21.3 ‰; ANOVA: $F_{3,13}$ = 6.62, $p < 0.01$; *a priori*: $F_{1,13}$ = 7.12, $p < 0.05$). At Senghor Seamount the extremes of the δ^{13}C range were also occupied by *Oncaea* spp. (-23.5 ‰) and scyphozoans (-18.1 ‰). δ^{13}C values of *L. maxima* were significantly higher at Senghor (-20.0 ‰) than at the far field (-21.1 ‰; *a priori*: $F_{1,13}$ = 7.16, $p < 0.05$). In comparison of both seamounts, *Rhincalanus cornutus* (-19.3 ‰) had a δ^{13}C significantly higher at Senghor than *Rhincalanus nasutus* (-20.5 ‰) at Ampère (ANOVA: $F_{3,24}$ = 10.82, $p < 0.001$; *a priori*: $F_{1,24}$ = 5.33, $p < 0.05$).

δ^{15}N ratios for POM varied between 1.1 ‰ and 3.1 ‰ at Ampère Seamount and were within the range of the far field values (0.8-4.7 ‰) with means of 1.9 ‰ and 2.8 ‰, respectively (Fig. 6-5b; see Table 6-A2 for full statistic results). At the far field site of Senghor δ^{15}N ratios ranged from 3.0 ‰ to 5.5 ‰ with a mean of 4.1 ‰. From the base of Senghor Seamount no samples were available.

Bathypelagic species from Ampère Seamount covered a broad δ^{15}N range with lowest mean δ^{15}N of 5.1 ‰ for *Oncaea* spp. and highest of 11.9 ‰ for chaetognaths (Fig. 6-5b). Exoskeletons had an average δ^{15}N of 10.0 ‰. In general δ^{15}N signatures from the far field were similar to Ampère. At Senghor Seamount *Oncaea* spp. also had the lowest mean ratio with 4.7 ‰. The highest δ^{15}N was reached by *Euchaeta* spp. (13.3 ‰). Data from the far field were similar, only *R. cornutus* had a significantly higher (9.5 ‰) mean δ^{15}N compared to Senghor (8.1 ‰; ANOVA: $F_{3,24}$ = 29.74, $p < 0.001$; *a priori*: $F_{1,24}$ = 8.15, $p < 0.01$). In comparison of both seamounts, *R. cornutus* had a δ^{15}N significantly higher at Senghor than *R. nasutus* at Ampère (*a priori*: $F_{1,24}$ = 6.92, $p < 0.05$).

Deep zooplankton covered a range from the 1st to the 3rd trophic level. At Ampère *Oncaea* spp. and *R. nasutus* both ranked on the base of the 1st level (Fig. 6-5b). *Euchaeta* spp. and *L. maxima* occupied level 2 and chaetognaths aimed the highest position on level 3. At Senghor *R. cornutus* was on the 1st level but occupied the 2nd level at the far field site. *Euchaeta* spp. and *L. maxima* had the highest trophic position (level 3) at Senghor. Both benthic crabs *Munidopsis aries* and *Willemoesia leptodactyla* ranked on the 3rd level at the Senghor far field site.

6.4.3 Trophic analyses in benthopelagic fishes

A total of 117 fishes from Ampère Seamount and the far field site were analysed for stable isotope ratios, representing 28 species of 21 families (Table 6-3). Stomach content analyses were done on 102 individuals. Collected fishes covered a size range from 9.0 to 130.5 cm and belonged to five different feeding types according to literature. At Senghor Seamount and the far field 31 fishes, representing 11 species of 8 families were measured for stable isotope ratios (Table 6-3). 11 stomachs were analysed, which were all empty. Size ranged from 8.0 to 76.0 cm, and three different feeding types were distinguished.

6.4.3.1 Stable isotope ratios

Around the plateau of Ampère Seamount mean $\delta^{13}C$ of the benthopelagic fish fauna ranged from -20.6 for *Callanthias ruber* on the summit (~150 m) to -17.7 for *Muraena helena* at the northernwestern rim (~160 m) (Fig. 6-6a; see Table 6-A3 for full statistic results). Mean $\delta^{13}C$ signatures did not differ significantly between summit and rim stations in those species which were captured in both locations (*Scomber colias*, *Pontinus kuhlii*, *Trachurus picturatus*), except for *Lepidopus caudatus* which had a mean $\delta^{13}C$ significantly higher at the rim (-18.5 ‰) than at the summit (-19.1 ‰; *t*-test: $t_3 = 4.88$, $p < 0.05$). The mean $\delta^{13}C$ of *Conger conger* was significantly higher at the upper southeastern slope (~310 m; -17.8 ‰) compared to the rim (-18.7 ‰; *t*-test: $t_4 = 6.27$, $p < 0.01$). Highest $\delta^{13}C$ on the upper northwestern slope (~490 m) was measured for *Zenopsis conchifer* (-18.0 ‰). On the mid slopes (~930-1200 m) mean $\delta^{13}C$ values covered a narrow range from -18.5 ‰ for *Synaphobranchus kaupii* to -17.5 ‰ for *Etmopterus pusillus*. The mean $\delta^{13}C$ of *Mora moro* was significantly higher at the southern (-17.8 ‰) compared to the northwestern station (-18.1 ‰; $t_{17} = 2.73$, $p < 0.05$). At the deep western slope (~2450 m) mean $\delta^{13}C$ values ranged from -20.3 ‰ for *Synaphobranchus kaupii* to -17.5 ‰ for *Cataetyx laticeps*. $\delta^{13}C$ signatures at the deep sea abyssal plain (~4410 m) of the far field site covered a range from -21.7 ‰ in *Histiobranchus bathybius* to -17.0 ‰ in *Coryphaenoides armatus*.

Around the Ampère summit plateau mean $\delta^{15}N$ signatures were lowest for *C. ruber* (8.1 ‰) and highest for *M. helena* (12.3 ‰) (Fig. 6-6b; see Table 6-A3 for full statistic results). Mean $\delta^{15}N$ signatures did not differ significantly between rim and summit stations in species which were captured at both locations (*S. colias*, *L. caudatus, P. kuhlii*), except for *T. picturatus* which had a mean $\delta^{15}N$ significantly higher at the rim (10.6 ‰) than at the summit (9.8 ‰; ANOVA: $F_{2,10} = 9.08$, $p < 0.01$; *post-hoc*: $p < 0.01$), but no difference was detected to the upper slope (10.3 ‰). At the northernwestern slope lowest mean $\delta^{15}N$ was measured for *Scomber scombrus* (9.7 ‰) and highest for *Z. conchifer* (11.4 ‰). At the mid slopes mean $\delta^{15}N$ ranged from 10.5 ‰ for *S. kaupii* to 12.7 ‰ for *Aphanopus carbo*. Mean $\delta^{15}N$ signature for *Deania calcea* was significantly higher at the southern slope (11.2 ‰) compared to the northwestern site (10.8 ‰; *t*-test: $t_5 = 5.96$, $p < 0.01$), as well as for *M. moro* with means of 12.1 ‰ and 11.4 ‰, respectively (*t*-test: $t_{17} = 2.92$, $p < 0.01$). On the deep western slope mean δ^{15}N values tended to increase slightly compared to the upper and mid slopes, ranging from 10.8 ‰ for *S. kaupii* to 14.6 ‰ for *C. laticeps*. At the deep far field site mean δ^{15}N values of benthopelagic fishes were similar to the slopes of Ampère and ranged from 10.8 ‰ in *H. bathybius* to 13.9 ‰ in *C. armatus*.

Table 6-3. Fishes collected in May 2009 and November/December 2010 at and around Ampère Seamount and in September/October2009 at and around Senghor Seamount, arranged according to depth of occurrence (for complete list and detailed catch information see Christiansen et al. 2015 and Vieira et al. subm.). Diet categories refer to: Whitehead et al. (1986); Martin & Christiansen (1997); Iken et al. (2001); Fock et al. (2002a); Reid et al. (2012); Froese & Pauly (2015).

Species	Family	Order	TL (cm)	n_{SI}	$n_{Stomach}$	$n_{Stomach\ empty}$	Diet
Ampère May 2009							
Lepidopus caudatus	Trichiuridae	Perciformes	89.5-132	2	14	7	P
Serranus atricauda	Serranidae	Perciformes	24-42	4	4	2	M
Trachurus picturatus	Carangidae	Perciformes	36.5-42.5	3	7	3	M
Scomber colias	Scombridae	Perciformes	36.5-54.5	5	5		ZM
Callanthias ruber	Callanthiidae	Perciformes	9-10	2	2		Z
Capros aper	Caproidae	Zeiformes	12	2	2		Z
Pontinus kuhlii	Scorpaenidae	Scorpaeniformes	19-31	5	4	2	M
Ampère Dec 2010							
Muraena helena	Muraenidae	Anguilliformes	108.5-110	2	0		P
Lepidopus caudatus	Trichiuridae	Perciformes	143.5	1	1		P
Serranus atricauda	Serranidae	Perciformes	40.5	1	0		M
Trachurus picturatus	Carangidae	Perciformes	35-45	6	6	1	M
Scomber scombrus	Scombridae	Perciformes	39-43.5	3	3		M
Scomber colias	Scombridae	Perciformes	39.5	1	0		M
Pontinus kuhlii	Scorpaenidae	Scorpaeniformes	18.5-40	4	4	2	M
Conger conger	Congridae	Anguilliformes	73.5-130.5	3	3	1	P
Helicolenus dactylopterus	Sebastidae	Scorpaeniformes	15.5-32.5	4	4	3	MB
Zenopsis conchifer	Zeidae	Zeiformes	80.5	1	1		MP
Aphanopus carbo	Trichiuridae	Perciformes	108-114	2	2		M
Deania calcea	Centrophoridae	Squaliformes	57-89	4	0		PM
Mora moro	Moridae	Gadiformes	33.5-61.5	14	3		G
Etmopterus pusillus	Etmopteridae	Squaliformes	39.5	1	0		PM
Synaphobranchus kaupii	Synaphobranchidae	Anguilliformes	33.5-66.5	7	7	3	MS
Bathypterois grallator	Ipnopidae	Aulopiformes	35.5	1	1	1	Z
Halosauropsis macrochir	Halosauridae	Notacanthiformes	56-64	2	2	2	B
Cataetyx laticeps	Bythitidae	Ophidiiformes	69.5	1	0		BM
Alepocephalidae unident.	Alepocephalidae	Osmeriformes	48	1	1		S
Bajacalifornia megalops	Alepocephalidae	Osmeriformes	53	1	1		S
Conocara salmoneum	Alepocephalidae	Osmeriformes	34-82.5	6	6		S
Histiobranchus bathybius	Synaphobranchidae	Anguilliformes	124	1	1		GS
Holcomycteronus squamosus	Ophidiidae	Ophidiiformes	42	1	1	1	S
Bathypterois longipes	Ipnopidae	Aulopiformes	14-27	7	1		ZM
Macrouridae unident.	Macrouridae	Gadiformes	50-52	2	2		GS
***Coryphaenoides* sp.**	Macrouridae	Gadiformes	54-66.5	2	1		GS
Coryphaenoides profundicolus	Macrouridae	Gadiformes	27-41	7	7		GS
Coryphaenoides armatus	Macrouridae	Gadiformes	68.5-80.5	8	6		GS
Senghor Oct 2009							
Exocoetus obtusirostris	Exocoetidae	Beloniformes	18.5-20	3	3	3	Z
Cheilopogon exsiliens	Exocoetidae	Beloniformes	26	1	1	1	Z
Hirundichthys speculiger	Exocoetidae	Beloniformes	25-27	2	2	2	Z
Antigonia capros	Caproidae	Zeiformes	20.5	1	0		ZM
Helicolenus dactylopterus	Sebastidae	Scorpaeniformes	8-44	6	0		M
Promethichthys prometheus	Gempylidae	Perciformes	57.5-62	4	0		M
Beryx splendens	Berycidae	Beryciformes	38	3	0		M
Bathytroctes macrolepis	Alepocephalidae	Osmeriformes	36.5	1	1	1	S
Ophidiidae unident.	Ophidiidae	Ophidiiformes	65	1	1	1	S
Holcomycteronus squamosus	Ophidiidae	Ophidiiformes	59-68	3	3	3	S
Coryphaenoides armatus	Macrouridae	Gadiformes	54.5-76	6	0		GS

TL, total length; n_{SI}, number of individuals used for stable isotope analysis; $n_{Stomach}$, total number of stomachs analysed; $n_{Stomach\ empty}$, number of empty stomachs. Diet abbreviations: B, benthivore (crustaceans, mollusks, polychaets, echinoderms); G, generalized feeder (B, M, organic falls, terrestrial garbage); M, mixed (crustacean, cephalopod, fish); P, piscivore (fish); S, predator-scavenger (living prey-carrion); Z, zooplanktivore (crustacean, mollusks).

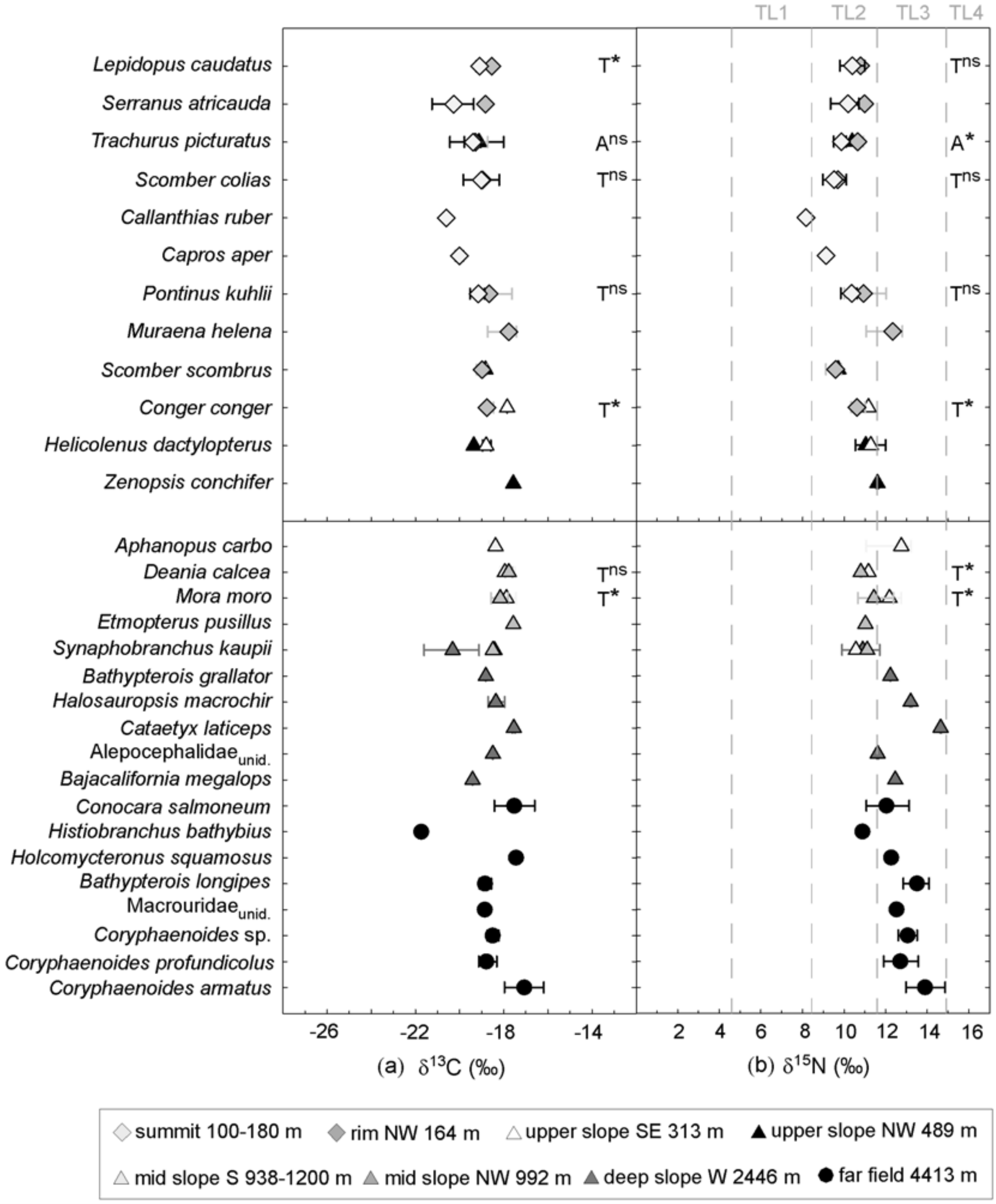

Fig. 6-6. Mean (a) δ^{13}C and (b) δ^{15}N signatures of benthopelagic fishes at Ampère Seamount in May 2009 and November/December 2010 and at the far field site. Fishes arranged according to depth of occurrence. See Fig. 6-5 and text for explanations and Table 6-A3 for full statistic results.

As for zooplankton the trophic level calculation for benthopelagic fishes from Ampère Seamount was based on the mean δ^{15}N of epipelagic POM for both seasons (4.4 ‰) (Fig. 6-6b). *C. ruber*, *Capros aper*, *S. colias* and *S. scombrus* occupied a middle position on the 2nd trophic level. *T. picturatus*, *L. caudatus, P. kuhlii*, *Serranus atricauda* and *C. conger* almost reached the 3rd level, which was occupied by *Helicolenus dactylopterus*, *M. helena* and *Z. conchifer*. Most species on the slopes of Ampère were also positioned at the 3rd trophic level, except for *C. laticeps* which ranged on level 4.

Based on an average δ^{15}N of 4.5 ‰ for surface POM at the far field site, *H. bathybius* had the lowest trophic position on the abyssal plain at the upper range of level 2. *Coryphaenoides profundicolus* occupied a position on the lower half of the 3rd level together with *Holcomycteronus squamosus* and *Bajacalifornia megalops*. *Bathypterois longipes* and *C. armatus* reached almost the 4th trophic level.

On the summit (~100 m) of Senghor Seamount *Antigonia capros* had the highest δ^{13}C ratio (-17.6 ‰) (Fig. 6-7a). *H. dactylopterus* on the summit was small in size (8.0-13.0 cm TL) while individuals collected from greater depth at the upper (~350-530 m) and mid northeastern slope (~730 m) were much larger (38.5-44.0 cm TL; Table 6-3). On the summit *H. dactylopterus* had a mean δ^{13}C of -18.3 ‰, but δ^{13}C signatures of the larger individuals from the upper (-17.0 ‰) and mid slope (-16.7 ‰) were significantly higher (ANOVA: $F_{2,6} = 36.63$, $p < 0.001$; *post-hoc*: $p < 0.01$; see Table 6-A3 for full statistic results). *Bathytroctes macrolepis* on the mid slope had the highest δ^{13}C signature of -14.0 ‰ overall. On the deep sea abyssal plain (~3300 m) of the far field station mean δ^{13}C ratios covered also a narrow range from -17.0 ‰ in *C. armatus* to -16.0 ‰ in Ophidiidae.

On Senghor summit *A. capros* had a mean δ^{15}N of 11.9 ‰ (Fig. 6-7b). Mean δ^{15}N signatures of *H. dactylopterus* increased with increasing size and depth and differed significantly between summit (10.4 ‰), upper (12.0 ‰) and mid slope (14.1 ‰; ANOVA: $F_{2,6} = 97.12$, $p < 0.001$; *post-hoc*: $p < 0.01$). At the deep far field site the lowest δ^{15}N was measured for *B. macrolepis* with 13.0 ‰, which was lower than on the mid slope of Senghor (14.3 ‰). The highest mean δ^{15}N was found for *H. squamosus* (15.2 ‰) and other unidentified members of the family Ophidiidae (15.8 ‰).

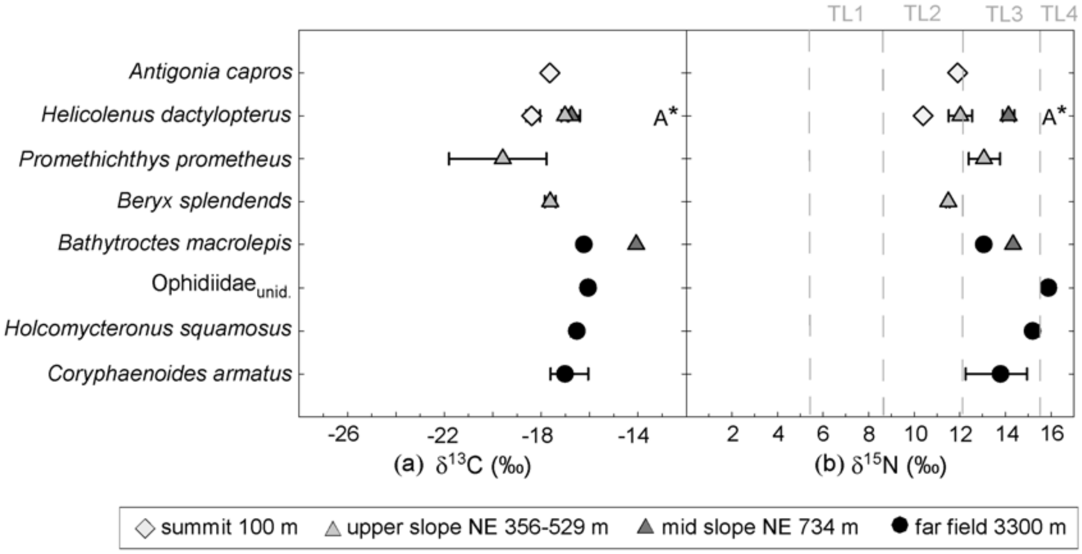

Fig. 6-7. Mean (a) δ^{13}C and (b) δ^{15}N signatures of benthopelagic fishes at Senghor Seamount in September/October 2009 and at the far field site. Fishes are arranged according to depth of occurrence. See Fig. 6-5 and text for explanations and Table 6-A3 for full statistic results.

For the fishes from Senghor the trophic level calculation was based on an average δ^{15}N of 5.6 ‰ for epipelagic POM (Fig. 6-7b). *A. capros* and *H. dactylopterus* at the summit and upper slope ranked on the 2nd trophic level, as well as *Beryx splendens*. *H. dactylopterus* at the mid slope and *Promethichthys prometheus* occupied level 3. Based on an average POM δ^{15}N of 4.9 ‰ *B. macrolepis* and *C. armatus* occupied the lower half of the 3rd level on the far field abyssal plain, whereas *H. squamosus* had a high 3rd level position. Ophiidae reached the 4th trophic level.

6.4.3.2 Stomach contents

Stomach content analyses of benthopelagic fishes from Ampère summit, slope and the adjacent abyssal plain provided 61 prey categories in a total of 74 stomachs of 21 species. 28 stomachs were empty (Table 6-3). Since stomachs of half of the species contained mainly unidentified crustacean and fish pieces or other unidentifiable fragments, only results from 9 fish species and one family with identifiable prey items are presented here (Table 6-4a, b).

The stomach content of *Callanthias ruber* contained many small cyclopoid copepods of the family Oncaeidae (42 %) (Fig. 6-8; Table 6-4a, b). *Capros aper* fed mainly on calanoid copepods (28 %) and other crustaceans (38 %) but also on non-crustacean organisms (22 %). The mackerels and *Trachurus picturatus* had the most diverse prey composition of copepods, other crustaceans and fishes, whereas the stomach content of *Lepidopus caudatus* comprised almost only fish pieces (89 %). The diet of *Bathypterois longipes* was composed mainly of crustaceans (97 %) as well as the diet of *Coryphaenoides profundicolus* and of the unidentified macrourid species, which contained a high number of the calanoid copepod *Metridia macrura*. The stomach content of *Coryphaenoides armatus* was mixed by fish pieces (53 %) and crustaceans (35 %).

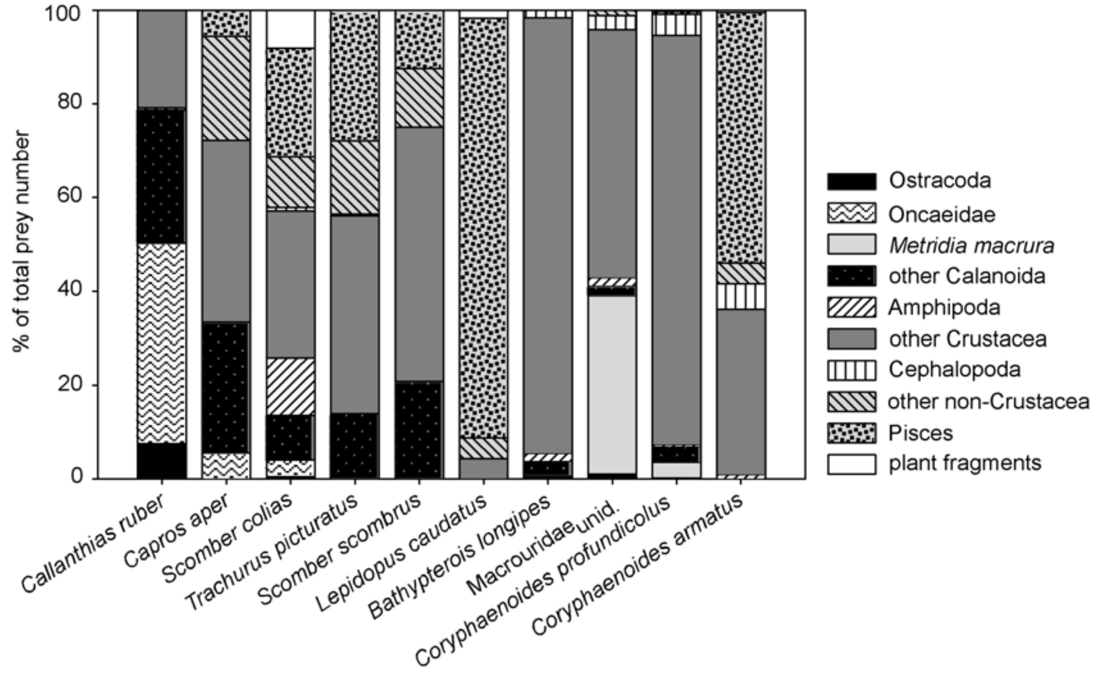

Fig. 6-8. Prey consumed by benthopelgic fishes at Ampère Seamount in May 2009 and in November/December 2010 and at the far field site as percentage of total prey number (%). Values refer to Table 6-4a, b.

Table 6-4a. Crustacean prey consumed by benthopelagic fish species at Ampère Seamount and the adjacent abyssal plain in May 2009 and November/December 2010.

		C. ruber	***C. aper***	***T. picturatus***	***S. colias***	***S. scombrus***	***L. caudatus***	***B. longipes***	**Macrouridae**	***C. profundicolus***	***C. armatus***
	Feeding type	**zooplanktivore**		**mixed feeder (crustacean/ cephalopod/ fish)**			**piscivore**	**zooplankti-/benthivore**	**predator-scavenger**		
Prey categories Crustacea	**Prey size range (mm)**	**Number of prey items**									
Cladocera	2-5				1						
Ostracoda	1-5	17			1			1	5	2	
Copepoda											
Harpacticoida											
Aegisthus spp.	2-5	2									
Miracia spp.	2-5								2		
Cyclopoida											
Oncaeidae	1-2	96	1		4						
Corycaeidae	1-5	4			2						
Calanoida unidentified	2-10	38	4	29	6	1		4	5	16	
Megacalanus spp.	5-10									2	
Eucalanus spp.	2-10	2			1						
Gaetanus spp.	2-5			2							
Aetedeidae	2-5	7		15							
Euchaeta spp.	2-10	3		5	2	1					
Scolecithridae	2-5	1									
Temora spp.	2-5				4						
Metridia macrura	5-10								154	18	
Pleuromamma spp.	2-5			23	1	3			2	1	
Lucicutia spp.	5-10	5							2		
Haloptilus spp.	2-5	5									
Candacia spp.	2-5	3	1	1							
Phyllopus spp.	2-5			1							
Mysidacea	10-25			2				4		1	
Euphausiacea, Furcilia	5-20	1		1	4	2				1	
Decapoda	30-190			4						1	1
Amphipoda	2-25				6			2	7	2	13
Hyperiidea	2-5	1			11						
Rhabdosoma spp.	5-10				1						
Isopoda	5-10									3	
Crustacea larvae	2-5				1			9			
Crustacea unidentified	5-10			3	3			3	66	24	
Crustacea pieces		40	7	219	35	9	5	102	137	455	442
Total Crustacea		**225**	**13**	**305**	**83**	**16**	**5**	**125**	**380**	**526**	**456**

Table 6-4b. Non-Crustacean prey consumed by benthopelagic fish species at Ampère Seamount and the adjacent abyssal plain in May 2009 and November/December 2010. n.q., not quantified.

		C. ruber	***C. aper***	***T. picturatus***	***S. colias***	***S. scombrus***	***L. caudatus***	***B. longipes***	**Macrouridae**	***C. profundicolus***	***C. armatus***
Prey categories non-Crustacea	**Prey size range (mm)**	**Number of prey items**									
Foraminifera	2-5			6							
Porifera spiculae$_{\text{n.q.}}$	5-30							+		+	+
Cnidaria											
Anthozoa fragments$_{\text{n.q.}}$	5-10			60		1			7 +		
Siphonophora fragments	10-20		3	1	8	1					
Worms unidentified	30-50								50		
Nematoda	5-30		1	2	1		2		1		4
Priapolida	5-20								1		1
Polychaeta fragments	5-10				3	2	1				11
Chaetognatha	5-10				1						
Mollusca											
Bivalvia	5-10				1						
Gastropoda pelagic	2-20			16	2		2		3		
Cephalopoda											
Beakers unident.	2-10			1			2	2	7	23	11
Sepioidea											
Heteroteuthis spp.	10								2	1	1
Teuthida											
Histioteuthis spp.	5-15								1	1	
Teuthowenia/ Galiteuthis spp.	5-30								4		
Taonius spec.	55								1		
Mantle pieces	30			1	1				62		
Thaliacea	80					1					
Pisces											
Fish unident.	100						1				
Caproidae juv.	35			3							
Cyclothone spp.	30			4							
Paralipididae	50					1					
Otholiths	2-5			8							
Jaws	5-50						1		2		
Vertebrae	2-770			94	34		70		329		
Scales	2-10		1	43		2	28		420	3	
Miscellaneous											
Gelatinous fragments$_{\text{n.q.}}$	20								+		
Shell fragments$_{\text{n.q.}}$				+					+		
Sand grains/ mud$_{\text{n.q.}}$									+		
Plant fragments	2-20				12		2				
Undefinable$_{\text{n.q.}}$				+		+	+		+		
Total non-Crustacea		**0**	**5**	**239**	**63**	**6**	**108**	**2**	**890**	**28**	**17**
Total prey items		**225**	**18**	**544**	**146**	**22**	**113**	**127**	**1346**	**554**	**397**

6.4.3.3 Benthopelagic fishes and potential food sources

For Ampère summit and the far field abyssal plain trophic relationships between benthopelagic fishes and their potential planktonic prey, as inferred from stomach contents, were estimated on the basis of stable isotope signatures. Around the summit of Ampère Seamount mean $\delta^{13}C$ ratios of pelagic prey ranged from -21.9 ‰ to -21.1 ‰, not indicating highly differing food sources (Fig. 6-9a). *Callanthias ruber* and *Capros aper* were enriched by 1.3 ‰ and 1.8 ‰, respectively, based on an average $\delta^{13}C$ of -21.9 ‰ for their potential prey. For all other benthopelagic fishes the $\delta^{13}C$ enrichment to their potential food sources was quite high, corresponding to two or three feeding steps. The mackerels, *Trachurus picturatus* and *Lepidopus caudatus* were enriched by 2.2-2.5 ‰, compared to their ingested food with average $\delta^{13}C$ values of -21.5 ‰ to -21.2 ‰. The potential prey for *Bathypterois longipes* and *Coryphaenoides profundicolus* had a mean $\delta^{13}C$ ratio of -21.6 ‰, resulting in an enrichment of 2.8 ‰ in both fishes. *Coryphaenoides armatus* was enriched by 3.6 ‰ based on its ingested prey with an average $\delta^{13}C$ of -20.7 ‰.

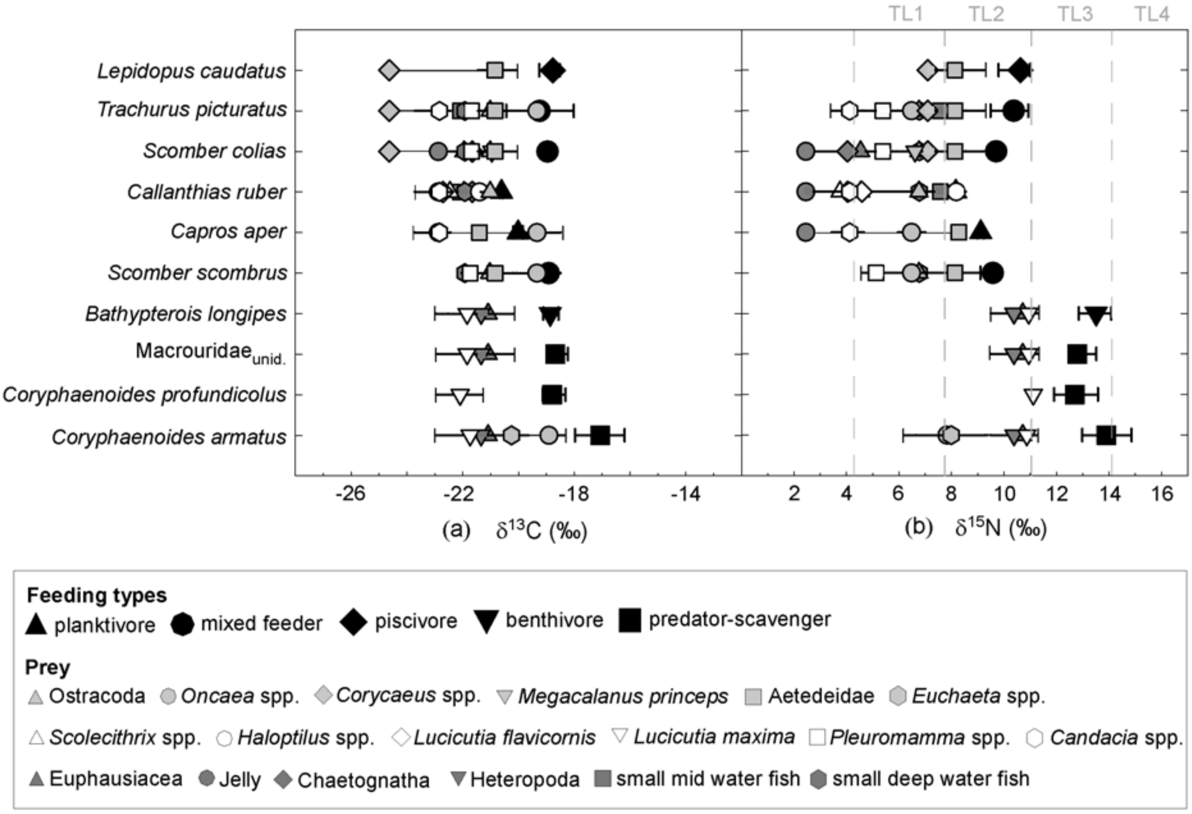

Fig. 6-9. Mean (a) $\delta^{13}C$ and (b) $\delta^{15}N$ stable isotope signatures of benthopelagic fishes and potential pelagic prey at Ampère Seamount in May 2009 and in November/December 2010 and at the far field site. Error bars representing minimum and maximum values for benthopelagic fishes and for total prey items. Fishes are arranged according to depth of occurrence. Symbols for benthopelagic fishes refer to feeding type. Trophic levels (TL) were estimated using mean $\delta^{15}N$ of epipelagic POM as baseline (TL1) and an increase of 3.4 ‰ per trophic level.

The potential pelagic prey taxa covered a mean $\delta^{15}N$ from 2.4 ‰ to 8.2 ‰ in the waters off Ampère summit and ranked on the first two trophic levels (Fig. 6-9b). Mean $\delta^{15}N$ of benthopelagic fishes located on the 2nd trophic level spanned from 8.1 ‰ to 10.6 ‰. Copepods covered nearly the total $\delta^{15}N$ range of all prey items and were important in the diet of zooplanktivores such as *C. ruber* and *C. aper* as well of the mixed feeding mackerels and *T. picturatus*. The average $\delta^{15}N$ of potential prey items for *C. ruber* and *C. aper* was 5.3 ‰ with enrichment in both fishes of 2.7 ‰ and 3.7 ‰, respectively, roughly corresponding to one trophic level. Similar enrichments were estimated for *Scomber scombrus* (2.7 ‰), *Scomber colias* (3.3 ‰) and *T. picturatus* (3.7 ‰) with a mean prey $\delta^{15}N$ of 6.2-6.8 ‰. The prey of the piscivorous *L. caudatus* had an average $\delta^{15}N$ of 8.0 ‰ and the enrichment was 2.6 ‰. Prey items of the deep-sea fishes at the far field site covered mean $\delta^{15}N$ ratios between 7.8 ‰ and 11.9 ‰ on the 2nd and 3rd trophic level. The enrichment to *C. profundicolus* and the unidentified macrourid species, ranking on the 3rd level, was 2.0 ‰ compared to an average $\delta^{15}N$ of 10.7 ‰ for potential prey. The zooplanktiovorous *B. longipes* was enriched by 2.7 ‰. *C. armatus* on the 4th level was enriched by 4.4 ‰ compared to an average $\delta^{15}N$ of 9.4 ‰ for its ingested prey.

6.5 Discussion

The principal objective of this study was to investigate trophic interactions within the pelagic community of zooplankton and micronekton and the associated benthopelagic fish fauna at a subtropical and a tropical NE Atlantic seamount in distinct trophic regions. We aimed to elucidate dietary sources within the zooplankton, primary food sources of the benthopelagic fishes and nutritional links between both communities.

6.5.1 Trophic structure of the pelagic community

6.5.1.1 Depth-related patterns

Stable isotope signatures of the pelagic community in the waters off Ampère and Senghor Seamount showed in general an increasing trend from the surface to the deep-sea as expected. Our observations are supported by previous studies on changes in the dominant feeding type of copepods and other mesozooplakton with an increase in carnivorous forms from the surface to around 2000 m but a rapid decrease and a shift to suspension feeders as the dominant feeding type in the lower bathypelagic zone (2000-6000 m) (Vinogradov & Tseitlin 1983). At depth more trophic steps are assumed between consumers and the source material (Polunin et al. 2001), and each single feeding step results in an average enrichment of ~1 ‰ in $\delta^{13}C$ and ~3.4 ‰ in $\delta^{15}N$ along the food chain (DeNiro & Epstein 1978; Minagawa & Wada 1984). Due to the smaller enrichment in $\delta^{13}C$ depth related trends are presumably more pronounced in the $\delta^{15}N$ than in the $\delta^{13}C$ signatures in the waters off Ampère and Senghor seamounts.

Usually it is assumed that the heavier ^{13}C is retained in the particulate fraction of bodies and faeces (Checkley & Entzeroth 1985), and therefore POM as source material sinking from the surface should be enriched in ^{13}C. More refractory components of detrital POC collected in deep mid-water samples often have $\delta^{13}C$ values more negative than surface POC but not always (Fry & Sherr 1984 and references therein). At Ampère and Senghor seamounts and the far field sites $\delta^{13}C$ values of mid-water POM were partly lower than of surface POM, as similarly observed by Benner et al. (1997), indicating selective decomposition of isotopically heavy components, such as carbohydrates and amino acids, and the relative enrichment of the remaining material in isotopically light lipids (Benner et al. 1997 and references therein). Similarly, Struck et al. (2001) reported decreasing or stable $\delta^{13}C$ values of suspended POC in the eastern Mediterranean. However, $\delta^{13}C$ values of collected POM may be highly variable depending on the mixture of labile components such as amino acids relative to refractory organic components such as cellulose or lignin, particle size and origin (Bishop et al. 1977), as observed in the deep-waters of Ampère Seamount and both far field sites, where no clear depth-related pattern existed.

In ^{15}N POM is usually also enriched with increasing depth, presumably by physico-chemical and microbial processes in the water column (Polunin et al. 2001) or by zooplankton uptake and excretion of ^{15}N enriched feces (Peterson & Fry 1987). Studies in the Pacific reported an average enrichment of 4-9 ‰ in $\delta^{15}N$ from surface to deep water POM (>200 m) (Altabet & McCarthy 1986; Saino & Hattori 1987). In our data, the ^{15}N enrichment was about 4-5 ‰ between epi- and mesopelagic layers, but bathypelagic POM had unexpected low $\delta^{15}N$ values. In a previous study on the Anaximenes Mountain and the adjacent Rhodes Basin we even found ^{15}N enriched POM in the meso- and bathypelagic zone (Denda & Christiansen 2011). Koppelmann et al. (2009) also reported enhanced $\delta^{15}N$ for suspended POM in the mid and deep eastern Mediterranean but depleted values for sinking POM. The same phenomena were observed by Altabet et al. (1991) in the North Atlantic suggesting that the incorporation of abundant dissolved nitrate with associated isotope fractionation by bacteria could favour a low $\delta^{15}N$ signal in sinking particles. However, Benner et al. (1997) could not explain a decreasing trend in $\delta^{15}N$ of suspended POM with depth by isotopic fractionation during decomposition in the water column. Thus we suppose that either the surface $\delta^{15}N$ signal of POM propagates downward to between 1000 and 4000 m with a time lag of two to three weeks (Altabet et al. 1991) resulting in the observed mismatch between epi- and bathypelagic signatures in our study, or that POM from the deep sampling sites of Ampère and Senghor was not of surface origin, instead POM might have been produced locally in the deep zone or transported horizontally from other more productive sites (see Altabet et al. 1991).

6.5.1.2 The epipelagic zone

In the epipelagic zone of Ampère Seamount $\delta^{13}C$ values of suspended POM were in the same range as at the adjacent Seine Seamount (Hirch 2009), but POM in the waters off Senghor was significantly enriched in $\delta^{13}C$. POM represents a mixture of living and dead phytoplankton, microzooplankton, bacteria and detritus, and differences in the phytoplankton composition between both regions may be one possible reason for the difference in $\delta^{13}C$. At Ampère and other NE Atlantic seamounts in higher latitudes with a deep nutrient depletion, for example Great Meteor Tablemount, the phytoplankton community comprises mainly nano- and picoplankton, which are specialised in low nutrient levels (Kaufmann 2004; Maranhão & Kaufmann 2008; Kaufmann et al. 2011). By contrast, in the tropical waters off Senghor higher nutrient concentrations and higher temperatures are supposed to favour larger diatoms and dinoflagellates (Kaufmann et al. 2011), and increasing particle size has been reported to be associated with increasing $\delta^{13}C$ values (Rau et al. 1990). Furthermore, diatoms are rich in ^{13}C due to bicarbonate uptake in nutrient rich waters and show a trend to higher $\delta^{13}C$ values at higher temperatures correlated with increasing growth rates (Fry & Wainright 1991).

$\delta^{15}N$ values of epipelagic POM and zooplankton were generally low in the area off Ampère Seamount, characteristic for the oligotrophic subtropical and tropical North Atlantic surface waters (Montoya et al. 2002). A seasonal shift was evident in the $\delta^{15}N$ of POM from lower ratios in May (~3.2 ‰) to higher values in November/December (~4.4 ‰), as observed by Hirch (2009) at Seine Seamount during November 2003 and April 2004. As Hirch (2009) already assumed, the enhanced $\delta^{15}N$ in late autumn compared to spring might be the result of recent upwelled deep-water nitrate, which is enriched in $\delta^{15}N$ (~5 ‰) compared to the near-surface nitrate (~2-3 ‰) (Montoya et al. 2002; Bourbonnais et al. 2009). While in May a shallow mixed surface layer of 20-30 m was present over Ampère Seamount, deeper mixing of about 80-100 m in November/December (Kaufmann & Diniz 2012; Denda & Christiansen 2014) presumably introduced deep-water nitrate into the euphotic zone by convective overturning (see Neuer et al. 2007). The following uptake by phytoplankton of the ^{15}N enriched nitrate features enhanced $\delta^{15}N$ values in the organic matter (Checkley & Miller 1989). After nitrate depletion and when ammonium becomes the dominant nitrogen source in the surface layer $\delta^{15}N$ declines, because trophic and excretory processes export ^{15}N enriched fecal pellets from the upper layer, while the lighter ^{14}N is retained in the surface waters in form of excreted ammonium of zooplankton and fish (Checkley & Entzeroth 1985; Checkley & Miller 1989). Beside these food-web processes the general $\delta^{15}N$ depletion in oligotrophic surface waters is attributed to an important input of isotopically light nitrogen through N_2 fixation also producing ^{15}N depleted organic matter (Minagawa & Wada 1986; Carpenter et al. 1997; Mahaffey et al. 2003). Since N_2 fixation is co-limited by iron and phosphorus in the surface waters of the eastern tropical Atlantic Saharan dust input may increase N_2 fixation by supplying both elements (Mills et al. 2004; Voss et al. 2004). Senghor Seamount lies within the sphere of the Saharan dust influence, but dust deposition at this location is highly episodic (see Chester et al. 1979; Prospero 1996; Bory et al. 2001). The $\delta^{15}N$ values of surface

POM were on average 5.6 ‰ at Senghor Seamount, not reflecting isotopically light organic matter in the upper mixed layer (20-30 m; see Denda & Christiansen 2014) as observed for Ampère Seamount in May, but can be ascribed to the high nitrate concentrations in the upper layer right at the thermocline over Senghor, being as high there as at Ampère only at 250 m depth (Kaufmann 2004; Kaufmann et al. 2011). Close to the equator high local nutrient availability and therefore low N_2 fixation rates were associated with the equatorial upwelling and circulation system as supposed by Voss et al. (2004) and Montoya et al. (2007). The increased nutrient availability at Senghor reflects the mesotrophic character of the waters south of the CVFZ (18.5° N, 21.0° W; Pierre et al., 1994; Morel 1996; Bory et al. 2001), but can not be attributed to a direct influence of filaments from the frontal system or the Mauritanian upwelling (see Onken & Klein 1991; Zenk et al. 1991). In September/October 2009 salinity isolines did not indicate the presence of the CVFZ close to the area and the regional chlorophyll distribution in the surface waters shows that neither the frontal system nor the Mauritanian upwelling affected the seamount during the cruise and during three months before (Dumont et al. subm.).

Epipelagic zooplankton at both seamounts had $\delta^{15}N$ values partly lower or of the same range than ratios of POM and ranked therefore also on the 1st trophic level, not reflecting the expected enrichment in ^{15}N between consumers and their diet. This can be attributed to a time lag between changes in the $\delta^{15}N$ signal of the food source and the conversion to consumer tissues (O'Reilly et al. 2002; Hirch 2009), which takes weeks to months depending on the turnover time of organisms (MacAvoy et al. 2001; Perga & Gerdeaux 2005). However, at both seamounts and the far field sites low trophic level position and low $\delta^{15}N$ and $\delta^{13}C$ values indicate herbivorous to omnivorous feeding behaviour as known for the copepods *Clausocalanus* spp. and *Lucicutia flavicornis* and for hyperiids and ostracods (feeding type according to Timonin 1971; Mauchline 1998; Koppelmann et al. 2003). *L. flavicornis* had lower $\delta^{15}N$ values at Ampère Seamount and the far field site than at Senghor and the far field, presumably due to feeding preference in the subtropical waters on cyanobacteria, which have a lower $\delta^{15}N$ than non N_2 fixing phytoplankton (Owens 1987). Similarly, gut contents of epipelagic *Lucicutia* sp. reflected greater preference for cyanobacteria than for phytoplankton as reported by Wilson & Steinberg (2010) for the subtropical Pacific. At Ampère Seamount isotope ratios of *Clausocalanus* spp. were slightly higher than those of *L. flavicornis*, which agreed with feeding studies by Cornils et al. (2007), describing *Clausocalanus* as an omnivorous, non-selective feeder on abundant particles in oligotrophic conditions. In the NW Mediterranean a mixed diet was reported for the genus with higher preference for ciliates than for phytoplankton (Broglio et al. 2004). *Oncaea* spp. had the lowest $\delta^{15}N$ values at each location in this study, but on the other hand is known for an opportunistic omnivorous to carnivorous feeding (Pfaffenhöfer 1993; Kattner et al. 2003). It is suggested to utilize a variety of prey and to feed on particles and organisms attached to marine snow and houses or body walls of salps, appendicularians or chaetognaths, (Ohtsuka & Kubo 1991; Ohtsuka et al. 1993; Go et al. 1998), but not on living phytoplankton (Kattner et al. 2003). Hirch (2009) found a similarly low range of $\delta^{15}N$

for *Oncaea* spp. at Seine Seamount but a fatty acid composition similar to the lipid composition of faecal pellets, which might reflect coprophagous feeding (Hirch 2009) as already observed by Huskin et al. (2004). But since faeces are enriched in ^{15}N, even this feeding mode should result in higher δ15N values than measured for *Oncaea* spp. in the seamount areas. Significantly higher δ^{15}N values at Senghor compared to Ampère as observed for *Oncaea* spp. and *Corycaeus* spp. might be attributed to the similarly enhanced δ^{15}N of the organic matter in the tropical waters, since the main food source of both copepods is far from clear at times. Other zooplankton classified as carnivorous, such as the copepod *Euchaeta* spp., chaetognaths (Hopkins 1985) and predatory siphonophores showed the expected enrichment in δ^{15}N as compared to the predominantly herbivores on a lower trophic level at both seamounts. The small laternfishes (Myctophidae) are opportunistic feeders on crustaceans, chaetognaths, fish eggs and larvae (Whitehead et al. 1986), which was reflected by their trophic position up on the 3rd level and highest δ^{15}N values in the epipelagic zone.

In the surface waters off Senghor Seamount and the far field site zooplanktivorous flying fishes were common, known to feed mainly on copepods, euphausiids and hyperiids (Parin 1970). All three species had very high δ^{13}C values, similar to ratios measured for *Exocoetus* sp. in the eastern tropical Pacific (Rau et al. 1983). But, their δ^{13}C signatures do not match to their potential prey items. Possibly flying fishes have relatively low lipid content in their muscle tissue, associated with a low amount of ^{12}C featuring relatively high δ^{13}C ratios. The variability in the δ^{15}N signatures may indicate different prey preferences among species. While *Exocoetus* sp. feeds mainly on small copepods and hyperiids (see van Noord et al. 2013), siphonophores and larval fishes become important in the diet of *Hirundichthys speculiger* (see van Noord et al. 2013), presumably causing the enhanced δ^{15}N values in this species, similar to those of the myctophids.

6.5.1.3 The mesopelagic zone

The assumed enrichment in ^{13}C and ^{15}N from prey to predator may also vary because isotopic fractionation per trophic step depends on diet quality, body size, excretory mechanisms and feeding rate of an organism (see Post 2002; Mill et al. 2007 and references therein). McCutchan et al. (2003) supposed a greater trophic shift in δ^{13}C for herbivores than for omnivores and for omnivores than for carnivores relative to the diet, as we also observed among the mesopelagic specimens, especially in the subtropical waters of Ampère Seamount and the far field. δ^{13}C and δ^{15}N values of mesopelagic zooplankton covered only a narrow range in the subtropical region, where signatures of omni- and zooplanktivores were almost in the same range than of herbi- and detrivores. At Senghor Seamount and the far field, however, isotope ratios showed a greater variability and were enriched in omni- and carnivores compared to detritus feeding specimens. At both seamounts mesopelagic zooplankton and small fishes ranged between the 2nd and 3rd trophic level, with low trophic positions for the herbivorous copepods *Calanoides carinatus* and *Subeucalanus monachus* (Mauchline 1998; Timonin et al. 1992). Whereas Timonin et al. (1992) reported active feeding on phytoplankton for *C. carinatus* in surface waters during upwelling in the Benguela system, the main distribution of *C. carinatus* in the waters around Ampère and Senghor seamounts was between 500 and 1000 m and that of *S. monachus* between 300 and 750 m (Denda unpubl.data). Thus we suppose both species to feed mainly on sinking phytodetritus from the surface. Contrary, species of *Euchaeta* are known for a predatory behaviour feeding on other small calanoid and cyclopoid copepods (Øresland 1991). The diet of the omnivorous decapods *Sergestes* spp. and *Acanthephyra* spp. was reported to consist mainly of chaetognaths, euphausiids and copepods but also of phytodebris and protists (Hopkins et al. 1994). The zooplanktivorous fish *Cyclothone alba/brauerii* feed mainly on copepods and other small crustaceans (Whitehead et al. 1986; Hopkins & Sutton 1998). Thus depending on the actual composition of the ingested food and the food quality the individual isotopic fractionation and the enrichment in $\delta^{13}C$ and $\delta^{15}N$ might be highly variable and, as at Ampère Seamount even smaller in omni- and zooplanktivorous predators compared to the detrivorous copepods, not showing the expected enrichment in the isotope signals along the food chain (see Fry & Sherr 1984). The general depletion of about 1 ‰ in $\delta^{13}C$ and 2 ‰ in $\delta^{15}N$ in the mesopelagic plankton at Ampère Seamount and the far field as compared to Senghor and the far field reflects the signals of the different phytoplankton communities at the surface, which become an important food source for deeper waters as sinking organic matter.

6.5.1.4 The bathypelagic zone

In the deep-waters isotope ratios showed a high variability, especially in $\delta^{15}N$ at both seamounts. As in the mid-waters the enrichment in $\delta^{13}C$ and $\delta^{15}N$ was variable among herbi-, omni- and carnivores and not consistent with increasing trophic level. However, the different surface signals of both regions were also reflected in the deep zone by the primary consumers *Rhincalanus nasutus* in the subtropical waters and *Rhincalanus cornutus* in the tropical region. Since both are known for herbivory as coarse filter feeders (Timonin et al. 1992; Teuber et al. 2014), we assume sinking phytodetritus as their main food source. But, we suppose also omnivory, especially for *R. cornutus* according to its intermediate isotope ratios, as also reported by Teuber et al. (2014) for the tropical SE Atlantic. $\delta^{15}N$ values of the small cyclopoid copepod *Oncaea* spp. were again comparatively low like in the epipelagic zone, maybe due to smaller sized food particles, which are more depleted in ^{15}N (Rau et al. 1990) than particles ingested by larger omnivores. At Ampère Seamount and the far field a $\delta^{13}C$ enrichment of about 0.4-1.0 ‰ in *R. nasutus* and *Disseta palumbii* relative to the $\delta^{13}C$ of exoskeletons might indicate direct feeding on these carcasses. The most abundant carcasses are those of copepods and it is assumed that their numbers do not build up in mid-waters because they are continuously eaten (Roe 1988). But reaching the bottom near water layers they might be an important food source in the deep pelagic zone. At Ampère Seamount and the far field *D. palumbii* aimed an intermediate trophic position and has been described as a typical suspension feeder feeding mainly on particles (Ohtsuka et al. 1997). At Seine Seamount storage lipids of this species reflected high proportions of saturated fatty acids usually present in phytodetritus (Hirch 2009), assuming detrivory as dominant feeding type for this copepod. At both seamounts *Lucicutia maxima* from the lower bathypelagic (2000-4000 m) is also assumed for detrivory, since it had δ^{15}N values in the same high range (10.5-12.1 ‰) as *Lucicutia longiserrata* in the deep eastern Mediterranean, which seems to be able to utilize suspended particles and may take advantage of the recycling of organic matter in the deep-sea (Koppelmann et al. 2009). Similar high δ^{15}N ratios of 10.3-11.1 ‰ were measured for *Megacalanus princeps* at Ampère and Senghor seamounts, which is characterized as suspension feeder in the upper bathypelagic zone (1000-2000 m) (Ikeda et al. 2006). On the other hand Teuber et al. (2014) supposed a higher degree of carnivory for *M. princeps* from lower mesopelagic depths, based on trophic marker fatty acid (carnivory/herbivory) ratios, supported by higher δ^{15}N values of >10 ‰. Since the carnivorous *Euchaeta* spp., chaetognaths and cephalopods had δ^{15}N values of 10.1-13.3 ‰ in the upper bathypelagic at both seamounts in our study, ratios of >10 ‰ might be an indication for carnivory in *M. princeps*. However, at Ampère Seamount and the far field δ^{15}N ratios of the small dragonfishes *Astronesthes neopogon* and *Photonectes braueri* were comparatively low, maybe due to migrating behaviour and feeding in shallower waters on mid-water fishes and crustaceans (Whitehead et al. 1986; Froese & Pauly 2015). On the abyssal plain at the far field site of Senghor the benthic crabs *Munidopsis aries* and *Willemoesia leptodactyla* had much higher δ^{13}C values than the planktonic species and occupied the highest trophic position with δ^{15}N values in the same range as found by Iken et al. (2001) at the Porcupine Abyssal Plain and by Reid et al. (2012) at the Mid-Atlantic Ridge. Both crabs are known for a mixed diet of detritus, crustaceans and other infauna (Cartes & Abelló 1992; Cartes et al. 2007) and are observed feeding on marine carrion (Kemp et al. 2006). The isotope ratios in our study reflect the predatory and scavenging feeding mode of both crabs (Cartes & Abelló 1992; Reid et al. 2012) on organic material of a higher decomposition stage. In the lower bathypelagic zone (2000-4000 m) a more opportunistic, detrivorous to omnivorous feeding type seemed to be common, where both large and small animals depend as much upon particles, detritus and carcasses as upon encounters with living prey (Roe 1988).

6.5.2 Trophic structure of the benthopelagic fish community

The topographies of Ampère and Senghor seamounts provide a suitable habitat for benthopelagic shallow and deep-water species, even for some which are usually restricted to the continental slope and coastal areas, such as *Conger conger* and *Muraena helena*. Thus most of the fishes collected around both seamounts are typical for shelves and seamounts in the Atlantic and the Mediterranean, whereas in the bathyal and abyssal regions of the seamounts and of the far field sites typical deep-sea fishes were found (Christiansen et al. 2015 and references therein; Vieira et al. subm. and references therein).

δ^{15}N signatures and the derived trophic positions of the benthopelagic fish species showed an increasing trend with body size and with depth, coincident with the vertical zonation of feeding types.

Zooplanktivores were mainly collected on the seamount summits and occupied the lowest trophic position of the fish community. Mixed-feeders appeared to be more pelagic around the summit plateau and the upper slope. The more piscivorous fishes were concentrated on the upper and mid slopes and had an intermediate trophic position. On the abyssal plains generalized feeders and predatory scavengers occupying the highest trophic position were caught. The increase of trophic level with depth was apparent by a $\delta^{15}N$ enrichment of ~3 ‰ for fishes from Senghor down to the mid slope, whereas at Ampère the $\delta^{15}N$ enrichment of ~6.5 ‰ from the summit to the deep slope indicates one more trophic level.

6.5.2.1 Food sources, nutritional links and resource partitioning

Some prey items of the benthopelagic fish fauna, especially mesopelagic copepods, are known for high contents of lipids (Lee & Hirota 1973), which, if not removed, results in lower (more negative) $\delta^{13}C$ values (DeNiro & Eppstein 1977; Wada et al. 1987). In order to avoid loss of the often very small material, lipids of zooplankton were not removed prior to the measurements, nor were lipids of fish tissue. Thus the $\delta^{13}C$ values of the potential prey organisms might be disproportionately low relative to the fish muscle tissue, which is generally low in lipid (DeNiro & Eppstein 1977; Wada et al. 1987). The difference between fish and potential food source might therefore be overestimated and has to be interpreted with some caution.

6.5.2.1.1 Ampère Seamount and the abyssal plain

The differences in stomach contents and stable isotope ratios between the seamount fishes at Ampère Seamount show a resource partitioning among the benthopelagic fishes through distinct vertical feeding positions and habitat choice, as suggested in previous studies on other seamounts (see Ehrich 1974; Pakhorukov 2008; Hirch & Christiansen 2010). Around the summit plateau of Ampère Seamount the predominantly zooplanktivorous and mixed-feeding species showed habitat choices associated with their prey preferences. Oncaeid copepods were the main prey in *Callanthias ruber* and were also ingested to a low amount by *Capros aper*. The $\delta^{13}C$ values of both species matched those of their potential crustacean prey with an enrichment of ~1.5 ‰ between the trophic levels. The importance of oncaeids in the diet of these species had already been observed on Seine Seamount (Christiansen et al. 2009), where *C. aper* also showed a substantial proportion of non-crustacean food. Since oncaeids were more abundant in the bottom near water layers over the summit plateau of Seine and Ampère seamounts than in the adjacent surface waters (Martin 2008; Denda et al. subm.), the predominance of this group as prey indicates a bottom associated feeding behaviour for *C. ruber* and *C. aper* or a selective feeding on oncaeids (Christiansen et al. 2009).

The diet of the two mackerel species and the jack mackerel covered a wide spectrum of prey items, respectively, but indicates also distinct feeding strategies: *Scomber colias* had a diet of oncaeid copepods together with amphipods, polychaetes and bivalves, suggesting a near-bottom feeding preference, whereas *Trachurus picturatus* and *Scomber scombrus* fed mainly on calanoid copepods and larger malacostraca as well as on cephalopods and fish, indicating a more pelagic distribution. The diverse food might contribute to the $\delta^{13}C$ enrichment of ~2.2 ‰ between these fishes and their prey, which is markedly higher than usually assumed for successive trophic levels.

This apparent habitat choice reflects the zooplankton distribution over Ampère summit as observed during the same study (see Denda & Christiansen 2014). Especially larger organisms (5-20 mm), including vertical migrators like euphausiids, were nearly absent over the summit, but increased towards the edge of the plateau and the upper and mid slopes, where they are available as food for the more pelagic fishes. A similar distribution pattern with larger zooplankton missing was observed over the summit of Seine Seamount (Martin & Christiansen 2009), and like in our study the predominance of small copepods in the stomachs of the near bottom fishes showed that these are not responsible for the absence of the larger plankton (Christiansen et al. 2009; Hirch & Christiansen 2010). Thus the topographic trapping of vertically migrating zooplankton on the summit seemed not to be a major mechanism for food supply at Ampère Seamount, as it was supposed by Fock et al. (2002a, b) for Great Meteor Tablemount. Hirch & Christiansen (2010) neither observed an important role of the topographic blockage for Seine Seamount; rather the seamount fishes were supported by current-driven advection of the planktonic prey. *Serranus atricauda*, a typical bottom-living fish on Ampère summit, is assumed to be a generalist predator feeding on benthic and epibenthic fishes, decapods and mysids (Morato et al. 2000), reflected by its isotope signature in the same range as for *Lepidopus caudatus*, which is predatory on decapods, amphipods, cephalopods and other fish including cannibalism in larger individuals (Klimpel et al. 2006). As top predator on the summit *Muraena helena* had the highest isotope values at the summit, whereas *Conger conger* showed similar signatures like the other bottom-living species, but is known from the Azores region to feed mainly on *C. aper* and *Macroramphosus* sp. (Morato et al. 1999).

Piscivores with a primarily nektonic diet appeared mainly on the upper and mid slopes of Ampère Seamount and generally had slightly enriched $\delta^{13}C$ and $\delta^{15}N$ signatures compared to the summit assemblage. The shark species *Deania calcea* is known as a principle fish eater of, for example, the bottom-living *Helicolenus dactylopterus* (Mauchline & Gordon 1983), which matches well with the difference of about 1 ‰ in our $\delta^{13}C$ values between both species. However, the diet of *D. calcea* and *Etmopterus* spp. can comprise a variety of predominantly benthopelagic prey, with fish as dominant food and euphausiids, decapods and squids of minor importance as reported by Mauchline & Gordon (1983). This mixed diet of micronekton, which was in a similar composition found in stomachs of *Synaphobranchus kaupii* in other studies (Merrett & Marshall 1981), might cause the relatively low $\delta^{15}N$ values of both sharks in the same range as for the cutthroat eel, showing that they are not high level predators. *Mora moro* is a large demersal species (Stefanescu et al. 1992) and isotope signatures were significantly different between both slope stations of Ampère Seamount, which might be attributed to the different depths of the stations and depth dependent feeding preferences. For the Catalan slope, Carrassón et al. (1997) reported *M. moro* to feed on benthic as well as on pelagic prey in depths of 700-800 m, whereas the diet of deeper individuals (1000-1400 m) was based on epi- and suprabenthic crustaceans, fish and cephalopods. These depth-related feeding strategies presumably caused the broader $\delta^{15}N$ range among species at the southern slope of Ampère Seamount with a tendency to lower ratios at 938 m than at 1200 m.

The abyssal predators and scavengers showed a broad $\delta^{15}N$ range which indicates a kind of resource partitioning also in the deep-sea due to distinct feeding strategies, as observed in the summit area of Ampère Seamount. The smaller, predominately plankti-/benthivores appeared mainly at the base of Ampère, like *Halosauropsis macrochir*, *Bathypterois grallator* and *Cataetyx laticeps*, but also on the abyssal plain with *Bathypterois longipes*. In the diet of *Halosauropsis macrochir* bathypelagic crustaceans, such as amphipods and decapods, including *Acanthephyra* sp., had been reported to be most important (Gordon & Duncan 1987). In our study the $\delta^{13}C$ enrichment of 1.4 ‰ between *Acanthephyra* spp. and *H. macrochir* indicates a possible direct feeding relationship between the two species, with *Acanthephyra* either impinging on the slopes or sinking as carrion and forming thereby a part of the predator-scavenger food chain as supposed by Reid et al. (2012). The exact diet of the rare *Cataetyx laticeps* is unknown (Mauchline & Gordon 1984; Whitehead et al. 1986; Gordon & Duncan 1987), but the family Bythitidae is generally noted to feed on small benthic invertebrates and fishes (Bray 2012). The high $\delta^{15}N$ signatures of *C. laticeps* at Ampère Seamount point to a strict benthic feeding on, for example, polychaetes and echinoderms, which had higher $\delta^{15}N$ values than several top predatory fishes in the abyssal North Atlantic (Iken et al. 2001). The tripod fishes *B. grallator* and *B. longipes* have been known to feed mainly on small benthopelagic crustaceans (Sulak 1977; Whitehead et al. 1986), but the relatively high $\delta^{15}N$ values of *B. longipes* in this study, which were in the same range or even higher than those of the larger scavengers, and the presence of small cephalopod beakers in the stomachs besides copepods, mysids and amphipods show that they are not restricted to zooplanktivorous feeding. We assumed macrourids to be end consumers in the abyssal food web, but their $\delta^{15}N$ values were lower than expected. *Coryphaenoides armatus* had a mixed diet of crustaceans, cephalopods and fish and is known to feed on carrion derived of epipelagic nekton (Martin & Christiansen 1997; Drazen et al. 2008), which have lower $\delta^{15}N$ values than the abyssal benthic prey (Drazen et al. 2008). Thus scavenging in macrourids as well as in alepocephalids and deep-sea eels may feature $\delta^{15}N$ values lower than in the plankti-/benthivorous species that do not feed on carrion. Scavenging might also cause the relative high $\delta^{13}C$ ratios in *C. armatus, Holcomycteronus squamosus* and *Conocara salmoneum* compared to the plankti-/benthivores, supposing lower lipid content associated with a higher $\delta^{13}C$ ratio for the epipelagic nekton as potential carrion than for the benthic prey, since lipid-rich organisms have very low $\delta^{13}C$ values (Post et al. 2007). The enhanced $\delta^{13}C$ values of *C. armatus* compared to the smaller *Coryphaenoides profundicolus* and the other macrourids are associated to a higher amount of fish ingested by the larger species, whereas the diet of the smaller ones was dominated by crustaceans. The same relationship between size and prey preference in macrourids had been observed by Martin & Christiansen (1997) in the NE Atlantic and by Drazen et al. (2008) in the NE Pacific.

6.5.2.1.2 Senghor Seamount and the abyssal plain

Within the few benthopelagic fishes studied at Senghor Seamount a resource partitioning is apparent similar to Ampère Seamount. On the summit of Senghor Seamount the predominantly zooplanktivorous *Antigonia capros* had unexpectedly high $\delta^{13}C$ and $\delta^{15}N$ signatures, which were in the same range as in the piscivorous *Zenopsis conchifer* from Ampère Seamount. On Great Meteor Tablemount both species were able to switch between crustacean prey, cephalopods and fish depending on the prey availability (Fock et al. 2002a, b). Thus we assume that *A. capros* fed mainly on fish at Senghor. The bottom-living *Helicolenus dactylopterus* was wide spread from the summit to the mid slope (100-734 m) of Senghor. Individuals became larger with depth and isotope ratios increased. *H. dactylopterus* is generally known for a mixed diet of both pelagic and benthic fishes and invertebrates (Whitehead et al. 1986), but off NW Africa it had been categorised as a highly selective benthic feeder mainly on ophiuroids (Merrett & Marshall 1981). Thus, we suppose that the relatively high isotope signatures of the larger individuals result from a predominantly benthic prey, which should be more enriched in $\delta^{13}C$ and $\delta^{15}N$ than the pelagic items at depth.

On the upper slope *Promethichthys prometheus* and *Beryx splendens* had comparably low isotope values, indicating a preference of pelagic prey from shallower waters, as supported by previous studies (Nakamura & Parin 1993; Vinnichenko 1997; Dürr & González 2002; Horn et al. 2010), which reported that the species ascend upwards during night and feed on fish, cephalopods and crustaceans. *B. splendens* was observed to follow actively the migrating prey (Vinnichenko 1997; Horn et al. 2010), reflected in the present study by its isotope ratios that match those of potential prey organisms like the decapods *Acanthephyra* spp. and *Sergestes* spp. as well as myctophids (see also Dürr & González 2002).

Within the abyssal fish community at the Senghor far field site *Coryphaenoides armatus* and *Holcomycteronus squamosus* occupied the highest trophic position, with their isotope ratios being in the same range as those of the abyssal benthic crabs. Iken et al. (2001 and references therein) observed the same feature at the Porcupine Abyssal Plain. For both, the crabs as benthic invertebrate top predators, as well as the more mobile predatory fishes scavenging plays an important role in their diet, so that they are not only dependant on abyssopelagic prey, but also on detritus and food falls of surface origin.

6.5.3 Conclusions on spatial differences in trophic pathways

The generally lower $\delta^{13}C$ and $\delta^{15}N$ values in the meso- and bathypelagic zooplankton of the subtropical waters as compared to the tropical region reflect the signals of different nutrient availability and phytoplankton communities from the surface, since sinking POM from the upper layers is an important food source for the deeper waters. The lower $\delta^{13}C$ values may also be an indication of a lipid content higher in the subtropical than in the tropical zooplankton, as tropical zooplankton generally do not accumulate large lipid stores (Lee et al. 2006), and high contents of lipids, which are depleted in ^{13}C because lipid synthesis favors incorporation of ^{12}C, result in low $\delta^{13}C$ ratios (Post et al. 2007). Significantly enriched $\delta^{15}N$ values in consumers at Senghor Seamount compared to Ampère might indicate more feeding steps along the food chain, pointing to different feeding conditions and trophic structures in a more complex food web in the tropics than in the subtropics.

A strong correlation between $\delta^{15}N$ and $\delta^{13}C$ values across all taxa at one sampling location, or the lack thereof, may indicate whether a food web is mainly dependent on a single primary food source, or relies on several energy providers. For example, a strong positive linear relationship for a bathypelagic assemblage suggests a linear food chain dependent on surface organic matter as basic energy source (Polunin et al. 2001; Drazen et al. 2008; Reid et al. 2012). Variable correlations in the distinct pelagic zones between the seamounts and the respective far field sites may indicate differences in the food web structure and feeding conditions and point, for example, to different shares of autochthonus and allochthonous food supply.

At Ampère Seamount a strong correlation between $\delta^{15}N$ and $\delta^{13}C$ suggests that the community relies on a single energy source resulting from, for example, local photosynthetically derived production (see Iken et al. 2001; Polunin et al. 2001), but that variable, advected food sources control the pelagic food web at the far field site, where no such relationship existed in the epi- and mesopelagic zones. The assumption that the higher trophic levels rely on autochthonus production at the seamount is, however, not supported by significant differences in the $\delta^{13}C$ values of POM and plankton of the epipelagic zone between both sites. Consistently, no evidence was found for hydrodynamic features generating and retaining autochthonus seamount production or trapping particles over Ampère at least during the cruise (Denda & Christiansen 2014; Denda et al. subm.). In meso- and bathypelagic waters, however, significantly differing $\delta^{13}C$ values of POM and typical suspension feeders at the seamount as compared to the open ocean might be indications of previous recirculation cells and associated downstream plankton production (Genin 2004; Genin & Dover 2007) over Ampère, whereas the stronger currents at the surface have advected and mixed plankton and particles off the seamount and the far field. In the bathypelagic zone correlations of $\delta^{15}N$ and $\delta^{13}C$ point to a rather homogenous surface-derived food source at both sites, which is in contrast to the more complex pathways in the upper waters of the open ocean as suggested above. Thus, despite possible differences in production and trophic pathways in the surface layers, the remaining nutritional sources seem to be comparable in the deep-sea.

Similar correlations between δ^{15}N and δ^{13}C in all pelagic zones of Senghor Seamount and the far field did not point to generally altered feeding conditions and trophic pathways between both sites. Significant differences in the δ^{13}C values of epipelagic POM and some omnivores as well as of bathypelagic detrivores, however, indicate food sources of different origin between the seamount and the open ocean. This may be attributed to a regional decrease in primary production from north to south, evident in a slightly enhanced net primary production at the reference site (~325 mg m^{-2} day^{-1}) as compared to Senghor (~280 mg m^{-2} day^{-1}) (Dumont et al. subm.). Since the reference site is located closer to the sphere of the CVFZ and the Mauritanian upwelling, advected filaments possibly cause varying nutritional sources and feeding conditions at this site as compared to Senghor Seamount at times.

In general the varying δ^{13}C and δ^{15}N signatures and correlations among the seamount systems and the far field sites indicate that the trophic structure of the pelagic and benthopelagic communities may be highly variable not only at seamounts, but also over the uniform abyssal plains of the two different trophic regimes.

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Table 6-A1. One-way ANOVA, *post-hoc* Bonferroni test and *t*-test for differences in $\delta^{13}C$ and $\delta^{15}N$ of POM and zooplankton between depth layers (epi = 0-100 m, meso = 100-1000 m, bathy = 1000-4000 m) at Ampère and Senghor seamounts and the far field sites (FF).

					$\delta^{13}C$					$\delta^{15}N$				
Taxon	**Depth zone**	**Test**	**N**	**Source**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**
	Ampère													
POM	epi, meso, bathy	ANOVA	19	Depth	2.033	2	1.016	7.461	<0.01	107	2	53.710	81.612	<0.001
				Error	2.180	16	0.136			10.530	16	0.658		
		post-hoc		epi *vs.* meso					>0.05					<0.001
		post-hoc		epi *vs.* bathy					<0.01					<0.01
		post-hoc		meso *vs.* bathy					<0.05					<0.001
Euchaeta	epi, meso	*t*	6	epi *vs.* meso		4	0.010	0.060	>0.05		4	1.530	3.055	<0.05
Chaetognatha	meso, bathy	*t*	8	meso *vs.* bathy		6	0.277	2.116	>0.05		6	1.195	3.649	<0.05
	Ampère FF													
POM	epi, meso, bathy	ANOVA	13	Depth	21.840	2	10.920	15.234	<0.01	74.505	2	37.253	23.784	<0.001
				Error	7.168	10	0.717			15.663	10	1.566		
		post-hoc		epi *vs.* meso					>0.05					<0.01
		post-hoc		epi *vs.* bathy					<0.05					>0.05
		post-hoc		meso *vs.* bathy					<0.01					<0.01
Oncaea		*t*	4	epi *vs.* bathy		2	1.070	4.157	>0.05		2	2.930	15.336	<0.01
Euchaeta	epi, meso	*t*	9	epi *vs.* meso		7	0.123	0.352	>0.05		7	2.383	3.504	<0.05
Lucicutia	epi, bathy	*t*	7	epi *vs.* bathy		5	0.492	0.904	>0.05		5	8.559	21.575	<0.001
Chaetognatha	meso, bathy	*t*	8	meso *vs.* bathy		6	0.125	0.337	>0.05		6	3.547	3.687	<0.05
	Senghor													
POM	epi, meso	*t*	13	epi *vs.* meso		11	0.089	0.343	>0.05		11	3.506	11.891	<0.001
Oncaea		*t*	6	epi *vs.* bathy		4	1.430	1.938	>0.05		4	1.575	4.310	<0.05
Euchaeta	epi, meso, bathy	ANOVA	15	Depth	7.624	2	3.812	5.855	<0.05	75.277	2	37.639	34.425	<0.001
				Error	7.812	12	0.651			13.120	12	1.093		
		post-hoc		epi *vs.* meso					<0.05					<0.01
		post-hoc		epi *vs.* bathy					>0.05					<0.001
		post-hoc		meso *vs.* bathy					>0.05					<0.01
Lucicutia	epi, bathy	*t*	5	epi *vs.* bathy		3	3.970	15.162	<0.01		3	8.180	16.918	<0.001
	Senghor FF													
POM	epi, meso, bathy	ANOVA	10	Depth	912.248	2	456.124	493.693	<0.001	67.716	2	33.858	14.853	<0.01
				Error	4.620	5	0.924			15.957	7	2.280		
		post-hoc		epi *vs.* meso					<0.001					>0.05
		post-hoc		epi *vs.* bathy					>0.05					>0.05
		post-hoc		meso *vs.* bathy					<0.001					<0.01
Euchaeta	epi, meso, bathy	ANOVA	9	Depth	2.449	2	1.224	3.046	>0.05	59.228	2	29.614	69.093	<0.001
				Error	2.412	6	0.402			2.572	6	0.429		
		post-hoc		epi *vs.* meso					>0.05					<0.01
		post-hoc		epi *vs.* bathy					>0.05					<0.001
		post-hoc		meso *vs.* bathy					>0.05					<0.05
Chaetognatha	epi, meso	*t*	4	epi *vs.* meso		2	1.355	13.466	<0.01		2	3.010	49.484	<0.001

ANOVA/ *a priori/ post-hoc* test: SQ, Sum-of-squares; df, degrees of freedom; MQ, Mean-square; F, F-ratio; p, probability of correlation.
***t*-test:** df, degrees of freedom; DM, Difference in Means; t, Pooled Variance t; p, probability of correlation.

Table 6-A2. One-way ANOVA, *a priori* hypothesis test and *t*-test for differences in δ^{13}C and δ^{15}N of POM and zooplankton between Ampère (Amp) and Senghor (Sen) seamounts and the far field sites (FF).

					δ^{13}C					**δ^{15}N**				
Taxon	**Location**	**Test**	**N**	**Source**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**P**	**SS**	**df**	**MQ** or **DM**	**F** or **t**	**p**
	0–100 m													
POM	Amp$_{2009}$, Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	30	Location	12.537	4	3.134	15.619	<0.001	17.900	4	4.475	10.226	<0.001
				Error	5.017	25	0.201			10.941	25	0.438		
		a priori		Amp$_{2009}$ *vs.* Amp$_{2010}$	1.757	1	1.767	8.806	<0.01	4.493	1	4.493	10.267	<0.01
		a priori		Amp$_{2010}$ *vs.* Amp FF	0.057	1	0.057	0.285	>0.05	0.019	1	0.019	0.044	>0.05
		a priori		Sen *vs.* Sen FF	2.814	1	2.814	14.023	<0.01	1.593	1	1.593	3.640	>0.05
		a priori		Amp *vs.* Sen	2.043	1	2.043	10.180	<0.01	15.626	1	15.626	35.707	<0.001
Ostracoda	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	16	Location	14.547	3	4.849	6.765	<0.01	0.821	3	0.274	0.297	>0.05
				Error	8.601	12	0.717			11.043	12	0.920		
		a priori		Amp *vs.* Amp FF	0.042	1	0.042	0.058	>0.05	0.535	1	0.535	0.581	>0.05
		a priori		Seng *vs.* Seng FF	13.401	1	13.401	18.698	<0.01	0.018	1	0.018	0.020	>0.05
		a priori		Amp *vs.* Seng	4.704	1	4.704	6.562	<0.05	0.653	1	0.653	0.709	>0.05
Oncaea	Amp$_{2010}$, Amp FF, Sen	ANOVA		Location	1.051	2	0.525	1.018	>0.05	4.569	2	2.285	25.537	<0.05
				Error	2.580	5	0.516			0.447	5	0.089		
		a priori		Amp *vs.* Amp FF	0.526	1	0.526	1.019	>0.05	0.593	1	0.593	6.628	>0.05
		a priori		Amp *vs.* Sen	1.021	1	1.021	1.978	>0.05	1.404	1	1.401	15.659	<0.05
Corycaeus	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	13	Location	5.559	3	1.853	3.304	>0.05	15.552	3	5.184	13.995	<0.01
				Error	5.048	9	0.561			3.334	9	0.370		
		a priori		Amp *vs.* Amp FF	0.034	1	0.034	0.061	>0.05	0.813	1	0.813	2.196	>0.05
		a priori		Sen *vs.* Sen FF	1.197	1	1.197	2.134	>0.05	0.028	1	0.028	0.076	>0.05
		a priori		Amp *vs.* Sen	1.114	1	1.114	1.986	>0.05	4.472	1	4.472	12.074	<0.01
Clausocalanus	Amp$_{010}$, Sen, Sen FF	ANOVA	10	Location	2.579	2	1.289	2.320	>0.05	0.093	2	0.047	0.079	>0.05
				Error	3.891	7	0.556			4.138	7	0.591		
		a priori		Sen *vs.* Sen FF	1.046	1	1.046	1.882	>0.05	0.000	1	0.000	0.000	>0.05
		a priori		Amp *vs.* Sen	0.889	1	0.889	1.600	>0.05	0.088	1	0.088	0.148	>0.05
Euchaeta	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	19	Location	3.190	3	1.063	2.013	>0.05	16.756	3	5.585	4.293	<0.05
				Error	7.925	15	0.528			19.515	15	1.301		
		a priori		Amp *vs.* Amp FF	0.001	1	0.001	0.002	>0.05	1.561	1	1.561	1.199	>0.05
		a priori		Sen *vs.* Sen FF	0.561	1	0.561	1.061	>0.05	0.341	1	0.341	0.262	>0.05
		a priori		Amp *vs.* Seng	0.764	1	0.746	1.447	>0.05	3.565	1	3.565	2.740	>0.05
Pleuromamma	Amp$_{2009}$, Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	20	Location	0.685	4	0.171	1.176	>0.05	26.613	4	6.653	14.111	<0.001
				Error	2.184	15	0.146			7.073	15	0.472		
		a priori		Amp$_{2009}$ *vs.* Amp$_{2010}$	0.000	1	0.000	0.003	>0.05	1.617	1	1.617	3.430	>0.05
		a priori		Amp$_{2010}$ *vs.* Amp FF	0.040	1	0.040	0.277	>0.05	6.165	1	6.165	13.076	<0.01
		a priori		Sen *vs.* Sen FF	0.403	1	0.403	2.771	>0.05	0.803	1	0.803	1.702	>0.05
		a priori		Amp *vs.* Sen	0.194	1	0.194	1.334	>0.05	0.382	1	0.382	0.810	>0.05
Candacia	Amp$_{2010}$, Amp FF, Sen	ANOVA	14	Location	0.272	2	0.136	0.238	>0.05	2.372	2	1.186	1.982	>0.05
				Error	6.287	11	0.572			6.584	11	0.599		
		a priori		Amp *vs.* Amp FF	0.270	1	0.270	0.473	>0.05	2.081	1	2.081	3.477	>0.05
		a priori		Amp *vs.* Sen	0.063	1	0.063	0.110	>0.05	0.114	1	0.114	0.191	>0.05

Labidocera	Sen, Sen FF	*t*	7	Sen *vs.* Sen FF		5	0.537	4.022	<0.05		5	0.079	0.364	>0.05
Euphausiacea	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	21	Location	10.915	3	3.638	7.130	<0.01	3.360	3	1.120	0.915	>0.05
				Error	8.676	17	0.510			20.813	17	1.224		
		a priori		Amp *vs.* Amp FF	0.966	1	0.966	1.893	>0.05	0.520	1	0.520	0.425	>0.05
		a priori		Sen *vs.* Sen FF	2.124	1	2.124	4.163	>0.05	2.126	1	2.126	1.737	>0.05
		a priori		Amp *vs.* Sen	1.650	1	1.650	3.233	>0.05	0.121	1	0.121	0.099	>0.05
Siphonophora	Amp$_{2010}$, Sen, Sen FF	ANOVA	15	Location	1.474	2	0.737	1.550	>0.05	1.319	2	0.660	3.554	>0.05
				Error	6.178	13	0.475			2.227	12	0.186		
		a priori		Sen *vs.* Sen FF	0.219	1	0.219	0.460	>0.05	1.313	1	1.313	7.072	<0.05
		a priori		Amp *vs.* Sen	0.810	1	0.810	1.705	>0.05	0.084	1	0.084	0.450	>0.05
Chaetognatha	Amp$_{2010}$, Sen, Sen FF	ANOVA	11	Location	1.272	2	0.636	2.127	>0.05	0.842	2	0.421	1.204	>0.05
				Error	2.392	8	0.299			2.799	8	0.250		
		a priori		Sen *vs.* Sen FF	0.249	1	0.249	0.832	>0.05	0.402	1	0.402	1.150	>0.05
		a priori		Amp *vs.* Sen	1.203	1	1.203	4.024	>0.05	0.620	1	0.620	1.773	>0.05
Leptocephalus	Sen, Sen FF	*t*	8	Sen *vs.* Sen FF		6	0.512	0.578	>0.05					
Myctophidae	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	24	Location	13.415	3	4.472	3.388	<0.05	76.834	3	25.611	13.595	<0.001
				Error	26.394	20	1.320			37.678	20	1.884		
		a priori		Amp *vs.* Amp FF	0.132	1	0.132	0.100	>0.05	0.931	1	0.931	0.494	>0.05
		a priori		Sen *vs.* Sen FF	0.019	1	0.019	0.015	>0.05	11.686	1	11.686	6.203	<0.05
		a priori		Amp *vs.* Sen	6.339	1	6.339	4.804	<0.05	6.825	1	6.825	3.623	>0.05
	100-1000 m													
POM	Amp$_{2009}$, Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	27	Location	30.550	4	7.637	12.781	<0.001	3.202	4	0.800	0.997	>0.05
				Error	13.146	22	0.598			17.669	22	0.803		
		a priori		Amp$_{2009}$ *vs.* Amp$_{2010}$	12.815	1	12.815	21.447	<0.001	0.012	1	0.012	0.015	>0.05
		a priori		Amp$_{2010}$ *vs.* Amp FF	4.545	1	4.545	7.606	<0.05	0.002	1	0.002	0.002	>0.05
		a priori		Sen *vs.* Sen FF	0.586	1	0.586	0.981	>0.05	0.487	1	0.487	0.607	>0.05
		a priori		Amp *vs.* Sen	12.231	1	12.231	20.469	<0.001	1.480	1	1.480	1.843	>0.05
C. carinatus	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	14	Location	1.431	3	0.477	0.187	>0.05	0.898	3	0.299	3.221	>0.05
				Error	25.484	10	2.548			0.929	12	0.093		
		a priori		Amp *vs.* Amp FF	0.092	1	0.092	0.036	>0.05	0.021	1	0.021	0.230	>0.05
		a priori		Seng *vs.* Sen FF	0.213	1	0.213	0.084	>0.05	0.153	1	0.153	1.648	>0.05
		a priori		Amp *vs.* Sen	0.104	1	0.104	0.041	>0.05	0.084	1	0.084	0.904	>0.05
S. monachus	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	10	Location	3.712	3	1.237	1.189	>0.05	3.121	3	1.040	4.511	>0.05
				Error	6.244	6	1.041			1.384	6	0.231		
		a priori		Amp *vs.* Amp FF	0.449	1	0.449	0.431	>0.05	0.762	1	0.762	3.302	>0.05
		a priori		Senghor *vs.* Sen FF	1.946	1	1.946	1.870	>0.05	0.316	1	0.316	1.371	>0.05
		a priori		Amp *vs.* Sen	0.051	1	0.051	0.049	>0.05	0.958	1	0.958	4.152	>0.05
Euachaeta	Amp$_{2009,}$ Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	16	Location	21.458	4	5.364	42.308	<0.001	34.166	4	8.541	58.790	<0.001
				Error	1.395	11	0.127			1.598	11	0.145		
		a priori		Amp$_{2009}$ *vs.* Amp$_{2010}$	0.077	1	0.077	0.610	>0.05	0.554	1	0.554	3.812	>0.05
		a priori		Amp$_{2010}$ *vs.* Amp FF	0.019	1	0.019	0.152	>0.05	0.001	1	0.001	0.009	>0.05
		a priori		Sen *vs.* Sen FF	0.011	1	0.011	0.085	>0.05	0.027	1	0.027	0.187	>0.05
		a priori		Amp *vs.* Sen	14.071	1	14.071	110.973	<0.001	23.972	1	23.972	164.999	<0.001

Sergestes	Amp$_{2010}$, Amp FF, Sen	ANOVA	11	Location	8.380	2	4.190	142.187	<0.001	8.995	2	4.498	7.086	<0.05
				Error	0.236	8	0.029			5.078	8	0.635		
		a priori		Amp *vs.* Amp FF	0.047	1	0.047	1.596	>0.05	0.116	1	0.116	0.183	>0.05
		a priori		Amp *vs.* Sen	6.864	1	6.864	232.923	<0.001	8.443	1	8.443	13.300	<0.01
Acanthephyra	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	20	Location	12.674	3	4.225	12.137	<0.001	47.727	3	15.909	55.045	<0.001
				Error	5.570	16	0.348			4.624	16	0.289		
		a priori		Amp *vs.* Amp FF	0.121	1	0.121	0.348	>0.05	1.958	1	1.958	6.776	<0.05
		a priori		Sen *vs.* Sen FF	0.156	1	0.156	0.449	>0.05	10.484	1	10.484	36.276	<0.001
		a priori		Amp *vs.* Sen	5.221	1	5.221	14.998	<0.01	5.491	1	5.491	19.000	<0.001
Chaetognatha	Amp$_{2010}$, Amp FF, Sen FF	ANOVA	10	Location	4.957	2	2.479	39.856	<0.001	4.690	2	2.345	6.756	<0.05
				Error	0.435	7	0.062			2.430	7	0.347		
		a-priori		Amp *vs.* Amp FF	0.022	1	0.022	0.357	>0.05	4.541	1	4.541	13.083	<0.01
Cyclothone	Amp$_{2009}$, Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	21	Location	13.940	4	3.485	6.926	<0.01	57.119	4	14.280	19.759	<0.001
				Error	8.051	16	0.503			11.563	16	0.723		
		a priori		Amp$_{2009}$ *vs.* Amp$_{2010}$	0.079	1	0.079	0.157	>0.05	1.907	1	1.907	2.639	>0.05
		a priori		Amp$_{2010}$ *vs.* Amp FF	0.263	1	0.263	0.522	>0.05	2.091	1	2.091	2.893	>0.05
		a priori		Sen *vs.* Sen FF	1.086	1	1.086	2.158	>0.05	1.011	1	1.011	1.399	>0.05
		a priori		Amp *vs.* Sen	2.139	1	2.139	4.251	>0.05	24.288	1	24.288	33.608	<0.001
A. hemigymnus	Amp$_{2010}$, Sen, Sen FF	ANOVA	6	Location	3.861	2	1.931	19.174	<0.05	7.878	2	3.939	1.597	>0.05
				Error	0.302	3	0.101			7.397	3	2.466		
		a priori		Sen *vs.* Sen FF	0.053	1	0.053	0.525	>0.05	1.381	1	1.381	0.560	>0.05
		a priori		Amp *vs.* Sen	3.258	1	3.258	32.359	<0.05	2.624	1	2.624	1.064	>0.05
	1000-4000 m													
POM	Amp$_{2010}$, Amp FF, Sen FF	ANOVA	9	Location	14.539	2	7.269	776.443	<0.001	7.782	2	3.891	2.426	>0.05
				Error	0.037	4	0.009			9.624	6	1.604		
		a priori		Amp *vs.* Amp FF	13.913	1	13.913	1486.017	<0.001	2.086	1	2.086	1.300	>0.05
Exoskeletons	Amp$_{2010}$, Amp FF	*t*	10	Amp *vs.* Amp FF		8	0.442	0.931	>0.05		8	0.069	0.172	>0.05
Amphipoda	Sen, Sen FF	*t*	7	Sen *vs.* Sen FF		5	1.382	2.423	>0.05		5	0.139	0.054	>0.05
M. princeps	Amp$_{2010}$, Sen	*t*	6	Amp *vs.* Sen		4	1.425	1.857	>0.05		4	0.812	1.014	>0.05
Rhincalanus	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	28	Location	13.433	3	4.478	10.816	<0.001	34.550	3	11.517	29.744	<0.001
				Error	9.936	24	0.414			9.293	24	0.387		
		a priori		Amp *vs.* Amp FF	0.086	1	0.086	0.207	>0.05	0.057	1	0.057	0.148	>0.05
		a priori		Sen *vs.* Sen FF	0.116	1	0.116	0.281	>0.05	3.154	1	3.154	8.145	<0.01
		a priori		Amp *vs.* Sen	2.207	1	2.207	5.331	<0.05	2.678	1	2.678	6.917	<0.05
Euchaeta	Sen, Sen FF	*t*	7	Sen *vs.* Sen FF		5	0.557	0.886	>0.05		5	0.336	0.609	>0.05
D. palumbii	Amp$_{2010}$, Amp FF	*t*	12	Amp *vs.* Amp FF		10	0.453	2.852	<0.05		10	0.139	0.524	>0.05
L. maxima	Amp$_{2010}$, Amp FF, Sen, Sen FF	ANOVA	17	Location	6.268	3	2.089	6.617	<0.01	5.602	3	1.867	2.357	>0.05
				Error	4.105	13	0.316			10.301	13	0.792		
		a priori		Amp *vs.* Amp FF	2.247	1	2.247	7.115	<0.05	0.003	1	0.003	0.003	>0.05
		a priori		Sen *vs.* Sen FF	2.261	1	2.261	7.159	<0.05	0.061	1	0.061	0.077	>0.05
		a priori		Amp *vs.* Sen	1.023	1	1.023	3.240	>0.05	1.890	1	1.890	2.385	>0.05
Scyphozoa	Amp$_{2010}$, Sen	*t*	6	Amp *vs.* Sen		4	0.717	2.529	>0.05		4	2.120	2.312	>0.05
Chaetognatha	Amp$_{2010}$, Amp FF	*t*	9	Amp *vs.* Amp FF		7	0.388	1.251	>0.05		7	0.343	0.422	>0.05

See Table 6-A1 for explanations.

Table 6-A3. One-way ANOVA, *post-hoc* Bonferroni test and *t*-test for differences in $\delta^{13}C$ and $\delta^{15}N$ of benthopelagic fishes between locations at Ampère and Senghor seamounts.

					$\delta^{13}C$					$\delta^{15}N$				
Species	**Location**	**Test**	**N**	**Source**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**	**SQ**	**df**	**MQ** or **DM**	**F** or **t**	**p**
	Ampère													
L. caudatus	sum, rim NW	*t*	5	sum *vs.* rim NW		3	0.561	4.878	<0.05		3	0.398	0.897	>0.05
T. picturatus	sum, rim NW, sl NW	ANOVA	13	Location	0.146	2	0.073	0.164	>0.05	1.142	2	0.571	9.077	<0.01
				Error	4.468	10	0.447			0.629	10	0.063		
		post-hoc		sum *vs.* rim NW					>0.05					<0.01
		post-hoc		sum *vs.* sl NW					>0.05					>0.05
		post-hoc		rim NW *vs.* sl NW					>0.05					>0.05
S. colias	sum, rim NW	*t*	11	sum *vs.* rim NW		9	0.493	1.977	>0.05		9	0.574	1.698	>0.05
C. conger	rim NW, sl SE	*t*	6	rim NW *vs.* sl SE		4	0.913	6.265	<0.01		4	0.558	2.678	>0.05
D. calcaeus	sl NW, sl S	*t*	7	sl NW *vs.* sl S		5	0.185	0.941	>0.05		5	0.368	5.957	<0.01
M. moro	sl NW, sl S	*t*	19	sl NW *vs.* sl S		17	0.285	2.725	<0.05		17	0.744	2.924	<0.01
	Senghor													
H. dactylopterus	sum, upper sl NE, mid sl NE	ANOVA	9	Location	4.942	2	2.471	36.625	<0.001	24.440	2	12.220	97.117	<0.001
				Error	0.405	6	0.067			0.755	6	0.126		
		post-hoc		sum *vs.* upper sl NE					<0.01					<0.01
		post-hoc		sum *vs.* mid sl NE					<0.001					<0.001
		post-hoc		upper *vs.* mid sl NE					>0.05					<0.01

sl, slope; sum, summit; see Table 6-A1 for explanations.

The fish fauna of Ampère Seamount (NE Atlantic) and the adjacent abyssal plain

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7.1 Abstract

An inventory of benthic and benthopelagic fishes is presented as a result of two exploratory surveys around Ampère Seamount, between Madeira and the Portuguese mainland, covering water depths from 60 to 4400 m. A total of 239 fishes were collected using different types of sampling gear. Three chondrichthyan species and 31 teleosts in 21 families were identified. The collections showed a vertical zonation with little overlap, but indications for an affinity of species to certain water masses were only vague. Although most of the species present new records for Ampère Seamount, all of them have been known for the NE Atlantic; endemic species were not found. The comparison with fish communities at other NE Atlantic seamounts indicates that despite a high ichthyofaunal similarity, which supports the *stepping stone* hypothesis of species dispersal, some differences can be attributed to the local features of the seamounts.

Keywords: deep-sea; fish distribution; ichthyofauna; seamounts; zoogeography

7.2 Introduction

Due to their vertical range and habitat diversity, seamounts often support high fish diversity, as compared to the surrounding ocean, and some are known as hotspots of endemic species (e.g. Shank

2010; Stocks et al. 2012). Seamounts are considered to act as *stepping stones* for species dispersal (Santos et al. 1995; Almada et al. 2001; Ávila & Malaquias 2003; Xavier & van Soest 2007; Shank 2010), bridging large oceanic areas in particular for shelf and slope dwelling species. Recently, studies of seamount ecosystems have received a great deal of attention by the scientific community, due their role as habitat providers for benthopelagic fishes and important spots for great pelagics (e.g. Clark et al. 2010; Morato et al. 2010). There is ongoing concern that seamount stocks are overfished and fishing is impairing the benthic communities (e.g. Clark 2001; Clark et al. 2006; Clark & Koslow 2007; Clark & Rowden 2009; Clark 2010; Norse et al. 2012).

Little has been known about the ichthyofauna at most NE Atlantic seamounts, in particular in the deeper regions. Although commercial fisheries have targeted many banks and seamounts, detailed scientific studies of the demersal and benthopelagic fish fauna are available only for a few of them. In particular, extensive sampling programmes were conducted at Great Meteor Bank and other seamounts south of the Azores (Maul 1976; Ehrich 1977; Kukuev 2004 and literature cited therein), and at Seine and Sedlo seamounts (Christiansen et al. 2009; Menezes et al. 2009; Menezes et al. 2012). Knowledge of the fish communities at Ampère Seamount is currently based on visual observations by Russian researchers covering the upper and middle slopes, but there is also anecdotal evidence that Ampère Seamount is a fishing ground for commercially valuable species, such as the black scabbardfish *Aphanopus carbo* (Bordalo-Machado et al. 2009) and the silver scabbardfish *Lepidopus caudatus* (pers. observation).

The fish survey at Ampère Seamount reported here was part of a comprehensive, multidisciplinary sampling programme, which also included hydrography, phyto- and zooplankton, benthos, biogeochemistry and sedimentology. The studies aimed at an advanced understanding of the seamount ecology, in comparison with other seamounts in the NE Atlantic and the Eastern Mediterranean, and addressed, for example, the relationships between flow field and plankton distribution, fluxes of organic matter, the trophic structure and the biodiversity of benthic and pelagic seamount communities. First results show that the oligotrophic nature of the sea area around Ampère is reflected in low zooplankton standing stocks, with no indications of an enhanced biomass at the seamount as compared to the surrounding ocean (Denda & Christiansen 2014). The major aim of the fish studies conducted on the P384 cruise of RV Poseidon and the M83/2 cruise of RV Meteor was to characterise the benthopelagic fish community at different depths, using various fishing gears and considering several locations at and around Ampère Seamount; including the summit, the slopes and an abyssal reference station. The results are compared to fish assemblages found at other NE Atlantic seamounts.

7.3 Materials and Methods

7.3.1 Study area

Ampère Seamount is part of the Horseshoe Seamounts Chain and located at 35° N, 013° W between the island of Madeira and the Portuguese southern coast, to the west of the Exclusive Economic Zone of Morocco (Fig. 7-1). Ampère rises from a base depth of ca. 4500 m to 55 m below the surface. It is separated from the neighbouring Coral Patch Seamount by a deep valley of 3400 m depth. The seamount has a conical shape with an elongated base and a small, rough summit plateau at 110-200 m, with a single narrow peak reaching to 55 m (Fig. 7-2). The slopes are steep and rocky with canyon-like structures particularly at the northern, eastern and southern sides (Halbach et al. 1993; Kuhn et al. 1996; Hatzky 2005), but sediment-covered flat areas exist as well. For comparison, a reference station on a flat, sedimentary abyssal plain in 4400 m depth, located ca. 70 nm south of Ampère Seamount at 33° 56’ N, 013° 16’ W, was also sampled (Fig. 7-1).

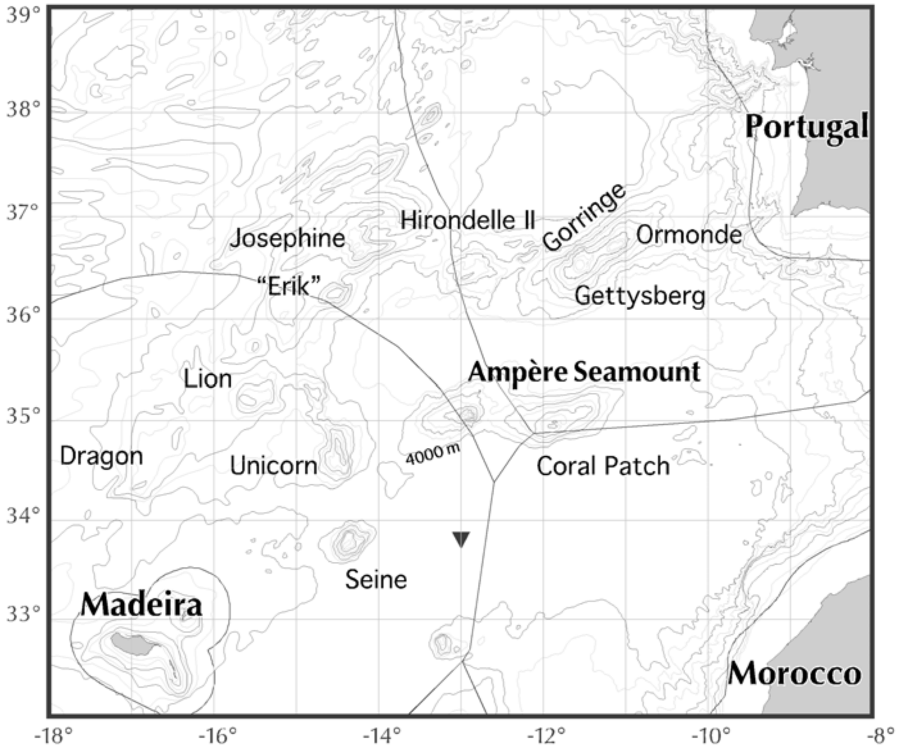

Fig. 7-1. The Horseshoe seamount chain. The location of the reference station south of Ampère Seamount is marked by a triangle. Depth contour interval 500 m. Bathymetric data source: GEBCO (IOC et al. 2003).

7.3.2 Sampling

The inventory of demersal fishes on Ampère Seamount was derived from sampling during the P384 cruise of RV Poseidon in May 2009, and the M83/2 cruise of RV Meteor in November/December 2010, using hooks-and-line, longlines, baited traps, beam trawl and otter trawl. The variety of sampling methods aimed at broadening the collection of fishes caught to several feeding types.

However, the rough and steep terrain of the seamount made benthopelagic trawling in the upper 2000 m extremely risky and led to the damage of the beam trawl during all tows and to the complete loss of one beam trawl. The otter trawl was deployed only below 2000 m. Stationary fishing gear (longlines, hook-and-line, traps) were used down to a maximum depth of 1200 m, except for small traps which were exposed in connection with lander deployments at 1700-2200 m.

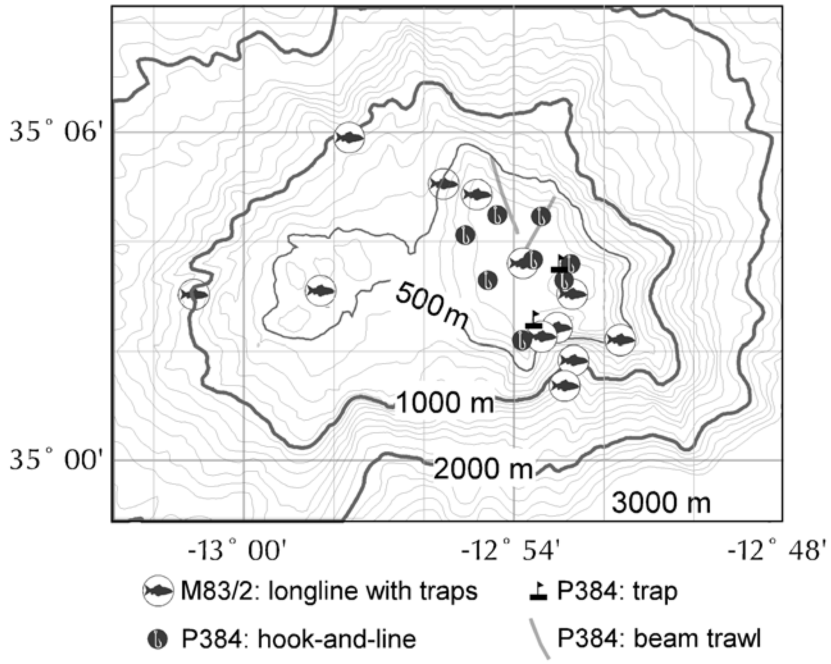

Fig. 7-2. Central area of Ampère Seamount with locations of stationary fishing gear and beam trawl tracks during cruise P384 and M83/2. Credit bathymetric data: J. Hatzky, AWI.

During the P384 cruise, hook-and-line fishing was performed opportunistically in the vicinity of the summit area at depths between 70 and 213 m (Fig. 7-2). Different hooks and various types of bait were used, including commercial fish lures, aluminium foil and pieces of sardines. Fish traps ("Madeira type", Fig. 7-3; Biscoito 1993) were baited with sardines and deployed for several hours, also in the summit area. A 2 m-beam trawl with 6 mm mesh (see Christiansen et al. 2009 for details) was towed twice at 123-133 m depth on the summit plateau (Fig. 7-2); bottom time was 10-15 min each.

During the M83/2 cruise, a total of 12 demersal longline sets were deployed between 60 m and 1200 m depth on the summit and on the upper slopes of the seamount (Fig. 7-2; Table 7-1). The basic design of the longline sets is shown in Fig. 7-4. From the third deployment on, a drift anchor was used instead of the weight at the end of the longline. In haul 7, a different design using 30 m-long branch lines with 10 snoods each was employed, similar to the longline "Type B" used by Menezes et al. (2009). In hauls 8-12, small buoys and weights were alternately attached to the main rope every 10 hooks. A total of 48-83 hooks of different size (straight # 3 and # 6; twisted # 6/0 and # 8/0) per set were baited with mackerels and sardines, and up to 8 traps of different design (Madeira-type fish trap, eel trap, crab trap and flatfish trap; Fig. 7-3) were attached either to the anchor weight or to the end of the main rope. Soak time was usually 5-6 h. Of the 12 longline/trap deployments, one longline was completely entangled and did not fish, and two longlines were lost. The total number of recovered hooks was ca. 500. Small traps made from 1.5 l plastic bottles were also attached to a lander system in four deployments at depths from 1700-2172 m.

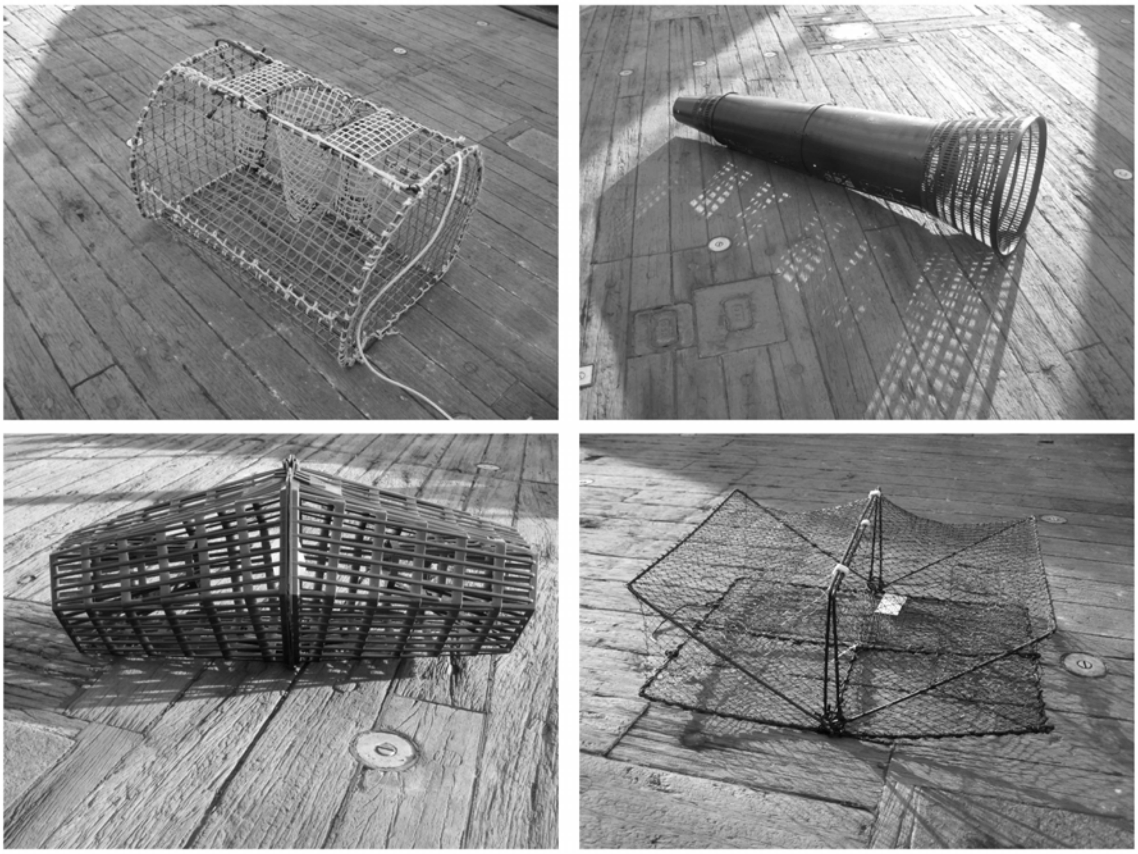

Fig. 7-3. Trap types used during cruises P384 and M83/2. Upper left: “Madeira type” (Biscoito 1993); upper right: “Apollo” eel trap; lower left: crab trap; lower right: flatfish trap.

Table 7-1. Features of the longline deployments during cruise M83/2.

Depl. no	Station no	Depth (m)	Position	No hooks	No traps	Observations
LL1	1094	314	upper slope SE	52	5	
LL2	1095	444	upper slope S	52		entangled, not fishing
LL3	1111	160	rim NW	48	8	
LL4	1112	490	upper slope NW	49	8	
LL5	1183	60	peak	52	7	36 hooks recovered. traps lost
LL6	1184	330	upper slope S			rope snapped
LL7	1195	127	summit plateau	60	2	
LL8	1216	938	middle slope S	83	2	42 hooks recovered
LL9	1228	991	middle slope NW	55	5	
LL10	1257	416	upper slope W	60	3	
LL11	1271	981	middle slope W			lost
LL12	1288	1200	middle slope S	55	2	

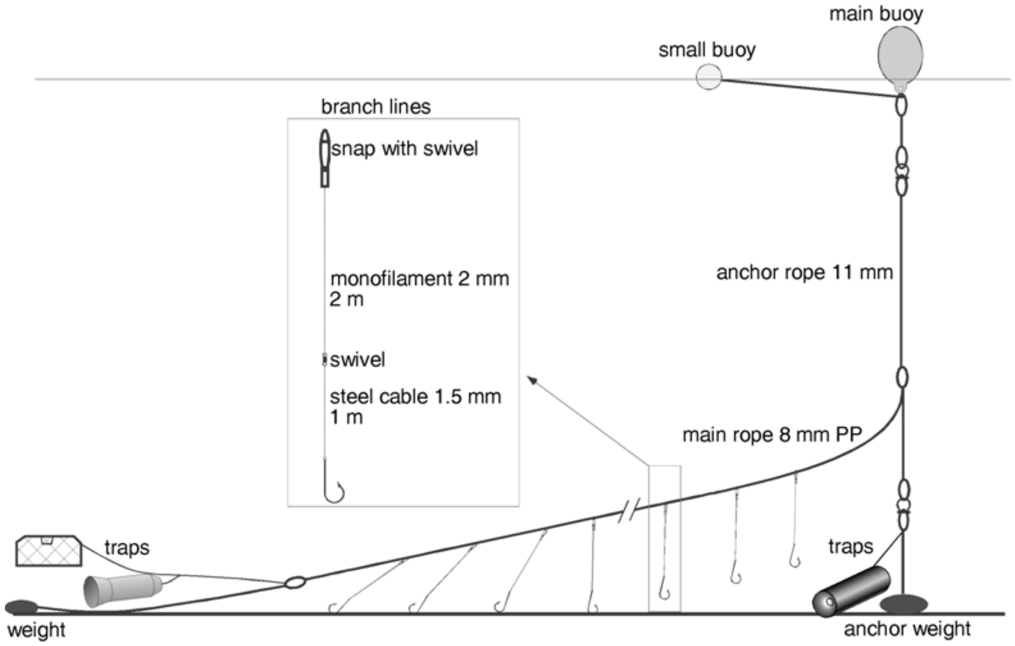

Fig. 7-4. Basic design of the longline used during cruise M83/2.

A 15 m-semiballoon otter trawl was towed on a single warp at 2-3 knots on the western lower slope of the seamount (approximately 2000-2100 m depth, bottom time approximately 30 min), and on the abyssal plain at the reference station south of Ampère Seamount (two hauls, both at 4415 m depth, bottom time approximately 180 and 120 min, respectively). The estimated horizontal net opening of the trawl was 8.6 m; the mesh size was 44 mm in the front part and 37 mm in the intermediate and rear parts, with a 13 mm inner liner in the cod-end.

Immediately after recovery of the catch, specimens were identified to the lowest taxonomic level possible using the keys in Whitehead et al. (1986). Total and standard lengths and weights of all specimens were measured and, where possible, stomachs were dissected and tissue samples taken for later analysis of DNA and isotopic ratios. Fishes from cruise P384 could not be landed due to lack of freezing facilities during transport, whereas all fishes from M83/2 were frozen at -20 °C to be transported to the University of Hamburg. Here, the onboard identifications were checked using a variety of taxonomic keys and descriptions (Sulak 1977; Whitehead et al. 1986; Sulak & Shcherbachev 1997; Nielsen et al. 1999; Franco et al. 2009; Froese and Pauly 2013). Less common species are being finally deposited at the Zoological Museum Hamburg.

7.4 Results

The list of fishes (Table 7-2) collected at Ampère Seamount includes a total of 239 specimens (pelagic bycatch in the otter trawl not included). 34 species belonging to 23 families were identified. Three species were Chondrichthyes and 31 were Actinopterygii. Perciformes (seven species), Anguilliformes and Gadiformes (five species each) were the most speciose orders in the collections.

Table 7-2. Fishes collected at and around Ampère Seamount, arranged according to depth of occurrence.

Species	Order	Family	N	Gear	Min Depth (m)	Max Depth (m)	Size (mm)
Muraena helena	Anguilliformes	Muraenidae	7	LL,T	60	164	940-1100 TL
Lepidopus caudatus	Perciformes	Trichiuridae	13	LL,HL	73	180	790-1380 SL
Serranus atricauda	Perciformes	Serranidae	6	LL,HL	75	213	210-375 SL
Trachurus picturatus	Perciformes	Carangidae	16	LL,HL	106	489	275-375 SL
Coris julis	Perciformes	Labridae	2	T	127	127	125-145 SL
Scomber scombrus	Perciformes	Scombridae	10	LL	127	164	335-415 SL
Scomber colias	Perciformes	Scombridae	11	LL,HL	127	180	310-480 SL
Callanthias ruber	Perciformes	Callanthiidae	2	BT	134	177	60-70 SL
Capros aper	Zeiformes	Caproidae	2	BT	134	177	90-110 SL
Pontinus kuhlii	Scorpaeniformes	Scorpaenidae	9	LL,HL,BT,T	164	170	150-330 SL
Conger conger	Anguilliformes	Congridae	3	LL, T	164	314	735-1305 TL
Helicolenus dactylopterus	Scorpaeniformes	Sebastidae	5	LL,T	314	489	125-275 SL
Malacocephalus laevis	Gadiformes	Macrouridae	1	LL	420	420	250 TL
*Dipturus batis*1)	Rajiformes	Rajidae	1	LL	420	420	580 TL
Zenopsis conchifer	Zeiformes	Zeidae	1	LL	489	489	705 SL
Aphanopus carbo	Perciformes	Trichiuridae	2	LL	938	938	1000-1080 SL
Deania calcea	Squaliformes	Centrophoridae	5	LL	938	992	570-890 TL
Mora moro	Gadiformes	Moridae	37	LL,T	938	1200	300-585 TL
Etmopterus pusillus	Squaliformes	Etmopteridae	2	LL	992	992	395-430 TL
Synaphobranchus kaupii	Anguilliformes	Synaphobranchidae	30	LL,OT,T	992	2050	335-730 TL
Simenchelys parasitica	Anguilliformes	Synaphobranchidae	6	T	1700	1700	n.a.
Bathypterois grallator	Aulopiformes	Ipnopidae	1	OT	2050	2050	295 SL
Halosauropsis macrochir	Notacanthiformes	Halosauridae	3	OT	2050	2050	550-640 TL
Cataetyx laticeps	Ophidiiformes	Bythitidae	1	OT	2050	2050	645 SL
Bajacalifornia megalops	Osmeriformes	Alepocephalidae	1	OT	2050	2050	480 SL
Conocara salmoneum	Osmeriformes	Alepocephalidae	7	OT	2050	4416	250-720 SL
Histiobranchus bathybius	Anguilliformes	Synaphobranchidae	1	OT	4416	4416	1210 SL
Bathypterois sp.	Aulopiformes	Ipnopidae	1	OT	4416	4416	125 TL
Holcomycteronus squamosus	Ophidiiformes	Ophidiidae	1	OT	4416	4416	375 SL
Bathymicrops regis	Aulopiformes	Ipnopidae	6	OT	4416	4419	90-110 SL
Bathypterois longipes	Aulopiformes	Ipnopidae	15	OT	4416	4419	65-195 SL
Coryphaenoides armatus	Gadiformes	Macrouridae	15	OT	4416	4419	660-860 TL
Coryphaenoides profundicolus	Gadiformes	Macrouridae	7	OT	4416	4419	270-410 TL
Coryphaenoides sp.	Gadiformes	Macrouridae	2	OT	4416	4419	540-665 TL
Echinomacrurus mollis	Gadiformes	Macrouridae	2	OT	4416	4419	50-205 TL
Rinoctes nasutus	Osmeriformes	Alepocephalidae	5	OT	4416	4419	125-195 SL

Gear abbreviations: HL, hook-and-line; LL, longline; T, trap; BT, beam trawl; OT, otter trawl. Size abbreviations: SL, standard length; TL, total length.

1) The taxonomic status of *D. batis* is currently under discussion. *D. batis* may actually consist of two nominal species, *D.* cf. *flossada* and *D.* cf. *intermedia* (Iglésias et al. 2010).

The collections showed a vertical zonation with little overlap. The upper depth guild, which included longline, hook-and-line, trap and beam trawl catches from 60-300 m, was most diverse and comprised a total of 11 species belonging to 10 families. The most frequently caught species were the pelagic or benthopelagic horse mackerel *Trachurus picturatus* with 16 specimens, silver scabbard fish *Lepidopus caudatus* with 13 species, and the two mackerel species, *Scomber colias* and *Scomber scombrus* with 11 and 10 specimens, respectively. The scorpionfish *Pontinus kuhlii* (9 specimens), the Mediterranean moray *Muraena helena* (7) and the blacktailed comber *Serranus atricauda* (6) were also relatively abundant in the catches, whereas the other species were rare with only two or three specimens each.The next depth guild from 300 to 500 m was covered by longline and traps. A total of five species were captured in this depth range including *Trachurus picturatus*, which was also caught above 300 m. Apart from the blackbelly rosefish *Helicolenus dactylopterus* with five specimens, only single fishes were caught from each family.

Longlines and traps were also employed between 900 and 1200 m. The predominant species in this depth layer was the common mora *Mora moro* with 37 specimens. Further a few specimens of the black scabbardfish *Aphanopus carbo*, Kaup's arrowhead *Synaphobranchus kaupii*, and two shark species, the birdbeak dogfish *Deania calcea* and the smooth lanternshark *Etmopterus pusillus*, were captured.

Synaphobrancus kaupii, was also caught on the lower slope of the seamount at about 2000 m, where it was the predominant species in the otter trawl catch with 30 individuals, corresponding to nearly 75 % of all specimens. Other families included Alepocephalidae, Bythitidae, Ipnopidae, Ophidiidae and Halosauridae with one species and 1-3 specimens each. The small traps attached to the lander system at 1700 m in two deployments captured six specimens of the Synaphobranchidae *Simenchelys parasitica*.

A total of 11 species were collected in the otter trawl on the abyssal plain at a depth of ca. 4400 m. The most abundant families were Macrouridae with 26 specimens (3 species), Ipnopidae with 22 specimens (3 species) and Alepocephalidae with 12 specimens (2 species). The families Synaphobranchidae and Ophidiidae were caught with one species and one specimen each. The most common species were the abyssal grenadier *Coryphaenoides armatus* and the abyssal spiderfish *Bathypterois longipes*, with 15 specimens each. One species was found in the otter trawl collections from both, 2400 m and 4400 m, the salmon smooth-head *Conocara salmoneum*.

In addition to the benthopelagic species, the otter trawl also collected pelagic species. Only a few particularly rare pelagic species have been analysed in detail so far, such as the first record in the North Atlantic of the cetomimid *Cetichthys indagator* (Vieira et al. 2012) and two large females of the anglerfish *Gigantactis vanhoeffeni*, and one unidentified *Gigantactis* female, which represent, to our best knowledge, the first records of adult *Gigantactis* females in the region (Bertelsen 1986; Swinney 1995; Santos et al. 1997).

7.5 Discussion

Contrary to the relatively well-known fish fauna of seamounts and islands around the Azores and Madeira (Maul 1976; Ehrich 1977; Shcherbachev et al. 1985; Santos et al. 1997; Arkhipov et al. 2004; Kukuev 2004; Menezes et al. 2006; Pakhorukov 2008; Christiansen et al. 2009; Menezes et al. 2009; Menezes et al. 2012), the ichthyofauna of the Horseshoe Seamount Chain (Fig. 7-1) and in particular of Ampère Seamount has been little studied until now. Visual observations were conducted on the summit area of Gorringe Bank (Gonçalves et al. 2004; Abecasis et al. 2009), and on the upper and middle slopes at Ampère Seamount and Josephine Bank; the latter was also trawled (Pakhorukov 2008). Recently, Wienberg et al. (2013) reported some fish species at Coral Patch Seamount from ROV observations above the middle slope.

The results presented here increase the number of fish species described from Ampère seamount substantially. Most of the 34 species collected at and around the seamount in this study are widely distributed in the Atlantic and in the Mediterranean (e.g. Merrett & Marshall 1981; Haedrich & Merrett 1988; Merrett 1992; Menezes et al. 2006; Pakhorukov 2008; Menezes et al. 2009; Menezes et al. 2012; Froese & Pauly 2013). Endemic species were not found. Except for the abyssal fishes *Conocara salmoneum*, *Bathymicrops regis*, *Coryphaenoides profundicolus* and *Echinomacrurus mollis*, all species have also been reported from waters around the Azores (Santos et al. 1997; Menezes et al. 2006; Menezes et al. 2012). Of all species listed here, *Conocara salmoneum* is reported explicitly in Portuguese waters for the first time, but data from Merrett (1992) already suggest its presence in the Madeiran EEZ.

In the 1980s, Soviet investigators surveyed Ampère Seamount together with Josephine Bank and most of the seamounts south of the Azores down to 1200 m depth by a submersible, the so-called underwater inhabited device (UID), and partly also with bottom trawls (Pakhorukov 2008). Table 7-3 lists all fish species at Ampère Seamount reported from Pakhorukov (2008) and the present study. Species are organised according to the main depth of catch/observation in these studies, and include occurrence and depth range at other NE Atlantic seamounts. The resulting inventory comprises a total of 52 identified species of benthic and benthopelagic fishes. From the visual observations at Ampère, Pakhorukov (2008) reports of 24 fish species, complemented by observations of their behaviour and the type of habitat. Only 6 of these species were recovered in this study, but on the other hand an additional 14 species were found between summit and middle slope at 1200 m. On the lower slope and surrounding abyssal plain at 1700, 2050 and 4400 m depth a further 14 species add to the ichthyocoenoses of Ampère Seamount. The little overlap between Pakhorukov's (2008) and the results from this study in the upper layers points to the importance of applying a wide variety of methods in order to assess the ichthyofauna as completely as possible.

The results from this study suggest a clear vertical zonation of the fishes at Ampère; however, part of this can probably be attributed to the rather small sample size and the few discrete sampling depths in our study, particularly in the upper 1200 m. Information which includes depth ranges at other NE Atlantic seamounts shows that many of the same species occur along a wide depth range (Table 7-3), thus making the allocation of single species to vertically discrete assemblages difficult.

Table 7-3. Inventory of fish species recorded at Ampère Seamount from the present study (C) and from Pakhorukov (2008, P), and comparative occurrences and depth ranges at NE Atlantic seamounts (this study; Ehrich 1977; Shcherbachev et al. 1985; Pakhorukov 2008; Abecasis et al. 2009; Christiansen et al. 2009; Menezes et al. 2009).

Species	**Ampère**		**JB**	**GB**	**SS**	**SSAz**	**Depth range (m) at NE Atlantic smts**		**Water mass**
	C	**P**					**Min**	**Max**	
Muraena helena	X			X			60	164	ENACW
Serranus atricauda	X			X			75	213	
Coris julis	X			X			127	127	
Scomber scombrus	X			X			127	164	
Macrorhamphosus scolopax		X	X	X	X	X	50	380	
Anthias anthias		X		X	X	X	50	390	
Antigonia capros		X	X			X	50	620	
Callionymus spp.		X	X			X	100	480	
Trachurus picturatus	X	X	X		X	X	100	500	
Hyperoglyphe sp.		X				X	125	600	
Scomber colias	X		X		X	X	127	330	
Callanthias ruber	X	X	X		X	X	134	345	
Capros aper	X		X	X	X	X	134	620	
Bothidae		X	X	X	X	X	160	340	
Pontinus kuhlii	X				X		160	350	
Zenopsis conchifer	X				X	X	160	489	
Conger conger	X			X	X		160	550	
Raja sp.		X	X	X	X		180	180	
Lophius piscatorius		X					200	450	
Malacocephalus laevis	X	X	X		X	X	420	420	
*Dipturus batis*1)	X						420	420	
Beryx splendens		X			X	X	27	1200	MOW
Polyprion americanus		X			X	X	50	1000	
Lepidopus caudatus	X	X	X		X	X	73	1000	
Helicolenus dactylopterus	X	X	X	X	X	X	180	760	
Hoplostethus mediterraneus		X	X			X	200	1200	
Hymenocephalus gracilis		X				X	260	1200	
Setarches guentheri		X	X			X	300	1140	
Epigonus telescopus		X			X	X	400	900	
Maurolicus amethystinopunctatus		X				X	430	1100	
Deania calcea	X	X	X		X	X	480	1400	
Argyropelecus aculeatus		X				X	500	1000	
Etmopterus pusillus	X				X	X	500	1200	
Mora moro	X		X		X	X	500	1300	
Aphanopus carbo	X			X	X	X	500	1600	
Ruvettus pretiosus		X					760	900	
Alepocephalus bairdi		X				X	980	1200	
Synaphobranchus kaupii	X				X		550	2050	bathyal NADW
Simenchelys parasitica	X				X		1700	1700	
Bajacalifornia megalops	X						2050	2050	
Cataetyx laticeps	X						2050	2050	
Halosauropsis macrochir	X						2050	2050	
Bathypterois grallator	X						2050	2050	
Conocara salmoneum	X						2050	4416	abyssal NADW/ANBW
Holcomycteronus squamosus	X						4416	4416	
Histiobranchus bathybius	X						4416	4416	
Bathymicrops regis	X					X	4300	4419	
Bathypterois longipes	X					X	4300	4419	
Rinoctes nasutus	X						4416	4419	
Coryphaenoides armatus	X						4416	4419	
Coryphaenoide profundicolus	X						4416	4419	
Echinomacrurus mollis	X						4416	4419	

JB, Josephine Bank; GB, Gorringe Bank; SS, Seine Seamount; SSAz, seamounts south of the Azores

1) See remark in Table 7-2.

Menezes et al. (2006; 2009 and literature quoted therein) identified vertically structured fish assemblages around the Azores archipelago and at Seine Seamount and related them to the water mass properties in the areas. During the Meteor cruise in December 2010 (Christiansen et al. 2012), Eastern North Atlantic central water (ENACW; 10-20 °C, 35.2-36.7 °C) characterized the upper 500 m below a 50-80 m thick, warm mixed layer. Between 600-1300 m depth Mediterranean outflow water (MOW; 13 °C, 38.4 PSU) was found, and underneath a mixing zone from 1400 to 2000 m, North Atlantic deep water (NADW; 1.5-4 °C, 34.8-35 PSU) and probably Antarctic bottom water (ANBW) formed the water layers in the lower bathyal and abyssal zones (Fig. 7-5).

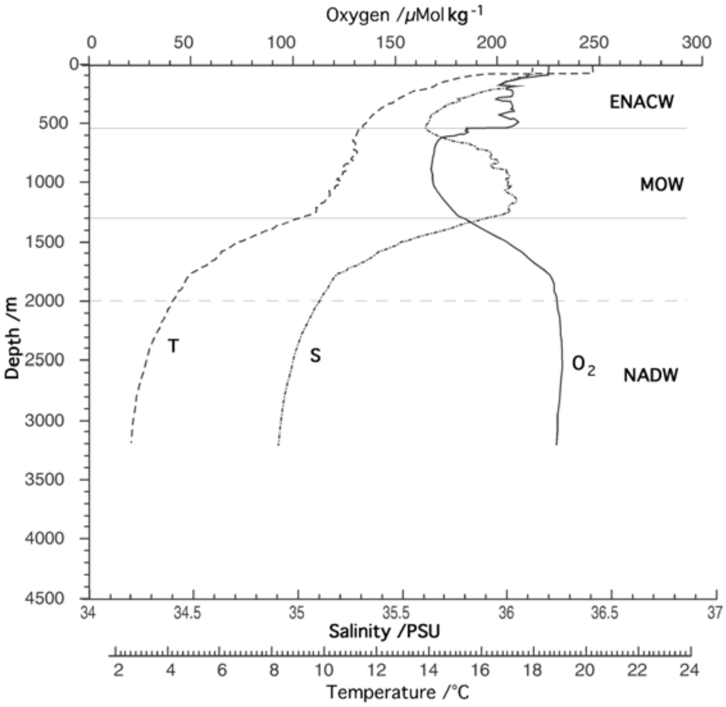

Fig. 7-5. Profiles of temperature, salinity and oxygen concentration at the southern slope of Ampère Seamount.

Both the summit and upper slope regions of Ampère Seamount down to about 600 m are under influence of the Eastern Atlantic central water/ Azores current. The benthic and benthopelagic fish communities in this depth stratum comprise 35 species (Table 7-3). Among this shallow fish community, 21 fish species seem to occur exclusively in this depth range, with four species being confined to the summit area down to 200 m. The remaining 14 species, including commercially exploited fish like alfonsino *Beryx splendens* Lowe, silver scabbardfish *Lepidopus caudatus*, and silver roughy *Hoplostethus mediterraneus*, have also been found deeper in the Mediterranean Outflow water between 600 and 1300 m. Only two species, *Ruvettus pretiosus* and *Alepocephalus bairdii*, seem to be restricted to this water mass of Mediterranean origin; however, this is based on only a small number of observations and should be judged with some caution. Generally, indications for an affinity of species to certain water masses are vague. Most of the fishes on the upper and middle slope of Ampère Seamount occur in a wide range of temperatures, salinities and oxygen concentrations.

The majority of the shallower species at Ampère were found in common with Gorringe Bank on the northern arc of the Horseshoes seamounts: *Conger conger*, *Muraena helena*, *Capros aper*, *Coris julis*, *Serranus atricauda*. However, *Pontinus kuhlii* (also observed at Seine and Great Meteor, Ehrich 1977; Christiansen et al. 2009; Menezes et al. 2009) and the widely distributed *Lepidopus caudatus*, which has been known from other NE Atlantic seamounts like the neighbouring Seine and Josephine and the more southern Great Meteor, Atlantis, Flamingo and Hyères (Ehrich 1977; Pakhorukov 2008; Menezes et al. 2009), were not observed at Gorringe (Abecasis et al. 2009), see Table 7-3. On the other hand, several species common at Gorringe were not found at Ampère, most of them being littoral fishes like Blenniidae or Labridae. However, the survey at Gorringe employed visual observations from divers and covered only the peaks at depths from 29-50 m, so the different methodologies involved do not allow for a comprehensive comparison of the fish communities between these seamounts, and *Lepidopus caudatus*, for example, has been known from commercial catches in the Gorringe area.

The upper and mid-slope collections included species that are usually found at the continental and island slopes, and, with the exception of the blue skate *Dipturus batis* (taxonomic status of this species is under discussion, see Iglésias et al. 2010), have been reported also from other seamounts in the NE Atlantic (Table 7-3). In particular, *Helicolenus dactylopterus*, *Aphanopus carbo*, *Mora moro* and *Deania calcea* have been observed at several seamounts in the Horseshoe region and to the north and south of the Azores (Pakhorukov 2008; Abecasis et al. 2009; Menezes et al. 2009). *Synaphobranchus kaupii* were also observed at Seine and Sedlo seamounts (Menezes et al. 2009), but not at other Horseshoe seamounts or at seamounts south of the Azores, which is probably due to the limited depth range of the samples there, since Almeida & Biscoito (2007) reported their presence at the Lucky Strike vent field on the mid-Atlantic Ridge south of the Azores

Due to the depth limitation to 1200 m in the observations of Pakhorukov (2008), the ichthyocoenoses found in this study on the lower slope of Ampère (1700 and <2000 m depth) and on the adjacent deep-sea abyssal plain (4400 m) supplement the species described from the regional seamounts substantially. With the exception of *Catetyx laticeps*, which is restricted to the Atlantic and Mediterranean, all of the fishes caught on the lower slope are species with a circumglobal distribution (Froese & Pauly 2013). They are usually found at bathyal depths, often with a wide depth range. However, no overlap was observed with the upper/mid slope species, except for the predominating species on the lower slope of Ampère, *Synaphobranchus kaupii*, which has been reported, for example, from Porcupine Seabight at depths from 230 to 2420 m (Merrett et al. 1991).

The Alepocephalidae *Conocara salmoneum* was the only species present on both the lower slope and the abyssal plain adjacent to Ampère Seamount. The fishes found here are typical abyssal species belonging to the northern and intermediate deep-sea fish assemblages as proposed for the NE Atlantic by Merrett (1992). Only the Ophidiidae *Holcomycteronus squamosus* was not included in those assemblages, but it is a particularly rare species known from a few scattered locations in the North Atlantic, with a certainly incomplete distribution record.

Despite the general similarities of the ichthyofaunal assemblages of the Northeast Atlantic seamounts, the comparisons also show some differences. These can partly be attributed to differing methodologies, as already indicated above, and to sampling effort. For example, the higher number of species collected with longlines by Menezes et al. (2009) at Seine Seamount is most probably due to the much higher fishing effort (>14000 hooks at Seine Seamount, as compared to ca. 500 recovered hooks at Ampère), and to the deeper-reaching sets (max. 2000 m *vs*. 1200 m). On the other hand, despite the differences in sampling effort, seven of the 20 species captured down to 1200 m at Ampère Seamount in this study had not been collected at Seine (all gears considered). Apart from possible dissimilarities in gear selectivity, true differences between the two seamounts like summit depth, topography, substrate or coral cover may play a role. For example, most of the species missing at Seine, including *Muraena helena*, *Serranus atricauda*, *Coris julis* and *Capros aper*, were captured at depths shallower than the Seine summit plateau. Furthermore, the much more rugged topography with basaltic outcrops of the Ampère summit area, as compared to the flat, sedimentary summit plateau of Seine, may provide suitable habitat for species, such as the moray eel *M. helena*, which depend on or prefer richly structured, rocky substrate (e.g. Bauchot 1986).

The relatively similar inventory of shelf and slope fish species in the summit and upper slope regions of the seamounts of the Horseshoe Chain and of the seamounts around the Azores supports the hypothesis of these topographic features being *stepping stones* for species dispersal within the larger NE Atlantic region, possibly powered by the large-scale current system (Azores current, Canary current) and westward propagating meddies. This may also apply to the benthopelagic deep-water fishes found at the seamount slopes, which are also dependent on suitable substrate at appropriate depths. However, a higher sampling effort and the use of genetic tools will be necessary to evaluate the biogeographic significance of Ampère Seamount and to assess the biogeographic links between the NE Atlantic seamounts.

This effort will also be important for designing conservation and management measures in order to mitigate eventually unsustainable impacts of fishing activities on the commercially targeted species such as several species found at Ampère, which are important in the southern Portuguese longline fisheries (Borges 2007), like *Lepidopus caudatus*, *Aphanopus carbo*, *Mora moro*, *Helicolenus dactylopterus* and *Pontinus kuhlii*, and, usually restricted to coastal areas, *Conger conger* and *Muraena helena*.

In conclusion, the data show, despite the comparatively low sampling effort, that Ampère Seamount hosts a rich and diverse fish community. Generally, the seamounts in the subtropical NE Atlantic appear to be very similar with respect to their ichthyofauna. However, the differences, for example between the adjacent and relatively well-sampled Ampère and Seine seamounts, point to the role of properties like substrate type and habitat complexity in shaping the final expression of community composition.

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Demersal fishes from Senghor Seamount and the adjacent abyssal plain (Central Eastern Atlantic)

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8.1 Abstract

Senghor Seamount is an important fishing ground around the Cape Verde archipelago in the Eastern central Atlantic. On an experimental field survey in September/October 2009 and December 2011 a total of 106 deep-sea fishes of 28 species belonging to 18 families were caught on the seamount summit, along the slopes and on the adjacent abyssal plane, using longlines, fish traps, beam trawl and otter trawl. We report 6 new records for the Cape Verde deep-sea fish fauna. Most species have been known from other areas of the Atlantic ocean, but these findings are an important contribution to our understanding of the distribution of deep-water fish species. The co-occurrence of northern and southern fish species at Senghor Seamount or the Cape Verde area in general, can be attributed to the large scale hydrographic regimes of different surface production merging at the Cape Verde frontal zone.

Keywords: deep-sea; ichthyofauna; seamounts; zoogeography

8.2 Introduction

Seamounts are underwater mountains, globally distributed in the ocean basins (Wessel et al. 2010), often showing high diversity as compared to the surrounding abyssal plain (Shank 2010; Stocks et al. 2012). Seamounts are also known to provide habitat and foraging ground for several demersal fish species and some studies exist which characterise the ichthyofauna in distinct regions of the NE

Atlantic (e.g. Haedrich & Merrett 1988; Merrett et al. 1991; Merrett 1992; Menezes et al. 2009; Christiansen et al. 2015), and particularly in the NW African region (Vakily et al. 2002). However, the distribution patterns and biology of the majority of the deep-sea fish species are still largely unknown.

Oceanographic research off the Cape Verde islands began in the mid-XIX century and the effort to study the wildlife of the archipelago is held until today. Some of the original work on marine fishes from Cape Verde was conducted by Franca & Vasconcelos (1962) and Lloris et al. (1991). Reiner (1996, 2005) reviewed the ichthyofauna of the Cape Verde Islands, while Monteiro et al. (2008), González et al. (2010, 2014), Brito et al. (2006), and Almeida et al. (2010) added new information on the marine fish communities of the archipelago. A compilation of data on coastal fish species, complementing the knowledge on the ichthyofauna from the Cape Verde archipelago with zoogeographic remarks, was given by Wirtz et al. (2013), Freitas (2014) and Hanel & John (2014), but information on deep-sea species remain scarce. Official data about the type and effort of fishing exerted on the Cape Verde offshore seamounts are scarce. The artisanal fleets contribute to most captures in the region (D´Oliveira Fonseca 2000; Benchimol et al. 2009), but are limited to the near-shore areas. However, the extent of the impact caused by industrial fisheries, in particular if international fishing vessels are included, is probably underestimated (MAAP/GEP 2004; Benchimol et al. 2009). Taking this into account, it is important to evaluate the deep-sea resources in order to characterize the role and conservation status of the seamounts around the Cape Verde archipelago.

Senghor Seamount, locally known as Nova Holanda Bank, is an important fishing area for the regional longline fishery and also supporting a small scale crab and lobster fishery (MAAP/GEP, 2004). Recent ROV surveys revealed that Senghor Seamount features various habitats for benthopelagic and benthic fishes, including soft bottom and hard substrate with rich coral cover (Christiansen & Koppelmann 2011). Benthopelagic fishing surveys off the Cape Verde archipelago were conducted during the 1980s and 1990s to investigate stock sizes of commercially important species along the islands' shelves and the adjacent seamounts (e.g. Magnússon & Magnússon 1985, 1987; Pálsson 1989; Thorsteisson et al. 1995). More recently, Menezes et al. (2004) investigated the demersal fish communities from Senghor Seamount, but provided very limited data on deeper reaching species. A valuable insight was given by Hanel et al. (2010) on the larval fish communities from Senghor, which were dominated by lanternfishes (Myctophidae). Hanel et al. (2010) anticipated an evident seamount effect related to the topographic features and oceanographic conditions in the region. However, Denda & Christiansen (2014) did not detect any current-topography related effect on the distribution and concentration of mesozooplankton as potential prey for seamount associated fishes at Senghor during the present study. No evidence was given for enhanced food availability, expressed by high concentrations of zooplankton biomass, at the seamount as compared to the surrounding ocean. Trophic analyses indicate that fish and benthic organisms were of major importance in the diets of seamount residents, rather than planktonic prey (Denda unpubl. data; Manuscript 3). Since Senghor provides special habitats for benthic organisms and hosts diverse and abundant communities of corals, hydroids, sponges, echinoderms, crustaceans and polychaetes (Christiansen & Koppelmann 2011; Chivers et al. 2013), the seamount is supposed to be an attractive location of enhanced food supply in the open ocean, at least of benthic organisms, for usually dispersed fish stocks as well as for typical shelf species.

Demersal fishes were sampled around Senghor Seamount at different depths above the summit plateau, the slopes and on the adjacent abyssal plain in the framework of a multidisciplinary study on seamount ecology. The main objective of the ichthyological surveys during the expeditions was to extend the knowledge of the deep-water biodiversity of the Cape Verde fish fauna.

8.3 Materials and Methods

8.3.1 Study site

Senghor Seamount is an isolated seamount located at 17° 12’ N, 021° 57’ W ca. 60 nm northeast of the island of Sal, Cape Verde (Fig. 8-1), within the sphere of the NE Atlantic tropical gyre (e.g. Mittelstaedt 1991; Lathuilière et al. 2008). The hydrographic regime is characterised by the North Equatorial Current system and seasonally by Mauritanian upwelling filaments (Mason et al. 2011), but also by northward flowing South Atlantic central water, merging at the Cape Verde frontal zone (CVFZ; e.g. Zenk et al. 1991). Senghor Seamount has a nearly circular shape with a base diameter of ca. 40 km, steep slopes and a small elliptical summit plateau, which is about 2.5 km wide and 5 km long. Water depth at the base of the seamount is about 3300 m; the minimum summit depth is 90 m. Video footage from the summit and upper slopes shows that the substrate structure varies between sediment covered areas and rocky outcrops (Christiansen & Koppelmann 2011). The flat sedimentary reference station was located ca. 60 nm north of Senghor Seamount at 18° 05’ N, 022° 00’ W with water depth about 3300 m, corresponding to the base depth of the seamount.

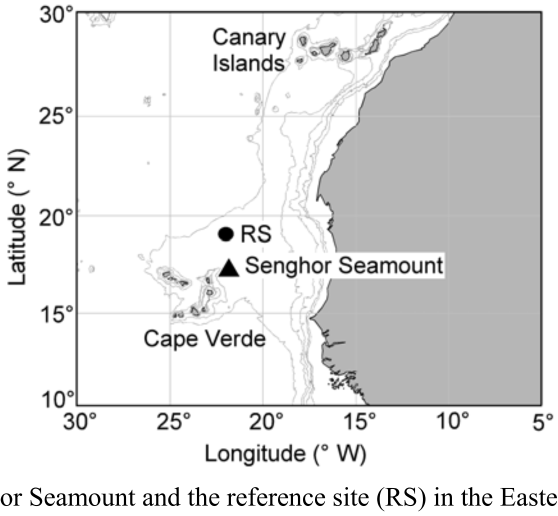

Fig. 8-1. Locations of Senghor Seamount and the reference site (RS) in the Eastern Atlantic.

8.3.2 Sampling

During the cruises M79/3 of RV Meteor in September/October 2009 and P423 of RV Poseidon in December 2011, fishes were sampled at distinct depths on the summit plateau and along the slopes of Senghor Seamount and on the adjacent abyssal plain (Fig. 8-2; Table 8-1). Depending on the area, different types of fishing gears were employed: demersal longline, fish traps, beam trawl and otter trawl, aiming primarily at demersal fishes, but pelagic species were collected as well during deployment and retrieving of the gear.

The longline sets were used on the summit and on the upper slopes of the seamount at several depths, ranging from 96 m to 758 m. A total of 100 hooks of different shape and size were attached to the main line by gangions approximately 60 cm in length and separated by approximately 2.5 m. The hooks were baited with squid. On seven of the longline sets a fish trap baited with squid was also deployed at the end of the longline, where the main anchor rope was attached.

The beam trawl (2 m beam length) was used to sample demersal fishes on the seamount summit at 103 m and on the upper slope at 260 m depth. The trawl was equipped with a 6 mm mesh net. The otter trawl (headrope length 15 m, mesh size 44 mm in the front part, 37 mm in the intermediate part and 13 mm inner liner in the cod-end) was used in deep waters at the reference station, at depths similar to those at the base of the seamount (ca. 3300 m).

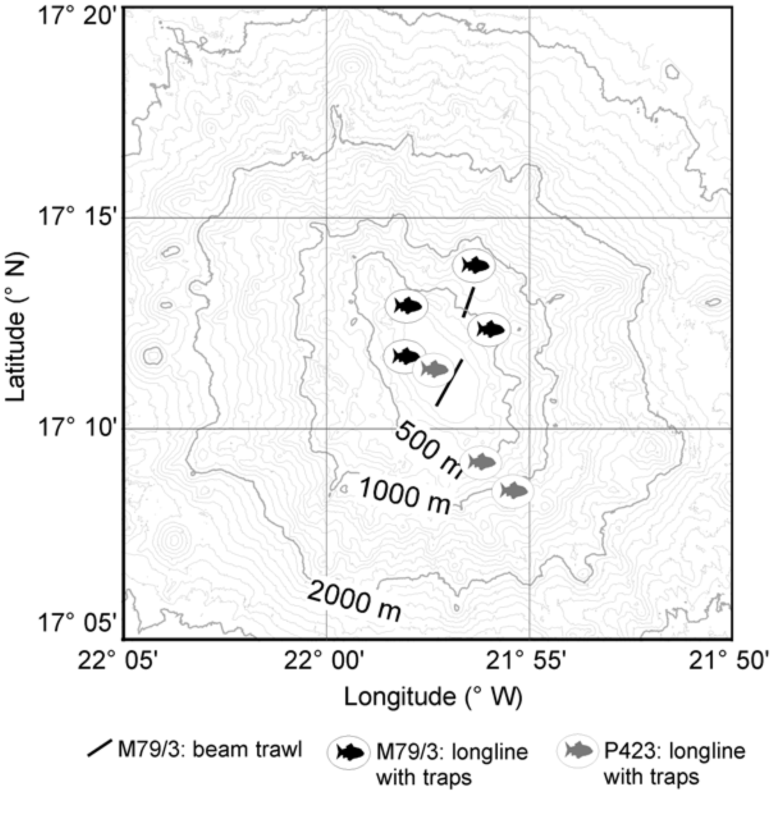

Fig. 8-2. Bathymetry and locations of beam trawl and longline deployments at Senghor Seamount on cruise M79/3 in September/October 2009 and P423 in December 2011.

Table 8-1. Trawl and longline deployments during expeditions M79/3 in September/October 2009 and P423 in December 2011 to Senghor Seamount. Gear abbreviations: BT, beam trawl; OT, otter trawl; LL, longline; LLT, longline with traps.

Station			Position		Water	
no	Gear	Date	Lat N	Long W	depth (m)	Location
M79/3		**2009**				
820	OT	30.09.	18° 01.70’	22° 04.27’	3310	abyssal plain
838	OT	02.10.	18° 05.50’	21° 57.99’	3299	abyssal plain
863	BT	04.10.	17° 11.05'	21° 56.90'	103	summit
976	BT	12.10.	17° 12.99’	21° 56.04	389	upper slope NE
876	LL	05.10.	17° 11.42’	21° 57.84’	116	summit
886	LLT	06.10.	17° 13.04'	21° 58.13'	350	upper slope N
926	LLT	09.10.	17° 12.62'	21° 56.13'	529	upper slope NE
961	LLT	11.10.	17° 13.77'	21° 56.45'	715	mid slope NE
1004	LLT	15.10.	17° 13.84'	21° 56.63'	739	upper slope NE
P423		**2011**				
743	LLT	13.12.	17° 11.52'	21° 57.19'	101	summit
755	LLT	14.12.	17° 09.42’	21° 56.16'	439	upper slope S
770	LLT	15.12.	17° 08.83’	21° 55.30'	986	mid slope SE

Immediately after recovery of the catch, all fishes were measured for total (TL) and standard length (SL) and weight (W; ± 1 mm and ± 1 g, respectively). Stomachs and gonads of selected species were dissected and tissue samples were taken for further DNA and stable isotope analyses. Fishes from cruise P423 could not be landed due to the lack of freezing facilities during transport, whereas all fishes from M79/3 were frozen at -20 °C to be transported to the University of Hamburg. Here, the onboard identifications were checked and specimens were identified to the lowest possible taxon following Whitehead et al. (1986) and Reiner (1996, 2005).

8.4 Results

We provide a list of 106 demersal fishes belonging to 28 species (excluding unidentified) in 18 families (Table 8-2). Two species in two families were Chondrichthyes, all others were Teleostei, Actinopterygii. Several pelagic fishes (44 specimens) were caught in the otter trawl during its descent or ascent through the water column, including members of families Nemichthyidae (1 species), Melanocetidae (1 species), Myctophidae (3 species), Melamphaidae (2 species), Phosichthyidae (1 species), Sternoptychidae (5 species and 2 unidentified) and Stomiidae (5 species and several unidentified specimens). These small mid-water fishes were not included in the list presented here. The most species-rich families were the Ophidiidae (N = 5), Ipnopidae (N = 3), and Macrouridae (N = 3), all caught in the otter trawl at 3300 m depth (Table 8-2). The most common species at bathyal depths were the grenadier *Coryphaenoides armatus* and the slimehead *Bathytroctes macrolepis*, with 15 and 13 individuals, respectively. Nine large adult females of *C. armatus* were caught having large ovaries containing ripening oocytes.

Top predator species collected in the longline sets included the elasmobranchs smooth lanternshark *Etmopterus pusillus*, sharpnose sevengill shark *Heptranchias perlo,* and bony fishes, such as the escolar *Promethichthys prometheus*. Some commercially important species were captured on the summit and slopes with the longlines, including the splendid alfonsino *Beryx splendens*, and the blackbelly rosefish *Helicolenus dactylopterus*. *H. dactylopterus* collected on the summit were much smaller in size (8.4-13.2 cm TL; 10-25 g TW) than the ones caught on the slopes (38.7-44.2 cm TL; 960-1390 g TW).

Table 8-2. List of fishes sampled at Senghor Seamount and the adjacent abyssal plain. N, number of individuals; TL, total length; SL, standard length; unid., unidentified; n.d., no data. Gear abbreviations: LL, longline; T, trap; BT, beam trawl; OT, otter trawl. Site abbreviations: sum, summit; up sl, upper slope; ab pl, abyssal plain.

Species	N	Gear	Site	Water depth (m)	TL (cm)	Remarks
ACTINOPTERYGII						
Anguilliformes						
Muraenidae						
Muraena helena	2	T	sum	195	n.d.	
Myrocongridae						
Myroconger compressus	2	T	up sl	356	34.0-47.5	These specimens were markedly smaller than those captured by Menezes et al. (2004), representing the northernmost record in the eastern Atlantic and the first occurrence associated with offshore seamounts.
Synaphobranchidae						Both species are ubiquitous in deep waters of the Atlantic and Indo-Pacific. *S. kaupii* has also been found at Seine, Sedlo and Ampère seamounts in the NE Atlantic (Menezes et al. 2009; Christiansen et al. 2015).
Ilyophis cf. *brunneus*	1	OT	ab pl	3285	44.5	
Synaphobranchus kaupii	4	T	up sl	530	15.5-27.1	
unid. Synaphobranchidae	7	LL	up sl	234	45.0-62.5	
Aulopiformes						
Ipnopidae						
Bathypterois grallator	2	OT	ab pl	3285	12.0-14.5	This species from the otter trawl hauls at the reference station has been known from scattered records along the Atlantic Ocean and Mediterranean Sea, but also in the Pacific Ocean (Franco et al. 2009). It has been found also on the lower slope of Ampère Seamount (Christiansen et al. 2015).
Bathypterois longipes	1	OT	ab pl	3285	22.5	This is a deep-sea species known from several locations in the NE Atlantic (Merrett & Marshall 1981), including seamounts south of the Azores (Shcherbachev et al. 1985) and in the vicinity of Ampère Seamount (Christiansen et al. 2015).
Ipnops cf. *murrayi*	6	OT	ab pl	3285-3300	14.8-17.0	The six specimens from the abyssal plain station represent the first records in the Cape Verde area, but are known from NW Africa (Merrett & Marshall 1981), Western and Southern Atlantic Ocean (Nielsen 1966). It is a rarely caught species.
Beryciformes						
Berycidae						
Beryx splendens	3	LL	up sl	530	38.3	The species is frequently found at seamounts and on the continental slopes (Paxton, 1999). Records for NE Atlantic seamounts include Seine and Sedlo seamounts (Menezes et al. 2009), Ampère Seamount and seamounts south of the Azores (Pakhorukov 2008). It is an important target for commercial fishery.
Gadiformes						
Macrouridae						
Coelorhynchus sp.	10	OT	ab pl	3300	11.0-28.5	
Coryphaenoides armatus	15	OT	ab pl	3285-3300	54.5-83.0	The species is ubiquitous in the world oceans, but the specimens caught north of Senghor Seamount include 9 females with ripening ovaries, representing a rare record for this species.

Coryphaenoides profundicolus	1	OT	ab pl	3285	99.8	This represents the southernmost record of this species and the first in Cape Verde waters. The species has been known to occur along the western African margin north of 20° N (Merrett & Marshall 1981) and in the temperate North Atlantic (Haedrich & Merrett 1988)
Coryphaenoides sp.	1	OT	ab pl	3285	59.3	
unid. Macrouridae	12	OT	ab pl	3285-3300	11.5-36.8	
Perciformes						
Caproidae						
Antigonia capros	1	BT	sum	100	20.5	This is the first record for Senghor Seamount, but the species has been caught in the Cape Verde area at several stations close to the islands before (Strømme et al. 1982). The species was common on the Great Meteor Bank and other seamounts south of the Azores (Ehrich 1977; Pakhorukov 2008), at Ampère and Josephine in the Horseshoe seamount chain (Pakhorukov 2008), but has not been reported from the NE Atlantic seamounts Seine, Sedlo and Gorringe (Abecasis et al. 2009; Menezes et al. 2009; Menezes et al. 2012).
Caristiidae						
Paracaristius sp.	1	OT	ab pl	n.d.	20.3	Only one specimen was collected in the otter trawl as pelagic bycatch. It is a rare bathypelagic genus. Two species of the family Caristiidae (*Paracaristius nemorosus* and *Platyberyx opalescens*) were reported to occur in the Cape Verde Region (Trunov et al. 2006; Stevenson & Kenaley 2011; Kukuev et al. 2012).
Chiasmodontidae						
Kali macrodon	1	OT	ab pl	n.d.	16.5	One specimen was collected in the otter trawl as pelagic bycatch. It represents the first occurrence in the Cape Verde region, the fifth specimen in the northeastern part of the Atlantic and the third specimen ever caught in tropical waters (Vieira et al. 2013).
Gempylidae						
Promethichthys prometheus	4	LL	up sl	530	57.5-62.0	Two with heads only. This species is found at continental slopes, around oceanic islands and submarine rises in tropical and warm temperate waters of all oceans (Nakamura & Parin 1993). It has not been reported from the more northern Eastern Atlantic seamounts, Seine, Sedlo, Ampère and Great Meteor (Pakhorukov 2008; Christiansen et al. 2009; Menezes et al. 2009; Menezes et al. 2012).
Ophidiiformes						
Aphyonidae						
Barathronus cf. *parfaiti*	1	OT	ab pl	3300	10.5	This specimen is the first record in Cape Verde, and the second in tropical waters. It is an extremely rare species (Nielsen et al. 1999) with only three records previously reported from west of the Azores, off the Bay of Biscay (Nielsen 1969), and west of Cape Blanc (Merrett & Marshall 1981).
Ophidiidae						
Acanthonus armatus	3	OT	ab pl	3285	31.2-32.5	Common species in tropical deepwaters of all oceans (Froese & Pauly 2015). First registered record in Cape Verde waters.
Bassozetus cf. *oncerocephalus*	1	OT	ab pl	3285	67.5	One unidentified *Bassozetus* has been reported by Merrett & Marshall (1981) from off W Africa at 21° N.
Brotulotaenia sp.	1	LL	up sl	234	75.0	
cf. *Holcomycteronus squamosus*	1	OT	ab pl	3300	64.0	
H. squamosus	1	OT	ab pl	3300	68.0	The specimen represents the first record in Cape Verde waters. It is a rare species with a few reports from scattered locations in the North Atlantic and off Angola (Froese & Pauly 2015). One unidentified *Holcomycteronus* has been reported by Merrett & Marshall (1981) from off W Africa at 21° N.

Porogadus sp.	3	OT	ab pl	3300	12.5-26.0	Probably *P. subarmatus*, but deeper taxonomic examination is needed. *P. subarmatus* is a very rare species. The type specimen was caught off Cape Verde (Nielsen et al. 1999; Froese & Pauly 2015). However, the *Porogadus* sp. reported in Merrett & Marshall (1981) from several locations off West Africa north of 17° N probably belong to this species as well. Another *Porogadus* species occurring in the area is *P. nudus* (Nielsen et al. 1999).
Osmeriformes						
Alepocephalidae						
Bathytroctes macrolepis	13	OT	ab pl	3285-3300	14.0-36.5	Merrett & Marshall (1981) reported the occurrence of several specimens along the W African margin. The species is known to occur in several locations in the North Atlantic (Haedrich & Merrett 1988; Santos et al. 1997) but also in the Pacific and Indian Ocean (Froese & Pauly 2015).
Platytroctidae						
Maulisia microlepis	1	OT	ab pl	3285	11.0	This species has mainly been collected in the eastern part of the Atlantic at locations northern than 40° N, but scattered reports exist also from the western African margin (Whitehead et al. 1986; Froese & Pauly 2015).
Notacanthiformes						
Halosauridae						
Aldrovandia affinis	1	OT	ab pl	3300	59.0	This is the first record in Cape Verde. The species shows a circumglobal distribution and it is common along the slopes of the West African margin north of 24° N (Merrett & Marshall 1981; Haedrich & Merrett 1988). This is also the largest specimen ever caught (Froese & Pauly 2015).
Scorpaeniformes						
Sebastidae						
Helicolenus dactylopterus	3	BT	sum	100	8.4-13.2	
	2	LL	up sl	356	38.7-40.0	
	1	LL	mid sl	735	44.2	
CHONDRICHTHYES						
Squaliformes						
Etmopteridae						
Etmopterus pusillus	2	LL	up sl	530	24.0-29.3	SL
Hexanchiformes						
Hexanchidae						
Heptranchias perlo	1	LL	up sl	356	65.0	SL

8.5 Discussion

The knowledge of the deep-sea fish communities below 1200 m around the Cape Verde archipelago is very limited. Merrett & Marshall (1981) studied the abyssal fish assemblages off NW Africa, but, with a few exceptions, their surveys were limited to locations east of 20° W, and most of their fishing effort focused on the area north of 20° N. Specific data for the deep waters off the Cape Verde archipelago are not available. The ichthyofauna of Senghor Seamount and of several other locations in the Cape Verde area was documented in particular through the longline survey of Menezes et al. (2004), covering a depth range from a few meters below the surface to 1200 m depth and showing a vertical zonation of species with affinities to certain water masses (Menezes et al. 2015), as also observed at other seamounts of the North Atlantic ocean (Bergstad et al. 2012; Christiansen et al. 2015).

The co-occurrence of northern and southern ichthyofaunal elements at Senghor Seamount, or the Cape Verde area in general, can be attributed to the large scale hydrographic regime with two water masses merging at the CVFZ, the North Atlantic central water (NACW) and the South Atlantic central water (SACW; e.g. Pérez-Rodríguez et al. 2001). The water mass distribution indicates that Senghor Seamount and the reference site, lie within the so called ‘shadow zone’, south of the CVFZ (see Tomczak 1981; Zenk et al. 1991; Pierre et al. 1994). At both sampling sites temperature and salinity were characteristic for SACW (9.7-15.2 °C; 35.2-35.7 PSU) between 150 and 600 m, lying below a warm mixed surface layer of about 30 m depth followed by a thermocline (Fig. 8-3; see also Denda & Christiansen 2014). Between 700 and 1200 m an intermediate layer of minimum salinity (34.92-34.98 PSU) corresponds to the Antarctic intermediate water (AAIW). Underneath North Atlantic deep water (NADW) lies between 1200 and 3300 m (6.1-2.5 °C; 34.9-35.0 PSU). In the lower bathyal and abyssal water layers a temperature of about 2.0 °C would be the common indicator for the Antarctic bottom water (AABW; Pierre et al. 1994).

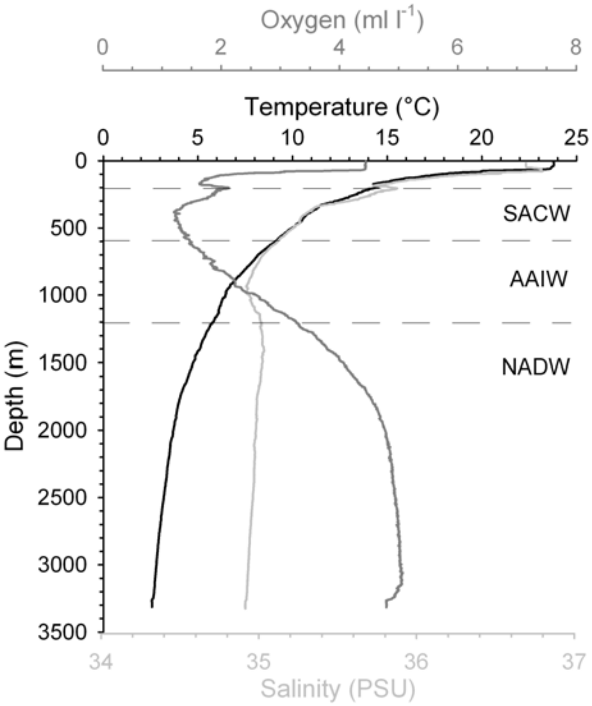

Fig. 8-3. Profiles of temperature (°C), salinity (PSU) and oxygen (ml l^{-1}) concentration at the reference site of Senghor Seamount.

The CVFZ is a strongly meandering feature and might reach near Senghor Seamount at times (Lázaro et al. 2005), but during the expedition in September/October 2009 salinity isolines did not indicate the presence of the front close to the area, nor showed the regional chlorophyll distribution in the surface waters that the frontal system affected the seamount during the cruise and during three months before (Dumont et al. subm.). The summit rim and the upper slope regions of Senghor Seamount down to about 700 m are usually influenced by SACW. In this depth range we caught eight species, which are typical for shelves and seamounts in the Eastern Atlantic north and south of the CVFZ, such as *Synaphobranchus kaupii*, *Etmopterus pusillus* and *Heptranchias perlo,* and also some which are usually restricted to the continental slope and coastal areas, such as *Muraena helena*, preferring rocky substrate (see Table 8-2 for details). Three of the species were caught for the first time at Senghor Seamount: the red eel *Myroconger compressus*, the ophidiiform fish *Brotulotaenia* sp. and the deep-body boarfish *Antigonia capros*. The northern most record offshore of *M. compressus* supports the important role of seamounts for the oceanic dispersal of typical shelf species between continental slopes or archipelagos. The species was previously caught in the coastal waters of the Cape Verde archipelago but not offshore in the area (Menezes et al. 2004), as well as *A. capros* (Strømme et al. 1982). The bottom living *Helicolenus dactylopterus* was wide spread from the summit to the mid slopes (100-734 m) of Senghor Seamount. Individuals became larger with depth, suggesting a size segregation of this species around the seamount, as also observed by Morales-Nin et al. (2003) and Colloca et al. (2010), with juvenile specimens occurring mainly in shallow waters of the summit while the adults are located mainly in deeper waters of the slopes. But the number of specimens caught is too small for final conclusions, and gear selection may also play a role. *Beryx splendens*, a commercially exploited species, is frequently found at seamounts and on the continental slopes in the NE Atlantic (Paxton 1999; Pakhorukov 2008; Menezes et al. 2009) in layers of the NACW (11.0-18.6 °C; 35.4-36.7 PSU; Tomczak 1981), but also deeper in the saltier waters of the Mediterranean outflow (600-1300 m; see Christiansen et al. 2015). Whereas *Promethichthys prometheus* is found at continental slopes, around oceanic islands and submarine rises in tropical waters of all oceans (Nakamura & Parin 1993), but is not known from the temperate NE Atlantic seamounts, Seine, Sedlo, Ampère and Great Meteor (Pakhorukov 2008; Christiansen et al. 2009; Menezes et al. 2009, 2012), maybe bounded to the south by the Mediterranean outflow. The species has been reported from landings in the Azores (Santos et al. 1997), but the origin of the catches is not clear.

The fishes collected on the abyssal plain adjacent to Senghor Seamount are typical deep-water species, but have not been known from the Cape Verde waters, yet, since deep-sea catches for this area hardly exist. To the authors' best knowledge, it is the first registered record of several deep-water species for the Cape Verde region, including *Acanthonus armatus*, *Ipnops* cf. *murrayi*, *Barathronus* cf. *parfaiti*, *Holcomycteronus squamosus*, *Aldrovandia affinis* and *Kali macrodon*, which has previously been reported by Vieira et al. (2013). Although some of the species are particularly rare (Fig. 8-4), all of them are known for the subtropical and tropical Eastern Atlantic, but usually north of 20° N (Merrett & Marshall 1981; Melo 2008).

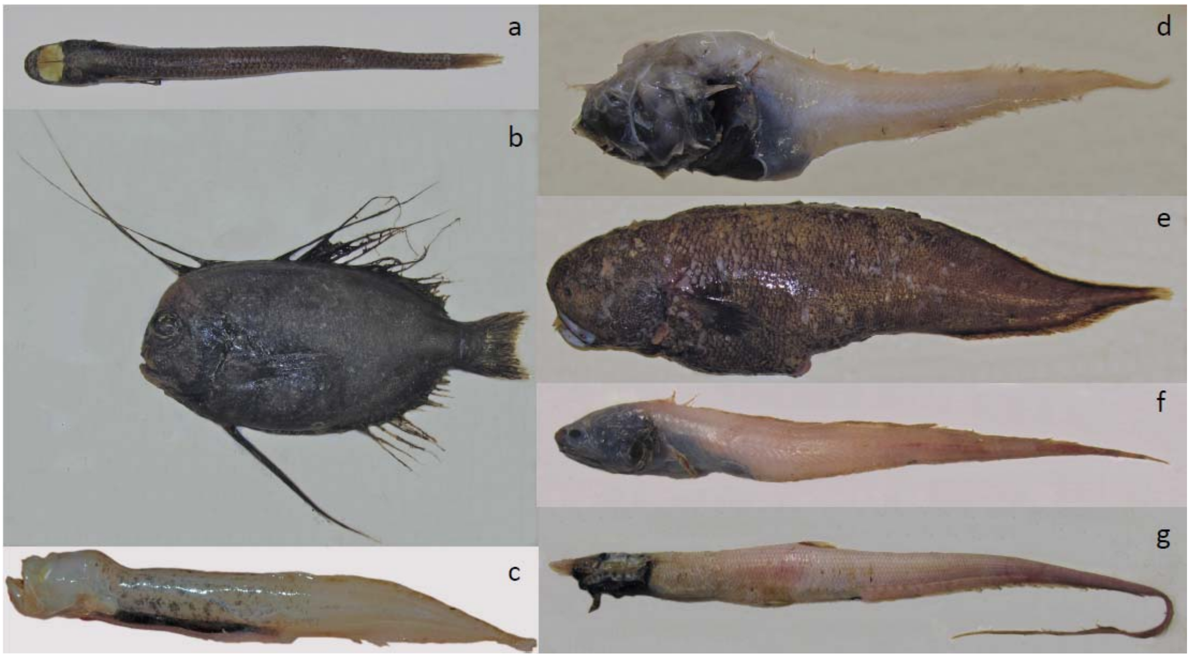

Fig. 8-4. Rare fishes collected on the abyssal plain adjacent to Senghor Seamount: a) *Ipnops* cf. *murrayi*; b) *Paracaristius* sp. (20.3 cm TL); c) *Barathronus* cf. *parfait* (10.5 cm TL); d) *Acanthonus armatus*; e) *Holcomycteronus squamosus* (68.0 cm TL); f) *Porogadus* sp.; g) *Aldrovandia affinis* (59.0 cm TL).

Most of the species we caught belong to the northerly (49-41° N), intermediate (38-30° N) and southerly (22-20° N) deep-sea fish assemblages of the eastern North Atlantic described by Merrett (1992). The composition of the dominant species changes among the three assemblages and the southerly one shows highest species richness (Merrett & Fasham 1998). *Coryphaenoides armatus*, for example, is the dominant species in the northerly assemblage and is known as one of the most abundant and widespread deep-demersal fish species in the North Atlantic Basin, becoming, however, less important south of 38° N in the waters off Morocco and NW Africa (Haedrich & Merrett 1990; Merrett 1992). It was also the dominant species in records from the Iceland Basin at 59° N, 020° W accounting for ~60 % of the total, whereas at 47° N, 020° W the species had a lower share of ~30 % (Martin & Christiansen 1997). In the southerly assemblage described by Merrett (1992) *C. armatus* made up 4 % (N = 12), according to the absolute numbers of individuals in our catches. The presence of *C. armatus* at the abyssal plain adjacent to Senghor Seamount, as one of the most abundant species in our otter trawl collections, is consistent with baited camera observations on the Cape Verde terrace (~120 nm SE of our abyssal station) and the Cape Verde abyssal plain (~210 nm SE of our abyssal station) of Henriques et al. (2002), who observed *C. armatus* as the main species attracted to bait.

Since there is still little knowledge about the reproduction of *C. armatus* as a common deep-water species, we might additionally mention at this point that the adult *C. armatus* females, we caught, had large ovaries containing ripening oocytes. The only record of *C. armatus* with ripe or close to ripe eggs was reported by Stein (1985) for individuals larger than 74 cm TL. The female with the ripest eggs was 96 cm long. Stein (1985) concluded that only very large females become sexually mature, that the reproduction may not be simultaneous within one population because not all the females with ripening eggs were at the same stage of ovarian development, and that the reproduction of the species may be semelparous. In our collection *C. armatus* females with ripening eggs were smaller in size covering a range from 54.5 to 83.0 cm TL (corresponding to 610-3280 g TW), which might challenge the hypotheses made by Stein (1985). Our findings support the assumption that *C. armatus* females mature at medium or even smaller size, making a semelparous reproduction unlikely.

Along the latitudinal gradient *Coryphaenoides profundicolus* becomes more abundant in the intermediate and southerly waters than *C. armatus* (Merrett 1992), however, not in our findings, which are the southernmost and first confirmed record of *C. profundicolus* in the waters off Cape Verde. Yet, *C. profundicolus* has been known to occur north of 20° N along the western African margin (Merrett & Marshall 1981) and in the temperate North Atlantic (Haedrich & Merrett 1988). *Bathypterois longipes* is also widespread, but dominant only in low latitudes (20-22° N; Merrett 1992) but in our catches, however, less abundant like *C. profundicolus*. Merrett (1992) associated the faunal change of the southerly assemblage as compared to the northern ones to the influence of upwelling and increased surface production along the continental margin of NW Africa. During our expedition and three months before the regional chlorophyll distribution in the surface waters shows that there was no influence from the Mauritanian upwelling in the area off Senghor Seamount and the reference station (Dumont et al. subm.). The net primary production indicates oligotrophic conditions in the waters off Senghor relative to the adjacent areas (Dumont et al. subm.). The less intense productivity at our abyssal station (18° N) south of the CVFZ as compared to the upwelling zone at Merrett's sampling site (20-22° N) north or within the CVFZ, might feature the observed change in the species composition between both deep-sea fish assemblages due to different food supply and feeding preferences. Replicate catches would be necessary for the Cape Verde region to verify this assumption statistically. However, the recent records and observations of the two macrourid species suggest that deep-sea fish communities and specimens are more widely distributed than previously assumed, and not mandatory restricted to northerly and southerly bounded assemblages. This is supported by the presence of species typical for southern waters in our catches. The aulopiform fish *Ipnops murrayi*, for example, is a particularly rare species usually known from the Western and Southern Atlantic and Indian and Pacific Oceans (Nielsen 1966), but also from scattered locations off NW Africa (Merrett & Marshall 1981). The rare *Holcomycteronus squamosus* is more likely distributed in the waters off Angola but also recorded at few scattered locations in the North Atlantic (Froese & Pauly 2015). One unidentified *Holcomycteronus* has been reported by Merrett & Marshall (1981) in the waters off West Africa at 21° N.

However, the patterns involving connectivity among the different deep-sea fish assemblages or the Eastern Atlantic seamount populations are still poorly known or are limited to commercially valuable species (White et al. 2009; Carlsson et al. 2011; Varela et al. 2013). In our study a transition is shown between northern and southern Atlantic fauna (Fig. 8-5), which emphasizes the role of Senghor Seamount in a broader bio-geographic context, contributing to our understanding on the distribution of deep-water fish species. Lloris et al. (1991) and Floeter et al. (2008) proposed that the Cape Verde archipelago is a boundary between the Mauritanian province and the southern West African region. In fact, most of the species presented here have a cosmopolitan distribution, but more northern Atlantic-Mediterranean affinities (Fig. 8-5; see Haedrich & Merrett 1988; Monteiro et al. 2008; Hanel & John 2014).

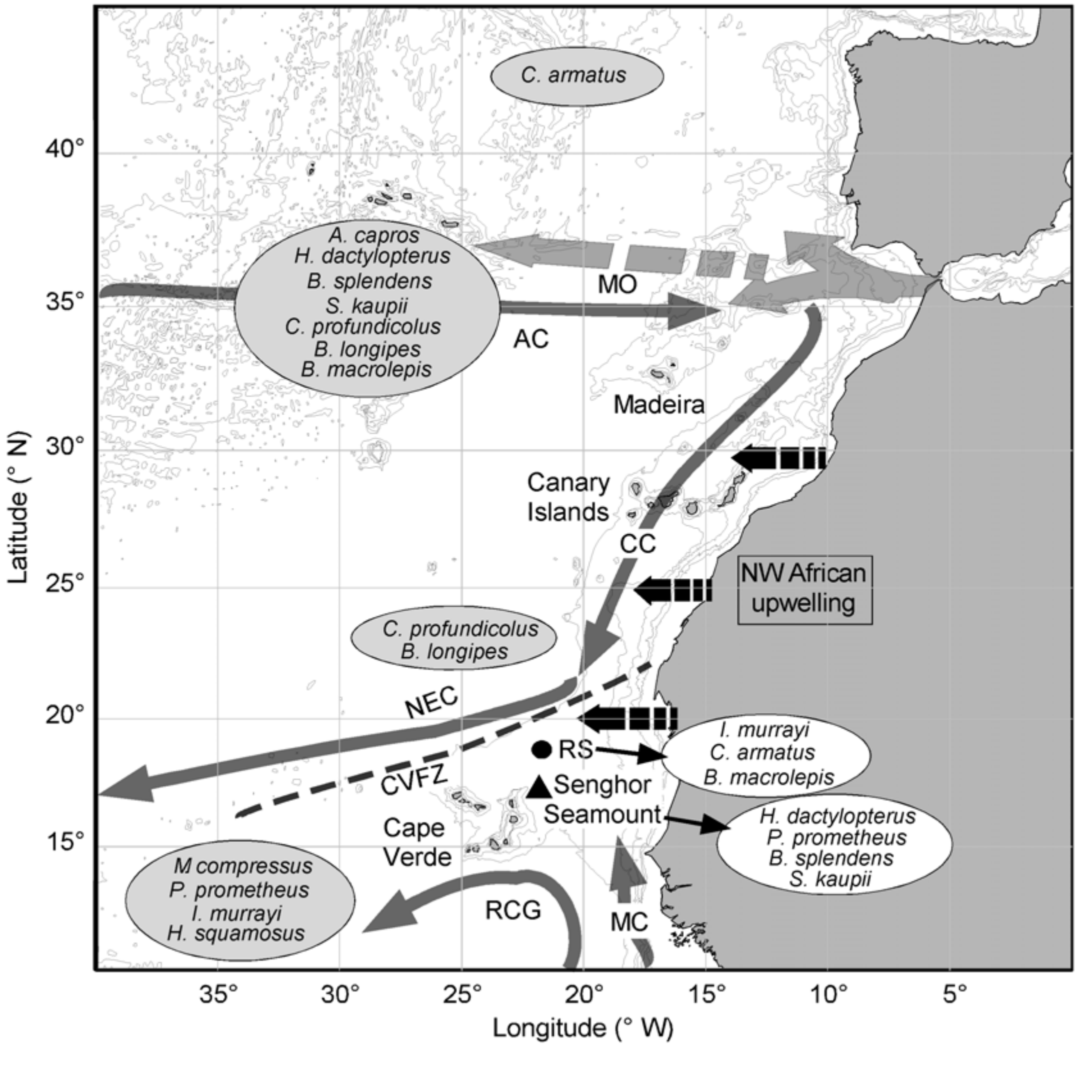

Fig. 8-5. Locations of Senghor Seamount and the reference site (RS) in the Eastern Atlantic with schematic surface circulation (after Lathuilière et al. 2008; Mason et al. 2011), NW African upwelling zones and fish assemblages. The most abundant fish species of the present study are listed for Senghor Seamount and the RS (white circles). Representative fish species caught at Senghor Seamount and the RS are grouped in four assemblages (grey circles) representing their main distribution in the Eastern Atlantic according to literature (see text). Within one assemblage species are arranged according to depth of occurrence. AC, Azores Current; CC, Canary Current; CVFZ, Cape Verde Frontal Zone; MC, Mauritania Current; MO, Mediterranean Outflow; NEC, North Equatorial Current; RCG, Recirculation Gyre.

The demersal fauna of Senghor Seamount is similar to that of subtropical NE Atlantic seamounts (Menezes et al. 2009; Christiansen et al. 2015), pointing out the role of seamounts as *stepping stones* for oceanic dispersal of benthopelagic fishes, particularly of typical shelf and slope species across large distances, for example, between continental margins and mid ocean ridges (Santos et al. 1995; Almada et al. 2001; Clark et al. 2010; Morato et al. 2010; Shank 2010) along the deep Atlantic ocean.

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9

General Discussion

The principal objective of this study was to compare the pelagic communities of two shallow seamounts, Ampère and Senghor, in contrasting regimes of the Eastern Atlantic. In the following, the seamount communities, their standing stocks and distributions are discussed first in their regional context in relation to the hydrographic and trophic conditions. The influence of large-scale processes and local seamount effects on the communities is assessed. Furthermore trophic interactions within the pelagic communities and with the associated benthopelagic fish fauna are elucidated and trophic pathways are discussed for each seamount and the surrounding open ocean.

9.1 The seamount communities affected by the large-scale current regime of the subtropical and tropical gyre

Zooplankton standing stocks and respiratory carbon demand as well as $\delta^{13}C$ and $\delta^{15}N$ signatures of POM and zooplankton were generally higher at Senghor as compared to Ampère Seamount and can be attributed to differences in productivity in the two areas (Manuscript 1-3). Ampère Seamount belongs to the sphere of the NE Atlantic subtropical gyre (37°-24° N), while Senghor Seamount is located in the adjacent cyclonic tropical gyre (19°-10° N). Both gyres are separated by the Cape Verde frontal zone (CVFZ; e.g. Zenk et al. 1991). Whereas the subtropical gyre to the north of the CVFZ is characterized by an oligotrophic regime (Longhurst 1995; Harrison et al. 2001), the waters south of the CVFZ are considered as nutrient-rich (Pierre et al. 1994; Morel 1996; Pastor et al. 2008) with a strong influence of the Mauritanian upwelling (e.g. Pastor et al. 2008; Mason et al. 2011) and enhanced chlorophyll concentrations which may extend up to 300-400 km from the shore (Lathuilière et al. 2008).

In the epi- and mesopelagic waters off Ampère Seamount mesozooplankton (0.3-20 mm) biomass standing stocks of ~4.5 g m^{-2} with a respiratory carbon demand of ~12 mg m^{-2} d^{-1} (Manuscript 1) confirm the generally reported low zooplankton biomass and respiration in the oligotrophic NE Atlantic gyre (Longhurst 1995; Robinson et al. 2002; Hernández-León & Ikeda 2005). Consistent with a general latitudinal increase in zooplankton biomass and respiration from the subtropical gyre towards the NW African upwelling (21-15° N) (Robinson et al. 2002), the mesozooplankton standing stock and respiratory carbon demand were about six times higher at Senghor than at Ampère. The difference in carbon demand between both areas can be attributed to the higher biomass and to the combined effects of higher temperature and smaller body size of individuals in the tropic waters, resulting in higher weight-specific respiration rates (Hernández-León & Ikeda 2005). Within the mesozooplankton community the smaller zooplankton (0.3-2 mm) contributed most to the total respiratory carbon demand at Senghor, emphasizing their importance for the carbon conversion in tropical waters, whereas at Ampère larger size groups (1-5 mm) gained higher shares. This reflects differences in the mesozooplankton composition between both areas with a higher proportion of smaller sized cyclopoid copepods, such as oncaeids, at Senghor and a higher amount of larger calanoid copepods at Ampère. Such a shift towards smaller sized copepods can generally be expected for tropical regions (Angel & de Baker 1982; Schneider 2002). A dispersal of Mediterranean species via the Mediterranean outflow or the formation of meddies (O'Neil Baringer & Price 1999) was not detected in the faunal composition at Ampère Seamount, at least not on the analysed taxonomic levels. In the bathypelagic zone the carbon demand at Senghor and Ampère was similar (~1.7 mg m^{-2} d^{-1}), suggesting that latitudinal differences in mesozooplankton biomass and their respiration rates become smaller at depth, and that, despite different production in surface layers, the food availability in the deep sea is comparable, pointing to differing vertical carbon fluxes with lower recycling rates in the oligotrophic subtropical gyre as compared to the more productive tropical areas.

Consistent with the latitudinal differences among the mesozooplankton communities, microzooplankton (0.055-0.3 mm) standing stocks and respiratory carbon demand were about three times higher at Senghor than at Ampère (Manuscript 2). The contribution of microzooplankton to the total zooplankton (0.055-20 mm) carbon demand of about 50 % in the waters off Ampère and 30 % at Senghor emphasizes the general importance of the small-sized plankton for the conversion of carbon in the biogeochemical cycle in subtropical and tropical areas (see King et al. 1978; Hernández-León et al. 1999; Calbet 2008). Size-specific differences in the contribution to the total carbon demand between the two trophic regimes may be attributed to the size structure of the phytoplankton communities and the corresponding availability as prey for small- and large-sized zooplankton. Over Ampère Seamount the phytoplankton community comprised mainly nano- and picoplankton (56-95 %), which are specialised in low nutrient levels (Kaufmann 2004; Kaufmann et al. 2011). In such a subtropical oligotrophic region microzooplankton is considered to be most important for the control of phytoplankton (Jackson 1980; Huskin et al. 2001), since the larger copepods (>0.2 mm) do not exploit the abundant picoalgae to a large extent (Huskin et al. 2001). Due to this high food availability for the microzooplankton half of the respiratory carbon demand can be ascribed to this size fraction in the area off Ampère Seamount. By contrast, the higher contribution of mesozooplankton to the total carbon demand at Senghor Seamount can be attributed to higher productivity in the area, providing favourable conditions for small-sized copepods (0.3-2 mm), supported by their enhanced abundance over Senghor. Usually larger phytoplankton cells, such as diatoms and dinoflagellates dominate in areas of higher productivity, showing high growth rates at high nutrient concentrations, while numbers of extremely small cells are depressed (Landry et al. 1995; Edwards et al. 1999). Consistent with the mesotrophic character of the waters south of the CVFZ (Pierre et al. 1994; Morel 1996) relative high nutrient concentrations were measured over Senghor Seamount (Kaufmann et al. 2011), supposing diatoms and dinoflagellates to be more abundant than nano- and picoplankton (Kaufmann et al. 2011) and primarily grazed by copepods, resulting in the observed higher biomass and carbon demand of meso- compared to microzooplankton at Senghor Seamount.

Differences in the surface production and in the composition of the pytoplankton community between the areas of the subtropical and tropical gyre were also reflected in the stable isotope signatures of POM from Ampère and Senghor seamounts (Manuscript 3). POM represents a mixture of living and dead phytoplankton, microzooplankton, bacteria and detritus. Since increasing particle size has been found to lead to increasing $\delta^{13}C$ (Rau et al. 1990), the higher $\delta^{13}C$ values in POM at Senghor Seamount as compared to Ampère may be attributed to the assumed enhanced abundance of larger diatoms and dinoflagellates in the tropical area. Furthermore, diatoms are enriched in ^{13}C due to bicarbonate uptake in nutrient rich waters and show a trend towards higher $\delta^{13}C$ values at higher temperatures (Fry & Wainright 1991). $\delta^{15}N$ ratios of epipelagic POM (3-4 ‰) and zooplankton were low in the area off Ampère Seamount, as characteristic for the oligotrophic subtropical and tropical North Atlantic surface waters (Montoya et al. 2002). The generally low $\delta^{15}N$ values in oligotrophic surface waters are attributed to the input of isotopically light nitrogen through N_2 fixation producing ^{15}N-depleted organic matter (Minagawa & Wada 1986; Carpenter et al. 1997; Mahaffey et al. 2003). Senghor Seamount lies within the sphere of episodic Saharan dust input (see Chester et al. 1979; Prospero 1996; Bory et al. 2001), which would potentially increase N_2 fixation in the surface waters by supplying the co-limiting elements, iron and phosphorus (Mills et al. 2004; Voss et al. 2004). However, the $\delta^{15}N$ values of POM (5-6 ‰) at Senghor did not reflect isotopically light organic matter in the surface waters, but can be ascribed to the high nitrate concentrations in the upper layer right at the thermocline, being as high there as at Ampère only at 250 m depth (Kaufmann 2004; Kaufmann et al. 2011). High local nutrient availability and therefore low N_2 fixation rates are typically found, for example, in upwelling systems (see Voss et al. 2004; Montoya et al. 2007). The increased nutrient availability at Senghor, associated with enriched $\delta^{15}N$ signals as compared to Ampère, reflects the mesotrophic character of the waters south of the CVFZ (18.5° N, 21.0° W; Pierre et al. 1994; Morel 1996; Bory et al. 2001), but cannot be attributed to a direct influence of filaments from the frontal system or the Mauritanian upwelling (see Onken & Klein 1991; Zenk et al. 1991) as primarily expected. In September/October 2009 salinity isolines did not indicate the presence of the CVFZ close to the area, and the regional chlorophyll distribution in the surface waters shows that neither the frontal system nor the Mauritanian upwelling affected the seamount during the cruise and during three months before (Dumont et al. subm.).

9.2 The zooplankton distribution affected by seamount associated flows and topographic blockage

Zooplankton standing stocks showed some small-scale spatial variability at each seamount, which may be attributed to some extent to the interaction of the local flow field with the seamount topography (Manuscript 1-2). At Ampère Seamount strong impinging currents of 15-25 cm s^{-1} from the northwest were present in the upper 250 m, whereas on the eastern and southern downstream side an area of lower current velocities was generated with some accumulation of microzooplankton (Manuscript 2). However, the general zooplankton distribution did not indicate any clear connection to the flow field; the expected biomass depletion on the upstream and enhanced biomass on the downstream side was not found. But the biomass of micro- and mesozooplankton was always reduced over the summit area as compared to the slopes, similar to previous studies in the NE Atlantic (Nellen 1973; Martin & Christiansen 2009). Especially larger size fractions (2-20 mm), which include most of the diel vertical migrators, were nearly missing over the summit, but increased towards the slopes over deeper waters during the night (Manuscript 1). This horizontal distribution pattern of the larger plankton across Ampère Seamount seems at first to correspond to the mechanism of the topographic blockage hypothesis (see Isaacs & Schwartzlose 1965; Genin et al. 1988; Genin et al. 1994) (Fig. 9-1): Vertically migrating zooplankton is blocked during its descent at dawn by the shallow topography and trapped on the summit during the day, where they can easily be consumed by resident predators (Fig. 9-1d). This mechanism, providing sufficient prey for seamount associated fishes, has generally been suggested to sustain fish aggregations at seamounts (Rogers 1994; Koslow 1997; Genin 2004). However, the predominance of small non-migrating copepods, such as oncaeids, in the stomachs of the near-bottom fishes *Callanthias ruber* and *Capros aper* showed that these are not responsible for the absence of the larger migrating plankton over Ampère Seamount (Manuscript 3; see also Christiansen et al. 2009; Hirch & Christiansen 2010). At Ampère it seems to be more likely that the advection of the vertically migrating zooplankton onto the summit area is blocked during the day when the deep migrating taxa stay at depths greater than the summit (Fig 9-1a) and also during the night when they do not ascend into waters shallower than the summit (Fig 9-1c), resulting in a gap formation over the plateau associated with a generally lower biomass (Genin et al. 1994; Rogers 1994; Haury et al. 2000). The biomass of the larger vertical migrators, like the copepod *Pleuromamma* spp. and euphausiids, increased towards the edges of the plateau and the slopes of Ampère, where they are available as prey for the more pelagic fish species, such as *Trachurus picturatus* and *Scomber scombrus* (Manuscript 3). Thus topographic trapping of vertically migrating zooplankton seems to be of minor importance for the food supply at Ampère Seamount, but the seamount fishes are rather supported by current-driven advection of the planktonic prey (Fig 9-1c), as similarly observed at the adjacent Seine Seamount (Hirch & Christiansen 2010). However, since time series are not available, topographic trapping cannot be completely excluded at Ampère Seamount (Fig. 9-1d).

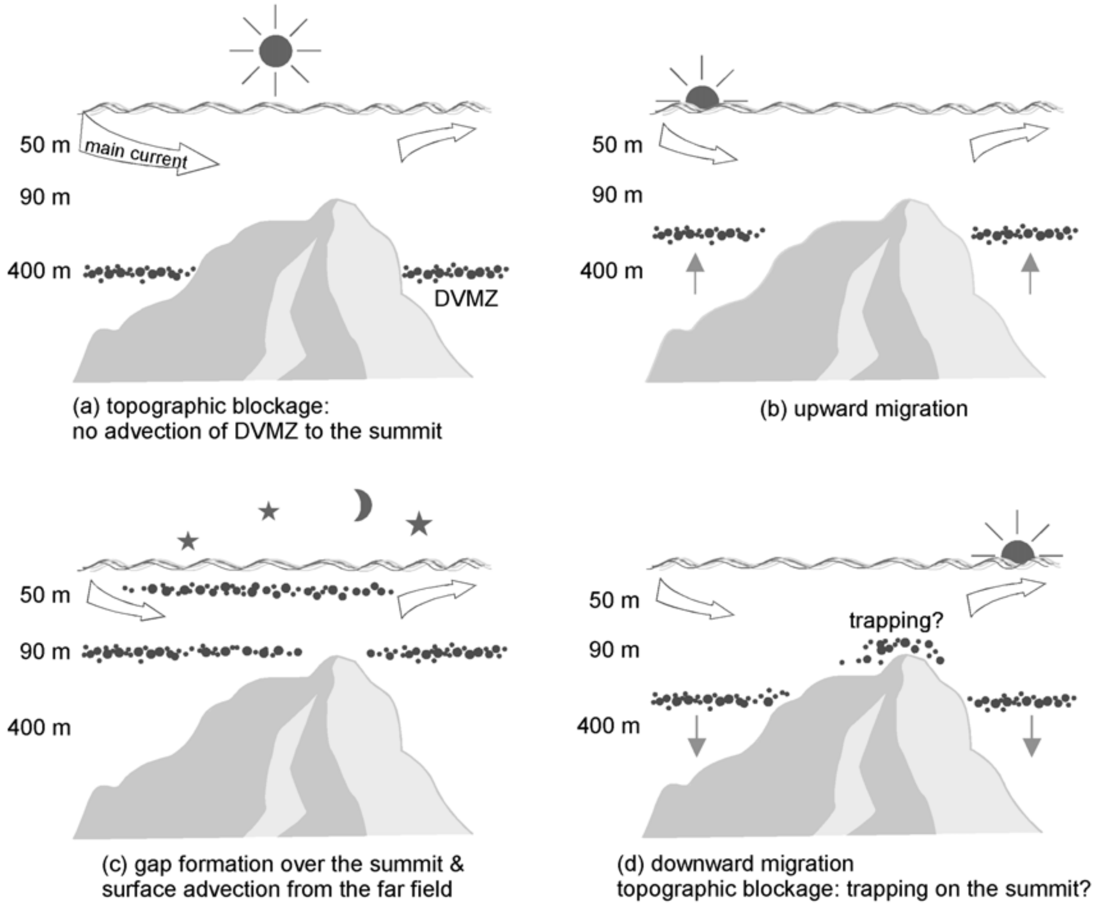

Fig. 9-1. Schematic diel vertical migration over Ampère Seamount: (a) during the day diel vertical migrating zooplankton (DVMZ) stay at depth greater than the summit and advection is blocked by the topography; (b) during dusk upward migration of DVMZ; (c) during the night DVMZ is forming a gap over the summit when they not ascend into depth shallower than the summit and their advection is still blocked by the topography, whilst there is surface advection from the far field; (d) during dawn downward migration of DVMZ possibly trapped on the summit during the next day.

Seamounts are often regarded as locations of enhanced productivity and, accordingly, biomass and abundance, as compared to the surrounding ocean. In the waters above Ampère some indication of a generally higher abundance of micro- and mesozooplankton was observed as compared to the open ocean. But differences were only small and not significant, and may rather reflect common or wind-driven patchiness than the expected local seamount effects through tidal resonance and seamount trapped waves (Manuscript 1-2). The region off Ampère Seamount is characterized by strong winds, as they came up during the winter cruise, mixing the surface layer (Kaufmann & Diniz 2012) and could break the thermal stratification as well as recirculating flows above the seamount. Moreover the upper water column of this region is frequently disrupted by long-lived meso-scale eddies generated and propagating in two permanent corridors north and south of the Azores front (Sangrà et al. 2009), which presumably prevent a build-up or, at least, a longer persistence of a recirculation cell over Ampère Seamount. In contrast to the expected current-topography interactions in the higher latitudes, at Ampère no seamount associated flow features were observed. Whereas at Senghor close to the equator, where the influence of the Coriolis force on the current regime is small, no tidal resonance exists (see Beckmann & Mohn 2002) and seamount associated flows were not expected, the plankton production and distribution as well as the retention potential seemed to be affected by the vertical displacement of isotherms and isohalines to some extent and by seamount surrounding flows.

At Senghor Seamount, steady impinging currents of 10-15 cm s^{-1} from the north/northeast were deflected by the seamount generating a calm area with low current velocities at the south/southwestern side above the lower edge of the summit plateau and the upper slope (Manuscript 2). Again, a substantial accumulation of zooplankton was not observed in this downstream area. In the upper 100 m the steady southwestward flow did not detectably interact with the seamount (see also Dumont et al. subm.), and mesozooplankton was evenly distributed across Senghor with a persistent higher biomass at 50 m than at 90 m, which points to a high proportion of non-migrating zooplankton residing in the layer of the fluorescence maximum at the bottom of the thermocline, as confirmed by the taxonomic composition (Manuscript 1). In contrast to Ampère the abundance of strong vertical migrators was relatively low over Senghor, and a gap formation over the summit was not observed. This suggests that topographic blockage of vertically migrating zooplankton is not a common mechanism for food supply at this tropical seamount. Trophic analyses of residents at Senghor Seamount, such as *Antigonia capros* and *Helicolenus dactylopterus*, indicate that fish and benthic organisms are of major importance in their diets, rather than planktonic prey (Manuscript 3).

An abundance of dinoflagellates much higher over Senghor Seamount than in the open ocean during December 2011 and February 2013, especially around the summit, suggests possible interactions between current and topography at times (Manuscript 2). The generation of a recirculation cell on the top of a seamount caused by a steady impinging flow would affect the local retention time of water masses and may accumulate passive particles at the seamount summit (Roden 1987; Beckmann & Mohn 2002; Genin 2004; Lavelle & Mohn 2010), whereas actively migrating zooplankton would be much less retained due to their interaction with deeper currents (Beckmann & Mohn 2002). Moreover, associated isopycnal doming enabling upwelling of deep nutrient-rich water into the euphotic zone over the seamount flanks could favour local increase of primary production (Roden 1987; Beckmann & Mohn 2002; Genin 2004). Since the abundance of other taxonomic groups than dinoflagellates was not higher over Senghor as compared to the reference site, it seems unlikely that local upwelling and retention lasted long enough for a transfer to higher trophic levels, which would require residence times in the order of several weeks to months according to the typical zooplankton generation times (Genin & Boehlert 1985; Dower & Mackas 1996; Genin & Dower 2007). It seems generally unlikely that a Taylor column could persist above Senghor Seamount for longer periods due to the high, primarily tide- and trade wind-driven, spatio-temporal current variability in the region (Dumont et al. subm. and references therein). Consistently, observations of currents did not detect any evidence for a recirculating flow in the upper 200 m during the cruises, neither in September/October 2009 (Dumont et al. subm.) nor in February 2013 (Manuscript 2). Instead, enhanced vertical mixing of the waters near the summit, indicated by vertical upward displacement of isotherms and isohalines in the upper 100 m near the thermocline due to variable tidal flow (Dumont et al. subm.), might induce nutrients and detritus to the surface mixed layer and increase dinoflagellate abundance at times (Fig. 9-2). Evidence for a general build-up of higher zooplankton biomass was not found over Senghor. Rather, total standing stocks of zooplankton were even lower at the seamount than in the unaffected ocean at times, supporting the assumption that zooplankton dynamics over a seamount are likely unrelated to possible local seamount-driven changes in the productivity and biomass of phytoplankton. Topography-generated upwelling is generally noted as an unlikely mechanism to affect secondary production and, unless trapping occurs, any enhancement of primary production would be shifted downstream as the nutrient-rich waters are advected away (Genin 2004; Genin & Dower 2007).

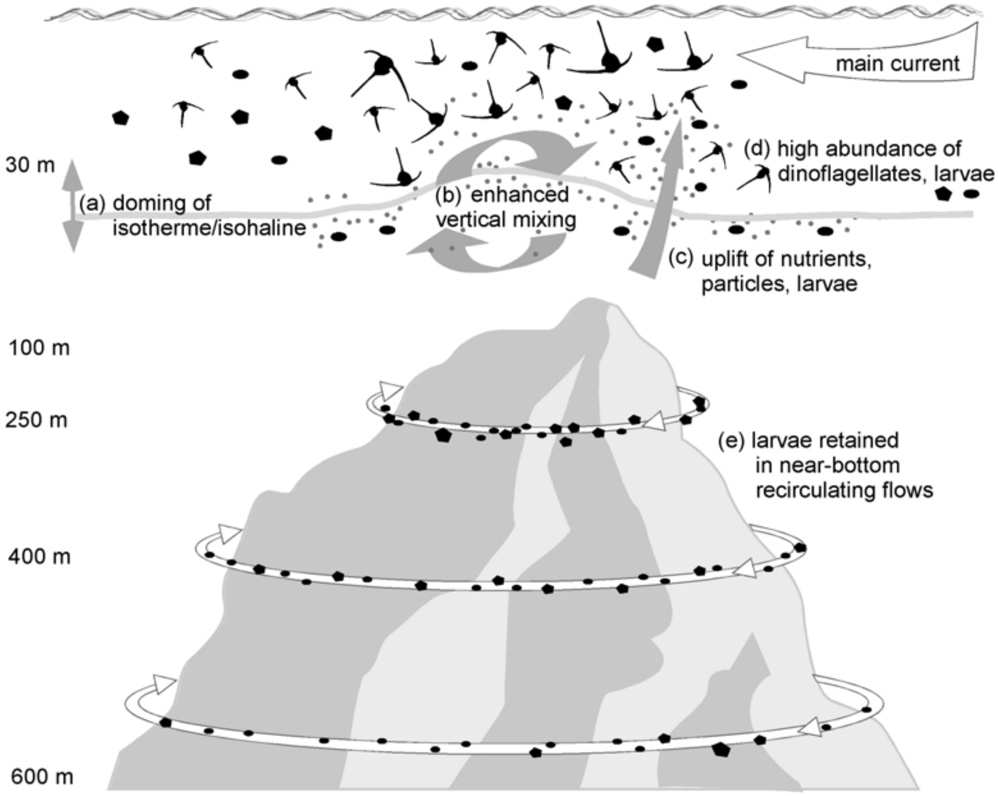

Fig. 9-2. Schematic flow dynamics and distribution of dinoflagellates and larvae at Senghor Seamount: (a) vertical upward displacement of isotherms and isohalines near the thermocline; (b) enhanced vertical mixing; (c) uplift of nutrients, particles and larvae into the upper mixed layer; (d) increased abundance of dinoflagellates and larvae in the upper mixed layer; (e) larvae retained in near-bottom recirculating flows between 250 and 600 m.

9.3 Seamounts as larval source in the ocean

Since both seamounts, Ampère and Senghor, provide special habitats for benthic organisms and host diverse and abundant communities of corals, hydroids, sponges, echinoderms, bryozoans, decapods and polychaetes (Christiansen & Koppelmann 2011; Lamont & Chivers 2012; Molodtsova & Vargas

2012; Chivers et al. 2013; Christiansen unpubl. data), they were expected to be a source for meroplanktonic larvae in the open ocean (Manuscript 2). At least Senghor was confirmed for significantly enhanced larval abundance in the seamount associated waters as compared to the open ocean during two sampling times, which suggests a retention potential for Senghor and supports the hypothesis by Mullineaux & Mills (1997) that larvae of benthic invertebrates are retained in flows near a seamount. However, evidence of flow features which potentially increase the retention time of water masses and larvae, like regions of closed streamlines above the seamount (Taylor caps), eddies formed in lee of the seamount, or rectified flows generated by seamount-trapped waves (see Mullineaux & Mills 1997 and references therein) was rarely found at Senghor. In the upper 200 m the steady southwestward flow across Senghor did not result in the generation of a recirculating flow (see also Dumont et al. subm.). Only in deeper waters from 250 to 400 m and down to 600 m the observations suggest weak recirculating near-bottom flows around Senghor (see also Dumont et al. subm.; Mohn unpubl. data), potentially retaining larvae close to the seamount, as indicated by small larval accumulations in the waters around the lower edge of the summit plateau and on the upper slopes (Fig. 9-2e). But since it is unlikely that this recirculating water extended into the surface layers because of high current variability (Dumont et al. subm.), the observed enhanced vertical mixing induced by tidal flow seems also to be the major mechanism for the high larval abundance in the upper mixed layer over Senghor. Trapped waves can generally be excluded as retention mechanism because Senghor is located equatorwards of 30° N, where trapped waves are not assumed to occur (Beckmann & Mohn 2002; Dumont et al. subm).

Over Ampère Seamount, on the other hand, the expected higher abundance of meroplanktonic larvae was not found, suggesting that larvae were not retained as result of the local flow field and thus did not accumulate at the seamount or that larval release was low during the short sampling period. Neither for Senghor nor for Ampère it is known, whether a potential retention time could last long enough for meroplanktonic larvae to complete their planktonic stages (~30 days) and settle at the seamount, or whether larvae are transported away from the seamount by lateral advection. These mechanisms of recruitment and dispersal of benthic invertebrates as well as larval traveling between isolated habitats, such as seamounts, still remain poorly understood (Clark et al. 2010; Lavelle & Mohn 2010; Shank 2010).

9.4 Depth and seamount related differences in trophic pathways

Trophic interactions among zooplankton and micronekton and nutritional links to the benthopelagic fishes from the summit and slopes of Ampère and Senghor indicate variable trophic structures in the different seamount systems and the open ocean (Manuscript 3). Trophic positions of zooplankton, micronekton and fishes were determined from $\delta^{15}N$ ratios, using epipelagic POM as baseline for the food web. Assuming an average $\delta^{15}N$ enrichment of 3.4 ‰ per trophic level (Minagawa & Wada

1984), epipelagic zooplankton occupied the 1st and 2nd trophic levels and included taxa known as herbivorous, omnivorous and carnivorous. Meso- and bathypelagic zooplankton comprised detrivorous, omnivorous or carnivorous feeding types and ranged between the 2nd and 3rd trophic level as well as the small zooplanktivorous mid-water fishes. Feeding types of benthopelagic fish species included mainly zooplanktivores and mixed feeders, but also benthivores, piscivores, and predator-scavengers. They had trophic positions between the 2nd and 4th trophic level.

In the surface waters of Ampère Seamount and the far field enhanced δ^{15}N values of POM in November/December as compared to May indicated recent upwelling of ^{15}N enriched deep-water nitrate (Montoya et al. 2002; Bourbonnais et al. 2009) due to enhanced turbulence and deeper mixing of the surface layer in late autumn as compared to spring. But this seasonal shift was not reflected in the zooplankton signatures at least during the same observation period. This can be attributed to a time lag between changes in the δ^{15}N signal of the food source and the conversion to consumer tissues (O'Reilly et al. 2002; Hirch 2009), which takes weeks to months depending on the turnover time of organisms (MacAvoy et al. 2001; Perga & Gerdeaux 2005). Such a time lag may explain why some epipelagic zooplankton had δ^{15}N values lower or in the same range as POM at both seamounts and ranked also on the 1st trophic level, not reflecting the expected enrichment in ^{15}N between consumers and their diet.

The assumed enrichment in ^{13}C and ^{15}N from prey to predator may also vary because isotopic fractionation per trophic step depends on diet quality, body size, excretory mechanisms and feeding rate of an organism (see Post 2002; Mill et al. 2007 and references therein). McCutchan et al. (2003) supposed a greater trophic shift in δ^{13}C for herbivores than for omnivores and for omnivores than for carnivores relative to the diet, as was also observed among the mesopelagic specimens in the present study, especially in the subtropical waters at Ampère Seamount and the far field. δ^{13}C and δ^{15}N values of mesopelagic zooplankton covered only a narrow range in the subtropical region, where signatures of omni- and zooplanktivores were quiet similar to those of phytodetrivores, not showing the expected enrichment in the isotope signals along the food chain (see Fry & Sherr 1984). At Senghor Seamount and the surrounding ocean, however, isotope ratios showed a greater variability and were enriched in omni- and carnivores compared to detritus feeding specimens. Like in the mesopelagic zone, the enrichment in ^{13}C and ^{15}N was variable among herbi-, omni- and carnivores also in the bathypelagic zone. Especially the δ^{15}N ratios showed a high variability in deep-waters at both seamounts, indicating a more complex food web structure at depth as compared to the primarily linear food chain in the waters above. A more opportunistic, detrivorous to omnivorous feeding type seemed to be common in the deep zone, where both large and small animals may feed on detritus as well as on carcasses and living prey (Roe 1988).

The generally lower $\delta^{13}C$ and $\delta^{15}N$ values in the meso- and bathypelagic zooplankton of the subtropical waters as compared to the tropical region reflect the signals of different nutrient availability and phytoplankton communities from the surface, since sinking POM from the upper layers is an important food source for the deeper waters. The lower $\delta^{13}C$ values may also be an indication of a lipid content higher in the subtropical than in the tropical zooplankton, as tropical zooplankton generally do not accumulate large lipid stores (Lee et al. 2006), and high contents of lipids, which are depleted in ^{13}C, result in low $\delta^{13}C$ values. Significantly enriched $\delta^{15}N$ values in consumers at Senghor Seamount compared to Ampère may indicate more feeding steps along the food chain, pointing to different feeding conditions and trophic structures in a more complex food web in the tropics than in the subtropics.

The strong correlation between $\delta^{15}N$ and $\delta^{13}C$ values of POM, zooplankton, micronekton and benthopelagic fishes in the epi- and mesopelagic zones at Ampère Seamount suggests a linear food chain based on a single energy source resulting, for example, from local photosynthetic derived production (see Iken et al. 2001; Polunin et al. 2001), whereas the lacking correlation at the open ocean reference site indicates varying nutritional sources and trophic pathways. The assumption that the higher trophic levels rely on autochthonus production at the seamount is, however, not supported by significant differences in the $\delta^{13}C$ values of POM and plankton of the epipelagic zone between both sites. Consistently, no evidence was found for hydrodynamic features generating and retaining autochthonus seamount production or trapping particles over Ampère at least during the cruise. In meso- and bathypelagic waters, however, significantly differing $\delta^{13}C$ values of POM and typical suspension feeders at the seamount as compared to the open ocean might be indications of previous recirculation cells and associated downstream plankton production (Genin 2004; Genin & Dover 2007) over Ampère, whereas the stronger currents at the surface have advected and mixed plankton and particles off the seamount and the far field. In the bathypelagic zone correlations of $\delta^{15}N$ and $\delta^{13}C$ point to a rather homogenous surface-derived food source at both sites, which is in contrast to the more complex pathways in the upper waters of the open ocean as suggested above. Thus, despite possible differences in production and trophic pathways in the surface layers, the remaining nutritional sources seem to be comparable in the deep-sea, as were biomass, abundance and respiration (Manuscript 1).

Similar correlations between $\delta^{15}N$ and $\delta^{13}C$ in all pelagic zones of Senghor Seamount and the open ocean did not point to generally altered feeding conditions and trophic pathways between both sites. Significant differences in the $\delta^{13}C$ values of epipelagic POM and some omnivores as well as of bathypelagic detrivores, however, indicate food sources of different origin between the seamount and the open ocean. This may be attributed to a regional decrease in primary production from north to south, evident in a slightly enhanced net primary production at the reference site (~325 mg m^{-2} day^{-1}) as compared to Senghor (~280 mg m^{-2} day^{-1}) (Dumont et al. subm.). Since the reference site is located closer to the sphere of the CVFZ and the Mauritanian upwelling, advected filaments possibly cause stronger varying nutritional sources and feeding conditions at this site associated with enhanced microzooplankton biomass as compared to Senghor Seamount at times.

In general the varying $\delta^{13}C$ and $\delta^{15}N$ signatures and correlations among the seamount systems and the far field sites indicate that the trophic structure of pelagic and benthopelagic communities may be highly variable not only at seamounts, but also over the uniform abyssal plains of the two different trophic regimes.

9.5 Nutritional links and resource partitioning among benthopelagic fishes

The topographies of Ampère and Senghor seamounts provide a suitable habitat for benthopelagic shallow and deep-water fishes, even for some which are usually restricted to the continental slope and coastal areas, such as *Conger conger* and *Muraena helena*. Thus most of the fishes collected at the summits and upper slopes of both seamounts are typical for shelves and seamounts in the Atlantic and the Mediterranean, whereas in the bathyal and abyssal regions of the seamounts and of the far field sites typical deep-sea fishes were found (Manuscript 4-5).

Differences in stomach contents and stable isotope signatures indicate a resource partitioning among the benthopelagic fishes at Ampère and Senghor seamounts and the abyssal plains (Manuscript 3), respectively, through distinct habitat choice, vertical feeding positions (Manuscript 4-5) and prey selection, as suggested in previous studies (see Ehrich 1974; Fock et al. 2002a, b; Pakhorukov 2008; Hirch & Christiansen 2010). The $\delta^{13}C$ and $\delta^{15}N$ signatures of the benthopelagic fishes were generally enriched by 1-4 ‰ compared to their potential pelagic prey. This indicates a close nutritional link to pelagic food sources for zooplanktivores and mixed feeders, mainly due to direct feeding on the pelagic organisms, or due to zooplankton sinking as carrion and forming thereby a part of the predator-scavenger food chain (see Reid et al. 2012) (see Fig. 9-3, 9-4 for schematic trophic pathways).

Zooplanktivores were mainly collected at the seamount summits and occupied the lowest trophic position of the fish community. Since oncaeid copepods were more abundant in the bottom near water layers over the summit plateau of Ampère Seamount (Manuscript 2), the predominance of this group as prey for *Callanthias ruber* and *Capros aper* indicates a bottom-associated feeding behaviour for these species (see also Christiansen et al. 2009; Hirch & Christiansen 2010). A near-bottom feeding preference was also suggested for *Scomber colias* which had a high proportion of epibenthic organisms in its diet.

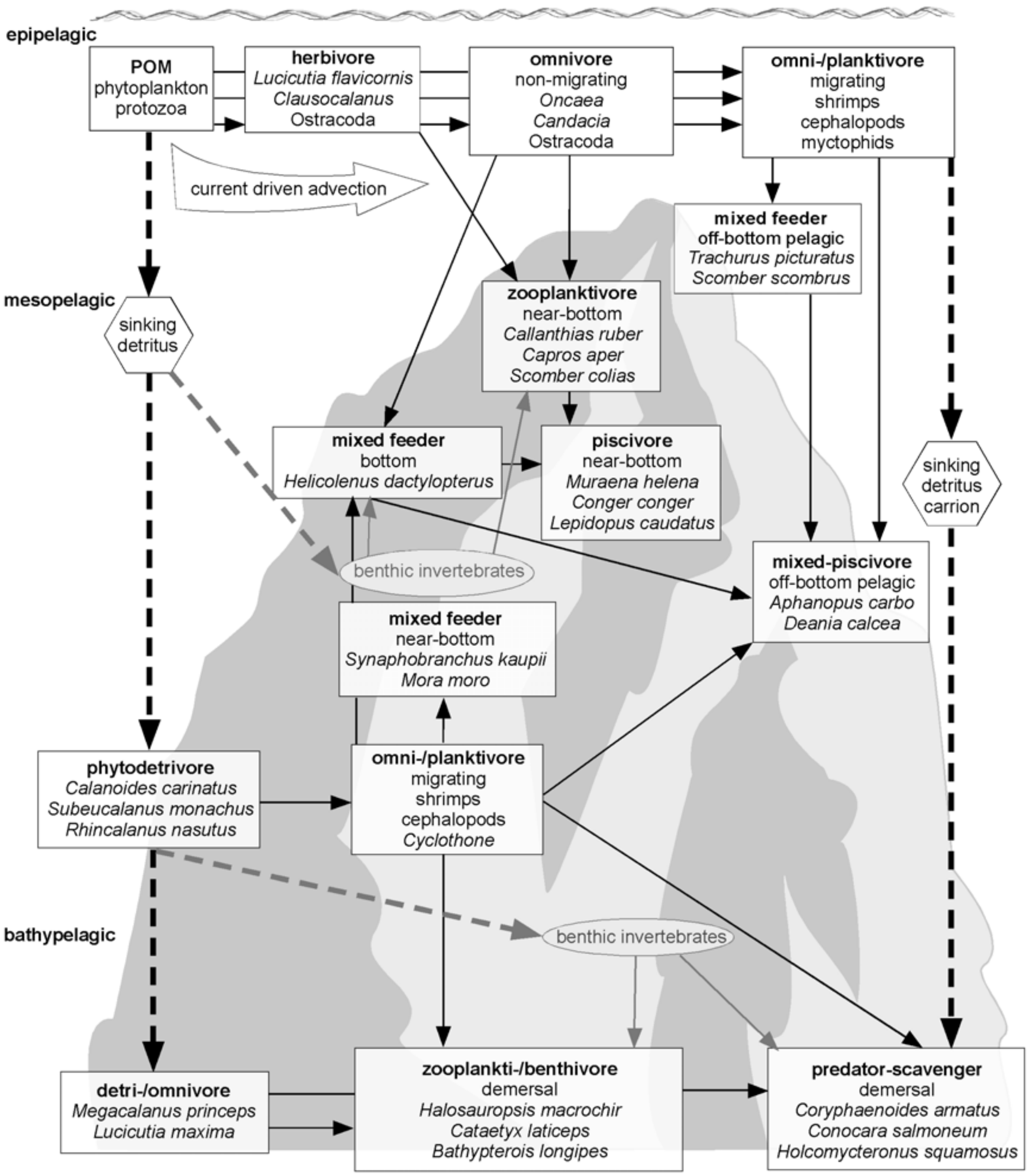

Fig. 9-3. Simplified trophic pathways from the epipelagic to the bathypelagic zone at Ampère Seamount between pelagic food sources and benthopelagic fishes with current-driven advection as the main mechanism for food supply. Representative zooplankton taxa and fish species are arranged according to depth of occurrence and grouped according to their habitat preference and feeding mode. Links on direct feeding are indicated by black arrows. Pathway of sinking material is indicated by broken arrows. Benthic invertebrates and links were added according to literature and are indicated by grey arrows.

Mixed feeders on crustaceans, cephalopods and fish, such as *Trachurus picturatus* and *Scomber scombrus*, appeared to be more pelagic around the summit plateau and above the upper slopes of Ampère, where the larger zooplankton and the micronekton was more abundant (Manuscript 1). For *Promethichthys prometheus* and *Beryx splendens* at the upper slopes of Senghor Seamount a diel vertically migrating behaviour and preference for macroplanktonic and micronektonic prey from shallower waters can be assumed due to their relative low isotope values as compared to the bottom-living plankti-/benthivorous *Helicolenus dactylopterus*, as reported in previous studies (Nakamura &

Parin 1993; Vinnichenko 1997; Dürr & González 2002; Horn et al. 2010). Piscivores with a primarily nektonic diet appeared mainly on the upper and mid slopes of Ampère Seamount and had slightly enriched $\delta^{13}C$ and $\delta^{15}N$ signatures compared to the summit assemblage. The shark species occupied an intermediate trophic position, showing that they are not high level predators, but rather feeding on a variety of predominantly benthopelagic and micronektonic prey.

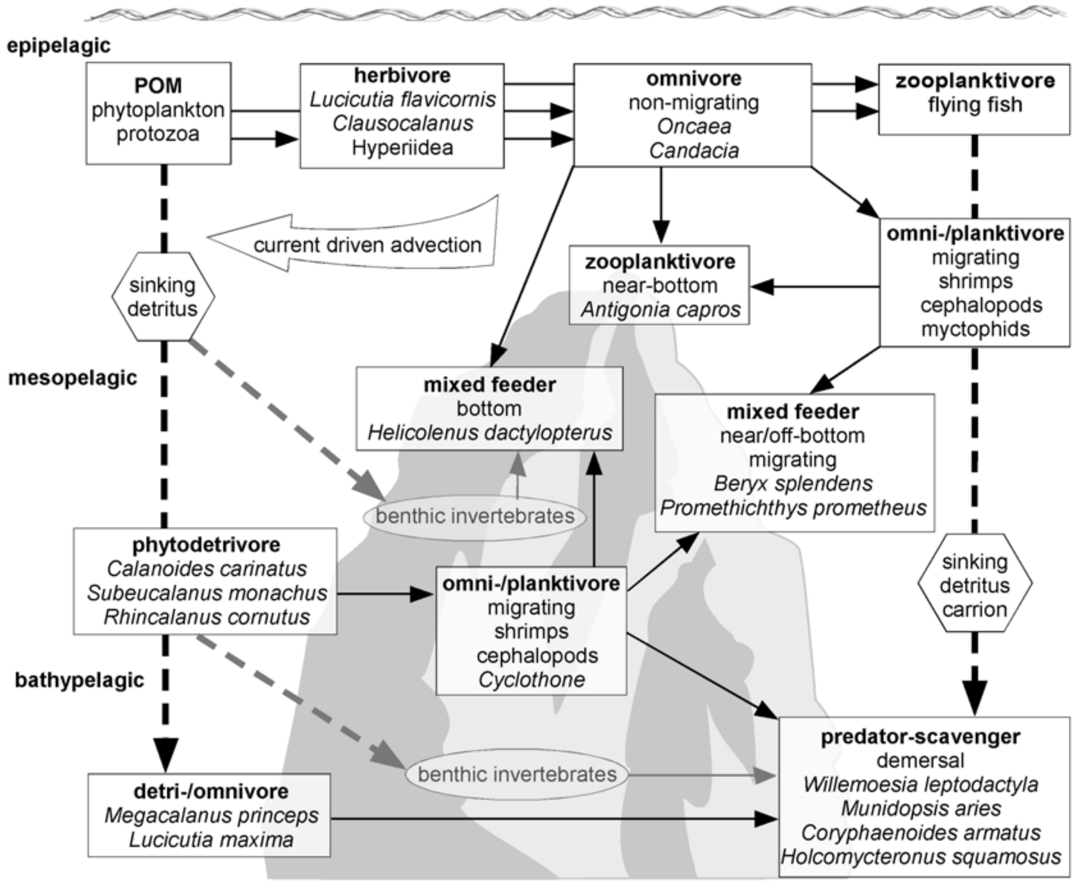

Fig. 9-4. Simplified trophic pathways from the epipelagic to the bathypelagic zone at Senghor Seamount with current-driven advection as the main mechanism for food supply. See Fig. 9-3 for explanations.

At the base of Ampère and on the abyssal plain mainly generalized feeders and predator-scavengers occupying the highest trophic position were caught, but also some species usually classified as plankti-/benthivorous, which had isotope signatures in the same range or even higher than those of the large predator-scavengers. This indicates either strict benthic feeding, as supposed for *Cataetyx laticeps*, on, for example, polychaetes and echinoderms, which have higher $\delta^{13}C$ and $\delta^{15}N$ values than several top predatory fishes in the abyssal North Atlantic (Iken et al. 2001), or that some species are not restricted to zooplanktivorous feeding as earlier assumed, such as the tripodfish *Bathypterois longipes*. Macrourids, the assumed end consumers in the abyssal food web, had unexpectedly low $\delta^{15}N$ values, which can be attributed to their scavenging feeding mode on carrion potentially derived of epipelagic nekton, which have lower $\delta^{15}N$ values than the abyssal benthic prey (Drazen et al. 2008). Within the macrourids a relationship between size and prey preference became obvious in the $\delta^{13}C$ ratios, associated with a higher amount of fish and probably carrion ingested by larger species, whereas the diet of the smaller ones was dominated by crustaceans (see also Martin & Christiansen 1997; Drazen et al. 2008). In general scavenging was observed to play an important role in the diet of the abyssal predatory fishes from the reference sites of Ampère and Senghor, but also for abyssal benthic crabs, verifying a direct trophic pathway from the surface to the deep-sea.

9.6 Conclusions

The differences in the zooplankton communities and the trophic variability between Ampère and Senghor seamounts are rather driven by the large-scale current systems in relation to the spheres of the subtropical and tropical NE Atlantic gyres than by local seamount effects. The zooplankton community at Ampère Seamount reflects the oligotrophic character of the region, while in the vicinity of Senghor the nutrient-rich waters south of the CVFZ feature a significantly higher biomass and respiratory carbon demand. Differences in surface primary production and in the composition of the phytoplankton communities as indicated in stable isotope signatures of POM propagate through the food web also into deeper layers. The contribution of microzooplankton to the total carbon demand emphasizes the general importance of the small-sized zooplankton for the conversion of carbon in the biogeochemical cycle, especially in oligotrophic waters, where they are an important link between small phytoplankton cells and larger planktivorous consumers. Despite possible differences in production and trophic pathways in the surface layers, in the deep-sea the remaining nutritional sources point to a homogenous surface-derived origin and seem to be comparable between both regimes as well as between the seamounts and the open ocean as were biomass, abundance and respiration. The fish fauna of Ampère and Senghor is typical for shelves, seamounts and abyssal regions in the Atlantic and the Mediterranean, pointing out the role of seamounts as *stepping stones* for oceanic dispersal of benthopelagic fishes, particularly of typical shelf and slope species across large distances, for example, between continental margins and mid ocean ridges along the deep Atlantic ocean.

The comparison with the unaffected open ocean reference sites gave no evidence of locally increased secondary production at the seamounts, expressed by high concentrations of zooplankton biomass. Rather, zooplankton biomass was even lower over the seamounts than in the surrounding ocean at times. As compared to Senghor, advected filaments of the CVFZ and the Mauritanian upwelling might cause varying nutritional sources and feeding conditions at the open ocean site, associated with enhanced microzooplankton biomass at times and significant differences in the $\delta^{13}C$ signals. Local current-topography interactions did not raise the total production within the seamount systems in general, but definitely affected the seamount associated communities and controlled their distribution mechanisms. The zooplankton distribution across Ampère Seamount seemed to be mainly driven by topographic blockage and gap formation of diel vertical migrators on the summit, while at Senghor the high proportion of non-migrating zooplankton was mainly controlled by food availability and strongly correlated to the layer of the fluorescence maximum. Enhanced vertical mixing through current-topography interactions near the summit of Senghor was supposed to be the major mechanism bringing nutrients to the surface mixed layer at times, associated with differing isotope signatures and increased dinoflagellate abundance as compared to the open ocean. This potential increase in production was, however, not expressed on higher trophic levels, showing that zooplankton production is likely unrelated to possible local seamount-driven changes in the productivity and biomass of phytoplankton. Since it seems generally unlikely that a Taylor column could persist above Senghor for extended periods due to the regional current regime, and no evidence for any recirculating flow was found over Ampère, nor for isotope signatures derived from autochthonus seamount production, the present results on zooplankton dynamics over both seamounts support the assumption that topography-generated upwelling and trapping is an unlikely mechanism to affect secondary production. Rather, horizontal current-driven advection of planktonic prey was assumed as major factor for the food supply to the resident fauna at Ampère and Senghor seamounts. However, in deeper waters weak near-bottom recirculating flows around Senghor retained larvae close to the seamount and thus Senghor was confirmed as an example for the expected higher retention potential for meroplanktonic larvae in seamount surrounding waters, and as a larval source for benthic invertebrates in the open ocean.

9.7 Perspectives

The present study provides insights into small-scale spatial and temporal variability of micro-and mesozooplankton distribution in relation to hydrographic conditions and to the local and large-scale flow fields at two seamounts in distinct trophic realms. Trophic interactions within zooplankton and micronekton and nutritional links to benthopelagic fishes were identified to elucidate distinct pathways in the pelagic food web. Our results, aiming to contribute to the understanding of processes on biophysical-coupling in seamount ecosystems, point to the need of further sampling effort and methods necessary to verify present assumptions.

Since sampling during a cruise of 3-5 weeks can represent only a snap-shot of a highly dynamic system, a higher temporal solution over a longer time period would be necessary to observe possible hydrodynamic processes and flow features that may not be persistent over the seamount, but affect plankton dynamics at times. The distinct plankton distribution patterns observed in this study may indicate previous current-topography interactions, but these processes cannot be confirmed. The topographic blockage of vertically migrating zooplankton seemed to be of minor importance at the seamounts studied, since zooplankton did not appear in high numbers in bottom-near catches over the summit during the day. However, the bottom-near zooplankton may have been generally undersampled due to the rough topography, where sampling very close to the bottom was not possible using classical plankton nets and epibenthos-sledge like gear would probably get stuck or be damaged, at least on the rocky areas, whereas any bottom contact would in turn destroy the vulnerable seamount biota. The use of optical or pumping devices could be a perspective to complement sampling in the layers within a few metres off the bottom.

Anaylses of the zooplankton composition at the lowest taxonomic level would be necessary for a detailed assessment of possible regional and local differences with respect to distinct water masses and current fields, such as the North and South Atlantic central water or the Mediterranean outflow. Morphological analyses should then be extended by genetics to verify species origin.

Although at least one seamount could be confirmed as larval source in the ocean with larvae retained in seamount surrounding flows, the maintenance on the benthic population remains unknown. For further assessment of the recruitment of benthic invertebrates or their dispersal, long-term experiments on larval settlement would be necessary as well as on larval drift away from the seamount and larval transport between isolated habitats. Drift experiments extended by numerical circulation models, would illustrate the distribution of passive particles in the surrounding flow field and improve our understanding on the mechanisms of oceanic dispersal and the role of seamounts as *stepping stones*. Genetic analyses should be done on larvae and benthic invertebrates to identify possible endemic species and assess connectivity between seamounts and continental margins, elucidating to which extent larval retention leads to speciation among seamount populations, or larval dispersal features species overlap between seamounts.

Estimates on the respiratory carbon demand are important to assess the role of organisms for the production, energy flow and carbon cycle in oceanic systems. In this study respiratory carbon demand was calculated from mean individual weight and habitat temperature using a multiple-regression model according to literature, which can only be an approximation especially for meso- and bathypelagic zooplankton, even if the results agreed well with respiration measurements in the subtropical and tropical NE Atlantic. However, indirect respiration measurements using a biochemical proxy, like the electron transfer system (ETS) activity, which is responsible for oxygen consumption in cell and organism (e.g. Owens & King 1975; Packard 1985; Ikeda et al. 2001), should provide more reliable data, also for specific taxa, and are a practical alternative compared to elaborate direct measurements.

For the identification of food sources and trophic relationships within marine food webs the combination of stomach contents and biochemical markers, such as stable isotopes, is an effective and common method. Stomach content analyses were not done on zooplankton, but would improve the interpretation of the stable isotope data considerably. In further trophic analyses these tools should be extended by additional biochemical markers, such as fatty acids. Since certain fatty acids can only be synthesised by distinct species of phytoplankton and macroalgae, and are transferred along the food chain between consumers (e.g. Dalsgaard et al. 2003), they may considerably help to track primary food sources in a seamount ecosystem and detect their origin, whether they result from autochthonus or allochthonus production. Especially in the oligotrophic region we supposed microzooplankton as important grazers on phytoplankton but also as dietary source for small zooplanktivorous consumers. For the identification of primary food sources and a better understanding of how the protistan and metazoan microzooplankton is linked in the food web, trophic analyses on this community are absolutely necessary in future studies. Another gap in our trophic study is the lack of pelagic fishes and squids, which are supposed to feed directly on macroplankton and micronekton and might be also attracted by the seamount fauna as high level consumers of the pelagic food chain, as well as whales and seabirds as top predators. In addition to the pelagic communities, benthic invertebrates should be included in the trophic analyses for the identification of nutritional sources and pathways, in particular whether the phytodetritus-based food chain relies on single photosynthetic production, or is also influenced by chemosynthetic energy sources in more complex food webs (e.g. Polunin et al. 2001; Drazen et al. 2008; Reid et al. 2012).

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Individual scientific contributions to the multiple-author manuscripts and outline of publications

Manuscript 1 - Zooplankton distribution patterns at two seamounts in the subtropical and tropical NE Atlantic

Anneke Denda & Bernd Christiansen

I conducted the sampling and did all laboratory and data analyses. All text writing was done by me in close cooperation with B. Christiansen, who critically reviewed the manuscript.
The manuscript is published in the peer reviewed journal Marine Ecology 35 (2014) 159-179.

Manuscript 2 - Microzooplankton and the dispersal of meroplanktonic larvae at two seamounts in the subtropical and tropical NE Atlantic

Anneke Denda, Christian Mohn, Helge Wehrmann & Bernd Christiansen

I conducted the sampling and the laboratory and data analyses. H. Wehrmann performed the biomass and taxonomic analyses of the microzooplankton samples from cruise M83/2. C. Mohn provided the ADCP data and contributed the respective methodological section. All other text writing was done by me in close cooperation with B. Christiansen, who critically reviewed the manuscript.
The manuscript is submitted to the peer reviewed Journal of the Marine Biological Association of the UK.

Manuscript 3 - From the epipelagic zone to the abyssal plain: Trophic interactions of zooplankton and benthopelagic fishes at two seamounts in the tropic-subtropical NE Atlantic

Anneke Denda, Benjamin Stefanowitsch & Bernd Christiansen

I developed the concept of this study and conducted the zooplankton sampling and taxonomic analyses. I was involved in the fisheries, taxonomic identification and biometric measurements of the fish species and performed the stomach content analyses. The preparation of the stable isotope samples for measurement was done by B. Stefanowitsch and me. The analyses were run at Biozentrum Klein Flottbek, Universität Hamburg, Hamburg by ourselves under the supervision of Dr. Christoph Reisdorff. All data evaluation and text writing was done by me in close cooperation with B. Christiansen, who critically reviewed the manuscript.
The manuscript will be submitted to a peer reviewed journal.

Manuscript 4 - The fish fauna of Ampère Seamount (NE Atlantic) and the adjacent abyssal plain

Bernd Christiansen, Rui P. Vieira, Sabine Christiansen, Anneke Denda, Frederico Oliveira & Jorge M. S. Gonçalves

I was involved in the sampling, taxonomic identification and biometric measurements of the fish species.
The manuscript is published in the peer reviewed journal Helgoland Marine Research 69 (2015) 13-23.

Manuscript 5 - Demersal fishes from Senghor Seamount and the adjacent abyssal plain (Central Eastern Atlantic)

Rui P. Vieira, Rui Coelho, Anneke Denda, Bettina Martin, Jorge M. S. Gonçalves & Bernd Christiansen

I was involved in the sampling, taxonomic identification and biometric measurements of the fish species as well as in text writing and reviewing of the manuscript.
The manuscript is submitted to the peer reviewed Journal Marine Biodiversity.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift „Zooplankton dynamics, fish zonation and trophic interactions at two seamounts in contrasting regimes of the Eastern Atlantic“ selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Anneke Denda

Hamburg, Juli 2015

Anneke Denda