Trophic interactions at seamounts

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English language evaluation of the Ph.D.-thesis of Stefanie Hirch

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The quality of English grammar and the vocabulary employed by the candidate fulfills the requirement for acceptance as a Ph.D. at the University of Hamburg.

Sincerely

Prof. Dr. Michael St. John

CONTENTS

SUMMARY

In recent years, seamounts have received increasing scientific attention. Although they are perceived as areas of high productivity, biological studies are still rare and little is known about the trophic ecology of seamount ecosystems. These systems are often characterised by dense aggregations of benthopelagic fishes, high biodiversity and high levels of endemism. The goal of the European OASIS project, within which this thesis was embedded, was to further our understanding of seamount ecosystems and their influence on the surrounding ocean through an interdisciplinary approach. The aim of the present thesis is to elucidate aspects of trophic ecology at two seamounts with different summit depths (Seine and Sedlo) in the subtropical NE Atlantic. In the thesis possible influences of the two seamounts on the food sources and diets of selected zooplankton species and on the respiration rates of the zooplankton community are investigated. A further aim of the thesis is to gain insight into the food sources and trophic structures of the epibenthic invertebrate and benthopelagic fish fauna on the summit plateau of Seine Seamount and their nutritional links to the surrounding ocean. Diets and trophic positions were investigated for selected species using fatty acid, stable isotope and gut content analyses. Zooplankton community respiration rates were estimated from electron transfer system (ETS) activity. Suspended particulate organic matter (POM_{susp}) was analysed as trophic baseline of the food web.

Fatty acid and stable isotope trophic markers indicated considerable temporal variability in POM_{susp} composition and zooplankton diets between surveys in November 2003, April 2004 and July 2004. In November, a trophic shift of the epipelagic zooplankton species towards low similar trophic positions compared to April and July was apparent from $\delta^{15}N$ values and suggested a preceding dominance of ^{15}N-depleted food sources. Marker fatty acids of POM_{susp} and the epipelagic zooplankton indicated elevated diatom abundance in April. In contrast to the pronounced temporal differences, spatial differences of POM_{susp} and zooplankton trophic marker signatures between seamount and remote reference sampling locations were small and indicated no seamount-related influence on POM_{susp} compositions or zooplankton diets at the two seamounts. Locally higher zooplankton respiration rates were occasionally observed at both seamounts, but these were not clearly elevated above the high temporal variability.

Trophic marker analyses as well as gut content analysis of the fish species indicated a close link between the pelagic food sources and the epibenthic and benthopelagic fauna on the summit plateau of Seine Seamount. Epibenthic invertebrates were closely linked to the pelagic particulate organic matter production either directly by suspension or deposit feeding or indirectly via the benthic food web through predation on detritivorous benthic primary consumers. The benthopelagic fish fauna was mainly sustained by direct feeding on pelagic prey, while benthic contributions to the diets were small. Pelagic versus benthic feeding was indicated by elevated levels of arachidonic acid (20:4(n-6)) concurrent with low proportions of the zooplankton marker fatty acid 18:1(n-9) in the storage lipids of benthivorous species. The presence of arachidonic acid suggested a possible contribution of rhodophytes as benthic primary food source to the resident seamount community. Epibenthic invertebrate and benthopelagic fish species occurred along a continuum of intermediate trophic positions rather than at discrete trophic levels. This indicated that the food web was dominated by opportunistic species that feed from different trophic levels. Resource partitioning regarding feeding habitats, prey selection and ontogenetic separation was apparent for zooplanktivorous fish species and presumably reduced dietary competition and promoted co-existence of the different species.

Zooplankton respiration rates and trophic marker signatures of POM_{susp} and the zooplankton species gave no indications of persistently enhanced feeding conditions of the zooplankton community at the seamounts compared to the surrounding ocean. The close nutritional link between epibenthic invertebrates and surface organic matter suggested rapid deposition of fresh detritus due to the shallow depth of the seamount summit plateau (~170 m), which might be temporally exhilarated by Taylor column-related downwelling. The lack of larger diel vertically migrating taxa and the dominance of non- or weakly-migrating copepods in the gut contents of zooplanktivorous fish species indicated the absence of enhanced food supply through topographic blockage of diel vertical migrators. The benthopelagic fish fauna, thus, appears to be mainly sustained by current-driven horizontal fluxes of zooplankton prey from the surrounding ocean.

ZUSAMMENFASSUNG

Seeberge gelangten in den letzten Jahren vermehrt in den Fokus der Wissenschaft. Obwohl für diese Ökosysteme allgemein eine hohe biologische Produktivität vermutet wird, gibt es nur wenige biologische Studien, die die Nahrungsökologie der Seebergökosysteme untersuchten. Diese Systeme zeichnen sich oftmals durch Fischreichtum, diverse Lebensgemeinschaften und einen erhöhten Anteil endemischer Arten aus. In einem interdisziplinären Forschungsansatz untersuchte das europäische OASIS-Projekt die Funktionsweise von Seebergökosystemen und deren Einfluss auf den umgebenden Ozean. Die vorliegende Arbeit beleuchtet als Teil des Projektes nahrungsökologische Aspekte an zwei unterschiedlich tiefen Seebergen (Seine und Sedlo) im subtropischen NO-Atlantik. Insbesondere sollten die Nahrungsquellen und Ernährungsweisen ausgewählter Zooplanktonarten und die Respirationsraten des Zooplanktons untersucht werden, um mögliche Einflüsse der Seeberge auf die Gemeinschaft aufzuklären. Zudem sollten die Nahrungsquellen und trophischen Beziehungen der epibentischen Wirbellosen und der benthopelagischen Fischfauna auf dem Gipfelplateau des Seine Seamounts sowie deren Nahrungsverbindung zum umgebenden Ozean aufgezeigt werden. Ernährungsgewohnheiten und trophische Positionen wurden für ausgewählte Arten anhand von trophischen Markern, d.h. Fettsäuren und stabilen Isotopen, und Mageninhaltsuntersuchungen bestimmt. Respirationsraten der Zooplanktongemeinschaft wurden mithilfe der Elektronen-transportsystem-Aktivität ermittelt. Als Basis der Nahrungskette wurde suspendiertes partikuläres Material (POM_{susp}) untersucht.

Untersuchungen der Fettsäuremarker und stabilen Isotope im November 2003, April 2004 und Juli 2004 wiesen auf eine deutliche zeitliche Variabilität in der Zusammensetzung des POM_{susp} und der Ernährungsweise des Zooplanktons hin. Im November zeigte sich im Vergleich zum April und Juli eine Verlagerung der trophischen Positionen des epipelagischen Zooplanktons zu einheitlich niedrigeren trophischen Ebenen. Dies deutet auf eine vorhergehende Dominanz ^{15}N-armer Nahrungsquellen hin. Fettsäuremarker zeigten dagegen eine erhöhte Diatomeen-Abundanz im April an. Im Gegensatz zu den ausgeprägten zeitlichen Unterschieden waren die räumlichen Unterschiede der trophischen Marker des POM_{susp} und der Zooplanktonarten zwischen seebergnahen Stationen und seebergfernen

Referenzstationen gering. Somit wurden keine Anzeichen für seebergbedingte Einflüsse auf die Zusammensetzung des POM_{susp} oder auf die Ernährungsweise des Zooplanktons an den zwei Seebergen gefunden. Zeitweise wurden lokal erhöhte Respirationsraten des Zooplanktons an den beiden Seebergen beobachtet, die jedoch nicht deutlich über der hohen zeitlichen Variabilität lagen.

Die Analysen der trophischen Marker und die Mageninhaltsanalysen der Fischarten deuten auf eine enge Verknüpfung zwischen den pelagischen Nahrungsquellen und der epibenthischen und benthopelagischen Fauna auf dem Gipfelplateau des Seine Seamount hin. Die epibenthischen Wirbellosen waren eng mit der Produktion des pelagischen partikulären organischen Materials verbunden, entweder direkt als Suspensions- oder Detritusfresser, oder indirekt über das benthische Nahrungsnetz durch Prädation an benthischen Detritusfressern. Die benthopelagische Fischfauna ernährte sich hauptsächlich direkt von pelagischer Beute, während der Anteil an benthischer Nahrung gering war. Eine benthische Ernährungsweise war durch einen erhöhten Gehalt an Arachidonsäure (20:4(n-6)) bei gleichzeitig niedrigen Mengen des Zooplanktonmarkers 18:1(n-9) in den Speicherlipiden benthivorer Arten gekennzeichnet. Das Vorhandensein arachidonischer Säure deutete auf einen möglichen Beitrag von Rhodophyten als benthische Nahrungsquelle für die ansässige Seeberggemeinschaft hin. Die trophischen Positionen der epibenthischen Wirbellosen sowie der benthopelagischen Fische lagen im Übergangsbereich zwischen den trophischen Ebenen eng beieinander. Dies deutet auf die Dominanz opportunistischer Arten im Nahrungsnetz hin, die sich von verschiedenen trophischen Ebenen ernähren. Eine Ressourcenaufteilung bezüglich des Nahrungshabitats, der Beuteselektion und der Trennung ontogenetischer Stadien wurde bei den zooplanktivoren Fischarten festgestellt. Sie reduziert vermutlich die Nahrungskonkurrenz und begünstigt dadurch eine Koexistenz verschiedener Arten.

Weder die Respirationsraten der Zooplanktongemeinschaften noch die trophischen Markersignaturen des POM_{susp} und der Zooplanktonarten gaben einen Hinweis auf dauerhaft verbesserte Nahrungsbedingungen der Zooplanktongemeinschaft an den beiden Seebergstandorten im Vergleich zu den ozeanischen Referenzstationen. Der enge Nahrungsfluss zwischen epibenthischen Wirbellosen und oberflächennahen organischem Material deutete auf eine schnelle Ablagerung von frischem Detritus

aufgrund der geringen Tiefe des Gipfelplateaus (ca. 170 m) von Seine Seamount hin. Dieser könnte zeitweilig durch einen Taylorsäulen-bedingten Abtrieb beschleunigt werden. Das Fehlen größerer vertikal wandernder Zooplanktonarten und die Dominanz von nicht oder schwach vertikal wandernden Copepoden in den Mageninhalten der zooplanktivoren Fische deutet darauf hin, dass keine erhöhte Nahrungszufuhr durch das Blockieren abwärtswandernder Vertikalwanderer an der Oberfläche des Seebergs stattfindet, sondern dass der Hauptmechanismus der Nahrungszufuhr zu den benthopelagischen Fischen auf Advektion von Zooplanktonbeute aus dem umgebenden Ozean beruht.

GENERAL INTRODUCTION

SEAMOUNT ECOSYSTEMS

Seamounts are undersea topographic features of mainly volcanic origin, which rise steeply from the sea floor for at least 1000 m (Menard 1964). They are common in all ocean basins and estimated numbers using satellite altimetry ranged from 70,000 to 100,000 with more than 50,000 of them situated in the Pacific (Wessel 1997) and more than 800 in the Atlantic (Epp and Smoot 1989).

As topographic obstacles, seamounts rise high through the water column into the open ocean where they interact with the prevalent ocean currents and tidal currents and create local changes in the hydrography. Due to the great diversity in size and shape of seamounts, these hydrographic effects are complex and include closed circulation cells known as Taylor columns, the formation of trapped waves, the amplification of tidal currents and locally enhanced turbulent mixing (e.g., Roden 1987, Kunze and Toole 1997, Beckmann and Mohn 2002). Taylor columns (or Taylor caps in stratified hydrographic conditions) are anti-cyclonic circulation cells trapped to the seamount summit region. Taylor columns generate upwelling above the flanks of the seamount, which may enhance local productivity, if the upwelling penetrates the euphotic zone, and downwelling in the centre above the summit, and they may enhance local particle retention (e.g., Roden 1987, Mullineaux and Mills 1997, Beckmann and Mohn 2002).

Seamounts are often associated with high biomass and diverse species assemblages, including species-rich benthic communities dominated by suspension feeders and dense aggregations of benthopelagic fishes (e.g., Rogers 1994, Richer de Forges *et al.* 2000, Koslow *et al.* 2001) as well as elevated abundances of zooplankton and micronekton (e.g., Genin 2004). Aggregations of pelagic fishes, sea turtles and marine mammals in the vicinity of seamounts further contribute to the local diversity and biomass (e.g., Rogers 1994, Klimley *et al.* 2005). Although commercial fisheries have exploited seamounts for more than 50 years, the trophic mechanisms supporting such enhanced biomasses at seamounts are still being discussed. Several hypotheses have been developed to explain how high standing stocks associated with seamount ecosystems

are sustained despite the often impoverished nutritional conditions of the ambient oceanic regions:

(1) The hypothesis of locally enhanced autochthonous seamount productivity proposed that a combination of Taylor column-generated nutrient upwelling and particle-retention above the seamount could result in a local increase in primary and secondary production that could sustain resident fish populations (Uda and Ishino 1958). Local upwelling and elevated chlorophyll concentrations related to Taylor column activity have been observed above a number of seamounts (Genin and Boehlert 1985, Dower *et al*. 1992, Dower and Mackas 1996, Mouriño *et al*. 2001), but support for the local enhancement of zooplankton secondary production remained weak (Uda and Ishino 1958, Genin and Boehlert 1985) and appeared inadequate to sustain large fish aggregations observed in the vicinity of seamounts (Tseitlin 1985, Koslow 1997).

(2) The sound-scattering layer interception hypothesis (Isaacs and Schwartzlose 1965) was based on acoustic records showing an encounter between descending scattering layers and the elevated topography off Baja California. The authors proposed an increased food supply for resident predators due to topographic blockage and trapping of the vertically migrating zooplankton and micronekton, which formed the sound-scattering layer, during descend. This mechanism has been suggested to provide sufficient prey to maintain fish aggregations at seamounts (Rogers 1994, Parin *et al.* 1997, Koslow 1997, Genin 2004) and was supported by gut content analyses of rockfishes (Genin *et al.* 1988) and pelagic armourheads (Seki and Somerton 1994) resident on seamounts, which contained vertically migrating zooplankton as dominant prey in their guts.

(3) The large-scale entrapment of water by topographically rectified currents could accumulate production advected to the area (Beckmann and Mohn 2002) and retain larvae around seamounts, further enhancing benthic recruitment (Mullineaux and Mills 1997, Beckmann and Mohn 2002), and possibly increase the downward flow of particulate organic matter to benthic communities over the centre of the seamount (Mullineaux and Mills 1997).

(4) Enhanced fluxes of suspended food particles advected to the seamounts from adjacent oceanic regions due to the amplification of near-bottom flows have also been

suggested to sustain high densities of resident seamount fauna (Tseitlin 1985, Genin *et al.* 1988, Koslow 1997, Genin 2004).

Considering the complexity of possible interactions between the seamount topography and the surrounding hydrography and biota, it is probable that more than one of the above mentioned mechanisms are operative in the vicinity of seamounts and that they may vary in time.

Seamounts are generally perceived as areas of high endemicity. Reported levels of endemism in benthic seamount fauna ranged from 15 % (Wilson and Kaufmann 1987) to potentially up to 34 % for individual seamounts (Richer de Forges *et al.* 2000). It has been hypothesised that mechanisms isolating seamount from other deep-sea habitats, like oceanic currents that trap larvae on seamounts and the presence of hard substrate habitats in the deep-sea, may lead to genetic isolation and enhanced speciation. However, recent studies have questioned the hypothesis of high seamount endemicity (McClain 2007, McClain *et al.* 2009). Seamounts are also thought to play a potential role as stepping stones for the trans-oceanic dispersal of continental shelf species by providing shallow topographic regions in the open ocean environment.

The association of commercially valuable fish species with seamounts resulted in the development of seamount trawling and long lining fisheries throughout the world's oceans (Clark 1999, Koslow *et al.* 2000). Many of the benthopelagic seamount-associated deep-sea fishes are noted for their extreme longevity (e.g., orange roughy 100+ years) and low productivity (Koslow 1996, 1997, Koslow *et al.* 2000). These life-history characteristics and the spatial restriction to often isolated seamount habitats render them exceptionally vulnerable to over fishing and stock collapse and many seamount fisheries have since been over exploited (Clark 1999, Koslow *et al.* 2000). Trawl fisheries have also been shown to have potentially severe impacts on the benthic fauna of seamounts (Koslow *et al.* 2000). The vulnerability of the seamount ecosystem to over exploitation emphasised the need for protection measures, such as marine protected areas for seamounts and management plans for sustainable exploitation of seamount resources. Improving scientific knowledge about the functioning of the seamount ecosystem is a prerequisite for the development of future conservation measures.

BIOCHEMICAL MARKERS IN TROPHIC ANALYSES

Biochemical markers, such as stable isotopes and fatty acids, have been used extensively in studies of trophic ecology in order to gain insight into energy flows through food webs, including marine systems (e.g., Davenport and Bax 2002, Dalsgaard *et al.* 2003). In contrast to gut content analysis, which provides information on recent food ingested by the consumer, biochemical markers provide an analysis of assimilated diet integrated over time.

Isotopic signatures of naturally occurring stable isotopes, i.e. the ratio of the rare heavier isotope to the common lighter isotope, change from prey to predator during chemical reactions of metabolic processes due to different reacting rates of similar molecules of slightly different mass (Peterson and Fry 1987). The different reacting rates result in the accumulation of the heavier isotope in the consumer, due to a preferential loss of lighter isotopes during respiration and excretion, and lead to a stepwise enrichment between prey and consumer tissue, termed trophic fractionation. Trophic fractionation occurs in a predictable way for the different elements and can be used to evaluate carbon sources and trophic position of an organism (e.g., Peterson and Fry 1987, Vander Zanden and Rasmussen 2001, Post 2002). The carbon stable isotopic composition of organisms ($\delta^{13}C$) changes little (< 1 ‰) between trophic levels and is used to evaluate the sources of carbon (DeNiro and Epstein 1978, 1981, Peterson and Fry 1987, Michener and Schell 1994). The nitrogen stable isotopic composition ($\delta^{15}N$), on the other hand, is typically enriched by 3-4 ‰ (average 3.4 ‰) per trophic level (Minagawa and Wada 1984). In relation to a trophic baseline value (generally representing primary producers) $\delta^{15}N$ is used to determine the trophic position of an organism.

The use of fatty acids biomarkers to trace predator-prey relationships in the ocean is based on the observation that particular fatty acids can only be biosynthesised by certain phytoplankton and macroalgal species and that these fatty acid patterns are transferred conservatively from primary producers to their consumers and among consumers (Dalsgaard *et al.* 2003 and references therein). Polar lipids (mainly phospholipids) have been traditionally viewed as structural lipids in biomembranes, while neutral lipids are generally thought to have a storage role (Hagen and Auel 2001, Lee *et al.* 2006, Kattner *et al.* 2007). In contrast to the conservative fatty acid composition of structural lipids of

consumers, which are relatively independent of dietary input, the fatty acid profiles of neutral lipids, which are used for energy storage, are readily influenced by dietary input (Sargent and Henderson 1995). Fatty acid biomarkers for marine primary producers are for example 16:1(n-7) and 20:5(n-3), which are characteristic for diatoms, while dinoflagellates produce generally higher amounts of 18:4(n-3) and 22:6(n-3) fatty acids. Oleic acid 18:1(n-9) is enriched in secondary consumers and is often used as a marker for carnivorous feeding (reviewed by Dalsgaard *et al.* 2003). Ratios of fatty acid biomarkers provide further indications on the feeding history of organisms. For example, the ratio of 16:0/16:1(n-7) fatty acids, which is higher in diatoms than other phytoplankton groups, has been applied to discriminate between diatom versus flagellate feeding (e.g., St. John and Lund 1996, Auel *et al.* 2002). The ratio 18:1(n-9)/18:1(n-7) has been frequently used to estimate the degree of carnivory versus herbivory (Graeve *et al.* 1997, Schmidt *et al.* 2006).

ELECTRON TRANSFER SYSTEM ACTIVITY AS PROXY FOR ZOOPLANKTON RESPIRATION

The assessment of respiration rates in planktonic communities is important for estimating energy flow in marine ecosystem and the determination of zooplankton-community respiration provides a useful indication of secondary production (Owens and King 1975). Direct determination of respiration usually involves the incubation of zooplankton in a controlled environment, which is time consuming and might be impractical when large and varied populations or deep-sea organisms are involved. Indirect respiration estimates using biochemical methods, like the electron transfer system (ETS) activity, offer a more practical alternative in these cases.

The electron transfer system is situated in the mitochondrion and chloroplast of eucaryotes and in the plasma membrane of procaryotes. It consists of a series of carrier molecules, which pass electrons from a high-energy compound to oxygen, the final low-energy electron acceptor. Consequently, its activity is responsible for oxygen consumption by both the cell and organism, and can be used as a biochemical proxy for respiration (e.g., Packard 1985, Ikeda *et al.* 2000, Giorgio and Williams 2005). The ETS activity is measured under substrate saturation and the method, thus, estimates the maximum overall activity of the enzymes associated with the respiratory electron

transfer system (Packard 1985). These *in vitro* measured rates might be higher than actual physiological rates in the field, where limitation of intracellular substrates can reduce enzyme activities (e.g., under low food conditions; Hernández-León and Gómez 1996). Potential respiratory oxygen consumption rates from ETS activity measurements need, therefore, to be converted to actual *in vivo* zooplankton respiration by using empirically determined respiration to ETS ratios (King and Packard 1975a, 1975b, Hernández-León and Gómez 1996).

The ETS activity is a measure for the potential of organisms to meet the physiological demands associated with different levels of activity. If physiological demands exceed the biochemical potential, the cells may adapt to the new situation by *de novo* synthesis of enzymes to increase the activity of the ETS (Ikeda *et al.* 2000). Important factors influencing respiration rates are, next to temperature and body size, the level of feeding activity and locomotion, together with the specific dynamic action (SDA), which describes the energy required mainly for growth (e.g., Ikeda *et al.* 2000, 2001 Hernández-León and Ikeda 2005, Thor 2000). A close correlation between respiration rates and ingestion rates of different copepod species has been observed in several studies (Lampert 1986, Thor 2000, Schmoker and Hernández-León 2003), and it was suggested that feeding and related swimming activity are responsible for the observed increase in respiration rate at increasing food levels. Zooplankton species have been found to react rapidly to increased food availability with increased respiratory intensity after prolonged time of starvation (Kiørboe *et al.* 1985, Hernández-León and Ikeda 2005) and to decreased food availability with a progressive decrease in respiration rates (Ikeda *et al.* 2000; Hernández-León and Ikeda 2005). Increases in zooplankton respiration rates determined from ETS activity associated with higher indices of grazing and primary productivity have been observed during phytoplankton blooms (Hernández-León *et al.* 2004), in cyclonic eddies (Hernández-León *et al.* 2001) and in ice-edge and frontal zone regions (Schalk 1990).

FOCUS OF THE PRESENT STUDY

The focus of this study was to elucidate nutritional sources and trophic interactions of zooplankton, epibenthic invertebrates and benthopelagic fishes within seamount food webs, and to investigate nutritional pathways linking the resident seamount fauna to the

surrounding ocean. Electron transfer system (ETS) activity as well as a combined method approach of fatty acid, stable isotope and gut content analyses were used to gain insight into the trophic ecology of the seamounts. Zooplankton-community respiration rates, estimated from ETS activities, and zooplankton trophic marker signatures were analysed at seamount and farfield reference locations of Seine and Sedlo Seamounts to detect possible seamount-related differences in feeding conditions. Trophic interactions of the resident epibenthic invertebrate and benthopelagic fish fauna were studied on the summit plateau of Seine Seamount using trophic marker and gut content analyses. Both investigated seamounts are situated within the oligotrophic biogeochemical province of the eastern North Atlantic Subtropical Gyre (NASE; Longhurst *et al.* 1995, 1998) (Fig. 1). Seine Seamount is located northeast of Madeira and is a single summit cone-shaped seamount with a summit plateau depth of about 170 m. Sedlo Seamount is located north of the Azores and is composed of three peaks, of which the shallowest one, with a summit depth of about 750 m, was investigated.

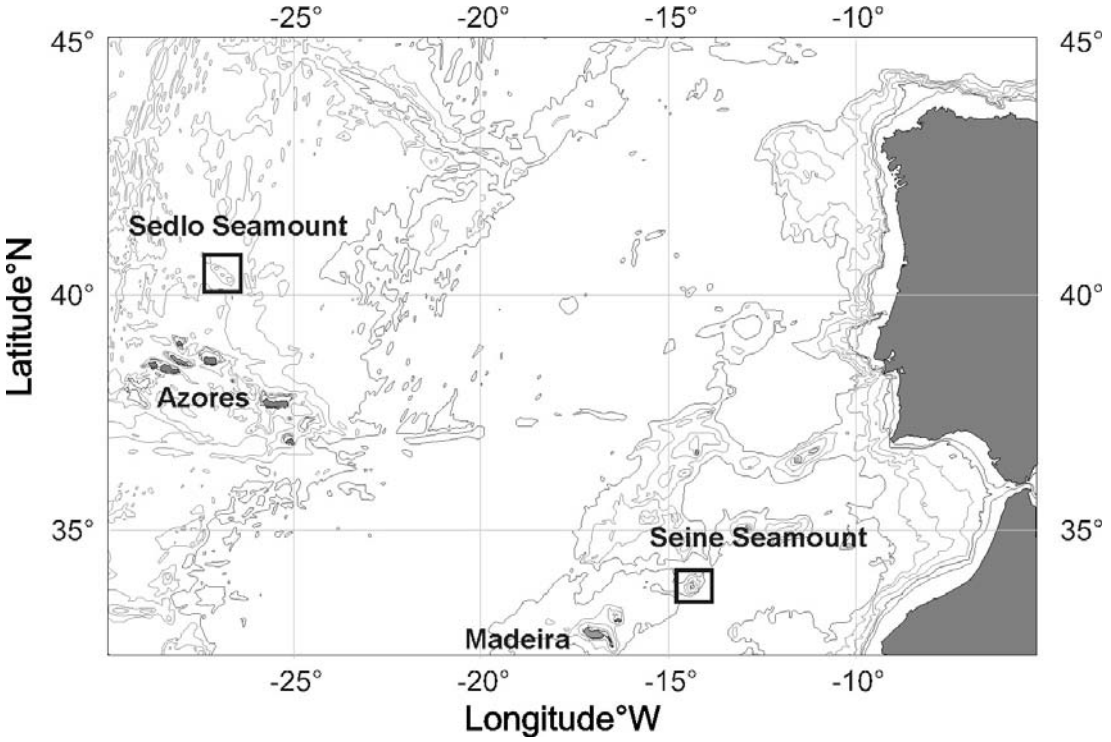

Fig. 1. Locations of the investigated seamounts in the NE Atlantic.

The following chapters focus on the respiration rates of the zooplankton community and, separately for the different faunal groups, on the trophic interactions of selected zooplankton, epibenthic invertebrate and benthopelagic fish species in relation to the seamount habitat.

In **Chapter II** "Zooplankton metabolism and carbon demand at two seamounts in the NE Atlantic", temporal and spatial differences in zooplankton-community respiration rates, estimated from electron transfer system (ETS) activity, were analysed at seamount and farfield reference locations of Seine and Sedlo Seamounts. The study specifically addressed the question whether zooplankton respiration rates at the seamounts support the hypothesis of locally enhanced productivity. If, according to the hypothesis, higher primary productivity at seamounts would offer higher food concentration to the local zooplankton, biomass-specific respiration rates, carbon demand and ultimately biomass of the local zooplankton standing stock would be expected to be enhanced compared to the surrounding open ocean.

Chapter III "Food sources and diets of zooplankton at two seamounts in the NE Atlantic: Are there seamount effects?" is focussed on the temporal and spatial differences in the suspended particulate organic matter compositions and in the diets and trophic positions of selected epi- and mesopelagic zooplankton species at Seine and Sedlo Seamounts. Possible seamount-related influences were investigated using stable isotope and fatty acid biomarker analyses. Special regard was given to the hypothesis of increased autochthonous production at seamounts and its potential influence on the local phytoplankton composition and zooplankton diets compared to the surrounding ocean.

In **Chapter IV** "Feeding ecology and food sources of selected epibenthic invertebrates on the summit plateau of Seine Seamount", the diets and trophic positions of epibenthic invertebrate species were investigated with respect to nutritional links to the pelagic food sources. Diets of the epibenthic invertebrates were analysed using stable isotope and fatty acid trophic markers and were compared to trophic marker signatures of suspended particulate organic matter and pelagic organisms sampled in the water column above the seamount.

The **Chapter V** "Food sources and trophic interactions of benthopelagic fish species on the summit plateau of Seine Seamount, NE Atlantic" analyses the diets and trophic

positions of benthopelagic fish species and their potential prey using the combined approach of gut content, stable isotope and fatty acid analyses. The study aimed to elucidate the nutritional link sustaining the benthopelagic fish community with special respect to the sound scattering layer interception hypothesis as mechanism of enhanced food supply.

In **Chapter VI** "The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: Composition, population structure and diets", the species composition, abundance and biomass of the benthopelagic fish assemblage are studied and the population structure and gut contents of abundant species are analysed.

ZOOPLANKTON METABOLISM AND CARBON DEMAND AT TWO SEAMOUNTS IN THE NE ATLANTIC

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ABSTRACT

Zooplankton metabolic rates, determined from electron transfer system (ETS) activity, were studied at two seamounts (Seine: 34°N, 14°W, summit depth ~170 m; Sedlo: 40°N, 27°W, summit depth ~750 m) of the NE Atlantic during three cruises in November 2003, April 2004 and July 2004. ETS activity and respiratory carbon demand were measured for samples taken at seamount and open ocean locations in order to probe the hypothesis of locally-enhanced seamount productivity. ETS activity and biomass revealed no consistent diel patterns of feeding activity and vertical migration at Seine and Sedlo Seamounts. Spatial differences of biomass-specific ETS activity were observed at both seamounts and coincided with differences in food abundance and quality. At Seine Seamount in April 2004, biomass-specific ETS activity was on average higher at the seamount locations compared to the open ocean, though the enhancement was of a lower magnitude than spatial and temporal variability and had no apparent influence on zooplankton respiratory carbon demand or biomass. A persistent pattern of reduced zooplankton biomass above the summit location at Seine Seamount in April 2004 and July 2004 resulted in a local reduction of respiratory carbon demand. At Sedlo Seamount in November 2003, large spatial differences in biomass-specific ETS activity observed at the seamount locations resulted in a large range of respiratory carbon demand at the seamount, but were not reflected in zooplankton biomass. The depth-integrated (0-150 m) median respiratory carbon demand of the zooplankton community estimated from day and night hauls was 2.1 mg C m^{-2} d^{-1} at Seine Seamount (range: 0.3 to 6.3) and 2.9 mg C m^{-2} d^{-1} at Sedlo Seamount (range: 1.6 to 12.0). The sporadic nature and low magnitude of locally higher zooplankton respiration rates at the

seamounts, which did not result in locally higher zooplankton standing stock biomass, lead us to reject the hypothesis that locally enhanced seamount productivity provides an autochthonous food supply to the resident fauna at Seine and Sedlo Seamounts. Instead, we conclude that the fauna at both seamounts are more likely supported by advection of food from the surrounding ocean.

Keywords: Zooplankton, Seamounts, Metabolism, ETS, North Atlantic, Sedlo, Seine

1. INTRODUCTION

Seamounts are common topographic features in all ocean basins (Smith and Jordan 1988, Epp and Smoot 1989) and a number of them have been found to support high abundances of demersal and epibenthic fish (Uda and Ishino 1958, Parin *et al*. 1997, Rogers 1994). Several hypotheses have been proposed as to how these dense fish populations are maintained, particularly in areas where the primary production is apparently insufficient to meet their metabolic requirements. These hypotheses are based on interactions between seamounts and the surrounding open ocean current regime and on the resulting changes in local hydrographic conditions (Roden 1987, Gonzales *et al*. 2001). Uda and Ishino (1958) first proposed that a combination of nutrient upwelling and particle retention by Taylor columns, i.e. an anti-cyclonic circulation cell trapped to the seamount summit region (e.g. Beckmann and Mohn 2002), can increase local primary production which would promote local secondary production that, in turn, would support local nektonic populations. Locally elevated chlorophyll concentrations have been observed above a number of seamounts (Dower *et al*. 1992, Genin and Boehlert 1985, Dower and Mackas 1996, Mourino *et al*. 2001), but support for the enhancement of zooplankton secondary production remains weak (Uda and Ishino 1958, Genin and Boehlert 1985). The trophic blockage hypothesis suggests that the trapping of diel vertically migrating zooplankton through advection at seamounts leads to enhanced availability of zooplankton, which can be easily consumed by benthic and bentho-pelagic organisms including fish (Isaacs and Schwartzlose 1965, Koslow 1997, Genin *et al*. 1988, Wilson and Boehlert 2004, Genin 2004, Haury *et al*. 2000). Aggregations of zooplankton might also be driven by behavioural response to vertical water mass movement caused by topographic interaction with ocean currents, when zooplankton swim vertically in order to maintain their depth (Genin 2004).

In this study, we investigated zooplankton metabolic rates at two seamounts in the northeast Atlantic to find possible evidence for locally increased primary and secondary production of plankton at seamounts. Enhanced primary productivity at seamounts would offer locally higher food concentration to the zooplankton community compared to the surrounding ocean waters. The level of feeding and animal activity, together with the specific dynamic action (SDA), which describes the energy required mainly for growth (Thor 2000), are important factors influencing respiration rates (e.g. Lampert 1984, Ikeda *et al*. 2000, Hernández-León and Ikeda 2005b), next to temperature and body size (Ikeda 1985, Ikeda *et al*. 2001, Hernández-León and Ikeda 2005b). A close correlation between respiration rates (measured by oxygen consumption in a flow through system) and ingestion rates (measured by gut fluorescence) of different copepod species has been observed in several studies (Lampert 1986, Thor 2000, Schmoker and Hernández-León 2003), and suggests that feeding and related swimming activity are responsible for the observed increase in respiration rate at increasing food levels. Zooplankton species have been found to react rapidly to increased food availability, with increased respiratory intensity after prolonged time of starvation (Kiørboe *et al.* 1985, Hernández-León and Ikeda 2005b) and to decreased food availability, causing starvation, with a progressive decrease in respiration rates (Ikeda *et al*. 2000; Hernández-León and Ikeda 2005b).

In subtropical gyres, many epipelagic copepod species, which constitute the most abundant group of the mesozooplankton (e.g. Head *et al*. 2002, Huskin *et al*. 2001a), appear to be limited in their abundance by predominantly low food availability that is hardly sufficient for metabolic needs and reproduction (Paffenhöfer *et al*. 2006). If increased local food availability were to occur, zooplankton respiration rates in the vicinity of seamounts would be expected to be enhanced compared to the surrounding open ocean, and to result in a local increase in the respiratory carbon demand of the zooplankton community. Increases in zooplankton respiration rates and indices of grazing associated with increased primary productivity have been observed in oligotrophic oceanic waters, e.g. around the Canary Islands during phytoplankton blooms (Hernández-León *et al*. 2004) and in cyclonic eddies (Hernández-León *et al*. 2001b), as well as in Antarctic (Schalk 1990) and temperate regions (Conover and Corner 1968).

The objectives of this study, which to our knowledge is the first to report on zooplankton metabolic rates in the vicinity of seamounts, were:

i. To determine zooplankton respiration rates from locations above Seine and Sedlo Seamounts and from far field open ocean locations, not influenced by topography in order to detect possible differences associated with the seamounts.

ii. To assess how these differences may vary on a spatial scale (i.e. between seamount locations) and on a temporal scale (between sampling periods). A specific question addressed was, "do zooplankton respiration rates at the seamounts support the theory of locally enhanced productivity?"

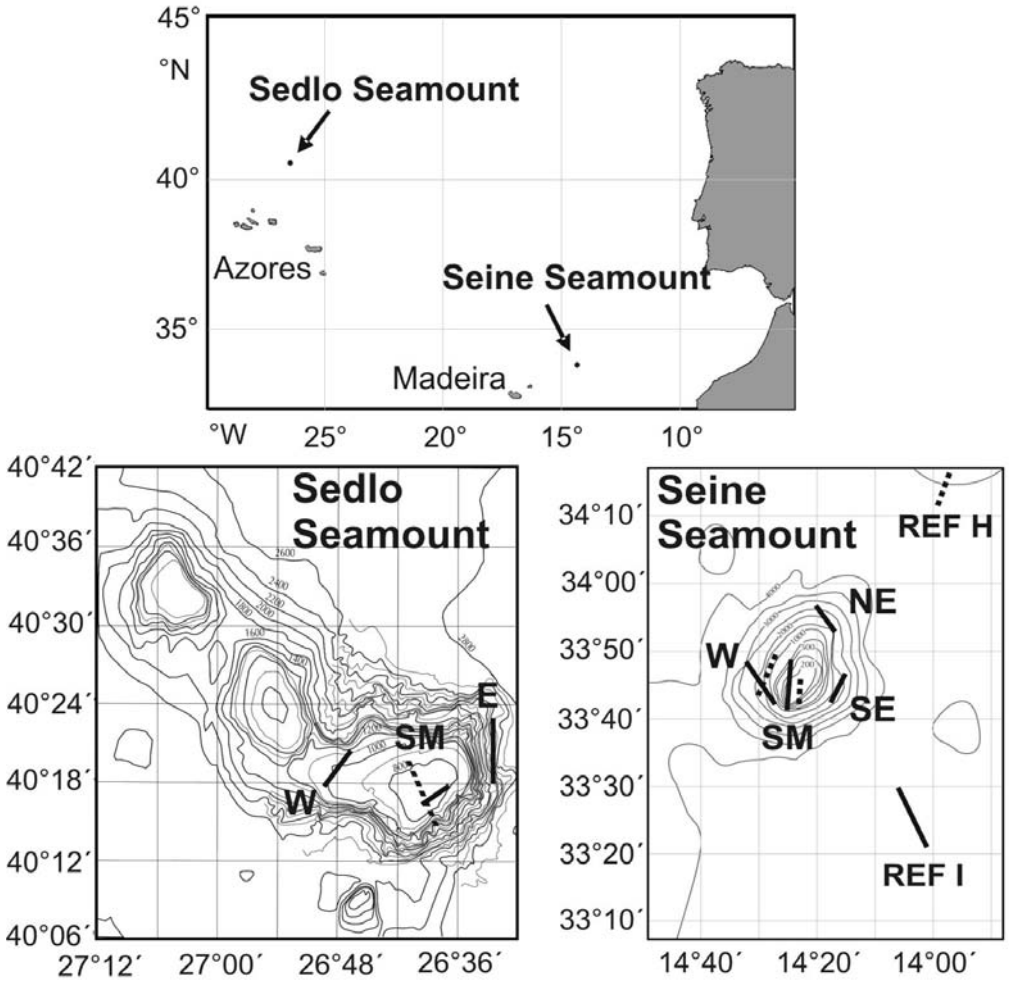

Figure 1. Location and bathymetry of Sedlo Seamount and Seine Seamount. The locations of the MOCNESS zooplankton hauls (Table 1) are shown for Sedlo Seamount in November 2003 (solid line) and July 2004 (broken line) and for Seine Seamount in April 2004 (solid line) and July 2004 (broken line). Haul locations are indicated as SM for the summit and E (east), NE (northeast), SE (southeast), and W (west) for the slope locations. REF H and REF I indicate the reference locations for Seine Seamount. The reference location for Sedlo Seamount is located outside the map at 40.0°N, 26.4°W.

2. MATERIALS AND METHODS

This investigation was part of an interdisciplinary study around two North Atlantic seamounts, Seine and Sedlo, within the framework of the European Project OASIS (OceAnic Seamounts: an Integrated Study) (Christiansen and Wolff, 2009). Both seamounts are located in the oligotrophic regime of the same biogeochemical region: the eastern North Atlantic Subtropical Gyre province (NASE). Seine Seamount is located northeast of Madeira (33°50'N - 14°20'W) and is a single summit cone-shaped seamount which rises from more than 4000 m to a summit plateau at ~170 m. Sedlo Seamount is located north of the Azores (40°25'N - 26°55'W) and is composed of 3 peaks, of which we investigated the shallowest that has a summit depth of ~750 m (Fig.1).

Table 1. Sampling data for MOCNESS zooplankton hauls.

Haul	Date	Sampling time (UTC)	Day/ Night	Seamount	Location	Sampling depths (m) horizontal samples
Meteor 60/1, November 2003						
M1	21./22.11.2003	23:40 - 02:38	N	Sedlo	E Slope	1000, 500, 50
M2	22.11.2003	14:00 - 16:46	D	Sedlo	E Slope	500, 300, 50
M3	23.11.2003	16:15 - 18:10	D	Sedlo	Summit	700
M4	24.11.2003	02:15 - 03:22	N	Sedlo	Summit	700, 500, 300, 50
M6	25.11.2003	14:37 - 17:02	D	Sedlo	W Slope	500, 50
M7	26.11.2003	02:40 - 04:41	N	Sedlo	W Slope	1000, 500, 300, 50
M9	29.11.2003	02:00 - 05:26	N	Sedlo	Reference	500, 50
M10	29.11.2003	13:50 - 17:30	D	Sedlo	Reference	300, 50
Poseidon 309, April 2004						
P1	28.03.2004	10:44 - 14:05	D	Seine	Reference I	1000, 500, 300, 50
P2	29.03.2004	13:34 - 16:48	D	Seine	Summit	150, 50
P3	29./30.03.2004	23:57 - 02:05	N	Seine	Summit	150, 50
P4	01.04.2004	10:36 - 13:20	D	Seine	W Slope	1000, 500, 300, 50
P5	01.04.2004	21:04 - 23:16	N	Seine	W Slope	1000, 500, 300, 50
P6	02./03.04.2004	21:22 - 00:04	N	Seine	Reference I	1000, 500, 300, 50
P7	03.04.2004	21:25 - 23:54	N	Seine	NE Slope	1000, 500, 300, 50
P8	04.04.2004	12:42 - 14:51	D	Seine	NE Slope	1000, 500, 300, 50
P9	05./06.04.2004	22:40 - 00:15	N	Seine	SE Slope	1000, 500, 300, 50
P10	06.04.2004	09:57 - 11:09	D	Seine	SE Slope	1000, 500, 300, 50
Discovery 282, July 2004						
D2	09.07.2004	03:01 - 04:02	N	Seine	Summit	150, 50, 50
D4	10.07.2004	12:51 - 16:10	D	Seine	Reference H	1000, 500, 300, 50
D5	16.07.2004	23:10 - 01:53	N	Seine	Reference H	1000, 500, 50
D6	17.07.2004	07:08 - 10:19	D	Seine	W Slope	1000, 500, 50
D7	17.07.2004	12:43 - 13.37	D	Seine	Summit	150, 50
D8	17.07.2004	20:13 - 23:13	N	Seine	W Slope	1000, 500, 50
D9	22.07.2004	14:59 - 17:06	D	Sedlo	Summit	700, 500, 50
D10	22.07.2004	22:10 - 01:14	N	Sedlo	Reference	1000, 500, 50

Zooplankton samples were taken during 3 cruises, in November 2003 (11th November – 6th December 2003; FS *Meteor*, M60/1), April 2004 (25th March – 8th April; FS *Poseidon*, P309) and July 2004 (30th June – 1st August; RSS *Discovery*, D282). Zooplankton were sampled using a MOCNESS multiple net system (Wiebe *et al*. 1985) with a 1 m^2 opening. The MOCNESS was equipped with nets of 0.333 mm mesh size and a CTD as well as a flowmeter and inclinometer to measure the volume of water sampled. Seine Seamount was sampled in April and July, while Sedlo Seamount was sampled in November and July (Table 1). At each seamount, day and night hauls were taken at locations above the summit and slopes of the seamounts and at open ocean reference locations, which were outside the influence of the seamounts (Fig.1, Table 1). The influence of a seamount on the hydrodynamic regime acts over a distance of some 20-40 km from the seamount centre (Beckmann and Mohn 2002), therefore the far field sampling sites at Seine and Sedlo Seamounts were chosen at distances of 40 km and 65 km from the seamounts, respectively.

Zooplankton for measurement of the respiratory activity (electron transfer system [ETS] activity) were sampled at discrete depth layers (50, 300, 500, 1000 m and close to the summit sea floor at Seine (~150 m) and Sedlo (~700 m) using horizontal tows (Table 1). Samples for zooplankton standing stock biomass were taken between these depths in oblique stratified tows with depth intervals of 200 m below 600 m, 100 m from 600-100 m depth, and 50 m in the surface water layers (Martin and Christiansen, 2009).

Zooplankton samples for measurement of ETS activity were fractioned using a 5 mm sieve to remove the rare larger organisms and gelatinous plankton which would disproportionably influence the respiration rates measured (respiration rates are size dependent, i.e. increase with decreasing body mass, see e.g. Hernández-León and Ikeda 2005b, Ikeda *et al*. 2001). The fraction > 5 mm was composed of mesopelagic fish, decapod shrimps, euphausiids, chaetognaths, salps, siphonophoran fragments and larvacean houses. The majority of these animals were larger than 2 cm, which were regarded as not being sampled representatively by the 1 m^2 MOCNESS (Martin and Christiansen, 2009). The < 5 mm sieve fraction was split in half with a Folsom plankton splitter (McEwen *et al*. 1954) and one half of each sample was frozen immediately at –80°C or in liquid nitrogen for subsequent analysis of ETS activity. The other half of the sample was stored at -20°C for biomass determination.

Zooplankton respiratory activity was determined by measuring the respiratory electron transfer system (ETS) activity according to the method described by Packard (1971) and modified by Kenner and Ahmed (1975). The biochemical method estimates, under substrate saturation, the maximum overall activity of the enzymes associated with the respiratory electron transfer system, which can be converted to potential respiratory oxygen consumption rates of organisms (Packard 1985). The enzymatic activity of the zooplankton assay was measured *in vitro* at 15 °C and was recalculated for *in situ* temperature using the Arrhenius equation and activation energy of 63 kJ mol^{-1} (Packard *et al*. 1975).

For the sampled depth layers, the *in situ* ETS-derived oxygen consumption rate was expressed as community ETS activity (µL O_2 m^{-3} h^{-1}), i.e. normalized to the volume of water sampled, and as biomass-specific ETS activity (µL O_2 g wwt^{-1} h^{-1}), i.e. normalized to the wet weight of the corresponding biomass sample. Zooplankton biomass was determined gravimetrically as wet weight from the frozen biomass samples and was converted to biomass concentration (mg wwt m^{-3}).

The respiratory carbon demands (mg C m^{-2} d^{-1}) of the depth integrated zooplankton standing stocks were calculated as the product of the biomass-specific respiration rates at the sampled depth layers and the standing stock biomass of the corresponding depth intervals from the oblique stratified tows (see above for depth intervals). Biomass-specific respiration rates were determined by adjusting the potential respiratory oxygen consumption rates from ETS activity measurements, re-calculated for the average *in situ* temperature of the corresponding biomass depth interval, to actual zooplankton respiration using a respiration (R) to ETS ratio of 0.5 (King and Packard 1975a, 1975b, Koppelmann *et al*. 2000, Hernández-León and Gómez 1996). This adjustment is necessary because ETS activity measured *in vitro* under substrate saturation might be higher than actual physiological rates in the field, where limitation of intracellular substrates, e.g. under low food conditions, can reduce enzyme activities (Hernández-León and Gómez 1996). A respiratory quotient (RQ) of 0.85 was used to convert the respiratory oxygen consumption rates to carbon dioxide production rates given in carbon units (King *et al*. 1978), which represent the carbon demand for zooplankton respiration. Carbon demand can be used as an index of minimum food requirements when assimilation efficiency and growth are not taken into account (Ikeda *et al*. 2000).

The standing stock biomass of zooplankton < 5 mm was determined as wet weight (g wwt m^{-2}) from size fractioned samples (<0.5 cm, 0.5 cm-2 cm, >2 cm) for the above mentioned depth intervals of the oblique stratified tows (Martin and Christiansen, 2009).

For statistical analyses of differences in vertical, diel and temporal distribution of zooplankton metabolism and biomass as well as correlation analysis between zooplankton *in situ* community ETS activity and biomass, the SPSS® (version 13.0.1) statistical package was used.

3. RESULTS

3.1 VERTICAL DISTRIBUTION OF ZOOPLANKTON METABOLISM

3.1.1 GENERAL TRENDS

Significant vertical differences of zooplankton community ETS activity (Kruskal-Wallis test; $p<0.001$), biomass concentration ($p<0.001$) and biomass-specific ETS activity ($p<0.05$) were observed for data pooled from all cruises and locations. The decrease with depth was most pronounced between the 50m and the mesopelagic depth layers (300 m, 500 m and 1000 m).

Correlation coefficients for the relationship between community ETS activity and biomass were significant and showed strong correlations at all seamount and reference locations (all $r > 0.90$), except at the Sedlo Seamount in November 2003 where the correlation was modest ($r = 0.666$) (Table 2).

Table 2.

Correlation coefficients (r) for zooplankton community ETS activity and biomass concentration at seamount (SM) and reference (REF) locations for the respective sampling periods. The number of measurement pairs is given as n. Significant correlations are marked with single asterisk (*) at $p < 0.05$, and with double asterisks (**) at $p<0.01$.

Seamount	Period	Location	*n*	*r*
SEINE	April 2004	SM	28	0.961**
		REF	8	0.924**
SEINE	July 2004	SM	11	0.966**
		REF	7	0.951**
SEDLO	Nov. 2003	SM	17	0.666**
		REF	4	0.984*
SEDLO	July 2004	SM+REF	6	0.924**

Day and night hauls were analysed for differences in ETS activity and biomass caused by diel vertical migration (DVM) of parts of the zooplankton community. Data from the day and night hauls at each location pooled from all cruises were tested separately for each depth layer using the Wilcoxon´s test for matched pairs (50 m (n = 11), 300 m (n = 4), 500 m (n = 8), and 1000 m (n = 6), with n = number of day and night pairs tested). Significant differences were found only at 500 m depth for community ETS activity and biomass (both $p<0.05$), both with higher median day values. Observed diel distributions of ETS activity and biomass concentrations at the sampled depth layers varied between sampling dates and locations (see 3.1.2 and 3.1.3).

3.1.2 SEINE SEAMOUNT

In April 2004, biomass-specific ETS activity at all sample locations was generally higher at night in the intermediate depth layers (150 m, 300 m and 500 m), while no trend was apparent at 50 m and 1000 m (Fig. 2a). Biomass concentrations were generally higher at night in the surface layer (50 m) and higher during the day in the intermediate depth layers (150 m, 300 m and 500 m), but were variable at 1000 m (Fig. 2b). Community ETS activity showed no clear trend in day/night distributions at 50 m and 300 m, but was mainly higher during the day at 500 m and higher during the night at 1000 m (Fig. 2c).

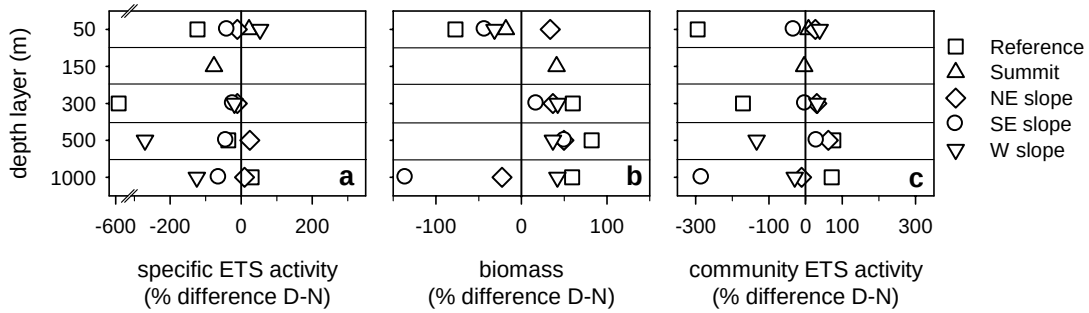

Figure 2. Day minus night differences at Seine Seamount locations in April 2004. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

In July 2004, biomass-specific ETS activity was higher during the night at 50 m and 150 m depths and higher during the day at 500 m depth, with no apparent trend at 1000 m depth (Fig. 3a). Diel differences in biomass concentration were generally characterized by higher day concentrations at all locations and depths (50 m, 150 m, and

500 m), although there was no apparent trend at 1000 m (Fig. 3b). At all sample locations, community ETS activity was higher during the night at 50 m and higher during the day at 500 m and above the summit at 150 m, while no trend was apparent at 1000 m depth (Fig. 3c).

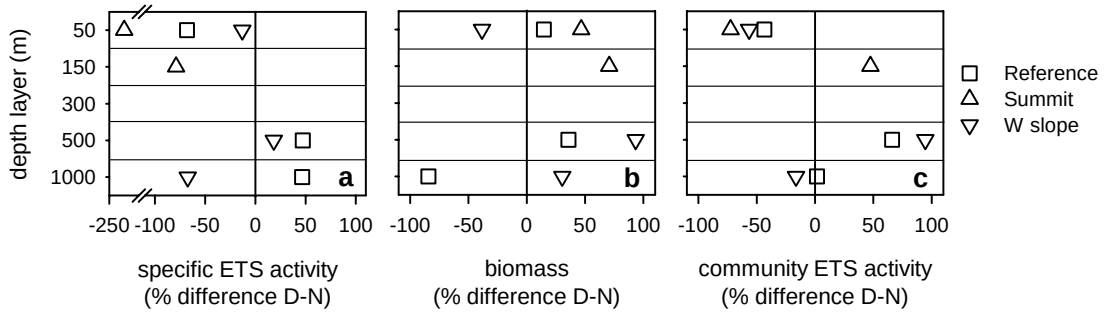

Figure 3. Day minus night differences at Seine Seamount locations in July 2004. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

3.1.3 SEDLO SEAMOUNT

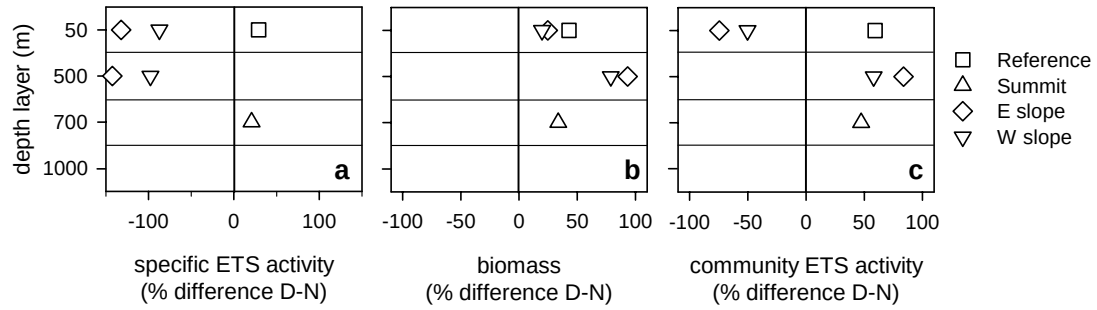

Figure 4. Day minus night differences at Sedlo Seamount locations in November 2003. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

At Sedlo Seamount in November 2003, day and night zooplankton samples were only available for one depth at the reference (50 m) and summit (750 m) locations and two depths (50 m and 500 m) at the eastern and western slope locations. At the eastern and western seamount slopes, zooplankton biomass-specific ETS activity (Fig. 4a) was higher during the night at both depths and biomass concentrations (Fig. 4b) were higher during the day at both depths, while community ETS activity (Fig. 4c) was higher at night at 50 m and higher during the day at 500 m. In contrast to the slope locations, biomass-specific and community ETS activities at the reference location at 50 m were

higher during the day, while the higher day biomass concentration was in agreement with observed values at the slopes. At 750 m, close to the summit sea floor, biomass-specific and community ETS activities as well as biomass were all higher during the day.

3.2 TEMPORAL VARIABILITY OF ZOOPLANKTON METABOLISM

For the analysis of temporal differences in metabolism and biomass, data from each seamount and relevant reference locations were pooled.

3.2.1 SEINE SEAMOUNT

Biomass-specific ETS activity (Fig. 5a) was significantly higher throughout the water column in July 2004 compared to April 2004 (50 m, $p=0.001$; 500 m, $p<0.01$; 1000 m, $p<0.05$; Mann-Whitney-U test), with more than an 8-fold higher median value and a much larger range at 50 m depth (July: 368 µl O_2 g wwt^{-1} h^{-1}, range=132-449; April: 43 µl O_2 g wwt^{-1} h^{-1}, range=17-60). Biomass concentrations (Fig. 5b), on the contrary, were significantly higher in April 2004 at 50 m and 500 m depth (both $p<0.05$), when average values were more than doubled and values at 50m were the highest of all cruises. Community ETS activity was higher at all depth levels in July 2004 (Fig. 5c), although significantly higher values were only found at 1000 m ($p<0.05$).

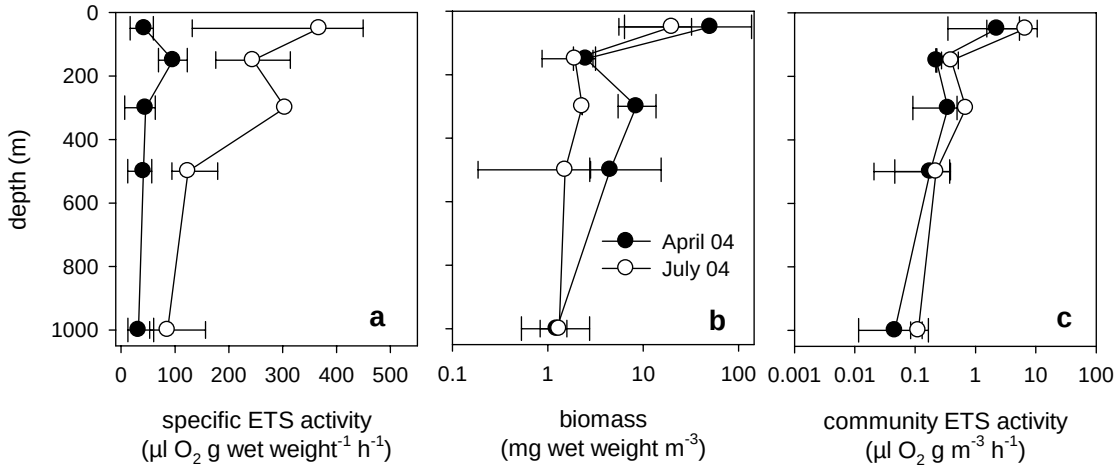

Figure 5. Temporal variability at Seine Seamount between April 2004 and July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale are given as median ± range. Thin error bar lines represent ranges for July.

Respiratory carbon demand of the zooplankton standing stock (0-150 m) was significantly higher in July 2004 ($p<0.05$) with a nearly 4-fold higher median value (3.5 mg C m^{-2} d^{-1} range=1.4-6.3) compared to April 2004 (0.9 mg C m^{-2} d^{-1}, range=0.3-3.2). The temporal difference in zooplankton standing stock biomass (0-150 m) was not significant ($p>0.05$) despite a more than 3-fold lower median value in July 2004 (1.9 g wwt m^{-2}, range=1.0-2.8) compared to April 2004 (6.6 g wwt m^{-2}, range=0.8-15).

3.2.2 SEDLO SEAMOUNT

Temporal differences of zooplankton ETS activity and biomass concentrations between November 2003 and July 2004 (Fig. 6) at the tested depth layers (50 m and 500 m) were not significant (all $p>0.05$, Mann-Whitney-U test). Biomass-specific ETS activity had higher median values at all depths in July 2004 (Fig. 6a), with 3-fold higher values at 50 m depth (370 µl O_2 g wwt^{-1} h^{-1}, range=238-502) compared to November 2003 (122 µl O_2 g wwt^{-1} h^{-1}, range=34-395). Median biomass concentrations were similar in November 2003 and July 2004 at all sampled depths (Fig. 6b), while median community ETS activity was higher in July 2004 at all depths and was more than doubled at 50 m (Fig. 6c).

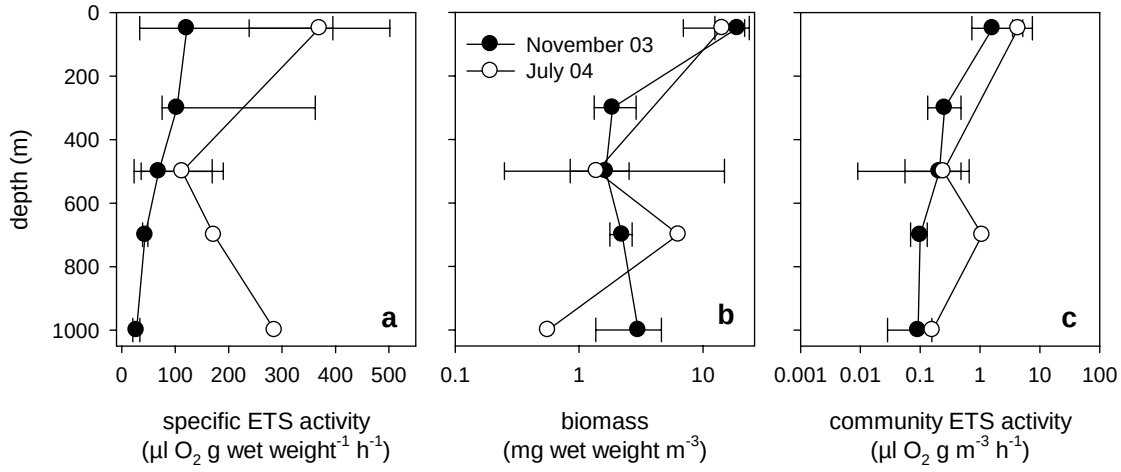

Figure 6. Temporal variability at Sedlo Seamount between November 2003 and July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale are given as median ± range. Thin error bar lines represent ranges for July.

Respiratory carbon demand values of the standing stock (0-700 m) were not significantly different between November 2003 (median: 5.0 mg C m^{-2} d^{-1}, range=1.5-15) and July 2004 (median: 3.1 mg C m^{-2} d^{-1}, range=2.6-3.6), although total biomass of

the zooplankton standing stock (0-700 m) was significantly higher ($p<0.05$) in November 2003 (median: 7.4 g wwt m^{-2}, range=4.9-12) compared to July 2004 (median: 2.3 g wwt m^{-2}, range=1.7-2.8).

3.3 SPATIAL DISTRIBUTION OF ZOOPLANKTON METABOLISM

3.3.1 SEINE SEAMOUNT

In April 2004, biomass-specific ETS activity was similar throughout the water column at the different locations, with generally lowest median values at the reference location (Fig. 7a). Biomass concentration, on the other hand, differed largely between locations at 50 m depth, while it was less variable between locations at the deeper layers (Fig. 7b). Lowest biomass concentrations were observed at 50 m and 150 m depth at the summit location. At the 50 m depth layer, median values were reduced by more than 80% compared to the other locations. For the same depth, biomass concentration was highest at the NE slope. Community ETS activity largely mirrored the spatial differences in biomass concentrations (Fig. 7c), resulting in a large range of values at 50 m depth, which were lowest above the summit and highest above the NE slope, while at the other depth layers values were more similar between locations. The correlation coefficients confirmed significant very strong correlations between zooplankton community ETS activity and biomass concentration at both seamount (r = 0.961) and reference (r = 0.924) locations (Table 2).

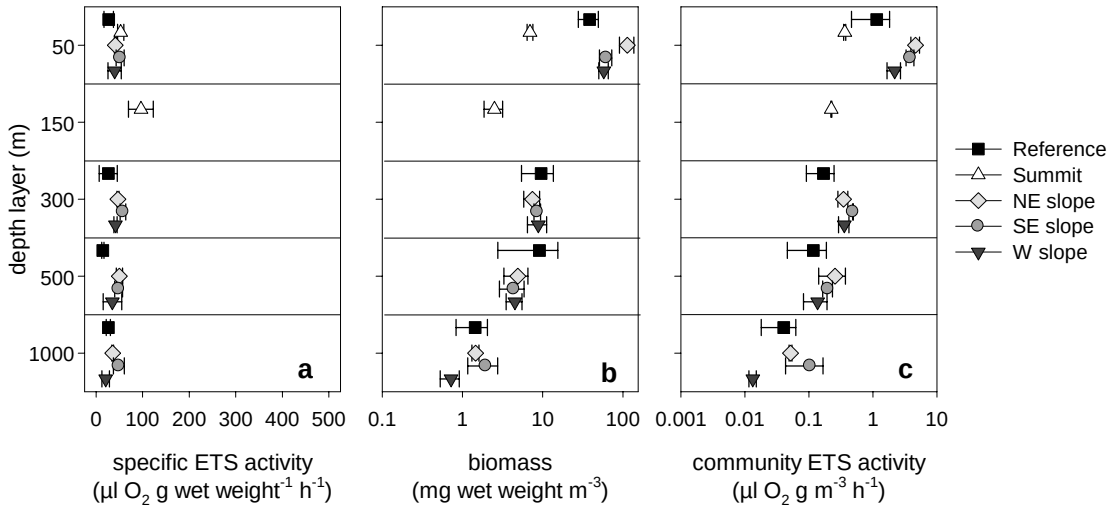

Figure 7. Intra-seamount variability at Seine Seamount in April 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the slopes (northeast, southeast and west) and at the reference location are given as median ± range for the sampled depth layers.

Differences in depth integrated (0-150 m) respiratory carbon demand of the standing stock (Fig. 8a) between sampling locations largely resembled those of the depth integrated (0-150 m) biomass distribution of the standing stock (Fig. 8b). Values of both were lowest above the summit, but showed no enhanced slope values, as were observed at the 50 m depth layer, indicating localized vertical differences in the distribution of biomass concentration and community ETS activity.

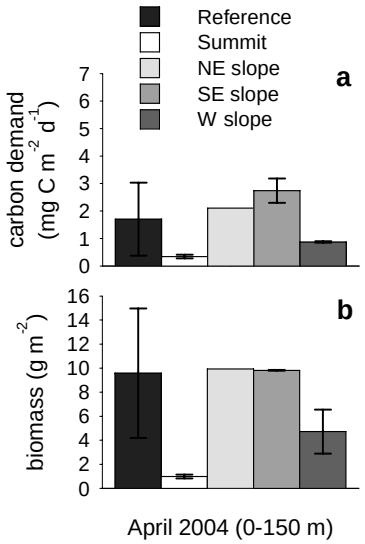

Figure 8.

Intra-seamount variability at Seine Seamount in April 2004. Comparison between water column-integrated (0-150 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the slopes (northeast, southeast and west) and at the reference location. Values are given as median ± range.

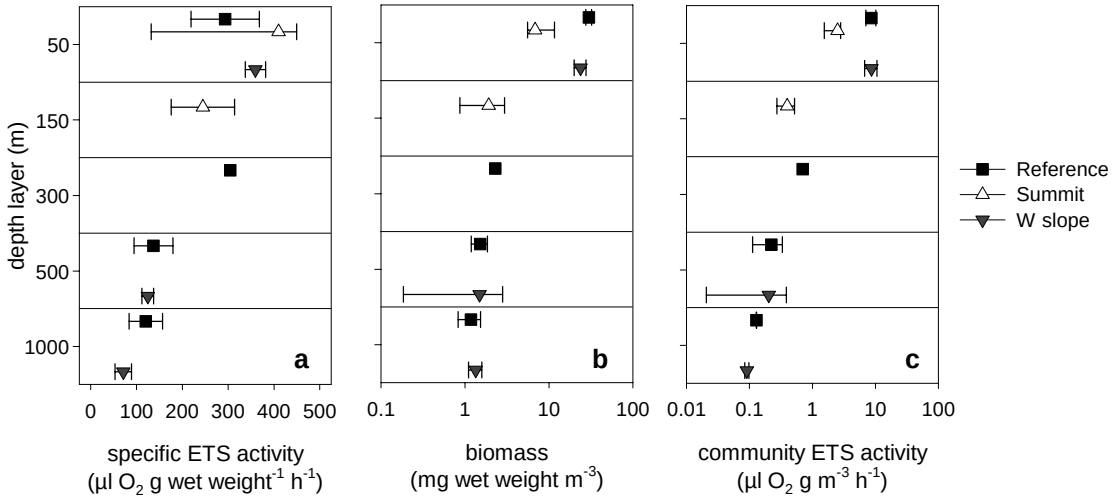

Figure 9. Intra-seamount variability at Seine Seamount in July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the western slope and at the reference location are given as median ± range for the sampled depth layers.

In July 2004, only three Seine Seamount locations (summit, West slope and reference) were sampled. Median values of biomass-specific ETS activity were similar among

seamount locations at the different depth layers (Fig. 9a). At 50 m depth, zooplankton biomass concentration above the seamount summit was, as in April 2004, strongly reduced compared to the other locations. The lowest summit biomass concentrations were found at 150 m depth (Fig. 9b). Community ETS activity at the seamount and reference locations was, as in April 2004, strongly correlated with biomass concentration (r = 0.966 and r = 0.951, respectively; Table 2) and showed a similar spatial distribution, with lowest community ETS activity at the summit location at 50 m depth (Fig. 9c).

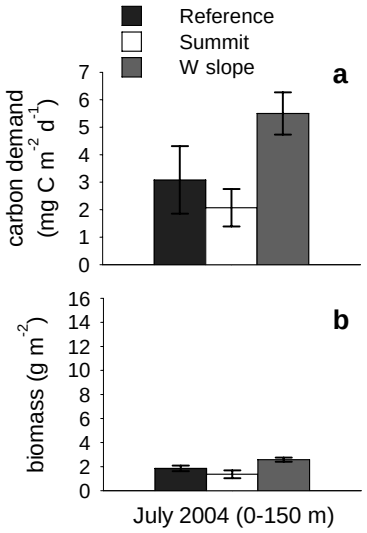

Figure 10.

Intra-seamount variability at Seine Seamount in July 2004. Comparison between water column-integrated (0-150 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the western slope and at the reference location. Values are given as median ± range.

Respiratory carbon demand of the standing stock (0-150 m; Fig. 10a) and standing stock biomass (0-150 m; Fig. 10b) in July 2004 were both lowest above the summit, though the difference to the other locations was less pronounced than in April 2004. Highest respiratory carbon demand and standing stock biomass were observed above the western slope.

3.3.2 SEDLO SEAMOUNT

In November 2003, biomass-specific ETS activity at Sedlo Seamount varied markedly between sampling locations at the 50 m, 300 m and 500 m depth layers. Average values were lowest at the summit and East slope locations and highest at the West slope, except at 500 m depth, where the West slope value was similar to the reference location (Fig. 11a). Biomass concentrations, by contrast, were relatively uniform among all locations at the different depth layers (Fig. 11b). Community ETS activity reflected the large differences in biomass-specific ETS activity among sampling locations rather than

biomass concentrations (Fig. 11c). This was consistent with the modest correlation between community ETS activity and biomass concentration for the seamount locations (r = 0.666), which for the reference location was very strong (r = 0.984) (Table 2).

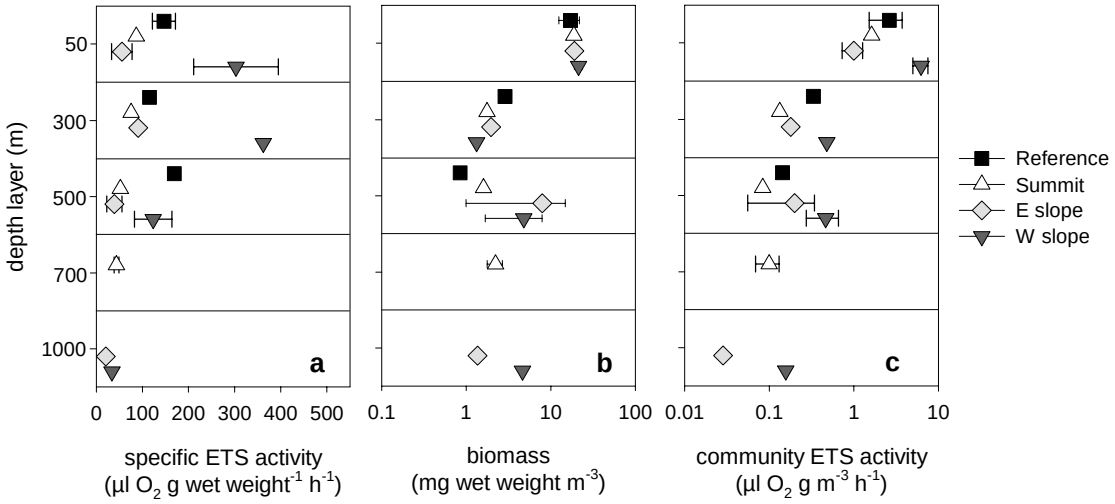

Figure 11. Intra-seamount variability at Sedlo Seamount in November 2003. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the slopes (east and west) and at the reference location are given as median ± range for the sampled depth layers.

Standing stock respiratory carbon demand values (0-700 m) at Sedlo Seamount in November 2003 (Fig. 12a) mirrored the same large intra-seamount differences observed for biomass-specific ETS activity at all depths. The average biomass of the standing stock (0-700 m) was similar among sampling locations (Fig. 12 b).

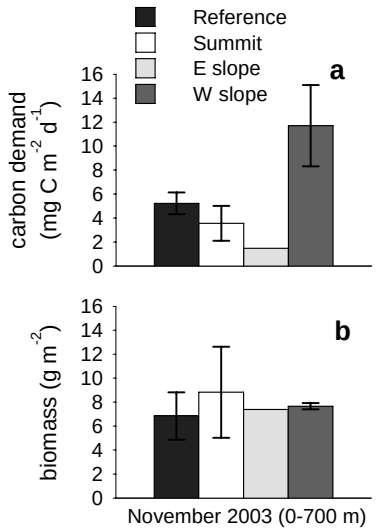

Figure 12.

Intra-seamount variability at Sedlo Seamount in November 2003. Comparison between water column-integrated (0-700 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the slopes (east and west) and at the reference location. Values are given as median ± range.

In July 2004, data from only one day haul at the summit and one night haul at the reference location were available for Sedlo Seamount. Biomass-specific ETS activity was higher above the summit at 50 and 500 m compared to the reference location (Fig. 13a). Zooplankton biomass concentrations above the summit were similar throughout the water column, but showed large vertical differences at the reference location, the value at 50 m being much higher and the one at 500 m being much lower than above the summit (Fig. 13b). Community ETS activity largely mirrored the biomass distribution at the depth layers, with a less pronounced difference between summit and reference locations at 50 m depth (Fig. 13c).

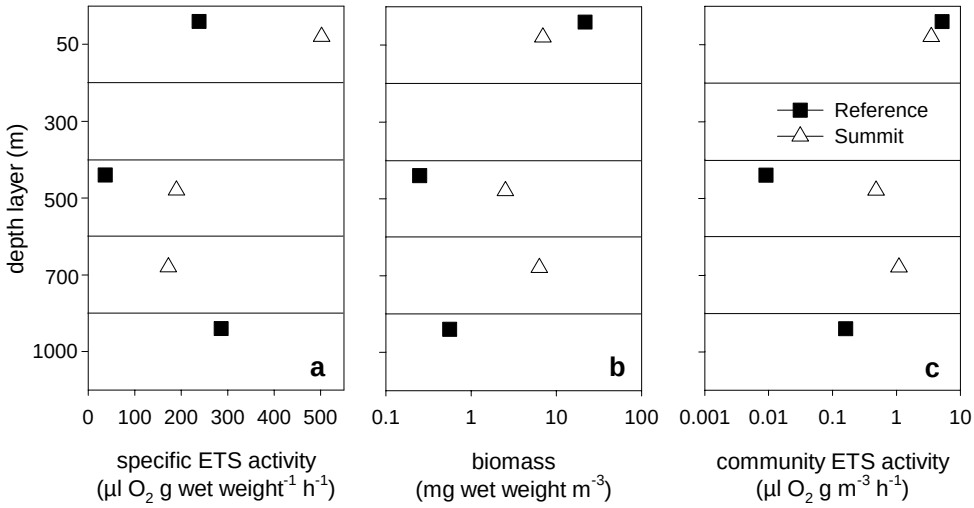

Figure 13. Intra-seamount variability at Sedlo Seamount in July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and at the reference locations are given for the sampled depth layers.

Standing stock respiratory carbon demand (0-700 m; Fig. 14a) and standing stock biomass (0-700 m; Fig. 14b) were generally similar at summit and reference locations.

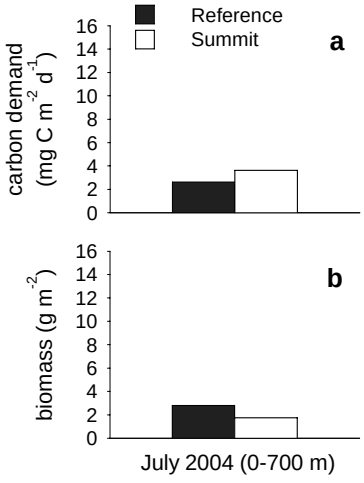

Figure 14.

Intra-seamount variability at Sedlo Seamount in July 2004. Comparison between water column-integrated (0-700 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and at the reference location.

4. DISCUSSION

4.1 VERTICAL AND TEMPORAL DIFFERENCES IN ZOOPLANKTON METABOLISM

The respiratory carbon demands of the zooplankton standing stock (integrated depth range: 0-150 m) from day and night samples ranged from 0.3-6.3 mg C m^{-2} d^{-1} and 1.6-12.0 mg C m^{-2} d^{-1} at Seine and Sedlo Seamounts, respectively. They were slightly lower at both sites than the average respiration rate of ~19 mg C m^{-2} d^{-1} (data taken from Hernández-León and Ikeda, 2005a) for the upper 200 m of the water column in the open ocean between 35 and 45° N, which covers the area of the studied seamounts. Hernández-León and Ikeda (2005a) estimated mesozooplankton community respiration rates using literature respiration rates mostly derived from direct incubation experiments on live specimens. The lower respiration rates observed at Sedlo and Seine Seamounts might, therefore, be due to differences in water column depth sampled as well as to differences in methods of respiration measurement and zooplankton sampling (the latter not being specified).

Community ETS activity decreased significantly with depth and was highly correlated with zooplankton biomass, except for Sedlo Seamount in November 2003 (see 4.2. for discussion). The observed decrease of *in situ* biomass-specific ETS activity with depth was due to decreasing temperature, as *in vitro* values were similar throughout the water column. The decrease of community ETS activity with depth is, thus, mainly caused by the decrease in water temperature and zooplankton biomass due to limited food availability at depth (King *et al*. 1978; Hernández-León *et al*. 2001a).

DVM is a common behaviour among zooplankton (e.g. Longhurst and Williams 1979, Hays *et al*. 2001). Classically, diel vertically migrating zooplankton and nekton feed in surface waters at night and return to depth at dawn (reviewed by Haney 1988, Pearre 2003). These diel rhythms of feeding and swimming behaviour have been found to cause diel rhythms in respiration, with higher oxygen consumption rates at night in migrating copepod species and lower or no day/night differences in species with less evident DVM behaviour (Pavlova 1994).

The distribution of zooplankton biomass and ETS activity observed at Seine and Sedlo Seamounts during the three cruises did not show consistent day/night differences

indicating DVM. Zooplankton biomass distributions followed the classical pattern at Seine Seamount in April 2004, but in July 2004, the pattern was only evident in higher day values at 500m depth, while at Sedlo Seamount in November 2003, day values were higher at both surface (50 m) and deeper layers (500 m). This biomass distribution resulted in significantly higher day values for pooled (all stations from all cruises) zooplankton biomass and community ETS activity at 500 m depth. The distribution of biomass-specific ETS activity was similarly ambiguous. At Sedlo Seamount in November 2003, it was generally higher at night at both 50 and 500 m depth, supporting DVM, but showed no surface pattern at Seine in April 2004, despite higher night values at 500 m depth, while in July 2004, higher night values at 50 m depth coincided with higher day values at 500 m depth. At Seine and Sedlo sampling locations, Martin and Christiansen (2009) generally observed no differences in zooplankton biomass between night and day hauls in the size class <0.5 cm, but they found indications of diel vertical migrations in the size fractions >0.5 cm. This agrees with previous reports suggesting that only the larger mesozooplankton (>1000 mm) contribute significantly to DVM in the Atlantic (e.g. Gallienne *et al*. 2001).

Other mesozooplankton studies in the north eastern Atlantic gyre have reported similarly contradictory results regarding diel rhythms of feeding and vertical migration. Huskin *et al*. (2001a) who investigated the size fractioned (200-500, 500-1000 and >1000 μm) mesozooplankton distribution of the upper 200 m at an open ocean station (TA2-11) midway between Seine and Sedlo Seamounts in April 1989, found no evidence for DVM from mesozooplankton biomass and copepod abundance in all size fractions, but a clear diel feeding rhythm with higher copepod gut contents at night. In contrast, Hernández-León *et al*. (1999), who studied mesozooplankton biomass and ETS activity in two size fractions (200-500 μm and >500 μm) in the upper 200 m over a 2,800 km east-west section in the tropical northeast central Atlantic Ocean (21°N) during August-September 1989, reported a clear signal of DVM for the larger mesozooplankton fraction (>500 μm) with higher average biomass at night in the upper 200 m and rather similar values in the 200–500 μm size class, while biomass-specific ETS activities of both size fractions did not differ between day and night. In a study including mesopelagic distributions of zooplankton biomass, metabolism and gut fluorescence in Canary Island waters, Hernández-Léon *et al*. (2001a) observed a

classical DVM biomass distribution of zooplankton >1 mm with higher night values in the upper 200 m and higher day values at around 500 m depth, while no clear pattern was apparent for the smaller (<1 mm) size fraction. They found no significant diel differences in biomass-specific gut fluorescence and ETS activity in either size fraction.

Diel vertical migrations are complex and the methods of collecting organisms or monitoring changes in their depths can affect how, or even whether DVMs are detected (Pearre 2003). In the present study, the limited discrete sampling depths might at times have missed the centre of migration-influenced maximum zooplankton densities during the different cruises.

Significant temporal differences in zooplankton biomass and respiration rates were found at both Seine and Sedlo Seamounts. Although subtropical gyres are generally regarded to be among the most stable environments of the ocean (Bienfang *et al*. 1984), several studies have shown a certain degree of temporal variability in primary production and chlorophyll *a* concentrations in the oligotrophic NASE province (e.g. Longhurst 1995, Harrison *et al*. 2001, Marañón *et al*. 2000, 2003, Teira *et al*. 2005 and references therein). These are generally characterized by maxima in phytoplankton standing stock (chlorophyll *a*) occurring in winter, sometimes as early as late fall (October), and lower chlorophyll *a* surface values in the summer months. Increases in phytoplankton biomass might be closely followed by the development of zooplankton biomass, as a reaction to increased food availability. This was observed during late winter in an area north of the Canary Islands, considered undisturbed by the islands (Hernández-León *et al*. 2004).

In the oligotrophic NASE province, phytoplankton biomass is dominated by small-sized cells (picoplankton and flagellates), with 71% of the cells <2 µm (Teira *et al*. 2005), ~85% of the cells <5 µm (Head *et al*. 2002) and 93% of the cells <10 µm (Neuer *et al*. 2007). Copepods are the main mesozooplankton group in the region (e.g. Head *et al*. 2002, Martin and Christiansen, 2009) and are able to ingest food particles from ~ 2 to 5 µm (Paffenhöfer 2003), although feeding is inefficient on small particles (e.g. Harris 1982, Lampitt and Gamble 1982) and elevated grazing rates have been observed when the larger phytoplankton particles (>10 µm) dominate (Dam *et al*. 1993, Sieracki *et al*. 1993, Calbet and Landry 1999). This suggests that only about 7 to 15% of the

autotrophic biomass could be directly used by mesozooplankton grazers and stresses the importance of heterotrophs, such as microzooplankton, and possibly detritus, in the diet of zooplankton in these oligotrophic waters (Huskin *et al*. 2001b, Head *et al*. 2002, Hernández-León *et al*. 2004). Phytoplankton biomass, measured as chlorophyll *a* concentrations, does not, therefore, necessarily represent available food for the mesozooplankton.

Kiriakoulakis *et al.* (2009) sampled suspended particulate organic matter (sPOM) on GF/F filters (0.7 μm pore size) at Seine and Sedlo Seamount locations using *in situ* pumps deployed at 50 m water depths. They determined chlorophyll *a* (see Tables 3 and 4), and also examined qualitatively the sPOM composition on the same filters using scanning electron microscopy. The authors reported phytoplankton sizes ranging mostly from 2 – 3 to 200 μm during all three cruises at Seine (April 2004 and July 2004) and Sedlo (November 2003 and July 2004) locations, although occasionally there were larger individuals and sub-micron spherical features (bacteria, archaea or cyanobacteria). This suggests that most of the sPOM present was of suitable size for copepod feeding. The composition of the main phytoplankton groups was similar during all cruises at both seamounts, except for a more diverse coccolithophorid assemblage in July 2004. However, some temporal changes in the proportional contribution of the main groups were discerned. Coccolithophores were the dominant group in April and July 2004, but were absent at Sedlo in November 2003. Diatoms were more abundant than dinoflagellates in November 2003 and April 2004, while dinoflagellates were more abundant than diatoms in July 2004. The abundance of microzooplankton, such as radiolaria, pelagic foraminifers and tintinnids, was low during all cruises.

Temporal differences in zooplankton biomass and respiration rates at the Seine Seamount were characterized by significantly higher zooplankton biomass in April 2004 and higher biomass-specific ETS activity in July 2004. Zooplankton biomass was more than 2-fold higher (depth-integrated 0-150 m as well as at the depth layers) in April 2004 and coincided with higher chlorophyll *a* values at most Seine locations compared to July 2004 (Table 3). The higher phytoplankton concentrations might indicate a late winter phytoplankton bloom resulting in enhanced zooplankton biomass. This observation agrees with both Head *et al*. (2002) and Huskin *et al*. (2001a, 2004) who noted higher mesozooplankton biomass and higher copepod abundances in the

upper 200 m in April 1999 compared with August 1998 at sampling stations located midway between Seine and Sedlo Seamounts at 22°W. Hernández-León *et al*. (2004) observed an increase in specific zooplankton ETS activity and gut fluorescence during late winter blooms preceding the development of zooplankton biomass in an oceanic area north of the Canary Islands. At Seine Seamount, biomass-specific ETS activity was significantly lower at the sampled depths in April 2004 compared to July 2004, despite indications of higher food abundance (chlorophyll *a* values) in April. This difference in biomass-specific ETS activity was only partly due to differences in ambient water temperature, as values were also significantly lower ($p<0.05$) before adjustment to *in situ* water temperatures, but might be caused by differences in food quantity and quality.

Table 3. Seine Seamount chlorophyll *a* (Chl) and phaeopigment (Phaeo) concentrations and phaeopigment/chlorophyll ratio of suspended particulate organic matter (sPOM; data from Kiriakoulakis *et al*., this volume), and depth integrated (0-150 m) chlorophyll *a* standing stock sampled as total particulate organic matter (tPOM) and gross primary production from bottle incubations (Pg; data from Arístegui *et al*., this volume) are listed for the sampling locations.

Seine Seamount	**Sampling locations**			
	Summit	**East slope**	**West slope**	**Reference**
Kiriakoulakis *et al*. (this volume) (sample depth: 50 m [~160 m])				
Chl (µg L^{-1})				
April 04	0.43 [0.03]	0.39	0.32	0.42
July 04	0.18 [0.03]	0.04	0.07	0.11
Phaeo (µg L^{-1})				
April 04	0.16	0.06	0.22	0.09
July 04	0.05 [0.03]	0.01	0.03	0.01
Phaeo/Chl ratio				
April 04	0.37 [3.90]	0.16	0.68	0.21
July 04	0.26 [0.92]	0.17	0.40	0.10
Arístegui *et al*. (this volume) (integrated depth layer: 0-150 m)				
Chl (mg m^{-2})				
April 04	51	40	41	20
July 04	21	22	31	27
Pg (mmol O_2 m^{-2} d^{-1})				
April 04	85	91	138	64
July 04	91	916	79	621

Arístegui *et al*. (2009) detected high amounts of phaeopigments, the degradation product of chlorophyll, from 50 m depth downward towards the summit sea floor at Seine Seamount in April 2004. Kiriakoulakis *et al*. (2009) also found higher phaeopigment/chlorophyll *a* ratios at 50 m depth at most Seine locations in April 2004, the highest ratio being located at 160 m depth above the summit (Tab 3). These high phaeopigment concentrations might indicate a senescent phase of the late winter bloom, with the sinking of detrital material resulting in poorer feeding conditions for a high mesozooplankton standing stock in April 2004. Additionally, the biomass of the

zooplankton standing stock (0-150 m) was about 3 times higher in April 2004 compared to July 2004, while integrated chlorophyll *a* values (0-150 m) were only about 1.5 to 2-fold higher (Table 3), i.e. the autotrophic biomass available for the zooplankton was lower in April 2004. The low biomass-specific respiration rates might, therefore, represent starvation conditions of the zooplankton community, as zooplankton has been found to decrease metabolic rates during prolonged starvation (see Section 1). Better feeding conditions in July 2004 are indicated by higher relative food abundance and a lower phaeopigment/chlorophyll ratio of the sPOM measured, and also by higher depth integrated gross primary production (Pg 0-150 m; Table 3) and indications of higher specific respiration of the POM (Arístegui *et al*., 2009) at Seine locations in July 2004, which indicate active growth conditions. The observed large temporal differences in zooplankton biomass and biomass-specific ETS activity resulted in significant temporal differences in the respiratory carbon demands of the zooplankton standing stock (0-150 m), which were 4-fold higher in July 2004, despite the lower zooplankton standing stock biomass.

Temporal differences of zooplankton respiration rates and biomass observed at Sedlo seamount and reference locations between November 2003 and July 2004 were similar to those at Seine Seamount, i.e. higher biomass in November 2003 and higher biomass-specific ETS activity in July 2004. Significantly higher (about 3-fold) zooplankton standing stock biomass (0-700 m) in November 2003 might be, as at Seine Seamount in April 2004, a result of biomass development following a bloom, since mixing events have been found to occur as early as October in the area (Neuer *et al*. 2007). The dominance of diatoms in the phytoplankton in November 2003 (Kiriakoulakis *et al*., 2009), a group known to grow efficiently under conditions of enhanced nutrient concentrations (Cushing 1989), supports this. However, possible bloom conditions were not supported by enhanced chlorophyll *a* values, which were similar during both cruises (Table 4).

The higher zooplankton standing stock biomass (0-700 m) in November 2003 coincided with lower average biomass-specific ETS activity at all depths compared to July 2004. As at Seine in April 2004, this might result from conditions of starvation due to low food quantity and quality. Similar phytoplankton standing stocks coincided with an about 3-fold higher zooplankton standing stock in November 2003 which imply a

reduced autotrophic biomass available as food for the zooplankton. Furthermore, higher ratios of phaeopigments to chlorophyll were observed in November 2003 (Table 4) and possibly indicate a senescent bloom offering a poorer food quality. Unlike Seine, temporal differences in biomass-specific ETS activity and biomass at Sedlo did not result in significant differences of the respiratory carbon demands of the zooplankton standing stock in the upper 700 m.

Table 4. Sedlo Seamount chlorophyll *a* (Chl) and phaeopigment (Phaeo) concentrations and phaeopigment/chlorophyll ratio of suspended particulate organic matter (sPOM; data from Kiriakoulakis *et al*., this volume), and depth integrated (0-150 m) chlorophyll *a* standing stock sampled as total particulate organic matter (tPOM) and gross primary production from bottle incubations (Pg; data from Arístegui *et al*., this volume) are listed for the sampling locations.

Sedlo Seamount	**Sampling locations**			
	Summit	**East slope**	**West slope**	**Reference**
Kiriakoulakis *et al*. (this volume) (sample depth: 50 m [~780 m])				
Chl (µg L^{-1})				
November 03	0.18 [0.0]	0.17	0.13	0.13
July 04	0.18 [0.04]	0.25 (90m)	0.38	0.09
Phaeo (µg L^{-1})				
November 03	0.11 [0.03]	0.12	0.12	0.29
July 04	0.00 [0.01]	0.13	0.07	0.00
Phaeo/Chl ratio				
November 03	0.61	0.71	0.88	2.18
July 04	0.00 [0.17]	0.50	0.18	0.00
Arístegui *et al*. (this volume) (integrated depth layer: 0-150 m)				
Chl (mg m^{-2})				
November 03	38	27	28	31
July 04	22	26	20	33
Pg (mmol O_2 m^{-2} d^{-1})				
November 03	43	206	78	20
July 04	51	155	92	-

Alternatively, the observed temporal differences in standing stock biomass and biomass-specific ETS activity at both Seine and Sedlo Seamounts might also be caused by temporal differences in zooplankton composition. With increasing seasonal stratification, nutrients in the euphotic zone become scarce, and are recycled rapidly through tight heterotrophic/autotrophic linkages of the microbial loop (e.g. Rivkin *et al*. 1996). These favour small nanoflagellates and picophytoplankton which are able to efficiently utilize low concentrations of nitrogen (Chisholm 1992) and grow rapidly (Tang 1995). Smaller-sized food particles would in turn probably favour smaller-sized copepod species and developmental stages. Weight-specific respiration rates increase with decreasing body mass (Hernández-León and Ikeda 2005b, Ikeda *et al*. 2001), while the influence of taxonomic differences is relatively modest (Ikeda 1985). A higher

proportion of smaller individuals during strong summer stratification in the upper ocean could, thus, result in higher summer biomass-specific ETS activity.

Kiriakoulakis *et al*. (2009), however, observed similar size ranges of phytoplankton for all three sampling cruises (see above). This observation agrees with the similar size distribution of the phytoplankton standing stock (0-200 m) in August 1998 and April 1999 reported by Head *et al*. (2002) and Huskin *et al*. (2001a, 2004) at stations midway between Seine and Sedlo Seamounts. For the same stations and sampling periods the authors also reported a similar size and species group composition of the mesozooplankton although biomass and abundances were higher in April 1999. These results suggest a generally uniform size and species composition of the mesozooplankton community during the three OASIS cruises which would support the importance of temporal differences in food availability for observed differences in zooplankton biomass and biomass-specific ETS activity.

4.2 SEAMOUNT EFFECTS ON ZOOPLANKTON METABOLISM

The most apparent possible seamount effect observed at Seine Seamount was the reduced mesozooplankton respiratory carbon demand (0-150 m) above the summit during both sampling cruises. This reduction was, however, not caused by differences in biomass-specific ETS activity, but rather by lower zooplankton standing stock biomass, since biomass concentration and community ETS activity at Seine Seamount were highly correlated. Martin and Christiansen (2009) concurrently studied the mesozooplankton biomass distribution of the same zooplankton hauls discussed in this paper and reported reduced biomass concentrations of zooplankton <0.5 cm and the almost complete absence of zooplankton >0.5 cm at the Seine summit location compared to the slope and open ocean reference locations during both seasons. The authors suggested that this reduction of larger, actively moving zooplankton is mainly caused by advection off the summit, or by active avoidance of the summit region, while predation by the resident seamount fish might explain the reduction of zooplankton smaller 0.5 cm. Christiansen *et al*. (2009) analyzed the stomach content of planktivorous benthopelagic and pelagic fishes caught above Seine summit in April 2004. The stomachs contained almost exclusively small copepods (<0.5 cm), but no larger prey organisms. A reduction in zooplankton biomass over submarine elevations

has been observed by several authors (Genin *et al*. 1994 and references therein). Daytime advection of migrators around the seamount, creating a "hole" above it, and higher levels of predation over shallow topographic features by epibenthic fish that ascend above the summits at night to feed are possible causes for the absence of the migrating zooplankton (Genin *et al*. 1988, Genin 2004, Haury *et al*. 1995, 2000).

A slight seamount effect on biomass-specific ETS activity may have occurred at Seine Seamount in April 2004, when biomass-specific rates were about 2-fold higher at the seamount locations compared to the reference location at all sampled depth layers. This higher biomass-specific ETS activity coincided with ~ 2-fold higher integrated (0-150 m) chlorophyll *a* values at the seamount locations compared to the reference location (Table 3). Higher food concentrations above the seamount might thus be a possible cause for the observed higher biomass-specific ETS activity, at least for the upper 150 m of the water column. The magnitude of this increase was, however, too low to result in a detectable impact on the respiratory carbon demand of the zooplankton standing stock, due to generally low biomass-specific ETS activity at that time.

Table 5. Mesozooplankton taxa composition in the surface 100 m at Seine Seamount in April 2004. Relative and individual abundances as well as the total abundance and biomass (wet weight) of zooplankton < 5 mm are given for a night haul at the summit and at the reference location (Martin, unpublished data). Total zooplankton abundance and biomass were used to calculate the mean individual biomass at both locations.

Seine Seamount (0-100 m)	**Summit location**		**Reference location**	
Zooplankton groups (<5mm)	**Abundance (%)**	**Abundance (ind 100 m^{-3})**	**Abundance (%)**	**Abundance (ind 100 m^{-3})**
Copepods	89	3470	83	57800
Other Crustaceans*	3	131	5	3680
Gelatinous Organisms**	4	142	2	1550
Molluscs	0	0	4	2630
Other Non-Crustaceans***	4	174	6	3910
Total abundance (ind 100 m^{-3})		**3917**		**69570**
Total biomass (mg wwt 100 m^{-3})		**1220**		**9790**
Mean ind biomass (mg wwt ind^{-1})		**0.32**		**0.14**

*Other Crustaceans: mainly ostracoda and crustacean larvae
**Gelatinous organisms: mainly siphonophora
***Other Non-Crustaceans: chaetognatha, polychaets, fish eggs, non-crustacean larvae

The observed differences in zooplankton biomass-specific ETS activity at Seine Seamount in April 2004 could also be a result of local differences in size and species composition. The species group composition analysed for night hauls (0-100 m) above

Seine summit and at the reference location in April 2004 (Martin, unpublished data; Table 5) showed, however, generally similar proportions of the main groups at both locations, despite markedly lower abundances in each zooplankton group above the summit compared to the reference location. For a first estimate of differences in the body size composition of the zooplankton, the mean individual biomass was calculated by dividing the total biomass concentration by the total abundance for each location (Martin, unpublished data; Table 5). The resulting mean individual biomass was slightly higher at the summit location (0.32 mg wwt ind^{-1}) compared to the reference location (0.14 mg wwt ind^{-1}), which indicates larger individuals above the summit and does not support the idea of smaller-sized zooplankton above the seamount being the reason for the observed higher biomass-specific ETS activities.

At Sedlo Seamount in November 2003, on the other hand, depth-integrated mesozooplankton respiratory carbon demand (0-700 m) reflected primarily the pronounced local differences in biomass-specific ETS activity at the seamount locations instead of the rather uniform zooplankton biomass (0-700 m). This was supported by a weaker correlation between biomass and community ETS activity compared to the reference location or to all Sedlo locations in July 2004. Local differences in biomass-specific ETS activity corresponded largely with local differences in POM quantity and quality in November 2003, suggesting differences in food availability to be a primary cause, despite rather similar chlorophyll *a* values at all sample locations (Table 4). In November 2003, biomass-specific ETS activity was highest above the western slope location and coincided with highest values of total particulate organic carbon (tPOC) and nitrogen (tPON) observed in the upper 1000 m of the water column above the western slope, as well as higher amounts of more labile material (lower C/N ratio) in the upper 200 m, compared to the other sampling locations (Vilas *et al*., 2009). At the same western slope, suspended POM had the highest lipid concentrations of all seamount locations, both absolute and relative to sPOC, at 50 m and 800 m depths (Kiriakoulakis *et al*., 2009). At 800 m depth, sPOM had also the highest proportion of polyunsaturated fatty acids (PUFAs, labile compounds which are essential food components and regarded as markers of organic matter quality: Kiriakoulakis *et al*. 2004). Lowest lipid concentrations were reported above the summit and the eastern slope locations, with the lowest proportion of PUFAs at 50 m depth above the eastern slope. This suggests

locally lower food quality and agrees with the lowest biomass-specific ETS activity found at these locations. At the reference location, where biomass-specific ETS activity values were intermediate, POM quality markers were contradictory. At 50 m depth the highest lipid concentration of all locations, inferring high sPOM quality, coincided with the highest phaeopigment/chlorophyll *a* ratio of all locations, inferring low sPOM quality (Pinturier-Geiss *et al*. 2001).

Whether the observed differences in biomass-specific ETS activity are due to local differences in size and species composition of the zooplankton cannot yet be answered. A thorough taxonomical analysis is underway (Martin and Christiansen, in prep.) and will give insight into possible changes of the zooplankton community. However, the relatively uniform distribution of depth-integrated zooplankton biomass values (0-700 m) at all Sedlo sampling locations might indicate a largely similar community composition.

The reported seamount effects are based on differences in zooplankton respiration rates and biomass observed at several seamount locations compared to one reference open ocean location for each seamount. These differences might, thus, partly be the result of this sampling imbalance against the open ocean and observed ranges in respiration rates and biomass might represent the general open ocean background variability.

4.3 IMPLICATIONS FOR TROPHIC PATHWAYS AT THE TWO SEAMOUNTS

According to prevailing hydrographical parameters, Taylor column generation at Seine Seamount is certainly possible and isopycnal doming over the shallow seamount may well extend into the euphotic zone (Mohn, pers. comm.). Both sets of conditions theoretically facilitate the influx of nutrient-rich deeper water into the surface layer. Evidence of potential nutrient enrichment in terms of enhanced phytoplankton biomass or primary production at the seamount, however, appears to be sporadic. Arístegui *et al*. (2009) reported a clear seamount effect on phytoplankton biomass in April 2004 when chlorophyll *a* values (0-150 m) were enhanced at the seamount locations compared to the reference location (Table 3), but detected no such enhancement in July 2004. As the authors concomitantly observed a proportionally higher enhancement of phaeopigments and only a slight increase in gross primary production at the seamount locations (Table 3), they suggested that the retention of organic matter, rather than an increase in local

primary production, was the main cause of increased phytoplankton biomass. Likewise, higher zooplankton biomass-specific ETS activity at the seamount was only observed in April 2004 and not in July 2004. The enhancement was also of a lower magnitude than the observed spatial and temporal variability and had no apparent effect on respiratory carbon demand of the standing stock; the latter was influenced mainly by lower zooplankton biomass above the summit. The intermittent nature of the chlorophyll *a* enrichment and weak evidence for enhanced zooplankton respiration rates observed at Seine Seamount, thus, do not seem to support the theory of locally enhanced primary and secondary production providing an autochthonous food supply to the seamount fauna (see Section 1). Instead, the persistently low zooplankton biomass above the summit compared to the other sampling locations rather supports the idea of an allochthonous food supply to the seamount fauna through advection from the surrounding ocean. Reduced summit biomass might, furthermore, result in increased spatial patchiness downstream of the seamount as reported for zooplankton biomass around seamounts by other authors (e.g. Genin *et al*. 1994, Haury *et al*. 2000).

At Sedlo Seamount in November 2003, mesozooplankton respiratory carbon demand (0-700 m) varied strongly among seamount locations resembling local differences in biomass-specific ETS activity while standing stock biomass (0-700 m) was similar at all sampling locations. There was some evidence for local differences in food quantity and quality influencing highest respiration rates observed at the western slope and lowest respiration rates at the summit and eastern slope locations (see 4.2 for discussion). Hydrographic data collected by White *et al*. (2009) from late March 2003 to early December 2003 revealed a complicated hydrographic regime at Sedlo Seamount. This was characterized by relatively persistent stronger currents close to the summit sea floor and a general anti-cyclonic flow around the seamount, likely due to Taylor Cone generation, which was present essentially throughout the measurement period. The anti-cyclonic flow reversed to cyclonic flow at 400 m depth, about 350 m above the summit depth, to form a cyclonic circulation cell located above the anti-cyclonic circulation cell. Modelling of the hydographic data further revealed the presence of a particularly strong anti-cyclonic flow pattern around the central peak of Sedlo seamount (White *et al*., 2009). These hydrographic conditions might be the cause for increased POM resuspension and retention above the trough between the two SE peaks resulting in

higher tPOM abundance detected by Vilas *et al*. (2009) above the western slope in November 2003. Whether up-welling nutrient-rich deep waters may reach the euphotic layer due to vortex pairing was not clear (White *et al*., 2009) and was not supported by clear evidence from locally enhanced chlorophyll *a* values or primary production (Table 4). Seamount-induced local phytoplankton biomass enhancements would have to be maintained for a few weeks to result in a zooplankton biomass response, as typical generation times for most zooplankton are in the order of weeks to months (Boehlert and Genin 1987). Despite the persistence of Taylor cone conditions during the four months preceding zooplankton sampling in November 2003, no increase in zooplankton biomass was observed at the western slope location. This suggests that, even if zooplankton production was locally enhanced at the seamount, any increased production was probably transported off the seamount by the general ocean current in the absence of an effective trapping mechanism for the zooplankton. Downstream transport of seamount-generated differences in zooplankton biomass (e.g. biomass reduction) has previously been reported by other authors (e.g. Genin *et al*. 1994, Haury *et al*. 2000). Thus, no clear evidence for locally enhanced seamount production at Sedlo Seamount was apparent, suggesting, like at Seine Seamount, advection of zooplankton to be the main food source supporting the seamount fauna.

5. CONCLUSIONS

Large temporal and spatial variability of zooplankton respiration rates and biomass were apparent at Seine and Sedlo Seamounts and coincided with local differences in food abundance and quality. Possible seamount effects on zooplankton biomass-specific ETS activity observed at the seamount locations compared to the open ocean locations were either characterized by an enhancement of activity at all seamount locations as at Seine Seamount in April 2004, although this was of a lower magnitude than spatial and temporal variability, with no apparent influence on zooplankton respiratory carbon demand, or by large local differences resulting in a larger range of respiratory carbon demand at the seamount, as at Sedlo Seamount in November 2003. In both cases no impact of enhanced respiration rates on zooplankton standing stock biomass was observed. Instead, a persistent pattern of zooplankton biomass reduction above the summit of Seine Seamount resulted in a concomitant reduction of respiratory carbon

demand. Due to a sampling imbalance against the open ocean, the reported seamount effects on respiration rates and biomass may also reflect variability in the open ocean background. The sporadic nature and low magnitude of enhanced zooplankton biomass-specific ETS activity and respiratory carbon demand compared to spatial and temporal variability at both seamounts lead us to reject the hypothesis that locally enhanced primary and secondary production provides an autochthonous food supply to the resident fauna at Seine and Sedlo Seamounts and to conclude that the fauna at both seamounts are more likely supported by advection of food from the surrounding ocean.

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REFERENCES

Arístegui, J., Mendonça, A., Vilas, J.C., Espino, M., Polo, I., Montero, M.F., Martins, A., 2009. Plankton metabolic balance at two north Atlantic seamounts. Deep-Sea Research Part II, in press.

Beckmann, A. and Mohn, C., 2002. The upper ocean circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. Ocean Dynamics, 52: 194-204.

Bienfang, P.K., Szyper, J.P., Okamoto, M.Y., Noda, E.K., 1984. Temporal and spatial variability of phytoplankton in a subtropical ecosystem. Limnology and Oceanography, 29: 527–539.

Boehlert, G. W. and Genin, A., 1987. A review of the effects of seamounts on biological processes. In: B. H. Keating, P. Fryer, R. Batiza, G. W. Boehlert (Eds.), Seamounts, Islands and Atolls. Geophysical monograph, vol 43, American Geophysical Union.

Calbet, A. and Landry, M.R., 1999. Mesozooplankton influences on the microbial food web: direct and indirect trophic interactions in the oligotrophic open ocean. Limnology and Oceanography, 44:1370–1380.

Chisholm, S. W., 1992. Phytoplankton size. In: Falkowski, P. G. and Woodhead, A. D. (Eds.), Primary Productivity and Biogeochemical Cycles in the Sea. Plenum Press, New York, 550 pp.

Christiansen, B. and Wolff, G.A., 2009. OASIS project description. Deep-Sea Research Part II, in press.

Christiansen, B., Martin, B., Hirch, S., 2009. The benthopelagic fish fauna of Seine Seamount, NE Atlantic: Composition, population structure and diets. Deep-Sea Research Part, in press II.

Conover, R. J. and Corner, E. D. S., 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. J. Mar. Biol. Assoc. UK, 48: 49–75.

Cushing, D. H., 1989. A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J. Plankton Res., 11, 1–13.

Dam, H.G., Miller, C.A., Jonasdottir, S.H., 1993. The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic bloom experiment. Deep-Sea Research Part II 40, 197–212.

Dower, J., Freeland, H., Juniper, K., 1992. A strong biological response to oceanic flow past Cobb Seamount. Deep-Sea Research, 39: 1139-1145.

Dower, J.F. and Mackas, D.L., 1996. "Seamount effects" in the zooplankton community near Cobb Seamount. Deep-Sea Research, 43 (6): 837-858.

Epp, D. and Smoot, N. C., 1989. Distribution of seamounts in the North Atlantic. Nature, 337: 254-257.

Gallienne, C. P., Robins, D. B., Woodd-Walker, R. S., 2001. Abundance, distribution and size structure of zooplankton along a 20° west meridional transect of the North East Atlantic Ocean in July. Deep-Sea Res. II, 48: 925–950.

Genin, A. and Boehlert, G. W., 1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. Journal of Marine Research, 43: 907-924.

Genin, A., Haury, L., Greenblatt, P., 1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep Sea Research, 35: 151-175.

Genin, A., Greene, C., Haury, L., Wiebe, P., Gal, G., Kaartvedt, S., Mier, E., Fey, C., Dawson, J., 1994. Zooplankton patch dynamics: daily gap formation over abrupt topography. Deep Sea Research I, 41: 941-951.

Genin, A., 2004. Biophysical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Marine Systems, 50: 2-20.

González, N., Anadón, R., Mouriño, B., Fernandez, E., Sinha, B., Escánez, J., Armas, D. D., 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: The role of mesoscale instabilities. Limnology and Oceanography, 46: 946-952.

Haney, J.F., 1988. Diel patterns of zooplankton behaviour. Bull. Mar. Sci., 43: 583-603.

Harris, R.P., 1982. Comparison of the feeding behaviour of Calanus and Pseudocalanus in two experimentally manipulated enclosed systems. Journal of the Marine Biological Association of the United Kingdom, 62: 71–91.

Harrison, W.G., Arístegui, J., Head, E.J.H., Li, W.K.W., Longhurst, A.R., Sameoto, D.D., 2001. Basin-scale variability in plankton biomass and community metabolism in the sub-tropical North Atlantic Ocean. Deep-Sea Research II, 48: 2241–2269.

Haury, L., Fey, C., Gal, G., Hobday, A., Genin, A., 1995. Copepod carcasses in the ocean I. Over seamounts. Marine Ecology Progress Series, 123: 57–63.

Haury, L., Fey, C., Newland, C., Genin, A., 2000. Zooplankton distribution around four eastern North Pacific seamounts. Progress in Oceanography, 45: 69-105.

Hays, G.C., Harris, R.P., Head, R.N., 2001. Diel changes in the near-surface biomass of zooplankton and the carbon content of vertical migrants. Deep-Sea Research II, 48: 1063-1068.

Head, R. N., Medina, G., Huskin, I., Anadón, R., Harris, R. P., 2002. Phytoplankton and mesozooplankton distribution and composition during transects of the Azores Subtropical Front. Deep-Sea Research II, 49: 4023–4034.

Hernández-León, S. and Gómez, M., 1996. Factors affecting the Respiration/ETS ratio in marine zooplankton. J. Plankton Res., 18: 239–255.

Hernández-León, S., Postel, L., Arístegui, J., Gómez, M., Montero, M.F., Torres, S., Almeida, C., Kühner, E., Brenning, U., Hagen, E., 1999. Large-scale and mesoscale distribution of plankton biomass and metabolic activity in the northeastern Central Atlantic. J. Oceanogr., 55: 471–482.

Hernández-León, S., Gómez, M., Pagazaurtundua, M., Portillo-Hahnefeld, A., Montero, I., Almeida, C., 2001a. Vertical distribution of zooplankton in Canary Island waters: implications for export flux. Deep-Sea Research I, 48: 1071–1092.

Hernández-León, S., Almeida, C., Gómez, M., Torres, S., Montero, I., Portillo-Hahnefeld, A., 2001b. Zooplankton biomass and indices of feeding and metabolism in island-generated eddies around Gran Canaria. J. Mar. Syst., 30: 51–66.

Hernández-León, S., Almeida, C., Bécognée, P., Yebra, L., Arístegui, J., 2004. Zooplankton biomass and indices of grazing and metabolism during a late winter bloom in subtropical waters. Mar. Biol., 145: 1191-1200.

Hernández-León, S. and Ikeda, T., 2005a. A Global Assessment of Mesozooplankton Respiration in the Ocean. Journal of Plankton Research, 27: 153-158.

Hernández-León, S. and Ikeda, T., 2005b. Zooplankton respiration. In: del Giorgio, P.A. and Williams, P.J.B. (Eds.), Respiration in aquatic ecosystems. Oxford University Press, pp. 57-82.

Huskin, I., Anadón, R., Medina, G., Head, R. N., Harris, R. P., 2001a. Mesozooplankton distribution and copepod grazing in the Subtropical Atlantic near the Azores: influence of mesoscale structures. J. Plankton. Res., 23: 671–691.

Huskin, I., Anadón, R., Woodd-Walker, R.S., Harris, R. P., 2001b. Basin-scale latitudinal patterns of copepod grazing in the Atlantik Ocean. Journal of Plankton Research, 23: 1361–1371.

Huskin, I., Viesca, L., Anadón, R., 2004. Particle flux in the Subtropical Atlantic near the Azores: influence of mesozooplankton. Journal of Plankton Research, 26: 403–415.

Ikeda, T., 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. Biol., 85: 1–11.

Ikeda, T., Torres, J. J., Hernández-León, S., Geiger, S. P., 2000. Metabolism. In R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley (Eds.), ICES Zooplankton Methodology Manual. Academic Press, San Diego, pp. 455–532.

Ikeda, T., Kanno, Y., Ozaki, K., Shinada, A., 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Mar. Biol., 139: 587–596.

Isaacs, J.D. and Schwartzlose, R.A., 1965. Migrant sound scatterers: interactions with the seafloor. Science, 150: 1810-1813.

Kenner, R. A., and Ahmed, S. I., 1975. Measurement of electron transport activities in marine phytoplankton. Mar. Biol., 33: 119-128.

King, F.D. and Packard, T.T., 1975a. Respiration and the activity of the respiratory electron transport system in marine zooplankton. Limnol. Oceanogr., 20: 849-854.

King, F. D. and Packard, T. T., 1975b. The effect of hydrostatic pressure on respiratory electron transport system activity in marine zooplankton. Deep-Sea Research, 22: 99–105.

King, F. D., Devol, A. H., Packard, T. T., 1978. Plankton metabolic activity in the eastern tropical North Pacific. Deep-Sea Research., 25: 689–704.

Kiørboe, T., Møhlenberg, F., and Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Mar. Ecol. Prog. Ser., 26: 85–97.

Kiriakoulakis, K., White, M., Bett, B. J., Wolff, G. A., 2004. Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. Deep-Sea Research I, 51: 1937-1954

Kiriakoulakis, K., Vilas, J.C., Blackbird, S.J., Arístegui, J., Wolff, G.A., 2009. Seamounts and organic matter – is there an effect? The case of Sedlo and Seine Seamounts. Part II. Composition of suspended particulate organic matter. Deep-Sea Research II, in press.

Koppelmann, R., Schäfer, P., Schiebel, R., 2000. Organic carbon losses measured by heterotrophic activity of mesozooplankton and $CaCO_3$ flux in the bathypelagic zone of the Arabian Sea. Deep-Sea Research II, 47: 169-187.

Koslow, J.A., 1997. Seamounts and the Ecology of Deep-Sea Fisheries. American Scientist, 85: 168-176.

Lampert, W., 1984. The measurement of respiration. In J. A. Downing and F. H. Rigler (Eds.), A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. Blackwell Scientific Publishers, Oxford, pp. 413–468.

Lampert, W., 1986. Response of the respiratory rate of Daphnia magna to changing food conditions. Oecologia, 70: 495-501.

Lampitt, R.S. and Gamble, J.C., 1982. Diet and respiration of the small planktonic marine copepod Oithona nana. Marine Biology, 66: 185–190.

Longhurst, A.R. and Williams, R., 1979. Materials for plankton modelling: Vertical distribution of Atlantic zooplankton in summer. Plankton Res., 1: 1-28.

Longhurst, A.R., 1995. Seasonal cycles of pelagic production and comsumption. Progress in Oceanography, 36: 77–167.

Marañón, E., Holligan, P.M., Varela, M., Mouriño, B., Bale, A.J., 2000. Basin-scale variability of phytoplankton from 50° N to 50° S in the Atlantic Ocean. Deep-Sea Research Part I, 47: 825–857

Marañón, E., Berhenfeld, M.J., González, N., Mouriño, B., Zubkov, M.V., 2003. High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure. Marine Ecology Progress Series, 257: 1–11.

Martin, B. and Christiansen, B., 2009. Distribution of zooplankton biomass at four seamounts in the NE Atlantic. Deep-Sea Research Part II, in press.

McEwen, G. F., Johnson, M. W., Folsom, T. R., 1954. A statistical analysis of the performance of the Folsom plankton splitter, based upon test observations. Arch. Met. Geophys. Bioklim., Ser. A, 6: 502-527.

Mouriño, B., Fernandez, E., Serret, P., Harbour, D., Sinha, B., Pingree, R., 2001. Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). Oceanologica acta, 24 (2): 1-20.

Neuer, S., Cianca, A., Helmke, P., Freudenthal, T., Davenport, R., Meggers, H., Michaela Knoll, M., Santana-Casiano, J. M., González-Davila, M., Rueda, M.-J., Llinás, O., 2007. Biogeochemistry and hydrography in the eastern subtropical North Atlantic gyre. Results from the European time-series station ESTOC. Progress in Oceanography, 72: 1–29.

Packard, T. T., 1971. The measurement of respiratory electron transport activity in marine phytoplankton. J. Mar. Res., 29: 235–244.

Packard, T. T., Devol, A. H., King, F. D., 1975. The effect of temperature on the respiratory electron transport system in marine plankton. Deep-Sea Research, 22: 237–249.

Packard, T.T., 1985. Measurement of electron transport activity of marine microplankton. Advances in Aquatic Microbiology, 3: 207-261.

Paffenhöfer, G.-A., Tzeng, M., Hristov, R., Smith, C.L., Mazzocchi, M.G., 2003. Abundance and distribution of nanoplankton in the epipelagic subtropical/tropical open Atlantic Ocean. Journal of Plankton Research, 25: 1535–1549.

Paffenhöfer, G.A., Mazzocchi, M.G., Tzeng, M.W., 2006. Living on the edge: feeding of subtropical open ocean Copepods. Marine Ecology, 27: 99–108.

Parin, N.V., Mironov, A.N., Nesis, K.N., 1997. Biology of the Nazca and Sala y Gómez Submarine Ridges, an outpost of the Indo-West Pacific Fauna in the eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. Adv. Mar. Biol., 32: 145-242.

Pavlova, E.V., 1994. Diel changes in copepod respiration rates. Hydrobiologia, 292/293: 333–339.

Pearre, S. Jr., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol. Rev., 78: 1-79.

Pinturier-Geiss, L., Laureillard, J. Riaux-Gobin, C., Fillaux, J., Saliot, A., 2001. Lipids and pigments in deep-sea surface sediments and interfacial particles from the Western Crozet Basin. Marine Chemistry, 75: 249-266.

Rivkin, R.B., Legendre, L., Deibel, D., Tremblay, J.E., Klein, B., Crocker, K., Roy, S., Silverberg, N., Lovejoy, C., Mesple, F., Romero, N., Anderson, M.R., Matthews, P., Savenkoff, C., Vezina, A., Therriault, J.C., Wesson, J., Berube, C., Ingram, R.G., 1996. Vertical flux of biogenic carbon in the ocean: is there food web control? Science, 272: 1163–1166.

Roden, G.I., 1987. Effects of seamounts and seamount chains on ocean circulation and thermohaline structure. In: B. H. Kaeting, P. Fryer, R. Batisa, and G. W. Boehlert (Eds.), Seamounts, Islands, and Atolls. Geopys. Monogr. Ser., 43, AGU, Washington D.C., 335-354.

Rogers, A. D., 1994. The biology of seamounts. Advances in Marine Biology, 30: 305-350.

Schalk, P.H., 1990. Biological activity in the Antarctic zooplankton community. Polar Biol. 10:405–411

Schmoker, C. and Hernández-León, S., 2003. The effect of food on the respiration rates of Daphnia magna using a flow-through system. Sci. Mar., 67 (3): 361-365.

Sieracki, M.E., Verity, P.G., Stoecker, D.K., 1993. Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic Spring Bloom. Deep-Sea Research II, 40: 213–225.

Smith, D. K. and Jordan, T. H., 1988. Seamount statistics in the Pacific Ocean. Journal of Geophysical Research, 93: 2899-2919.

Tang, E. P. V., 1995. The allometry of algal growth rates. J. Plankton Res., 17: 1325–1335.

Thor, P., 2000. Relationship between specific dynamic action and protein deposition in calanoid copepods. J. Exp. Mar. Biol. Ecol., 245: 171–182.

Teira, E., Mouriño, B., Marañón, E., Péreza, V., Pazó, M.J., Serreta, P., Armas, D. de, Escánez, J., Malcolm, E., Woodward, S., Fernández, E., 2005. Variability of chlorophyll and primary production in

the Eastern North Atlantic Subtropical Gyre: potential factors affecting phytoplankton activity. Deep-Sea Research I, 52: 569–588.

Uda, M. and Ishino, M., 1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish., 44: 105-129.

Vilas, J.C., Arístegui, J., Kiriakoulakis, K., Wolff, G.A., Espino, M., Polo, I., Montero, M.F., Mendonça, A., 2009. Seamounts and organic matter – is there an effect? The case of Sedlo and Seine Seamounts; Part 1. Distributions of dissolved and particulate organic matter. Deep-Sea Research Part II, in press.

White, M., Mohn, C., Bashmachnikov, I., Jose, F., Pelegrí, J.L., 2009. Dynamics at an elongated, intermediate depth seamount in the north Atlantic (Sedlo Seamount, 40 20'N, 27 50'W). Deep-Sea Research Part II, in press.

Wiebe, P.H., Morton, A.W., Bradley, A.M., Backus, R.H., Craddock, J.E., Barber, V., Cowles, T.J., Flierl, G.R., 1985. New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar. Biol., 87: 313-323.

Wilson, C.D. and Boehlert, G.W., 2004. Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific. Journal of Marine Systems 50: 39-60.

FOOD SOURCES AND DIETS OF ZOOPLANKTON AT TWO SEAMOUNTS IN THE NE ATLANTIC: ARE THERE SEAMOUNT EFFECTS?

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ABSTRACT

Stable isotopes and fatty acid biomarkers were used to investigate the food sources and diets of selected epi- and mesopelagic zooplankton species sampled at two seamounts (Seine: 34°N, 14°W, summit depth: 170 m; Sedlo: 40°N, 27°W, summit depth: 750 m) in the NE Atlantic during three cruises in November 2003, April 2004 and July 2004. Samples of suspended particulate organic matter (POM_{susp}) and zooplankton were taken at seamount and reference farfield locations in order to test the hypothesis of locally enhanced seamount productivity and its relation to zooplankton feeding conditions. Selected zooplankton species included herbivores, omnivores and carnivores. Stable isotope and fatty acid biomarkers indicated pronounced temporal differences in POM_{susp} compositions and diets of the zooplankton species at Seine Seamount. In November 2003, there was a mismatch between high $\delta^{15}N$ values of POM_{susp} and low $\delta^{15}N$ values of epipelagic zooplankton species. This was probably the result of a time-lag in isotopic equilibration of zooplankton to isotopic changes in the food sources. In April 2004, storage lipid fatty acid compositions of epipelagic zooplankton were rich in diatom markers and reflected elevated diatom abundance indicated in the total lipids of POM_{susp}. Significantly lower $\delta^{15}N$ values observed in mesopelagic species in April compared to July in 2004 might be related to the spring bloom that resulted in increased downward flux of sinking organic matter particles with lower $\delta^{15}N$ values. In contrast to the pronounced temporal differences, the biomarker signatures between the farfield and seamount locations at Seine and Sedlo Seamounts did not show evidence for locally enhanced feeding conditions of the zooplankton fuelled by seamount-related nutrient-upwelling as proposed by the hypothesis of locally-enhanced seamount productivity.

1. INTRODUCTION

Seamounts are common topographic features in all ocean basins (Smith and Jordan 1988, Epp and Smoot 1989, Rogers 1994) and are often associated with high biomass and diverse species assemblages, including species-rich benthic communities dominated by suspension feeders and dense aggregations of benthopelagic fishes (Genin *et al.* 1986, Rogers 1994, Koslow 1997, Parin *et al*. 1997, Richer de Forges *et al.* 2000, Koslow *et al.* 2001). Several hypotheses have been developed to explain how high standing stocks associated with seamount ecosystems are sustained despite the often impoverished nutritional conditions of the ambient oceanic regions. These hypotheses are based on interactions between seamounts and the surrounding open ocean current regimes that influence local hydrographic conditions (Roden 1987, Gonzales *et al*. 2001) and include enhanced local *in situ* productivity and the aggregation or increased flux of prey in the seamount environment (Roger 1994, Koslow 1997, Genin 2004). The hypothesis of locally enhanced autochthonous seamount productivity proposed that a combination of Taylor column-generated nutrient-upwelling and particle-retention above the seamount could result in a local increase in primary and secondary production that could sustain resident fish populations (Uda and Ishino 1958). Taylor columns (or Taylor caps in stratified hydrographic conditions) are anti-cyclonic circulation cells trapped to the seamount summit region, which generate upwelling above the flanks of the seamount and downwelling in the center above the summit and may enhance local particle retention (e.g., Mullineaux and Mills 1997, Beckmann and Mohn 2002). Retention times of water and particles over a seamount would have to be in the order of zooplankton generation times (weeks or months) to allow higher trophic levels to respond to higher primary productivity in the vicinity of the seamount. Local upwelling and elevated chlorophyll concentrations related to Taylor column activity have been observed above a number of seamounts (Genin and Boehlert 1985, Dower *et al*. 1992, Dower and Mackas 1996, Mouriño *et al*. 2001), but support for the local enhancement of zooplankton secondary production remained weak (Uda and Ishino 1958, Genin and Boehlert 1985) and appeared inadequate to sustain large fish aggregations observed in the vicinity of seamounts (Tseitlin 1985, Koslow 1997). Additional hypotheses have therefore been proposed to explain the higher abundances of zooplankton (Fedosova 1974), micronekton (Boehlert and Genin 1987) and resident benthic and benthopelagic fauna (Genin *et al.* 1986, Rogers 1994, Koslow 1997, Parin *et al*. 1997, Richer de

Forges *et al.* 2000, Koslow *et al.* 2001) in the vicinity of seamounts. These include the sound-scattering layer interception hypothesis (Isaacs and Schwartzlose 1965), which suggests increased food supply to the seamount fauna due to topographic blockage and trapping of the vertically migrating zooplankton and micronekton during descend. Local aggregations of zooplankton might also be driven by behavioural response to seamount-induced vertical water mass movement, when zooplankton swim vertically in order to maintain their depth (Genin 2004).

In this study, we aimed to test the hypothesis of locally-enhanced seamount productivity by using a biochemical trophic marker approach to investigate possible seamount-related changes in particulate organic matter composition and zooplankton diet at two seamounts in the northeast Atlantic. Stable isotopes and fatty acids have been used extensively in studies of trophic ecology, including marine systems (e.g. Davenport and Bax 2002, Dalsgaard *et al.* 2003 and references therein, Koppelmann *et al.* 2009). Isotopic signatures change from prey to predator in a predictable way for the different elements and can be used to evaluate carbon sources and trophic position of an organism (e.g. Peterson and Fry 1987, Vander Zanden and Rasmussen 2001, Post 2002). The carbon stable isotopic composition of organisms ($\delta^{13}C$) changes little (< 1 ‰) between trophic levels and is used to evaluate the sources of carbon (DeNiro and Epstein 1978, 1981, Peterson and Fry 1987, Michener and Schell 1994). The nitrogen stable isotopic composition ($\delta^{15}N$), on the other hand, is typically enriched by 3-4 ‰ (average 3.4 ‰) per trophic level and is used to estimate the trophic position of a consumer (Minagawa and Wada 1984). The use of fatty acid biomarkers to trace predator-prey relationships in the ocean is based on the observation that particular fatty acids can only be biosynthesised by certain phytoplankton and macroalgal species and that these fatty acid patterns are transferred conservatively from primary producers to their consumers and among consumers (Dalsgaard *et al.* 2003 and references therein). In contrast to the conservative fatty acid composition of structural lipids (mainly phospholipids) of consumers, which are relatively independent of dietary input, the fatty acid profiles of neutral lipids, which are used for energy storage, are readily influenced by dietary input (Sargent and Henderson 1995). In this study, the fatty acid signature of the neutral lipid fraction was used to investigate the diets of the zooplankton species studied.

Phytoplankton production in the oligotrophic subtropical gyres is generally nutrient limited and phytoplankton communities in the oligotrophic area of the North Atlantic Subtropical Gyre, where the investigated seamounts are located, are dominated by small flagellates and picoplankton (<2 µm) while larger diatoms, dinoflagellates and coccolithophorids constitute <10 % of phytoplankton stocks (Head *et al.* 2002, Huskin *et al.* 2004, Teira *et al.* 2005, Neuer *et al.* 2007). A number of studies have shown that copepod feeding is inefficient on small particles (e.g., Harris 1982, Lampitt and Gamble 1982). Elevated grazing rates have been observed when the phytoplankton biomass is dominated by large particles (diatoms) and much reduced when dominated by small (<10 µm) flagellates (Dam *et al.* 1993, Sieracki *et al.* 1993). Dietary shifts from an omnivorous towards a more herbivorous diet with a preference for diatoms during increased diatom abundance or diatom blooms have been reported for a number of copepod and euphausiid species (Fessenden and Cowles 1994, Schnetzer and Steinberg 2002). They have been suggested as an adaptive response to situations of low phytoplankton availability, with omnivory being unnecessary under phytoplankton bloom conditions (Fessenden and Cowles 1994). Diatoms are known to grow efficiently under conditions of enhanced nutrient concentrations and have been reported as a dominant group in mixing conditions (Cushing 1989, St. John and Lund 1996). Enhanced nutrient concentrations due to deep-water upwelling at the seamounts could result in an abundance of diatoms in the local phytoplankton composition compared to the surrounding stratified and nutrient-depleted ocean waters. Local zooplankton populations would in turn preferentially utilize these higher diatom abundances in the vicinity of the seamounts.

We expected to see these seamount-related differences in phytoplankton composition and zooplankton diet expressed in the biomarker signatures. Lipid compositions of diatoms are characterized by the fatty acids 16:1(n-7) and 20:5(n-3), while dinoflagellates and haptophytes usually contain high amounts of 18:4(n-3), 18:5(n-3) and 22:6(n-3) fatty acids (reviewed by Dalsgaard *et al.* 2003). The ratio of 16:0/16:1(n-7) fatty acids, which is higher in diatoms than other phytoplankton groups, has been applied in several studies to discriminate between diatom versus flagellate feeding (St. John and Lund 1996, Mayzaud *et al.* 1999, Auel *et al.* 2002). The ratio 18:1(n-9)/18:1(n-7) has been frequently used to estimate the degree of carnivory versus

herbivory (Graeve *et al.* 1997, Mayzaud *et al.* 1999, Schmidt *et al.* 2006). We expected the lipid compositions of suspended particulate organic matter and the zooplankton in the vicinity of seamounts to contain higher proportions of diatom marker fatty acids and a higher ratio of 16:1(n-7)/16:0 fatty acids concurrently with a lower ratio of 18:1(n-9)/18:1(n-7) than at the stratified, flagellate dominated reference locations outside the sphere of influence of the seamounts.

In oligotrophic open oceans, $\delta^{15}N$ values of near-surface suspended particles are well below that of deep-water nitrate due to utilization of isotopically lighter ammonium and/or production of isotopically depleted organic matter through N_2-fixation by diazotrophs in stratified conditions (Checkley and Miller 1989, Checkley and Entzeroth 1985, Montoya *et al.* 2002, 2004). Isotopic shifts in phytoplankton $\delta^{15}N$ values have been reported associated with upwelling of deep-water nitrate into the euphotic zone during mixing conditions (Montoya *et al.* 2002, O´Reilly *et al.* 2002). We expected to see this isotopic shift towards higher $\delta^{15}N$ values in phytoplankton and zooplankton in the vicinity of the seamounts if seamount-induced upwelling and enhanced local productivity had occurred.

The aim of this study was to investigate the temporal and spatial differences in the food sources and diets of epi- and mesopelagic zooplankton species with respect to possible seamount-related effects at two seamounts in the NE Atlantic using the combined approach of stable isotope and fatty acid biomarker analyses.

Specific objectives were:

1. to identify the dietary sources of the zooplankton species studied at the two seamounts,
2. to investigate temporal changes in zooplankton diet with regard to changes in the composition of suspended particulate organic matter,
3. to analyse possible seamount-related influences on the diet and trophic position of the zooplankton species focussing on the hypothesis of increased autochthonous production at seamounts.

2. MATERIALS AND METHODS

Sample collection. This investigation was part of an interdisciplinary study around two North Atlantic seamounts, Seine and Sedlo, within the framework of the European Project OASIS (OceAnic Seamounts: an Integrated Study; Christiansen and Wolff 2009). Both seamounts are situated within the oligotrophic biogeochemical province of the eastern North Atlantic Subtropical Gyre (NASE; Longhurst *et al.* 1995, 1998). Seine Seamount is located northeast of Madeira (33°50'N - 14°20'W) and is a single summit cone-shaped seamount, which rises from more than 4000 m to a summit plateau at ~170 m (Fig. 1). Sedlo Seamount is located north of the Azores (40°25'N - 26°55'W) and is composed of three peaks, of which we investigated the shallowest with a summit depth of ~750 m (Fig. 1).

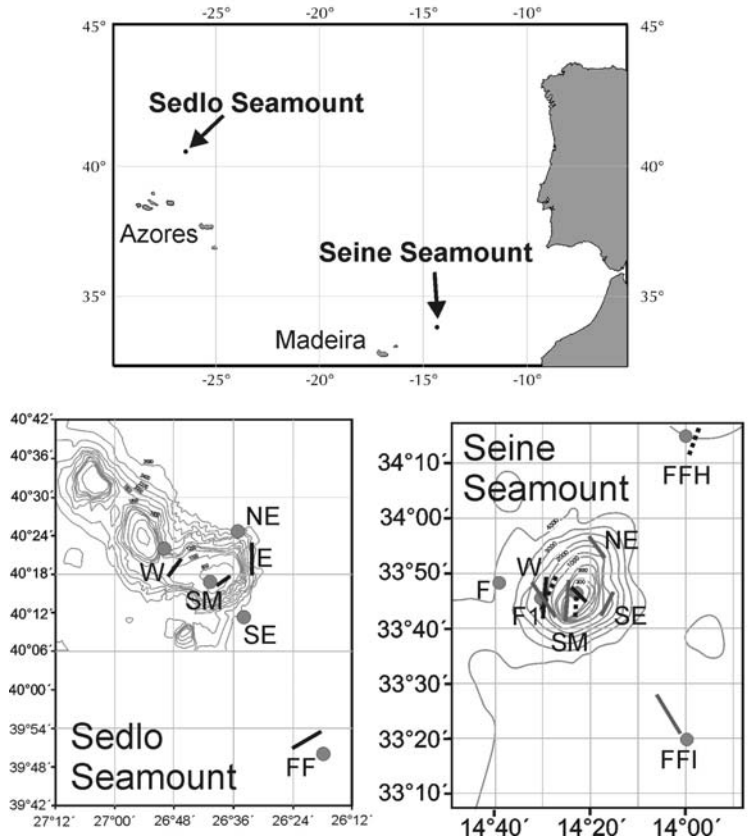

Fig. 1. Location and bathymetry of Sedlo and Seine Seamounts. The locations of the MOCNESS zooplankton hauls (Tab. 1) are shown for Seine and Sedlo Seamounts in November 2003 (solid black line) and for Seine Seamount in April 2004 (solid grey line) and July 2004 (broken line). Haul locations are indicated as SM for the summit and E (east), NE (northeast), SE (southeast), and W (west) for the slope locations. FF indicates the farfield location at Sedlo Seamount, FFH and FFI indicate the farfield locations for Seine Seamount. POM_{susp} water sample locations (filled circles) are either the same as for MOCNESS haul locations, or indicated as F1 and F for the west slope at Seine Seamount and NE and SE at the east slope of Sedlo Seamount.

Measurements of the current regime at Seine Seamount indicated that a Taylor column generation is certainly possible and isopycnal doming over the shallow seamount may well extend into the euphotic zone (Mohn, pers. comm.), which would theoretically facilitate the influx of nutrient-rich deeper water into the surface layer. The impact of mesoscale eddies, usually derived from Mediterranean Outflow Water, on the anti-cyclonic flow resulted in strong mesoscale temporal variability in the local current regime (Bashmachnikov *et al.* 2009). The current regime at Sedlo Seamount indicated a complex hydrographic situation with cyclonic circulation closer to the surface and anti-cyclonic circulation below and closer to the seamount summit and possible links between them (Mohn *et al.* 2009). Due to variable background forcing and interaction of the seamount with Mediterranean Outflow Water patches, these flow patterns are probably not a permanent feature (Bashmachnikov *et al.* 2009, Mohn *et al.* 2009). Whether upwelling nutrient-rich deep water reaches the euphotic layer due to vortex pairing is not clear (Mohn *et al*. 2009).

Zooplankton and suspended particulate organic matter (POM_{susp}) samples were taken during three cruises, in November 2003 (11th November – 6th December 2003; FS *Meteor*, M60/1), April 2004 (25th March – 8th April; FS *Poseidon*, P309) and July 2004 (30th June – 1st August; RSS *Discovery*, D282). Seine Seamount was sampled during the surveys in November, April and July, while Sedlo Seamount was sampled in November (Tab. 1). At each seamount, water particles were filtered from CTD water and day and night zooplankton hauls were taken at locations above the summit and the slopes of the seamounts and at farfield locations (Fig.1, Tab. 1). The influence of a seamount on the hydrodynamic regime acts over a distance of some 20-40 km from the seamount centre (Beckmann and Mohn 2002), therefore the farfield sampling sites at Seine and Sedlo Seamounts were chosen at distances of 40 km and 65 km from the seamounts, respectively.

Zooplankton was sampled using a 1 m^2-Double-MOCNESS (Multiple Open/Closing Net and Environmental Sensing System, Wiebe *et al.* 1985) with a 1 m^2-opening and equipped with 20 dark coloured nets (10 nets at each side) of 0.333 µm mesh size. In November 2003, a 10 m^2-MOCNESS with a 10 m^2-opening equipped with 6 nets of 1.6 mm mesh size was also used. The nets were sequentially opened and closed at defined depths and depth was controlled by a temperature corrected pressure sensor.

Table 1. Sampling data for MOCNESS zooplankton hauls and CTD-Rosette water sampling for suspended particulate organic matter.

Gear-Haul	Date	Sampling time (UTC)	Location	Sampling depth (m)	Water depth (m)	Latitude N	Longitude W
Meteor 60/1, November 2003							
Sedlo Seamount							
ROS-682	19.11.2003	23:40 - 02:38	E slope-NE	50	2660	40°25.0	26°35.0
ROS-683	19.11.2003	14:00 - 16:46	W slope	50	1420	40°21.9	26°49.9
ROS-687	20.11.2003	16:15 - 18:10	Summit-SM	50	757	40°17.3	26°41.3
ROS-695	21.11.2003	02:15 - 03:22	E slope-SE	50	2656	40°11.6	26°33.9
ROS-738	29.11.2003	02:40 - 04:41	Farfield-FF	50	2876	39°50.0	26°17.9
MOC-01	21./22.11.2003	23:40 - 02:38	E slope	0 - 1000	2697	40°17.9	26°32.6
MOC-02	22.11.2003	14:00 - 16:46	E slope	0 - 1000	1963	40°17.7	26°33.1
MOC-03	23.11.2003	16:15 - 18:10	Summit-SM	0 - 800	837	40°15.3	26°40.2
MOC-04	24.11.2003	02:15 - 03:22	Summit-SM	0 -770	800	40°16.1	26°39.1
MOC-06	25.11.2003	14:37 - 17:02	W slope	0 - 1000	1183	40°20.6	26°47.5
MOC-07	26.11.2003	02:40 - 04:41	W slope	0 - 950	989	40°19.2	26°48.4
MOC-09	29.11.2003	02:00 - 05:26	Farfield-FF	0 - 2800	2850	39°46.9	26°24.9
MOC-10	29.11.2003	13:50 - 17:30	Farfield-FF	0 - 3500	3796	39°57.6	26°14.0
Seine Seamount							
ROS-748	03.12.2003	08:38 - 08:46	Summit-A	50	178	33°46.0	14°22.0
MOC-11	03.12.2003	16:00 - 17:21	Summit	50 - 100	190	33°44.7	14°20.9
10MOC-3	03.12.2003	10:09 - 12:33	W slope	0 - 1000	1195	33°42.1	14°30.1
Poseidon 309, April 2004, Seine Seamount							
ROS-13-3	28.03.2004	08:05 - 08:13	Farfield-FFI	50	4400	33°19.8	13°59.3
ROS-18-4	29.03.2004	21:37 - 21:43	Summit-SM	50	171	33°46.0	14°21.8
ROS-22-1	30.03.2004	21:20 - 21:32	W slope-F	50	4008	33°48.0	14°40.1
ROS-28-1	01.04.2004	14:13 - 14:20	W slope-F1	50	2479	33°46.0	14°30.9
MOC-01	28.03.2004	10:44 - 14:05	Farfield-FFI	50 - 1000	4406	33°20.0	14°00.0
MOC-02	29.03.2004	13:34 - 16:48	Summit-SM	50 - 150	174	33°41.4	14°25.5
MOC-04	01.04.2004	10:36 - 13:20	W slope	50 - 1000	1188	33°42.4	14°27.7
MOC-05	01.04.2004	21:04 - 23:16	W slope	50 - 1000	1173	33°42.1	14°27.5
MOC-06	02./03.04.2004	21:22 - 00:04	Farfield-FFI	50 - 1000	4406	33°24.3	14°03.1
MOC-07	03.04.2004	21:25 - 23:54	NE slope	50 - 1000	1547	33°51.8	14°16.9
MOC-08	04.04.2004	12:42 - 14:51	NE slope	50 - 1000	1595	33°52.0	14°16.9
MOC-09	05./06.04.2004	22:40 - 00:15	SE slope	50 - 1000	1360	33°43.0	14°18.6
MOC-10	06.04.2004	09:57 - 11:09	SE slope	50 - 1000	1478	33°43.9	14°17.5
Discovery 282, July 2004, Seine Seamount							
ROS-432-2	07.07.2004	18:20 - 00:02	W slope-F	50	4038	33°48.3	14°39.6
ROS-434-2	08./09.07.2004	21:15 - 00:10	Summit-SM	50	175	33°46.1	14°22.5
ROS-439-2	10.07.2004	5:10 - 10:47	Farfield-FFH	50	4079	34°15.1	14°00.0
MOC-02	09.07.2004	03:01 - 04:02	Summit	0-140	167	33°43.8	14°24.8
MOC-04	10.07.2004	12:51 - 16:10	Farfield-FFH	0-1000	4113	34°12.6	14°01.8
MOC-05	16./17.07.2004	23:10 - 01:53	Farfield-FFH	0-1000	4105	34°12.3	14°01.2
MOC-06	17.07.2004	07:08 - 10:19	W slope	0-1000	2191	33°43.5	14°31.0
MOC-07	17.07.2004	12:43 - 13.37	Summit-SM	0-140	174	33°44.0	14°22.5
MOC-08	17.07.2004	20:13 - 23:13	W slope	0-1000	1951	33°43.4	14°29.6

Abbreviations: ROS: CTD-Rosette with Niskin bottles
MOC, 10MOC: MOCNESS plankton net, 1 m² or 10 m² opening

Zooplankton samples were taken with stratified oblique hauls starting at the greatest sampling depth and progressing up towards the surface at a ships speed of 2 knots. Sampling depths at the farfield location and above the slopes of the seamount covered the upper 1000 m. Directly upon recovery of the MOCNESS, specimen for stable isotope and lipid analyses were sorted on board in a temperature controlled laboratory at 4°C or at ambient temperature conditions on ice using a dissecting microscope. Epi- and mesopelagic zooplankton species were selected on the basis of their abundance and presence during the 3 surveys and with the aim to cover a range of feeding types and trophic levels. Depending on species size, each sample consisted of 1 to 250 individuals (Tab. 2). Stable isotope samples were stored at -20°C and lipid samples at -80°C or in liquid nitrogen until further analyses.

Table 2. Sampling depth and number of stable isotope and lipid samples per species (number of pooled specimens per sample in brackets).

			Sedlo		**Seine**					
Species	Acronym	Depth (m)	November 03		November 03		April 04		July 04	
			n_{SI}	n_{Lip}	n_{SI}	n_{Lip}	n_{SI}	n_{Lip}	n_{SI}	n_{Lip}
POM_{susp}	POM	50	15	5	3	1	12	3	9	3
Copepoda										
Oncaea spp.	Onca	50-150	5 (64-103)	1 (37)	2 (74-85)	1 (100)	6 (50-120)	6 (46-150)	4 (81-105)	3 (100-107)
Lucicutia flavicornis	Lfla	50-150	-	-	3 (100-113)	3 (104-113)	8 (68-103)	3 (41-99)	3 (100-108)	1 (100)
Clausocalanus spp.	Clau	50-150	7 (99-244)	4 (100-203)	-	1 (120)	6 (60-127)	2 (100-110)	4 (84-101)	2 (100-111)
Euchaeta spp.	Euch	50-150	3 (24-50)	-	-	-	3 (83-100)	-	-	-
Pleuromamma xiphias	Pxip	50-100, 500-600	3 (3-15)	3 (10-15)	-	-	5 (40-65)	5 (5-30)	6 (10-21)	3 (10-15)
Disseta palumbii	Dpal	800-1000	1 (10)	2 (3-6)	1 (83)	-	8 (18-60)	8 (12-30)	6 (15-30)	3 (10)
Ostracoda										
Ostracoda	Ostr	50-150	-	-	3 (63-200)	1 (100)	2 (100-102)	1 (95)	-	-
Euphausiacea										
Euphausia hemigibba	Ehem	50-100, 500-600	5 (1-3)	3 (1-5)	-	-	8 (1-2)	6 (1)	6 (1-3)	5 (1-2)
Pteropoda										
Cavolinia inflexa	Cinf	50-450	4 (6-40)	-	1 (22)	1 (10)	1 (30)	1 (25)	-	-
Chaetognatha										
Sagitta spp.	Sagi	50-100	-	-	1 (19)	1 (10)	2 (11-16)	1 (15)	-	-
Eukrohnia hamata	Eham	500-600	3 (6-14)	-	-	-	2 (6-17)	2 (6-10)	-	-
Eukrohnia fowleri	Efow	800-1000	6 (3-45)	2 (3-5)	2 (25-29)	-	8 (4-17)	7 (4-9)	5 (2-6)	3 (1-3)
Pisces										
Cyclothone alba	Calb	500-600	3 (1-2)	3 (1)	1 (1)	-	8 (1)	6 (1)	7 (1-2)	5 (1)
Cyclothone pallida	Cpal	800-1000	-	-	-	-	2 (1)	-	1 (1)	-

Water samples for stable isotope and lipid analyses of suspended particulate organic matter (POM_{susp}) were collected at 50 m depth using Niskin bottles mounted on a CTD rosette. Prior to filtration, the sampled water was passed through a 300 µm mesh sieve to remove larger zooplankton organisms, which would bias the POM_{susp} data. Water for stable isotope (10-20 l per filter) and for lipid (20 l per filter) samples were vacuum

filtered immediately on board at low pressure on pre-combusted (450°C; 5 h) GF/C filters (Whatman®; 55 mm diameter; nominal pore size 1.2 µm). All filter samples were wrapped in muffled (450ºC; 5 h) aluminium foil and immediately frozen at -20ºC (stable isotope samples) and -80ºC or in liquid nitrogen (lipid samples) until further analysis.

Stable isotope analysis. For analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures, frozen samples of POM_{susp} and zooplankton were lyophilised for at least 48 h.
Isotopic analyses of the lyophilised POM_{susp} filter samples were performed simultaneously for carbon and nitrogen stable isotopes by elemental analyser /continuous flow isotope ratio mass spectrometry (Thermo-Finnigan Delta$^+$ Advantage Mass Spectrometer/Costech EAS Elemental Analyser) at UCSB/MSI Analytical Laboratory. The analytical error of this method is ≤0.25 ‰ for $\delta^{13}C$ and $\delta^{15}N$.

Lipids of lyophilised tissue samples were removed for the 2 mesopelagic fish species prior to analysis using Soxhlet extraction with a dichloromethane:methanol mixture (DCM:MeOH 2:1, v:v) for 4 - 6 hours (Bligh and Dyer 1959) to avoid a bias in $\delta^{13}C$ values, as lipids are depleted in ^{13}C (Peterson and Fry 1987, Wada *et al.* 1987). Afterwards the samples were lyophilised again (48 h) and ground to a homogenous powder using pestle and mortar. Lipids of invertebrate zooplankton samples were not removed to avoid loss of biomass of the often very small sample quantities. Carbonates, which would introduce a positive bias in $\delta^{13}C$ measurements, because of less negative $\delta^{13}C$ values (DeNiro and Epstein 1978, Fry 1988, Rau *et al.* 1991, Cloern *et al.* 2002), were removed from calcareous zooplankton samples (ostracods, pteropods) by adding 1 mol l^{-1} hydrochloric acid (HCl) drop-by-drop to each powdered sample until CO_2 release stopped. To minimize loss of dissolved organic matter, the samples were not rinsed with de-ionised water after the treatment (Jacob *et al.* 2005). The samples were dried at 60°C and ground to homogenous powder again. Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) analyses of the pulverised zooplankton samples were performed simultaneously with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyser via a THERMO/Finnigan Conflo II- interface at the GeoBio-Center^{LMU} in Munich, Germany. Standard deviation for repeated measurements of lab standard material (peptone) were <0.15 ‰ for nitrogen and

carbon. Standards used for nitrogen and carbon stable isotope determination were atmospheric N_2 and Peedee Belemnite (PDB), respectively.

Stable isotope values were expressed in δ-notations as parts per thousand (‰), where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively:

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

The ratio of nitrogen stable isotopes ($\delta^{15}N$) is typically enriched by 3-4 ‰ (average 3.4 ‰) relative to its diet and is used to estimate the trophic position of a consumer (Minagawa and Wada 1984). In this study, trophic levels were estimated using mean $\delta^{15}N$ of surface suspended particulate organic matter (POM_{susp}) as baseline value of the pelagic food web and a $\delta^{15}N$ trophic-enrichment factor of 3.4 ‰ per trophic level.

Fatty acid analysis. Frozen zooplankton samples and POM_{susp} filters were lyophilised for at least 48 h prior to lipid extraction.

Lipids of zooplankton samples were extracted with minor modifications as described by Hagen (2000) based on the method of Folch *et al.* (1957) using ultrasonic disruption in a dichloromethane (DCM):methanol (MeOH) (2:1/v:v) mixture and a washing procedure with aqueous KCl solution (0.88%). A known amount of internal standard (nonadecanoic acid) for quantification of fatty acids was added to the sample prior to extraction. Lipid classes of the total lipid extracts were separated by solid phase extraction according to the method of Peters *et al.* (2006) using 1 ml glass columns filled with 100 mg SiOH (CHROMABOND®, Macherey-Nagel) on a vacuum manifold. Prior to sample load, the columns were washed with a solvent sequence of acetone, diethylether, and hexane:diethylether-mixtures to remove residues. After column conditioning with 4 ml of hexane, a subsample of the total lipid extract dissolved in hexane were added. The neutral lipid fraction was eluted with 2.5 ml hexane:diethylether (95:5/v:v) and 2.5 ml hexane:diethylether (1:1/v:v). For fatty acid analyses, subsamples of the neutral lipid fractions were hydrolysed and fatty acids converted to their methyl ester derivatives (FAME) by adding 250 µl hexane and 1 ml of 3% concentrated sulphuric acid (H_2SO_4) in methanol to the dried extracts. The solution was left to react at 80°C for 4 h. After cooling, 4 ml of aqua bidest. were added, and FAMEs were extracted three times with 2 ml hexane (Kattner and Fricke, 1986).

Samples were analysed using a gas chromatograph (Agilent 6890N) equipped with a DB-WAX column (30 m length × 0.32 mm inner diameter, 0.25 μm film thickness) operated with helium as carrier gas (constant flow 2.0 ml min^{-1}). The following oven temperature program was used: 40°C held for 5 min, 40-150°C at 10°C min^{-1}, 150°C held for 5min, 150-220°C at 2°C min^{-1}, 220°C held for 20 min. Samples were injected using a temperature programmed vaporizer injector (Gerstel® CIS3) in solvent vent mode (injection volume 5 μl, injection speed 10 μl s^{-1}, injection temperature -40°C (temperature program: -40–40°C at 6°C s^{-1} after 0.51 min, 40°C held for 0.1 min, 40-250°C at 12°C s^{-1}, 250°C held for 2.0 min), vent flow 50 ml min^{-1}, vent pressure: 34 kPa, splitless time 0.5-1.5 min, purge flow: 50 ml min^{-1}, split flow: 20 ml min^{-1}). The FAMEs were detected by flame ionisation (FID, detector temperature: 250°C, hydrogen flow: 30 ml min^{-1}, air flow: 350 ml min^{-1}, makeup (N_2) flow: 30 ml min^{-1}) and identified by comparing retention times with those obtained from known standards (Supelco™ 37 Component FAME Mix, single FAME standards: nonadecanoic acid (C19:0), Octadecatetraenoic acid (C18:4n3)) and/or from the literature. Data was processed using Agilent GC ChemStation Software©. Total fatty acids were calculated as the sum of all identified fatty acid from the chromatogram.

Lipid extraction and analyses of the POM_{susp} filter samples were carried out with minor modifications according to Kiriakoulakis *et al.* (2004). The lyophilised filter samples were placed in glass extraction thimbles and a known amount of an internal standard (5α(H)-cholestane) was added. The filters were then extracted (24 h) in a soxhlet apparatus using a dichloromethane (DCM):methanol (MeOH) solvent mixture (2:1, v:v). The solvent extract was evaporated to dryness under vacuum and the residue taken up in a minimum volume of DCM and then passed through anhydrous sodium sulphate into a vial. The solvent was removed by evaporation under nitrogen and an aliquot of the total extract (50%; re-dissolved in DCM) was transferred to a 5 ml Reacti-Vial with a Teflon screw-cap, evaporated to dryness and transmethylated with 1.5 ml of 10 % methanolic acetyl chloride (10% of redistilled acetyl chloride added very slowly to chilled MeOH; 0°C). The solution was left to react (40ºC; 12 h; Christie, 1982) in the dark. Subsequently, the sample was evaporated to dryness with a stream of N_2, re-dissolved in DCM and stored at -20°C prior to GC-MS analysis. GC-MS analyses were performed on the derivatised (*bis*-trimethylsilyltrifluoroacetamide; BSFTA, 1 % TMS;

30-50 µL; 40°C; 0.5 - 1 h), transmethylated extracts using a Trace 2000 Series gas chromatograph fitted with an on-column injector and a fused high-temperature silica column (60 m × 0.25 mm i.d.; 5 %; DB5-HT equivalent; J&W) with helium as the carrier gas (ca. 1.6 ml min^{-1}). A retention gap of deactivated fused silica (1 m × 0.32 mm i.d.) was used at the front of the column. The oven was programmed from 60°C to 170°C at 6°C min^{-1} after 1 minute, then up to 315°C at 2.5°C min^{-1} and held for 10 minutes. The GC column was fed directly into the EI source of a Thermoquest Finnigan TSQ7000 mass spectrometer (ionisation potential 70 eV; source temperature 215°C; trap current 300 µA), operated in Full Data Acquisition mode, (50 - 600 Thompsons cycled every s) and data was processed using Xcalibur software. Compounds were identified either by comparison of their mass spectra and relative retention indices with those available in the literature and/or by comparison with authentic standards. Quantitative data were calculated by comparison of peak area of the internal standard with those of the compounds of interest, using the total ion current chromatogram. The relative response factors of the analytes were determined individually for 36 representative compounds using authentic standards. For analytes without authentic standards, the response factors for similar compounds of the same class and/or similar structure were used. Total fatty acids were calculated as the sum of all identified fatty acid from the chromatogram.

Statistical analysis. Statistical analyses were performed using the software SPSS. Normal distribution and homogeneity of variance of data was tested using the Shapiro-Wilk and the Levene test, respectively. Temporal and spatial differences were tested when the sample number was ≥3 for each variable. Temporal differences in stable isotope and FA ratios of zooplankton between 2 surveys at Seine Seamount were tested using either the T-test or the Mann-Whitney test. Temporal differences in isotopic signatures of POM_{susp} and *L. flavicornis* between the 3 surveys at Seine Seamount were tested using one-way ANOVA followed by a *post-hoc* Tukey-HSD test. Spatial differences in stable isotope ratios of POM_{susp} between the different sampling locations at Seine and Sedlo Seamounts were tested using either one-way ANOVA followed by a *post-hoc* Tukey-HSD test or the Kruskal-Wallis test. Spatial differences in stable isotope ratios of zooplankton species between farfield and pooled seamount locations were tested using either the T-test or the Mann-Whitney test.

3. RESULTS

3.1. TEMPORAL DIFFERENCES AT SEINE SEAMOUNT

3.1.1. STABLE ISOTOPES

The $\delta^{15}N$ values of POM_{susp} ranged from 0.3 ‰ in July to 4.4 ‰ in November and differed significantly between the 3 surveys ($p<0.01$, one-way ANOVA). In November, when only the summit location was sampled, the $\delta^{15}N$ values were significantly higher (mean: 4.1 ‰), compared to April and July (mean: 2.0 and 1.6 ‰, respectively; both $p<0.01$, *post-hoc* Tukey-HSD), while differences between April and July were not significant ($p>0.05$, *post-hoc* Tukey-HSD) (Fig. 2A). The $\delta^{13}C$ values of POM_{susp} ranged from -24.4 ‰ in November to -22.8 ‰ in April and temporal differences were not significant ($p>0.05$, one-way ANOVA) (Fig. 2B).

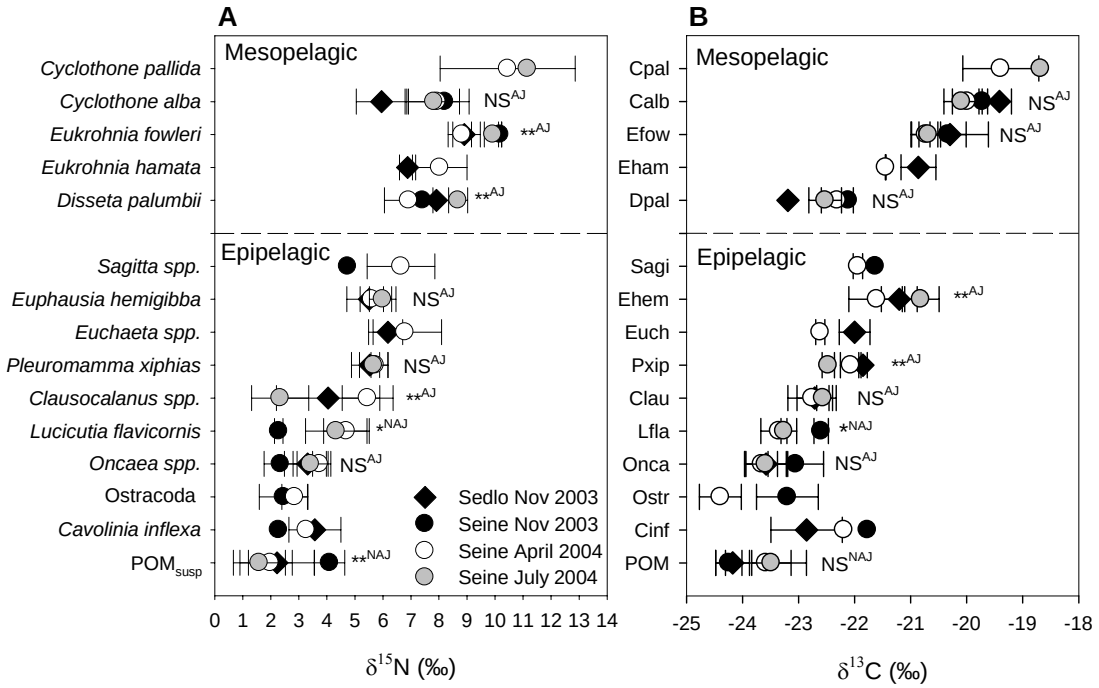

Fig. 2. Stable isotope signatures (mean ± SD) for (A) $\delta^{15}N$ and (B) $\delta^{13}C$ of POM_{susp} and epi- and mesopelagic zooplankton species pooled for all sampling locations for the surveys in November 2003, April 2004 and July 2004. Temporal differences at Seine Seamount were tested using either the T-test for April and July 2004 comparisons (AJ) or the one-way ANOVA followed by a *post-hoc* Tukey-HSD test for comparisons of all 3 surveys (NAJ); significance of tests is given as NS for not significant ($p>0.05$), * for $p<0.05$ and ** for $p<0.01$.

The range of $\delta^{15}N$ values covered by epipelagic zooplankton species sampled during the 3 surveys at Seine Seamount ranged from 0.8 ‰ for *Clausocalanus* spp. in July to 8.2 ‰ for *Euchaeta* spp. in April. Species like the pteropod *Cavolinia inflexa*, Ostracoda

and the copepod *Oncaea* spp. occupied the lower half of the total range, while the copepods *Pleuromamma xiphias* and *Euchaeta* spp., the euphausiid *Euphausia hemigibba* and the chaetognath *Sagitta* spp. had $\delta^{15}N$ values in the upper half of the total range. The $\delta^{15}N$ values of the copepods *Clausocalanus* spp. and *Lucicutia flavicornis* were most variable and covered the largest part of the total range (Fig. 2A). In contrast to POM_{susp}, mean $\delta^{15}N$ values of epipelagic zooplankton species sampled in November were lower than those in April and July and were similar among all species (mean: ~ 2.3 ‰), except for the chaetognath *Sagitta* spp. (4.7 ‰, Fig. 2A). Mean $\delta^{15}N$ values of these epipelagic species were, thus, nearly 2 ‰ lower than those of POM_{susp}. Small sample sizes in November allowed statistical testing only for the copepod *L. flavicornis* and differences in $\delta^{15}N$ between November and the other two surveys were significant (one-way ANOVA: $p<0.01$, *post-hoc* Tukey-HSD: both surveys $p<0.05$). Between April and July, differences in $\delta^{15}N$ were small and not significant ($p>0.05$, T-test), except for *Clausocalanus* spp., which had significantly higher values in April ($p<0.05$, T-test; Fig. 2A).

The $\delta^{13}C$ values for epipelagic zooplankton species at Seine Seamount ranged from -24.4 ‰ for Ostracoda in April to -20.3 ‰ for *E. hemigibba* in July. Temporal differences between species were most pronounced between the survey in November and the surveys in April and July, but in contrast to $\delta^{15}N$ values, mean $\delta^{13}C$ values for zooplankton species were higher in November than in April and July (Fig. 2B). The differences in $\delta^{13}C$ between the November and the other two surveys were significant for the copepod *L. flavicornis* ($p<0.01$, one-way ANOVA, *post-hoc* Tukey-HSD: both surveys $p<0.05$), while sample size was too small for the other species to allow for statistical testing. Differences in $\delta^{13}C$ between April and July were generally small and not significant ($p>0.05$), except for slightly higher values in April for *P. xiphias* ($p<0.01$, T-test) and higher values in July for *E. hemigibba* ($p<0.01$, T-test; Fig. 2B).

The mesopelagic species covered a range of $\delta^{15}N$ values from 6.0 ‰ for the copepod *Disseta palumbii* in April to 12.2 ‰ for the gonostomatid fish *Cyclothone pallida* in April. Mean $\delta^{15}N$ values were similar for the chaetognath *Eukrohnia hamata* and the gonostomatid fish *Cyclothone alba* from shallower mesopelagic depths (500-600 m), while at lower mesopelagic depths (800-1000 m) mean $\delta^{15}N$ values increased between species from the copepod *D. palumbii* to the chaetognath *Eukrohnia fowleri* and were

highest for *C. pallida*. At mesopelagic depths, temporal differences in $\delta^{15}N$ values at Seine Seamount were either not apparent, like for *C. alba* ($p>0.05$, T-test for April/July) and *C. pallida*, or were significantly higher in July compared to April, like for the copepod *D. palumbii* and the chaetognath *E. fowleri* (both $p<0.05$), while $\delta^{15}N$ values in November were within the range of the other two surveys and revealed no pattern (Fig. 2A).

The $\delta^{13}C$ values for mesopelagic species at Seine Seamount ranged from -22.9 ‰ for *D. palumbii* in July to -18.7 ‰ *C. pallida* in July and were generally similar for all 3 surveys with no significant differences between April and July ($p>0.05$, T-test; Fig. 2B). At the shallower mesopelagic depth layer, mean $\delta^{13}C$ values for *E. hamata* were lower than for *C. alba*, while at the lower mesopelagic depth layer, mean $\delta^{13}C$ values increased from strongly depleted values for *D. palumbii* to higher values for *E. fowleri* and highest values for *C. pallida*, and the increase was more pronounced for $\delta^{13}C$ than for $\delta^{15}N$ values.

3.1.2 FATTY ACID BIOMARKERS

Temporal differences in the fatty acid composition of the total lipids of POM_{susp} were pronounced between the 3 surveys at Seine Seamount (Fig. 3A, Tab. 3). In November, when only the summit location was sampled, the fatty acid composition of POM_{susp} was distinguished from that in April and July by the lack of the saturated fatty acid (SFA) 14:0, by the highest proportion of mono-unsaturated fatty acids (MUFA, 31 %), mainly 18:1(n-9) and 20:1(n-9), and by the lowest proportion of poly-unsaturated fatty acids (PUFA, 16 %), mainly 18:2(n-6).

The fatty acid composition of POM_{susp} in April showed a high degree of local variability, as total fatty acids at the summit and farfield location consisted exclusively of SFA (mainly 14:0, 16:0 and 18:0), while the sample at the West slope location contained the lowest proportion of SFA (47 %) and the highest proportion of PUFA (44 %) of all samples analysed. Poly-unsaturated fatty acids were dominated by the flagellate markers 22:6(n-3), 18:5(n-3) and 18:4(n-3), but also contained the highest proportion of the diatom marker 20:5(n-3) of all samples. Mono-unsaturated fatty acids of POM_{susp} in April were dominated by the diatom marker 16:1(n-7) and contained the lowest proportion of the carnivory marker 18:1(n-9) of all samples.

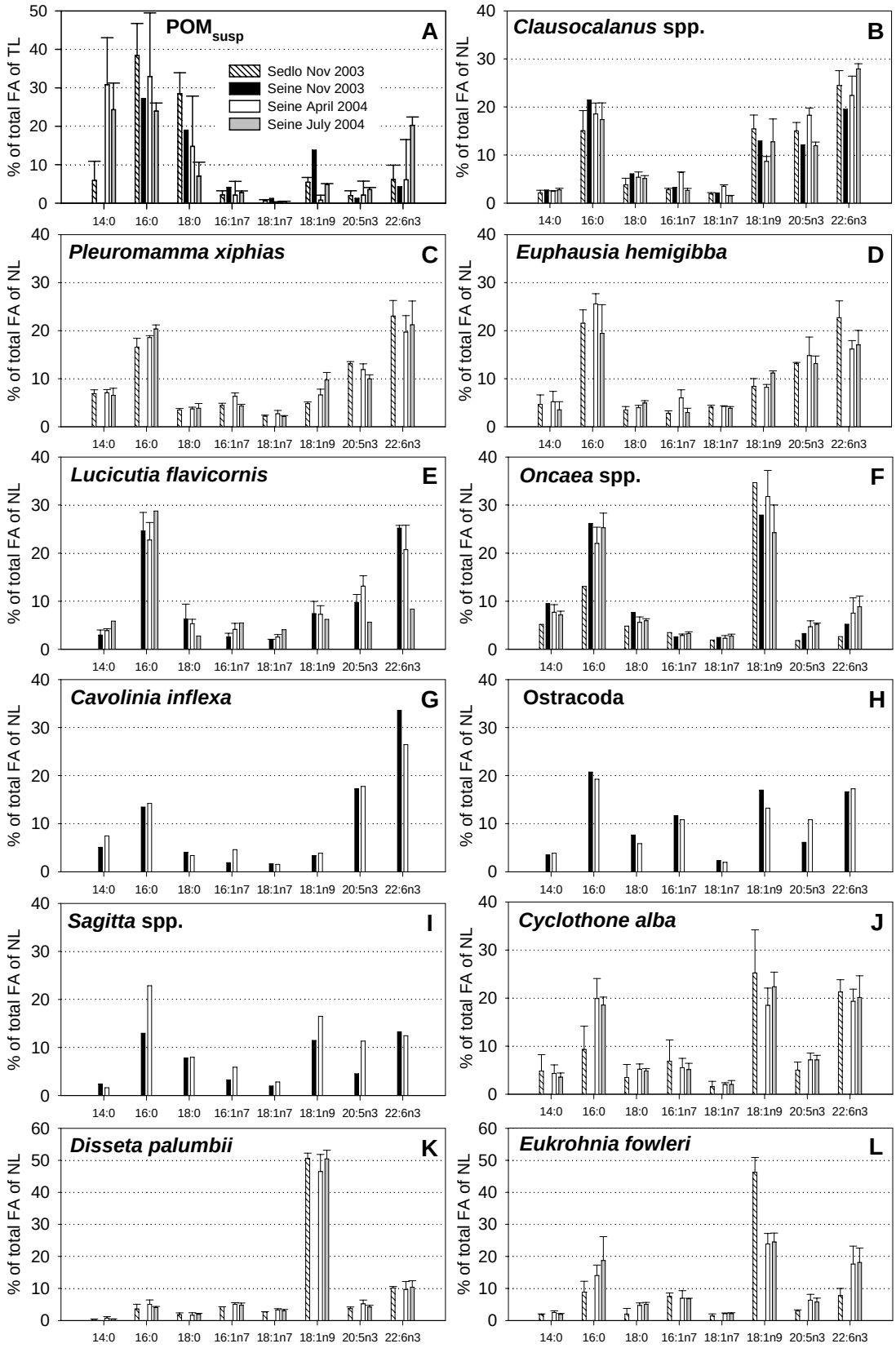

Fig. 3. Relative composition of the most abundant fatty acids (mean ± SD) in the total lipids of POM_{susp} (A) and the storage lipids of epipelagic (B-I) and mesopelagic (J-L) zooplankton species pooled for all seamount and farfield locations for the surveys in November 2003, April 2004 and July 2004 at Seine and Sedlo Seamounts.

Table 3. Fatty acid composition (mean % of total fatty acids ± SD) of total lipids of POM_{susp} and storage lipids of zooplankton species sampled at Seine and Sedlo Seamounts during November 2003, April 2004 and July 2004.

	Sedlo								Seine									
FA	POM	Clau	Px	Ehem	Onc	Calb	Dpal	Efow		POM		*Clausocalanus* spp.			*P. xiphias*		*E. hemigibba*	
	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	April	July	Nov	April	July	April	July	April	July
	(n=5)	(n=4)	(n=3)	(n=3)	(n=1)	(n=3)	(n=2)	(n=2)	(n=1)	(n=3)	(n=3)	(n=1)	(n=2)	(n=2)	(n=5)	(n=3)	(n=6)	(n=5)
14:0	5.9±5.0	2.0±0.5	6.9±0.8	4.7±1.9	5.2	4.8±3.4	0.3±0.1	1.9±0.2	0.0	30.8±12.2	24.3±6.9	2.7	2.5±0.1	2.7±0.4	7.1±0.7	6.5±1.5	5.2±2.1	3.5±1.7
15:0	1.8±0.4	1.2±0.2	3.2±0.1	2.1±0.4	3.9	0.7±0.3	0.1±0.0	0.3±0.1	1.2	2.5±1.3	1.0±0.1	1.7	0.9±0.1	1.4±0.1	2.0±0.2	1.9±0.2	1.4±0.4	1.4±0.4
16:0	38.4±8.4	13.4±2.5	16.6±1.8	21.5±2.8	13.1	9.3±4.9	3.6±1.4	8.8±3.4	27.2	32.9±16.6	23.9±2.1	21.5	18.5±2.3	17.4±3.5	18.6±0.4	20.3±0.8	25.6±2.1	19.4±6.0
17:0	0.9±1.0	1.5±0.2	2.4±0.2	2.1±0.1	3.0	0.7±0.4	0.3±0.1	0.7±0.2	1.0	0.0±0.0	0.0±0.0	1.9	1.5±0.1	1.4±0.1	2.7±0.2	2.3±0.1	1.8±0.5	2.1±0.3
18:0	28.4±5.5	3.3±0.5	3.5±0.3	3.5±0.7	4.8	3.5±2.7	1.8±0.6	2.0±1.8	19.0	14.7±13.1	7.0±3.6	6.1	5.4±1.1	5.1±0.6	3.7±0.3	3.9±1.0	4.0±0.5	4.9±0.5
20:0	1.9±0.4	0.0±0.0	0.0±0.0	0.0±0.0	0.0	0.0±0.0	0.0±0.0	0.0±0.0	2.2	0.8±0.7	0.5±0.1	0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
22:0	0.8±0.6	0.1±0.0	0.6±0.2	0.4±0.2	1.0	0.4±0.8	0.0±0.0	0.0±0.0	3.0	0.4±0.4	0.2±0.2	0.4	0.3±0.2	0.2±0.0	0.5±0.3	0.5±0.1	0.2±0.1	0.6±0.7
16:1(n-7)	2.1±1.1	2.6±0.2	4.4±0.5	2.8±0.5	3.5	6.9±4.4	4.3±0.0	7.5±1.1	4.1	2.1±3.6	2.7±0.4	3.3	6.4±0.1	2.6±0.4	6.3±0.7	4.3±0.3	6.0±1.7	3.0±0.9
18:1(n-9)	5.4±1.2	16.1±2.9	4.8±0.4	8.4±1.6	34.7	25.2±9.0	50.6±1.6	46.2±4.6	13.8	0.7±1.3	4.8±0.3	12.9	8.7±1.0	12.8±4.7	6.6±1.2	9.7±1.6	8.2±0.6	11.2±0.4
18:1(n-7)	0.6±0.3	1.9±0.2	2.2±0.2	4.1±0.4	1.9	1.6±1.1	2.7±0.1	1.4±0.6	1.2	0.1±0.2	0.5±0.0	2.1	3.5±0.3	1.5±0.1	2.7±0.7	2.1±0.2	4.2±0.2	3.8±0.4
20:1(n-11)	0.0±0.0	0.5±0.1	0.0±0.0	0.0±0.0	0.0	1.3±0.3	1.2±0.2	1.9±0.1	0.0	0.0±0.0	0.0±0.0	0.3	0.2±0.0	0.5±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
20:1(n-9)	0.5±1.0	0.7±0.2	1.1±0.2	1.0±0.1	5.2	3.2±1.3	5.0±0.3	3.2±0.1	7.9	0.0±0.0	0.2±0.3	0.7	0.2±0.2	0.7±0.1	1.3±0.3	2.5±0.7	0.9±0.3	2.1±0.4
22:1(n-11)	0.0±0.0	0.7±0.4	0.3±0.1	0.6±0.7	0.0	2.5±1.3	5.7±1.2	4.7±2.5	0.0	0.0±0.0	0.0±0.0	1.0	0.1±0.2	0.4±0.1	0.5±0.3	0.5±0.1	0.1±0.2	0.0±0.0
22:1(n-9)	0.6±0.8	0.1±0.1	1.2±0.7	0.8±0.4	1.6	1.4±0.4	2.0±0.2	0.9±0.5	3.4	0.1±0.3	0.1±0.1	0.4	0.1±0.1	0.1±0.1	0.7±0.3	0.8±0.3	0.3±0.1	1.0±0.9
24:1	0.0±0.0	1.5±0.6	2.9±2.5	0.0±0.0	1.5	2.4±0.3	2.1±0.0	4.4±3.0	0.6	0.0±0.0	0.0±0.0	0.8	1.0±0.3	1.0±0.2	1.9±0.6	1.6±0.3	0.1±0.4	0.9±2.0
18:2(n-6)	1.8±1.6	1.5±0.2	1.2±0.1	1.8±0.3	2.9	1.6±0.2	1.8±0.2	0.6±0.7	10.5	0.5±0.9	3.9±1.7	2.6	1.7±0.5	2.0±0.6	1.7±0.3	1.9±0.2	1.7±0.2	2.6±0.7
18:3(n-3)	0.0±0.0	1.3±0.1	1.6±0.3	1.7±0.2	1.3	0.8±0.1	1.0±0.0	0.6±0.1	0.0	0.0±0.0	0.0±0.0	1.2	1.1±0.1	1.2±0.4	1.8±0.2	1.3±0.3	1.7±0.3	1.7±0.2
18:4(n-3)	1.2±1.6	3.1±0.5	3.6±0.2	2.3±0.2	1.1	0.8±0.6	1.0±0.0	1.1±0.6	0.0	2.6±4.6	2.6±0.5	2.8	1.9±0.6	2.1±0.8	3.5±0.8	2.6±0.7	1.9±0.7	1.4±0.5
18:5(n-3)	1.4±1.0	0.5±0.2	1.1±0.1	0.2±0.3	0.8	0.8±0.6	0.0±0.0	0.0±0.0	0.9	3.3±5.7	4.6±2.6	0.9	0.1±0.0	0.7±0.0	1.0±0.2	1.3±0.4	0.2±0.6	0.9±0.9
20:2(n-6)	0.0±0.0	0.7±0.0	0.6±0.3	0.8±0.1	1.7	0.6±0.6	0.4±0.1	0.3±0.0	0.0	0.0±0.0	0.0±0.0	0.5	0.4±0.1	0.6±0.0	0.5±0.2	0.4±0.1	0.5±0.1	1.0±0.4
20:3(n-6)	0.0±0.0	0.2±0.1	0.4±0.2	0.3±0.1	0.0	0.4±0.4	0.2±0.0	0.2±0.1	0.0	0.0±0.0	0.0±0.0	0.2	0.3±0.1	0.5±0.1	0.3±0.1	0.2±0.0	0.3±0.1	0.4±0.2
20:4(n-6)	0.0±0.0	0.8±0.0	0.8±0.2	2.5±0.7	0.8	1.2±0.8	0.5±0.0	0.5±0.0	0.0	0.1±0.2	0.1±0.1	1.0	1.3±0.3	1.1±0.4	1.2±0.2	0.9±0.0	2.9±0.7	3.3±0.4
20:3(n-3)	0.0±0.0	0.4±0.0	0.4±0.1	0.5±0.1	1.4	0.3±0.3	0.3±0.0	0.2±0.0	0.0	0.0±0.0	0.0±0.0	0.3	0.2±0.0	0.3±0.1	0.4±0.1	0.4±0.1	0.3±0.1	0.8±0.6
20:4(n-3)	0.0±0.0	2.7±0.6	1.5±0.0	0.9±0.3	0.5	1.7±0.3	1.2±0.1	0.5±0.1	0.0	0.0±0.0	0.0±0.0	1.7	1.5±0.1	1.5±0.9	1.4±0.1	1.0±0.1	0.6±0.2	1.0±0.3
20:5(n-3)	2.0±1.2	15.8±0.7	13.1±0.5	13.2±0.2	1.8	5.0±1.7	3.7±0.5	2.9±0.3	0.0	2.1±3.6	3.5±0.5	12.1	18.3±1.5	11.9±0.8	11.9±1.2	10.0±0.8	14.8±3.9	13.1±1.6
22:2	0.0±0.0	0.0±0.1	0.2±0.0	0.2±0.2	1.3	0.3±0.5	0.0±0.0	0.1±0.0	0.0	0.0±0.0	0.0±0.0	0.0	0.0±0.0	0.1±0.1	0.1±0.1	0.1±0.1	0.1±0.1	0.3±0.5
22:6(n-3)	6.1±3.7	25.7±1.6	23.0±3.2	22.7±3.5	2.6	21.3±2.6	10.1±0.5	7.8±2.2	4.2	6.0±10.5	20.2±2.2	19.5	22.4±4.0	27.9±1.1	19.7±3.5	21.2±4.9	16.2±1.8	17.0±3.0
∑ minor FA	0.3±0.5	1.8±0.5	2.4±0.7	1.1±0.4	4.4	1.4±0.8	0.2±0.0	1.4±1.2	0.0	0.0±0.0	0.0±0.0	1.3	1.4±0.0	2.3±0.2	1.9±0.7	1.7±0.7	0.9±0.4	2.1±1.6
∑ SFA	78.1±8.3	22.0±3.3	34.3±1.0	34.8±3.5	33.7	19.8±7.7	6.3±2.2	13.9±1.8	53.5	82.2±30.8	56.9±6.7	34.5	29.4±3.8	29.2±4.3	35.7±1.6	36.5±2.9	38.7±4.5	33.0±6.6
∑ MUFA	9.4±2.4	24.7±3.2	18.2±3.5	18.0±1.4	49.9	45.4±15.7	73.5±0.8	70.7±1.1	30.9	3.1±5.4	8.3±0.3	22.3	20.9±0.6	20.8±4.0	21.0±2.8	22.2±2.8	20.0±2.3	22.9±2.9
∑ PUFA	12.4±8.6	53.3±1.8	47.5±2.6	47.3±4.1	16.4	34.8±8.3	20.2±1.4	15.5±0.7	15.6	14.7±25.5	34.9±7.0	43.2	49.7±4.5	49.9±0.3	43.3±3.2	41.3±5.0	41.2±5.9	44.1±4.7
16:1(n-7)/16:0	0.05±0.02	0.20±0.04	0.27±0.02	0.13±0.03	0.26	1.05±0.91	1.28±0.50	0.89±0.23	0.15	0.15±0.26	0.11±0.03	0.15	0.35±0.04	0.15±0.01	0.34±0.04	0.21±0.01	0.24±0.06	0.15±0.02
18:1(n-9)/18:1(n-7)	9.8±3.7	8.8±2.7	2.2±0.3	2.1±0.5	18.0	23.5±21.1	19.0±0.2	38.1±20.8	11.6	2.0±3.4	10.2±0.8	6.1	2.5±0.5	8.3±3.5	2.5±0.6	4.5±0.4	1.9±0.1	2.9±0.3

Table 3. Continued.

FA	Seine																	
	L. flaviconis			*Oncaea* spp.			*C. inflexa*		Ostracoda		*Sagitta* spp.		*C. alba*		*D. palumbii*		*E. fowleri*	
	Nov	April	July	Nov	April	July	Nov	April	Nov	April	Nov	April	April	July	April	July	April	July
	n=3	n=3	n=1	n=1	n=6	n=3	n=1	n=1	n=1	n=1	n=1	n=1	n=6	n=5	n=8	n=3	n=7	n=3
14:0	2.9±1.0	3.8±0.3	5.8	9.5	7.7±1.5	7.1±0.8	5.1	7.5	3.5	3.9	2.4	1.6	4.3±1.8	3.5±0.8	0.7±0.4	0.4±0.0	2.4±0.5	1.9±0.2
15:0	1.7±0.3	2.2±0.5	3.0	1.0	0.7±0.3	1.2±0.3	1.0	1.0	1.5	1.3	1.4	0.6	0.8±0.2	0.7±0.0	0.2±0.0	0.1±0.0	0.4±0.0	0.4±0.1
16:0	24.6±3.8	22.7±3.6	28.7	26.2	22.0±3.3	25.2±3.0	13.5	14.2	20.7	19.2	13.0	22.9	19.8±4.1	18.5±1.6	5.0±1.3	4.0±0.3	14.0±3.2	18.7±7.4
17:0	2.7±0.6	3.1±0.1	4.0	0.7	0.5±0.1	0.9±0.3	1.1	0.9	1.8	1.2	1.9	1.8	1.0±0.2	0.9±0.2	0.3±0.1	0.3±0.0	1.0±0.1	1.0±0.2
18:0	6.2±3.1	5.3±0.9	2.8	7.7	5.5±1.1	5.9±0.4	4.0	3.4	7.6	5.8	7.8	8.0	5.2±1.0	4.8±0.4	1.6±0.7	1.9±0.2	4.6±0.7	4.9±0.6
20:0	0.0±0.0	0.0±0.0	0.0	0.0	0.0±0.0	0.0±0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.00
22:0	0.5±0.6	0.1±0.1	1.6	0.3	0.2±0.1	0.3±0.2	0.0	0.0	0.2	0.3	0.0	0.0	0.3±0.1	0.2±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
16:1(n-7)	2.5±0.8	4.1±1.2	5.5	2.6	2.8±0.2	3.2±0.3	1.9	4.6	11.7	10.8	3.3	5.9	5.4±1.9	5.1±1.3	5.0±0.4	4.7±0.6	6.9±2.3	6.7±0.1
18:1(n-9)	7.3±2.5	7.2±1.7	6.2	27.9	31.7±5.4	24.2±5.7	3.3	3.9	17.0	13.3	11.5	16.5	18.4±3.5	22.3±3.0	46.4±5.3	50.4±2.7	23.9±3.2	24.5±2.7
18:1(n-7)	2.0±0.0	2.5±0.5	4.0	2.5	2.3±0.5	2.7±0.4	1.7	1.5	2.3	2.0	2.0	2.8	2.0±0.3	2.0±0.8	3.2±0.4	3.0±0.3	2.1±0.2	2.1±0.3
20:1(n-11)	0.0±0.0	0.0±0.0	0.0	0.0	0.0±0.0	0.0±0.0	0.2	0.2	0.5	0.4	0.0	0.6	0.5±0.1	0.6±0.1	1.2±0.5	1.3±0.2	1.0±0.2	0.6±0.4
20:1(n-9)	1.0±0.4	0.9±0.1	1.5	3.3	4.5±0.8	3.4±1.0	1.2	1.0	0.6	0.3	1.7	0.7	1.3±0.5	1.4±0.4	4.0±0.6	3.7±0.2	3.0±1.1	2.0±0.3
22:1(n-11)	0.4±0.4	0.3±0.2	1.1	0.0	0.0±0.0	0.0±0.0	0.6	0.2	0.8	1.4	0.0	0.0	1.4±1.0	1.9±1.6	5.9±0.9	5.1±0.4	3.6±1.7	1.6±0.9
22:1(n-9)	0.7±0.2	0.6±0.0	2.8	1.3	1.2±0.2	1.2±0.2	0.0	0.2	0.3	0.3	2.3	1.5	1.3±0.6	0.6±0.2	1.6±0.4	1.5±0.4	1.2±0.5	1.1±0.2
24:1	1.7±0.4	0.5±0.4	2.0	1.4	1.3±0.3	1.5±0.5	0.0	0.0	0.8	1.2	4.4	1.9	2.8±0.9	2.0±0.7	2.2±0.5	2.0±0.3	5.4±2.4	3.7±1.2
18:2(n-6)	2.1±0.1	1.5±0.1	1.9	1.1	1.0±0.1	1.2±0.3	2.0	2.1	1.5	2.2	1.8	1.9	1.1±0.2	1.3±0.1	2.0±0.4	1.9±0.0	0.9±0.1	0.9±0.1
18:3(n-3)	1.1±0.0	1.3±0.0	2.2	0.6	0.7±0.1	0.8±0.1	1.5	2.4	1.0	1.6	1.8	1.0	0.8±0.2	0.7±0.0	1.0±0.2	1.0±0.1	0.6±0.0	0.7±0.1
18:4(n-3)	1.4±0.2	1.7±0.1	3.1	0.7	0.8±0.2	1.2±0.1	2.3	4.1	1.7	3.0	2.0	1.4	1.2±0.5	0.8±0.2	1.0±0.3	0.9±0.2	0.8±0.3	0.9±0.3
18:5(n-3)	0.6±0.2	0.6±0.2	1.1	0.4	0.3±0.0	0.4±0.2	0.7	0.6	0.5	0.5	3.7	0.8	0.4±0.1	0.7±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
20:2(n-6)	0.4±0.0	0.6±0.0	0.8	0.7	0.4±0.2	0.5±0.1	2.5	1.9	0.4	0.3	3.0	0.4	0.3±0.0	0.3±0.0	0.5±0.1	0.4±0.0	0.2±0.0	0.2±0.0
20:3(n-6)	0.1±0.1	0.4±0.0	0.4	0.4	0.2±0.1	0.3±0.0	0.2	0.3	0.0	0.0	5.1	0.5	0.2±0.1	0.2±0.0	0.3±0.1	0.2±0.0	0.1±0.0	0.0±0.0
20:4(n-6)	1.0±0.3	1.4±0.2	1.5	0.4	0.3±0.2	0.4±0.0	1.9	1.8	1.0	1.0	2.6	1.4	1.4±0.6	1.3±0.6	0.9±0.2	0.7±0.1	1.1±0.5	1.3±0.7
20:3(n-3)	0.3±0.1	0.3±0.0	0.6	0.7	0.5±0.2	0.6±0.1	2.4	1.5	0.0	0.0	0.0	0.0	0.3±0.1	0.1±0.0	0.3±0.1	0.2±0.0	0.1±0.0	0.1±0.0
20:4(n-3)	1.0±0.8	1.4±0.3	2.5	0.8	1.1±0.0	1.2±0.0	0.9	1.3	0.7	1.0	5.4	2.8	1.1±0.3	1.0±0.1	0.8±0.1	0.8±0.1	0.4±0.1	0.4±0.0
20:5(n-3)	9.7±1.6	13.1±2.1	5.6	3.3	4.6±1.2	5.2±0.2	17.2	17.7	6.1	10.8	4.5	11.3	7.1±1.3	7.1±0.9	5.1±1.1	4.2±0.5	6.3±1.8	5.7±1.2
22:2	0.0±0.0	0.0±0.0	0.0	0.2	0.2±0.1	0.2±0.1	0.1	0.3	0.0	0.0	3.1	0.4	0.3±0.2	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0
22:6(n-3)	25.2±0.5	20.7±5.0	8.4	5.2	7.4±3.1	8.8±2.2	33.6	26.4	16.6	17.3	13.3	12.5	19.3±2.5	20.1±4.5	9.6±2.4	10.3±2.0	17.6±5.5	18.1±4.4
∑ minor FA	1.5±0.3	2.5±1.3	2.7	1.2	0.7±0.6	1.0±0.2	1.2	1.1	1.3	1.0	2.3	0.8	0.7±0.2	0.6±0.2	0.1±0.1	0.0±0.0	1.2±0.2	1.2±0.3
∑ SFA	40.0±2.1	38.5±5.9	46.9	46.3	37.4±4.2	41.6±4.9	24.7	27.1	35.6	32.0	26.5	34.8	31.9±5.2	29.1±1.3	7.93±2.1	6.88±0.7	22.9±3.8	27.3±8.2
∑ MUFA	16.5±3.8	18.0±0.5	24.9	39.2	44.3±5.6	36.8±7.8	9.6	12.3	34.4	30.0	25.9	30.2	33.9±4.1	36.8±5.2	69.9±6.3	72.1±2.7	48.2±2.6	43.4±5.6
∑ PUFA	43.4±1.7	43.4±5.6	28.2	14.5	18.2±4.7	21.4±3.4	65.6	60.6	30.0	38.0	47.7	35.0	34.0±3.0	34.0±5.8	22.0±4.8	20.9±2.4	28.7±4.4	29.1±6.7
16:1(n-7)/16:0	0.10±0.04	0.18±0.08	0.19	0.10	0.13±0.03	0.13±0.02	0.14	0.32	0.56	0.56	0.25	0.26	0.30±0.18	0.27±0.06	1.10±0.41	1.20±0.28	0.51±0.18	0.39±0.13
18:1(n-9)/18:1(n-7)	3.7±1.3	3.0±1.4	1.5	11.4	14.±4.1	8.9±1.8	2.0	2.5	7.3	6.7	5.8	5.8	9.1±0.8	12.±3.3	14.±2.7	16.±2.2	11.±1.9	11.±0.5

In July, the mean proportion of SFA in POM_{susp} was highest (57%) and had a similar fatty acid composition to the West slope in April, while the mean proportion of PUFA (35 %) was a little lower than in April, but also dominated by flagellate markers (22:6(n-3), 18:5(n-3) and 18:4(n-3)), but with lower proportions of the diatom marker 20:5(n-3). Mono-unsaturated fatty acids were dominated by the carnivory marker 18:1(n-9) and contained lower proportions of the diatom marker 16:1(n-7) compared to the West slope in April.

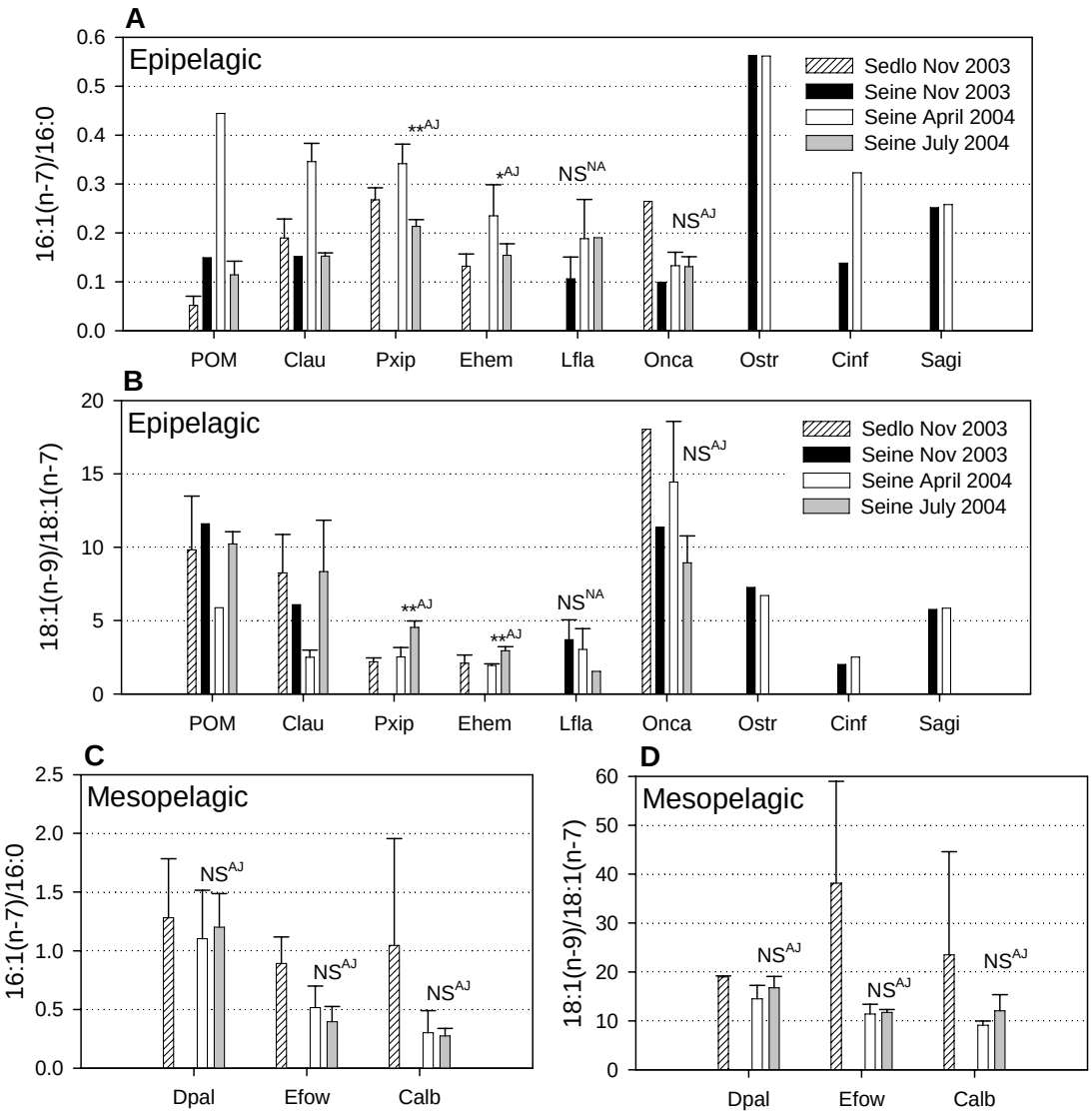

Fig. 4. Ratios of 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) fatty acids (mean ± SD) in the total lipids of POM_{susp} (A,B) and storage lipids of epi- (A,B) and mesopelagic (C,D) zooplankton species pooled for all sampling locations from the surveys in November 2003, April 2004 and July 2004 at Seine and Sedlo Seamounts. Temporal differences at Seine Seamount were tested using the T-test for April and July 2004 comparisons (AJ) or for November 2003 and April 2004 comparisons (NA). Significance of tests is given as NS for not significant ($p>0.05$), * for $p<0.05$ and ** for $p<0.01$.

The fatty acid marker ratios 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) support the temporal differences in POM_{susp} composition indicated by the different phyto- and zooplankton fatty acid marker proportions. The ratio 16:1(n-7)/16:0, indicative for diatom abundance, was highest in April at the West slope location (0.44) and markedly lower in November (0.10) and July (mean: 0.11; range: 0.10-0.15) suggesting higher diatom abundance during the April survey (Fig. 4A). Values of the fatty acid marker ratio 18:1(n-9)/18:1(n-7), indicative for metazoan or metazoan-derived particle abundance (e.g., faecal pellets) versus diatom abundance in POM_{susp}, were lowest in April (5.9) and similarly high in November (11.6) and July (10.2), also suggesting a higher proportion of diatoms in POM_{susp} in April (Fig. 4B).

Temporal differences were also apparent in the fatty acid composition of the storage lipids of epipelagic zooplankton species (Fig. 3B-I). The fatty acid signatures of the copepods *Clausocalanus* spp. and *P. xiphias* and the euphausiid *E. hemigibba* (Fig. 3B-D) were dominated by PUFA during all cruises (41-50 % of total fatty acids, while SFA were second most abundant (29-39 %) and MUFA least abundant (20-23 %). Dominant fatty acids in the storage lipids of these species were the saturated 16:0, the poly-unsaturated 20:5(n-3) and 22:6(n-3), and the mono-unsaturated 18:1(n-9), which were present in similar proportions in the 3 species. Temporal differences were characterized by higher mean proportions of the diatom marker fatty acids 16:1(n-7) and 20:5(n-3) and lower mean proportions of the carnivory marker 18:1(n-9) in April compared to July, and for *Clausocalanus* spp. also compared to November. This temporal pattern was even more apparent in the fatty acid marker ratios and largely reflected the pattern in POM_{susp} (Fig. 4A,B). Mean ratios of 16:1(n-7)/16:0, indicative for feeding on diatoms, were higher for *Clausocalanus* spp., *P. xiphias* and *E. hemigibba* in April compared to July, and for *Clausocalanus* spp. also compared to November. The differences between April and July were significant for *P. xiphias* and *E. hemigibba* ($p<0.01$ and $p<0.05$, respectively; T-test), while small sample size prevented statistical testing for *Clausocalanus* spp. (Fig. 4A). The temporal pattern was reversed for the fatty acid marker ratio 18:1(n-9)/18:1(n-7), indicative of carnivory versus herbivory, which was lower in April for *Clausocalanus* spp., *P. xiphias* and *E. hemigibba* compared to July, and for *Clausocalanus* spp. also compared to November. Differences

between April and July were significant for *P. xiphias* and *E. hemigibba* (both $p<0.01$, T-test) (Fig. 4B).

The copepod *L. flavicornis* (Fig. 3E) had fatty acid signatures similar to the 3 above mentioned species in November and April, including higher mean proportions of the diatom marker fatty acids 16:1(n-7) and 20:5(n-3) in April. In July, however, proportions of poly-unsaturated 20:5(n-3) and 22:6(n-3) were much lower while proportions of the mono-unsaturated 16:1(n-7) were as high as in April and for 18:1(n-9) were similar for all cruises. Temporal differences in the fatty acid ratios 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) of *L. flavicornis* revealed no clear pattern between the 3 surveys and were not significant between November and April ($p>0.05$, T-test; Fig. 4A,B).

In contrast to the calanoid copepods, the storage lipids of the poecilostomatoid copepod *Oncaea* spp. were dominated by SFA (37-46 % of total fatty acids) and MUFA (37-44 %), while PUFA, mainly 20:5(n-3) and 22:6(n-3), were least abundant (14-22 %, Fig. 3F). Dominant fatty acids were the saturated 16:0 and mono-unsaturated 18:1(n-9). *Oncaea* spp. contained the highest mean proportions of 18:1(n-9) of all epipelagic species and these were higher in April compared to November and July. The 16:1(n-7)/16:0 ratios for *Oncaea* spp. were similar between the 3 surveys ($p>0.05$, T-test: April-July; Fig. 4A). The 18:1(n-9)/18:1(n-7) ratio was highest in April (14.4) with markedly lower mean ratios in November (11.4) and July (8.9), although differences were not significant compared to July ($p>0.05$, T-test) (Fig. 4B).

The storage lipids of the pteropod *C. inflexa* (Fig. 3G) contained the highest proportions of PUFA of all zooplankton species (~63 %), which were dominated by the flagellate marker fatty acid 22:6(n-3) with the diatom marker 20:5(n-3) being second most abundant. Saturated fatty acids (~26 %) were dominated by 16:0, while MUFA were least abundant and contained the lowest proportion of the carnivory marker fatty acid 18:1(n-9) of all zooplankton species. Fatty acid proportions of *C. inflexa* were generally similar for the November and April surveys, except for a higher proportion of 22:6(n-3) and slightly lower proportion of 16:1(n-7) in November. The marker ratio 16:1(n-7)/16:0 was more than twice as high in April compared to November with values

similar to those of *Clausocalanus* spp. (Fig. 4A), while the 18:1(n-9)/18:1(n-7) ratio was similar for both surveys and among the lowest of all zooplankton species (Fig. 4B).

Storage lipid fatty acid signature of Ostracoda (Fig. 3H) were generally similar to those of *Clausocalanus* spp., *P. xiphias* and *E. hemigibba*, but were characterized by about equal proportions of SFA, MUFA and PUFA, due to higher proportions of the diatom marker 16:1(n-7), which were the highest of all zooplankton species, and slightly higher proportions of the carnivory marker 18:1(n-9), while proportions of 22:6(n-3) and 20:5(n-3) were slightly lower. Temporal differences in fatty acid proportions between November and July were small with a slightly higher proportion of 20:5(n-3) in April concurrent with a slightly lower proportion of 18:1(n-9). Due to the high abundance of the diatom marker 16:1(n-7), the 16:1(n-7)/16:0 ratios were the highest of all zooplankton species and were similar in November and April (Fig. 4A). The18:1(n-9)/18:1(n-7) ratio was also similar in November and April (Fig. 4B).

The storage lipid composition of the chaetognath *Sagitta* spp. varied considerably between the November and April survey (Fig. 3I). PUFA were more abundant in November (48%) with equal proportions of SFAs and MUFA, while in April proportions were about equal for all 3 groups. Fatty acids were dominated by 16:0, 18:1(n-9) and 22:6(n-3) and in April including also 20:5(n-3). Despite pronounced temporal variability in fatty acid proportions, the 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) ratios were similar for both surveys (Fig. 4A,B).

The storage lipids of the mesopelagic fish *C. alba* (Fig. 3J) contained about equal proportions of SFA, MUFA and PUFA which were dominated by 16:0, 18:1(n-9) and 22:6(n-3), respectively. Proportions of the most abundant fatty acids were similar for the April and July survey, when this species was sampled, except for slightly lower mean proportions of 18:1(n-9) in April. The 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) ratios were in the range of those for epipelagic species and were similar in April and July (both $p>0.05$, T-test; Fig. 4C,D).

The deep mesopelagic copepod *D. palumbii* (Fig. 3K) differed markedly in storage lipid fatty acid composition from the other zooplankton species and contained the highest proportion of the carnivory marker fatty acid 18:1(n-9) (~50 % of the total fatty acids) and the lowest proportion of SFA (~7 % of total fatty acids) of all species studied.

Storage lipids were, thus, dominated by MUFA (~71 %) with PUFA constituting about 21 % (mainly 22:6(n-3) and 20:5(n-3)). Fatty acid proportions were generally similar in April and July. The 16:1(n-7)/16:0 ratios were more than twice as high as those for the other epi- and mesopelagic species because of the very low proportions of 16:0, while 18:1(n-9)/18:1(n-7) ratios were also higher than for the other mesopelagic species, but in the range of values for *Oncaea* spp. Both ratios were similar in April and July for *D. palumbii* (both $p>0.05$, T-test; Fig. 4C,D).

The fatty acid proportions of the deep mesopelagic chaetognath *E. fowleri* (Fig. 3L) were dominated by MUFA (~46 %) with SFAs (~25 %) and PUFA (~29 %) being similar abundant. Dominant fatty acids were 16:0, 18:1(n-9) and 22:6(n-3). Proportions of the most abundant fatty acids were generally similar in April and July. The 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) ratios were similar to *C. alba* and in the range of those for epipelagic species and were similar in April and July (both $p>0.05$, T-test; Fig. 4C,D).

3.2. Spatial differences at Seine and Sedlo Seamounts

3.2.1. Seine

In April, mean $\delta^{15}N$ and $\delta^{13}C$ of POM_{susp} were lowest at the West slope location and had similar mean values at the summit and farfield locations, but differences were not significant ($p>0.05$, Kruskal-Wallis; Fig. 5A,B). Epipelagic zooplankton species had similar mean $\delta^{15}N$ and $\delta^{13}C$ values at the sampled seamount and farfield locations and differences between the summit or pooled seamount locations and the farfield location were all not significant ($p>0.05$, T-test or Mann-Whitney; Fig. 5A,B). Among mesopelagic zooplankton species, *D. palumbii* had significantly higher $\delta^{15}N$ and $\delta^{13}C$ values at the farfield location ($p<0.05$, Mann-Whitney and $p<0.01$, T-test, respectively; Fig. 5A,B). Mean $\delta^{15}N$ values of the other mesopelagic species were also higher at the farfield location, although for *C. alba* these differences were not significant ($p>0.05$, T-test), while the other species had insufficient sample sizes for statistical testing. Mean $\delta^{13}C$ values of the other species were generally similar and for *C. alba* revealed no significant differences between farfield and the pooled seamount locations ($p>0.05$, T-test).

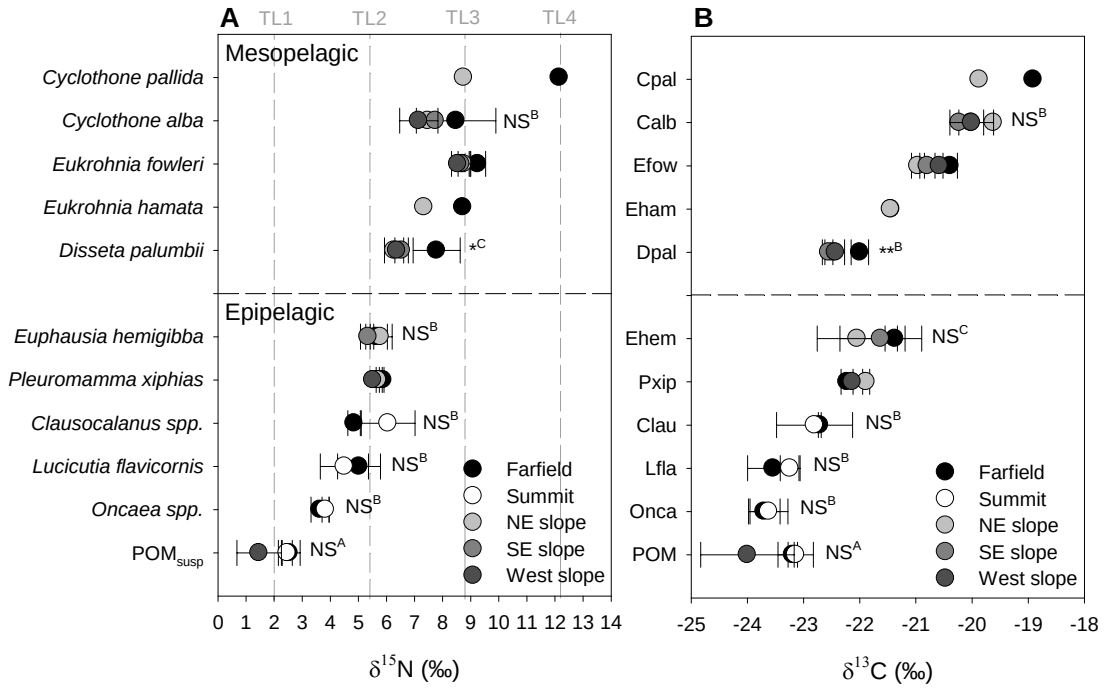

Fig. 5. Stable isotope signatures (mean ± SD) for (A) $\delta^{15}N$ and (B) $\delta^{13}C$ of POM_{susp} and epi- and mesopelagic zooplankton species at seamount and farfield locations of Seine Seamount in April 2004. Trophic levels (TL) were estimated using mean $\delta^{15}N$ of POM_{susp} pooled from all locations as TL1 and assuming an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level. Spatial differences in stable isotope signatures of POM_{susp} between sampling locations were tested using the Kruskal-Wallis-Test (^{A}). Spatial differences of zooplankton isotopic signatures between data pooled for all seamount (summit and slope) locations and the farfield location were tested using the T-test (^{B}) or the Mann-Whitney-Test (^{C}). Significance of tests is given as NS for not significant (p>0.05), * for p<0.05 and ** for p<0.01.

Assuming mean $\delta^{15}N$ of POM_{susp} pooled from all locations (2.0 ‰ in April) as the base and 1st trophic level (TL1) of the pelagic food web and a $\delta^{15}N$ increase of 3.4 ‰ per trophic level, epipelagic zooplankton species occupied the first two trophic levels (Fig. 5A). *Oncaea* spp. and *L. flavicornis* ranged on intermediat trophic positions in the upper half between the 1st and 2nd trophic level. *Oncaea* spp. occupied the lowest trophic position of the species sampled during the survey with ~1.7 ‰ higher $\delta^{15}N$ values than POM_{susp}. The $\delta^{15}N$ values of *Clausocalanus* spp., *P. xiphias* and *E. hemigibba* ranged around the base of the 2nd trophic level with *Clausocalanus* spp. showing the largest range of values. Mesopelagic species occupied trophic positions between the 2nd and 4th trophic level with most species positioned on the 3rd trophic level and *C. pallida* at the farfield location occupying the highest trophic position close to the 4th trophic level (Fig. 5A). The copepod *D. palumbii* had the lowest $\delta^{15}N$ values of all mesopelagic species at each location.

The ratios of 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) fatty acids in April could only be calculated for the POM_{susp} sample from the West slope location, as total fatty acids of the samples from the farfield and summit locations consisted exclusively of SFA. At the West slope location the 16:1(n-7)/16:0 ratio was highest (0.44) and the 18:1(n-9)/18:1(n-7) ratio lowest (5.9) of all surveys (Fig. 6A,B).

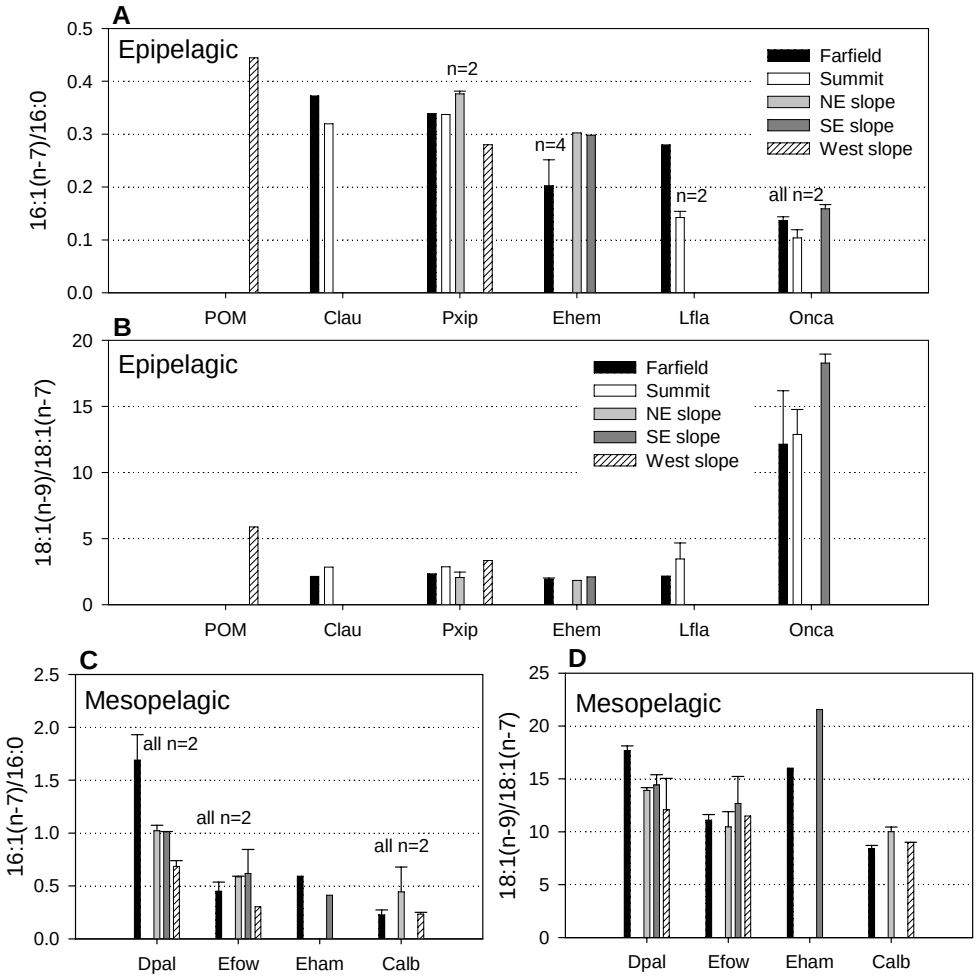

Fig. 6. Ratios of 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) fatty acids (mean and ranges) in the total lipids of POM_{susp} (A,B) and storage lipids of epi- (A,B) and mesopelagic (C,D) zooplankton species at the different sampling locations at Seine Seamount in April 2004. n = number of samples at a location if >1.

Spatial differences in the 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) ratios of the epipelagic *Clausocalanus* spp., *P. xiphias* and *E. hemigibba* in April were generally smaller than the observed temporal differences (Fig. 6A,B). Of the 2 species with no significant temporal differences, namely *L. flavicornis* and *Oncaea* spp., spatial variability of the marker ratios was similar to temporal variability for *Oncaea* spp. and revealed no apparent pattern, while *L. flavicornis* had a markedly higher 16:1(n-7)/16:0 ratio at the

farfield compared to the summit locations concurrent with similar 18:1(n-9)/18:1(n-7) ratios.

Among the mesopelagic species in April, *D. palumbii* showed the largest spatial variability for the 16:1(n-7)/16:0 ratio, which was strongly elevated at the farfield location compared to the seamount locations (Fig. 6C). Considerable variability in 16:1(n-7)/16:0 ratios within as well as between locations were also apparent for the other mesopelagic species, namely *E. hamata*, *E. fowleri* and *C. alba*, although they were of lower magnitude compared to *D. palumbii* and without apparent spatial patterns. The ratios of 18:1(n-9)/18:1(n-7) were also variable within as well as between locations for all mesopelagic species, with slightly elevated mean ratios at the farfield location for *D. palumbii*, while no spatial pattern was apparent for the other species (Fig. 6D).

In July, mean $\delta^{15}N$ values of POM_{susp} at Seine Seamount were lower at the summit location compared to the more similar West slope and farfield locations, but the differences were not significant ($p>0.05$, one-way ANOVA; Fig. 7A). Spatial differences in $\delta^{13}C$ of POM_{susp} were significant ($p<0.01$, one-way ANOVA) with lower values at the farfield location compared to the more similar summit and West slope locations (both locations $p<0.01$, *post-hoc* Tukey-HSD; Fig. 7B).

Among the epipelagic species, mean isotopic differences between the summit and farfield locations were similar to those of POM_{susp} for *Oncaea* spp., with lower $\delta^{15}N$ and higher $\delta^{13}C$ values at the summit location, while for *Clausocalanus* spp. no spatial differences were apparent (Fig. 7A,B). The diel vertical migrators *P. xiphias* and *E. hemigibba* had similar $\delta^{15}N$ and $\delta^{13}C$ values at the West slope and farfield locations (*P. xiphias*: both $p>0.05$, T-test; Fig. 7A,B).

The $\delta^{15}N$ and $\delta^{13}C$ values for the mesopelagic copepod *D. palumbii* and chaetognath *E. fowleri* were also similar at the seamount and farfield locations (*D. palumbii*: both $p>0.05$, Mann-Whitney), while *C. alba* had significantly higher $\delta^{15}N$ values at the farfield location compared to the summit ($p<0.01$, T-test) concurrent with similar $\delta^{13}C$ values ($p>0.05$, T-test; Fig. 7A,B).

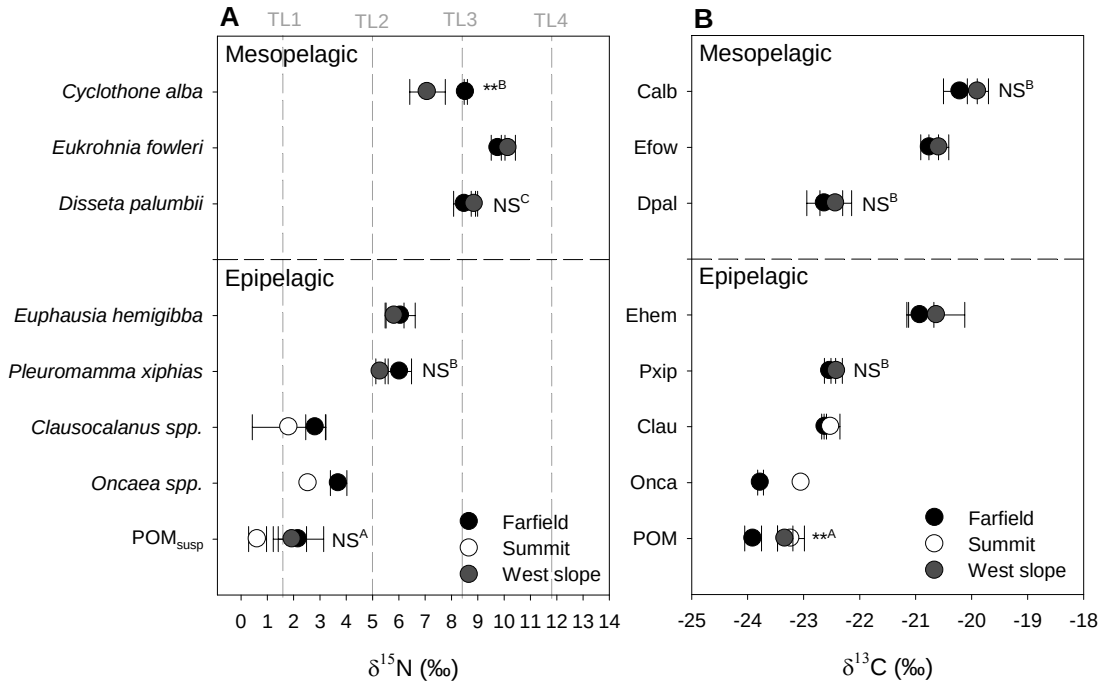

Fig. 7. Stable isotope signatures (mean ± SD) for (A) $\delta^{15}N$ and (B) $\delta^{13}C$ of POM_{susp} and epi- and mesopelagic zooplankton species at seamount and farfield locations of Seine Seamount in July 2004. Trophic levels (TL) were estimated using mean $\delta^{15}N$ of POM_{susp} pooled from all locations as TL1 and assuming an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level. Spatial differences of POM_{susp} stable isotope signatures between sampling locations were tested using one-way ANOVA followed by a *post-hoc* Tukey-HSD test (^{A}). Spatial differences of zooplankton isotopic signatures between data pooled for all seamount (summit and slope) locations and the farfield location were tested using the T-test (^{B}) or the Mann-Whitney-Test (^{C}). Significance of tests is given as NS for not significant (p>0.05), * for p<0.05 and ** for p<0.01.

According to $\delta^{15}N$ values, epipelagic zooplankton species ranged in the first two trophic levels, when mean $\delta^{15}N$ of POM_{susp} pooled for all locations (1.8 ‰ in July) was assumed as base of the pelagic food web (Fig. 7A). *Oncaea* spp., *P. xiphias* and *E. hemigibba* occupied similar trophic positions as in April. *Oncaea* spp. took an intermediate position between the 1st and 2nd trophic level, while *P. xiphias* and *E. hemigibba* were situated in the lower half between the 2nd and 3rd trophic level. *Clausocalanus* spp., occupied a much lower trophic position in July compared to April, with $\delta^{15}N$ values close to those for POM_{susp} (Fig. 7A). Mesopelagic species occupied trophic positions between the 2nd and 4th trophic level as in April (Fig. 7A). The deep mesopelagic species *D. palumbii* and *E. fowleri*, however, had both higher $\delta^{15}N$ values in July (~1 ‰ and 2 ‰, respectively), while the fish *C. alba*, from shallower mesopelagic depths, remained at a similar trophic position.

The 16:1(n-7)/16:0 fatty acids ratio of the total lipids of POM_{susp} was slightly elevated at the summit location compared to the farfield and West slope locations (Fig. 8A), although the increase was small compared to observed temporal differences, while the 18:1(n-9)/18:1(n-7) ratios were largely similar at all locations (Fig. 8B).

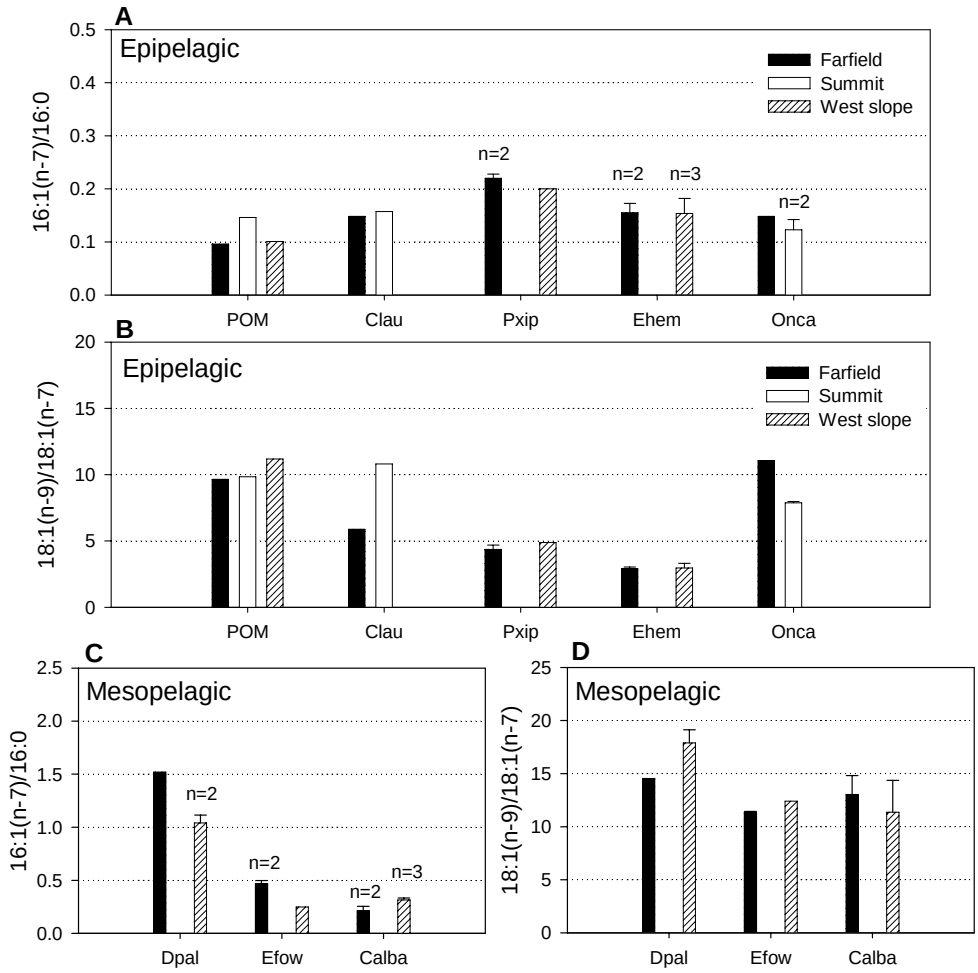

Fig. 8. Ratios of 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) fatty acids (mean and ranges) in the total lipids of POM_{susp} (A,B) and storage lipids of epi- (A,B) and mesopelagic (C,D) zooplankton species at the different sampling locations at Seine Seamount in July 2004. n = number of samples at a location if >1.

The 16:1(n-7)/16:0 ratios of the storage lipids of the epipelagic zooplankton were similar at farfield and seamount locations for all species, including ratios for *Clausocalanus* spp. and *Oncaea* spp. at the summit location (Fig. 8A). The 18:1(n-9)/18:1(n-7) ratios of *Clausocalanus* spp. and *Oncaea* spp., on the other hand, differed markedly between summit and farfield locations, although without a pattern, as *Clausocalanus* spp. had a higher ratio at the summit location and *Oncaea* spp. at the

farfield location (Fig. 8B). Ratios of 18:1(n-9)/18:1(n-7) fatty acids were similar for *P. xiphias* and *E. hemigibba* at farfield and West slope locations.

For the mesopelagic zooplankton, no clear spatial patterns were apparent in the fatty acid marker ratios. The deep-mesopelagic species *D. palumbii* and *E. fowleri* had higher 16:1(n-7)/16:0 ratios at the farfield location compared to the West slope, while ratios were similar for *C. alba* (Fig. 8C). Mean 18:1(n-9)/18:1(n-7) ratios were similar between farfield and West slope locations for *E. fowleri* and *C. alba*, but were higher at the West slope for *D. palumbii* (Fig. 8D).

3.2.2. SEDLO

At Sedlo Seamount in November, spatial differences in $\delta^{15}N$ values of POM_{susp} were significant ($p<0.01$, one-way ANOVA) with significantly higher values at the farfield location (mean: 4.5 ‰) compared to the summit, East and West slope locations (pooled mean: 1.7 ‰; all $p<0.01$, *post-hoc* Tukey-HSD; Fig. 9A). The $\delta^{13}C$ values of POM_{susp} at farfield and seamount locations were similar ($p>0.05$, one-way ANOVA) (Fig. 9B).

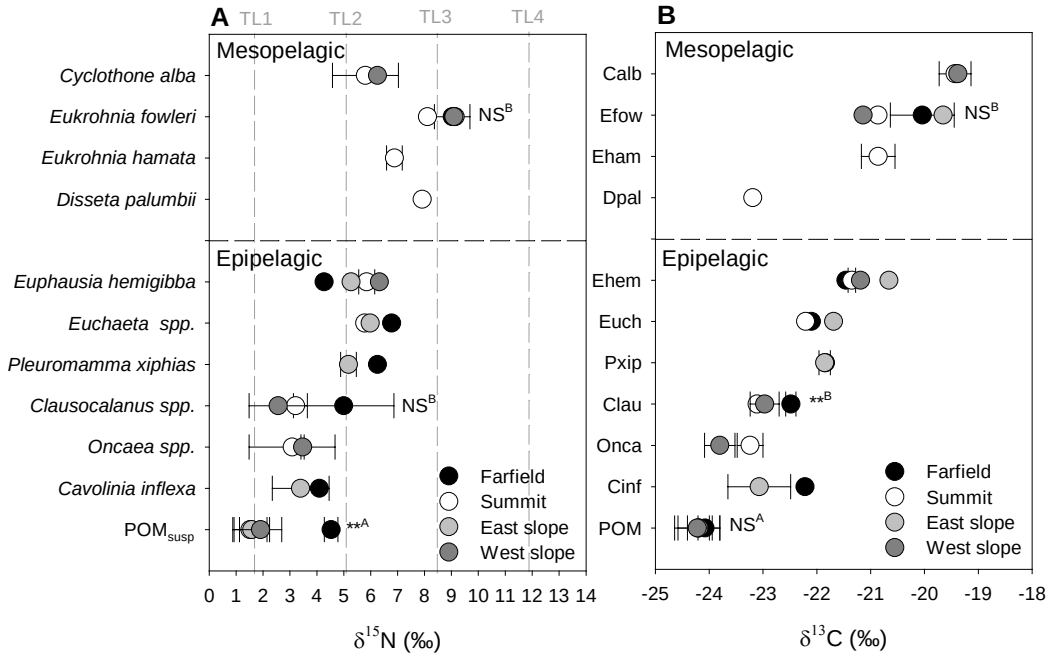

Fig. 9. Stable isotope signatures (mean ± SD) for (A) $\delta^{15}N$ and (B) $\delta^{13}C$ of POM_{susp} and epi- and mesopelagic zooplankton species at seamount and farfield locations of Sedlo Seamount in November 2003. Trophic levels (TL) were estimated using mean $\delta^{15}N$ of POM_{susp} only from summit and slope locations as TL1 (see discussion) and assuming an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level. Spatial differences of POM_{susp} stable isotope signatures between sampling locations were tested using one-way ANOVA followed by a *post-hoc* Tukey-HSD test (^{A}). Spatial differences of zooplankton isotopic signatures between data pooled for all seamount (summit and slope) locations and the farfield location were tested using the T-test (^{B}). Significance of tests is given as NS for not significant ($p>0.05$), * for $p<0.05$ and ** for $p<0.01$.

The higher $\delta^{15}N$ values of POM_{susp} at the farfield location were not clearly apparent in the epipelagic zooplankton species and spatial differences were not significant for *Clausocalanus* spp. (both $p>0.05$, T-test), while sample size for the other species was insufficient for statistical testing (Fig. 9A). The $\delta^{13}C$ values were significantly higher at the farfield location compared to seamount locations for *Clausocalanus* spp. ($p<0.01$, T-test; Fig 9B), while values were similar or variable without apparent spatial patterns for the other epipelagic species (Fig. 9B).

The chaetognath *E. fowleri* was the only mesopelagic species sampled at farfield and seamount locations and spatial differences of $\delta^{15}N$ and $\delta^{13}C$ values were not significant (both $p>0.05$, T-test). While not sampled at the farfield, $\delta^{15}N$ and $\delta^{13}C$ values for *C. alba* were similar among seamount locations (Fig. 9A,B).

Determination of the trophic baseline using mean $\delta^{15}N$ of POM_{susp} pooled for all locations was difficult due to significantly enriched $\delta^{15}N$ values at the farfield location. As these enriched $\delta^{15}N$ values of POM_{susp} at the farfield location were not reflected in the epipelagic zooplankton species, mean $\delta^{15}N$ of POM_{susp} pooled only from seamount locations (1.7 ‰) was used as base of the pelagic food web to estimate the trophic position of the zooplankton species sampled at Sedlo Seamount (Fig. 9A). Epipelagic zooplankton species at Sedlo Seamount ranged in the 1st and 3rd trophic levels (Fig 9A) with species occupying similar trophic positions to those of Seine Seamount in April and July. *Clausocalanus* spp., *Oncaea* spp. and *C. inflexa* were positioned on intermediate trophic positions between the 1st and 2nd trophic level, with *Clausocalanus* spp. covering the largest range of values, while *Euchaeta* spp., *E. hemigibba* and *P. xiphias* ranged in the lower half between the 2nd and 3rd trophic level (Fig 9A). Mesopelagic species occupied trophic positions between the 2nd and 4th trophic level (Fig 9A) and $\delta^{15}N$ values were generally in a similar range as observed at Seine Seamount, except for lower values for *C. alba*. The fish *C. alba* and chaetognath *E. hamata* from shallower mesopelagic depths occupied lower trophic positions between the 2nd and 3rd trophic level than the deeper mesopelagic *D. palumbii* and *E. fowleri*, which occupied positions just below the 3rd trophic level and in the lower half between the 3rd and 4th trophic level, respectively (Fig 9A).

The fatty acid marker ratios of 16:1(n-7)/16:0 for POM_{susp} were similar at the seamount and farfield locations, while the 18:1(n-9)/18:1(n-7) ratios at the summit and East slope

locations were markedly lower than at the farfield and West slope location at Sedlo Seamount (Fig. 10A,B). The epipelagic species *Clausocalanus* spp., *P. xiphias* and *E. hemigibba* did not reflect the spatial differences in the 18:1(n-9)/18:1(n-7) ratio observed for POM_{susp} and had similar values for both ratios at the farfield and seamount locations of Sedlo Seamount, except for a higher 18:1(n-9)/18:1(n-7) ratio at the summit location for *Clausocalanus* spp. (Fig. 10A,B). Mesopelagic species were only sampled at summit and slope locations at Sedlo Seamount, so that a comparison with the farfield location was not possible. However, large spatial differences in both fatty acid marker ratios between the different seamount locations were apparent for all mesopelagic species, although without clear spatial patterns (Fig. 10C,D), and were much larger than those observed for the same species at Seine Seamount (Fig. 4C,D).

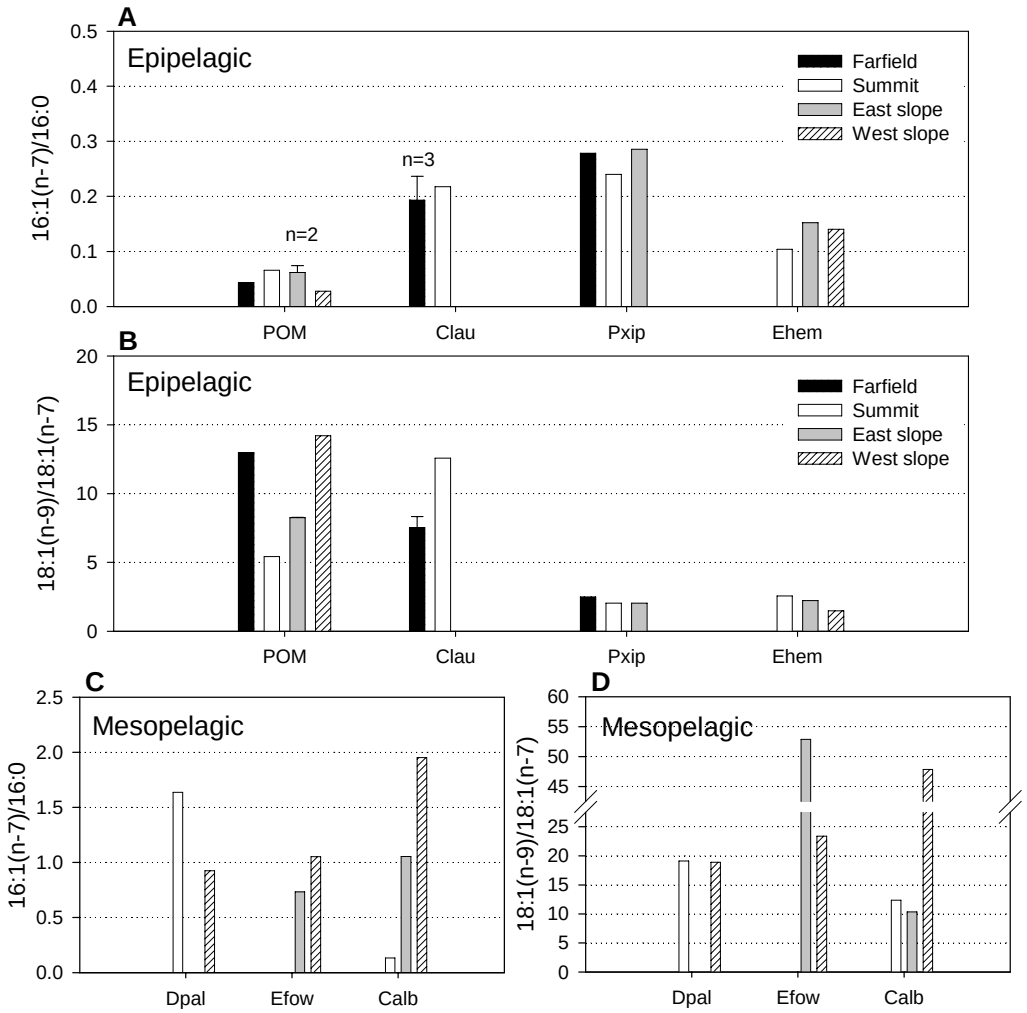

Fig. 10. Ratios of 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) fatty acids (mean and ranges) in the total lipids of POM_{susp} (A,B) and storage lipids of epi- (A,B) and mesopelagic (C,D) zooplankton species at the different sampling locations at Sedlo Seamount in November 2003. n = number of samples at a location if >1.

4. DISCUSSION

4.1. TEMPORAL CHANGES IN POM_{SUSP} COMPOSITION AND ZOOPLANKTON DIET

POM_{SUSP} COMPOSITION

Temporal changes in near-surface POM_{susp} composition at Seine Seamount locations were evident from stable isotope and fatty acid signatures for the 3 surveys conducted in November 2003 and April 2004 and July 2004. Carbon and nitrogen isotopic ratios of POM_{susp} were within the range of values previously reported for marine particulates (e.g. Fry and Sherr 1984, Owens 1987, Montoya *et al.* 2002). Significantly elevated $\delta^{15}N$ values of POM_{susp} at Seine Seamount in November compared to April and July coincided with a deep mixing of the upper ocean layer (mixing depth: 90 m) above the seamount, which was slightly shallower than the maximum depth of the winter mixed layer (150 m) in the region (Bashmachnikov *et al.* 2009). The elevated $\delta^{15}N$ values in November might, thus, be the result of recent upwelling of ^{15}N enriched deep-water nitrate and subsequent uptake and conversion into phytoplankton biomass. In oligotrophic open ocean areas, there is a strong isotopic contrast between deep-water nitrate, which has an average $\delta^{15}N$ of ~4.5 ‰ over broad reaches of the ocean and near-surface suspended particles, which have a $\delta^{15}N$ well below that of typical subsurface nitrate (e.g. Montoya *et al.* 2002 and references therein). Proposed mechanisms responsible for $\delta^{15}N$ depletion in surface waters are (1) food-web processes that preferentially export ^{15}N-enriched faecal pellets from the upper water column while retaining isotopically lighter ammonium from heterotroph excretion (especially copepods) in the surface layer (Checkley and Miller 1989, Checkley and Entzeroth 1985) and (2) production of isotopically depleted organic matter through N_2-fixation by diazotrophs (e.g. Montoya *et al.* 2002, 2004). Below the euphotic zone, the increase in $\delta^{15}N$ of PON with depth has been ascribed to biological degradation and/or denitrification that leaves nitrate with high $\delta^{15}N$ values (Michener and Schell 1994).

Temporal differences in the fatty acid composition of the total lipids of POM_{susp} at Seine Seamount reflected most likely changes in phytoplankton and microzooplankton composition of the organic matter particles during different periods of production. In November, the fatty acid signature of POM_{susp} was dominated by saturated fatty acids (SFA, 16:0 and 18:0) and characterized by the lack of 14:0, which is a prominent

constituent of phytoplankton lipids (Sargent and Whittle 1981), as well as the lowest proportion of poly-unsaturated fatty acids (PUFA) together with the highest proportion of mono-unsaturated fatty acids (MUFA) of all surveys. Mono-unsaturated fatty acids consisted mainly of 18:1(n-9) and 20:1(n-9), which are abundant in zooplankton (Wakeham 1995, Dalsgaard *et al.* 2003) and/or their remains (e.g., carcasses, exuviae**,** faecal pellets; Tanoue and Hara 1986, Matsueda *et al.* 1986, Najdek *et al.* 1994). The combination of saturated 18:0 and monoenes of the (n-9) family (18:1(n-9), 20:l(n-9), 22:1(n-9)) has been reported to be associated with periods of minimum phytoplankton growth during bloom initiation or lag phase (Mayzaud *et al.* 1989). With regard to recent deep-water nitrate upwelling indicated by elevated $\delta^{15}N$ values of POM_{susp}, the fatty acid signature of POM_{susp} in November might reflect a period of minimum growth.

In April, fatty acids of POM_{susp} consisted either exclusively of saturated fatty acids (at the farfield and summit locations) or contained the highest proportion of phytoplankton marker fatty acids observed during all surveys (at the West slope location). Unsaturated fatty acids are more labile and degrade faster than SFA (Wakeham *et al.* 1984, Rice *et al.* 1986), and their lack in the SFA dominated samples could indicate that POM_{susp} consisted of refractory detritus. This was, however, not supported by higher proportions of bacterial marker fatty acids or elevated $\delta^{15}N$ values, as $\delta^{15}N$ increases with increasing degree of biological degradation of organic matter (Michener and Schell 1994, Checkley and Miller 1989). The lipids of the West slope sample, on the other hand, contained high proportions of PUFA, which are indicative of bloom conditions (Mayzaud *et al.* 1989, Bergé and Barnathan 2005, Dalsgaard *et al.* 2003). They also contained the highest proportion of the diatom marker fatty acids 16:1(n-7) and 20:5(n-3), together with the lowest proportions of the zooplankton marker fatty acid 18:1(n-9), while flagellates remained dominant according to proportions of flagellate markers (18:4(n-3), 18:5(n-3) and 22:6(n-3); Dalsgaard *et al.* 2003). The fatty acid marker ratio 16:1(n-7)/16:0 supported a higher abundance of diatoms in POM_{susp} at the West slope location with higher values in April compared to July. The ratios in April and July were similar to values reported for a mixed flagellate/diatom and a flagellate-dominated phytoplankton biomass, respectively, in the North Sea (St. John and Lund 1996). This fatty acid composition might indicate bloom conditions in April. Concurrently determined chlorophyll *a* concentrations at Seine Seamount, which were highest in

April compared to November and July (Kiriakoulakis *et al.* 2009, Kiriakoulakis unpublished data), further supported enhanced phytoplankton abundance in April. The observed large variability in the fatty acid composition of POM_{susp} in April (i.e., between fresh phytoplankton and refractory detritus) might reflect highly progressed bloom conditions with high proportions of senescent phytoplankton, as suggested by high chlorophyll *a* /phaeopigment ratios (Kiriakoulakis *et al.* 2009), and a patchy distribution due to strong vertical mixing (upper-ocean mixed-layer depth at Seine Seamount in April: 150 m; Bashmachnikov *et al.* 2009).

High proportions of SFA and abundant PUFA dominated by flagellate marker fatty acids characterized the fatty acid composition of POM_{susp} in July. This fatty acid signature is characteristic for POM_{susp} compositions in stratified summer conditions and reflected the minimum mixing depth of the upper ocean mixed layer (20-50 m in July/August; Bashmachnikov *et al.* 2009) reported for the 3 surveys.

EPIPELAGIC ZOOPLANKTON

According to fatty acid and stable isotope signatures, the epipelagic zooplankton species studied were mainly omnivorous feeders, although herbivorous and carnivorous species were also represented. The predominantly carnivorous diets of the copepod *Euchaeta* spp. (Maucheline 1998) and the chaetognath *Sagitta* spp. (Tönnesson and Tiselius 2005) were reflected in their high trophic level position according to their $\delta^{15}N$ values. The storage lipids of the copepod species *Clausocalanus* spp., *P. xiphias* and *L. flavicornis*, and the euphausiid *E. hemigibba* were characterized by high proportions of phytoplankton marker fatty acids (mainly 22:6(n-3) and 20:5(n-3)) and substantial amounts of the carnivory marker fatty acid 18:1(n-9), and indicated omnivorous feeding on phyto- and zooplankton. These results agreed with studies of gut contents of *P. xiphias* and *E. hemigibba*, which reported a similar and diverse diet of phytoplankton, heterotrophic prey (proto-and metazoans) and detritus (Kinsey and Hopkins 1994, Schnetzer and Steinberg 2002). Feeding experiments with *Clausocalanus* spp. revealed a mixed diet with a preference for ciliates over phytoplankton and for bigger (>5µm) phytoplankton over smaller (<5µm) phytoplankton in a natural food medium (Kleppel *et al.* 1988, Broglio *et al.* 2004). Species of the family Lucicutiidae have been described as omnivorous/detritivorous (Maucheline 1998 and references therein) and the fatty acid

signature of *L. flavicornis* in July, which was characterized by higher amounts of the saturated fatty acid 16:0 and lower amounts of phytoplankton marker fatty acids compared to the other surveys, might indicate a higher proportion of detritus in the diet of *L. flavicornis* in July, as this signature is typical for detritus (Reemtsma *et al.* 1990). Isotopic signatures generally confirmed the omnivorous feeding mode of these species, which occupied an intermediate trophic level position, according to their $\delta^{15}N$ values. The slightly higher trophic positions occupied by the larger diel vertically migrating species *P. xiphias* and *E. hemigibba* compared to the 2 smaller calanoid copepod species are most likely due to the size-related ability to feed on larger, higher trophic level prey.

The lowest trophic positions regarding $\delta^{15}N$ values were occupied by the herbivorous pteropod *C. inflexa* and the omnivorous Ostracoda and *Oncaea* spp. Pteropods feed non-selectively on phytoplankton down to bacteria-sized particles, which they capture with mucus sheets (e.g. Silver and Bruland 1981). The storage lipids of *C. inflexa* confirmed this feeding mode as they were dominated by the highest proportion of phytoplankton marker fatty acids concurrent with the lowest proportion of the carnivory marker fatty acid 18:1(n-9). Planktonic ostracoda are predominantly omnivores /detritivores (Longhurst 1979) and the storage lipids of the Ostracoda contained proportions of phytoplankton and carnivory marker fatty acids largely similar to those of the calanoid copepod species. The storage lipids were, however, characterized by the highest proportion of the diatom marker fatty acid 16:1(n-7) of all epipelagic species, which might indicate a feeding preference for diatoms, although flagellates were also consumed. Poecilostomatoid copepods of the genera *Oncaea* have been reported to be mainly omnivorous (Wu *et al.* 2004, Ohtsuka *et al.* 1996). The storage lipid fatty acid composition of *Oncaea* spp. was dominated by the highest proportion of the carnivory marker fatty acid 18:1(n-9) of all epipelagic species studied and contained high amounts of the saturated fatty acid 16:0 and low amounts of phytoplankton marker fatty acids. A similar fatty acid composition was reported for total lipids of *Oncaea* species from Arctic and Antarctic waters, except for their much lower amounts of the saturated fatty acid 16:0 (Kattner *et al.* 2003). The authors suggested an omnivorous and/or carnivorous feeding behaviour of the species, including feeding on detritus but not on living phytoplankton. The low trophic level of *Oncaea* spp. observed in this study

would not support a predominantly carnivorous feeding behaviour, but members of *Oncaea* have also been observed feeding on faecal-pellet material and marine snow (Skjoldal and Wassmann 1986, Lampitt *et al.* 1993, Huskin *et al.* 2004 and references therein). The similarity of the storage lipid fatty acid composition of *Oncaea* spp. with those reported for lipids of faecal pellets, which generally are dominated by the fatty acids 16:0 and 18:1(n-9) (Tanoue and Hara 1986, Matsueda *et al.* 1986, Najdek *et al.* 1994), might, thus, suggest coprophagy of the species investigated.

Temporal differences in both stable isotope and fatty acid biomarker signatures were observed in the epipelagic zooplankton species studied. Stable isotope signatures indicated pronounced lower average $\delta^{15}N$ values for all species sampled in November compared to April and July, which contrasted with the significantly enriched $\delta^{15}N$ values for POM_{susp}. These were higher than those of the zooplankton species, except for the carnivorous *Sagitta* spp. This trophic mismatch was most likely the result of a time lag between changes in $\delta^{15}N$ of the food source and the equilibration to these changes in the $\delta^{15}N$ of consumer tissues, which has been previously reported for aquatic ecosystems (O´Reilly *et al.* 2002). Equilibration of $\delta^{15}N$ in consumer tissues may take several days to several months (Dalerum and Angerbjörn 2005, Perga and Gerdeaux 2005) depending on the turnover time of an organism (Fry & Arnold, 1982, Hesslein *et al.* 1993, MacAvoy *et al.* 2001). In this study, the observed trophic mismatch most likely reflected recent changes in $\delta^{15}N$-signatures of POM_{susp} due to recent upwelling of $\delta^{15}N$-enriched deep-water nitrate into the euphotic zone, which had not been integrated into the $\delta^{15}N$ signal at consumer trophic levels. The lower average $\delta^{15}N$ values of the zooplankton in November compared to April and July occurred independent of feeding mode and trophic position occupied. The lower trophic level species, like *C. inflexa*, Ostracoda, *Oncaea* spp. and *L. flavicornis*, had shifted towards a similar average $\delta^{15}N$ values suggesting a dietary shift towards the same $\delta^{15}N$-depleted food source. For the higher trophic level chaetognath *Sagitta* spp. the lower $\delta^{15}N$ value observed in November reflected more likely an isotopic shift of the baseline of the food web, rather than a more herbivorous feeding.

The dietary shift of the zooplankton suggested by $\delta^{15}N$-signatures in November was, however, not mirrored in the storage lipid fatty acid signatures of the species, which contained no elevated proportions of phytoplankton marker fatty acids indicative for a

more herbivorous feeding mode. Instead, phytoplankton marker fatty acid proportions of the zooplankton were either generally similar to those from April (e.g., *Oncaea* spp., Ostracoda and *L. flavicornis*) or contained lower proportions of diatom marker fatty acids compared to April (e.g., *C. inflexa*, *Clausocalanus* spp., *Sagitta* spp.). The absence of a signal for increased herbivory in the zooplankton storage lipid fatty acids might be the result of different equilibration times of consumers to changes of $\delta^{15}N$ and fatty acid signature in the food sources, with fatty acid signatures of the storage lipids equilibrating faster than stable isotope signatures of whole individuals. Storage lipid fatty acid signature of the zooplankton in November did not reflect the low phytoplankton marker proportions in the fatty acid signature of POM_{susp}, which might indicated another time-lag in the equilibration of zooplankton storage lipid fatty acids to a recent change in POM_{susp} composition. Reported equilibration times for fatty acid signatures of consumers ranged from several days to several weeks (St. John and Lund 1996, Fraser *et al.* 1989, Kirsch *et al.* 1998).

The mismatches in biomarker signatures observed between POM_{susp} and zooplankton species might, thus, indicate a high temporal variability of POM_{susp} composition in November, as the winter months in the region studied are characterized by periods of strong vertical mixing of the surface layer and, hence, variable environmental conditions (Bashmachnikov *et al.* 2009).

In April and July, stable isotope signatures of POM_{susp} and the zooplankton species were generally similar, indicating more stable trophic conditions than in November. Flagellate markers generally dominated phytoplankton marker fatty acids in the storage lipids of the epipelagic zooplankton in April and July, but some of the species contained significantly higher proportions of diatom marker fatty acids in April. The storage lipids of these species, namely the herbivorous pteropod *C. inflexa* and the omnivorous *Clausocalanus* spp., *P. xiphias* and *E. hemigibba*, reflected the elevated value of the fatty acid marker ratio 16:1(n-7)/16:0 for POM_{susp} at the West slope in April, indicative of increased diatom abundance. Dietary shifts towards more herbivorous diets with a preference for diatoms during increased diatom abundance or diatom blooms have been reported for a number of copepod and euphausiid species (Fessenden and Cowles 1994, Schnetzer and Steinberg 2002), including *P. xiphias* (Schnetzer and Steinberg 2002). Concurrent with the elevated proportions of diatom marker fatty acids in the storage

lipids of the above mentioned species were, except for the herbivorous pteropod, the lowest values for the 18:1(n-9)/18:1(n-7) ratio, indicative of increased herbivory, and suggested more herbivorous feeding for these species in April.

Fatty acid marker ratios of the other epipelagic zooplankton species, i.e. *Oncaea* spp., *L. flavicornis*, Ostracoda and *Sagitta* spp., did not clearly reflect the observed temporal differences in diatom abundances, which might be due to differences in food choice. For *Oncaea* spp., *L. flavicornis* and *Sagitta* spp., this might be explained by utilizing a higher proportion of food items other than phytoplankton, e.g. faecal pellets, detritus and small crustaceans, respectively, while the high proportion of the diatom marker fatty acid 16:1(n-7) of the Ostracoda in November and July suggested a more specialised feeding behaviour on 16:1(n-7)–rich food sources independent of temporal phytoplankton group abundances.

The elevated value of the fatty acid marker ratio 16:1(n-7)/16:0 for POM_{susp} in April most likely did not indicate diatom bloom conditions at that time, but rather a situation of mixed flagellate and diatom composition with elevated but not dominant diatom abundance. The elevated ratios observed in some of the zooplankton species are of similar or slightly lower magnitude than those in POM_{susp} and reflect more likely a non-selective feeding on higher diatom abundances rather than a dietary switch to herbivorous feeding.

MESOPELAGIC ZOOPLANKTON

The selected mesopelagic species were either detritivorous like the copepod *D. palumbii* (Harding 1974, Pearre 2003), or carnivorous like the chaetognaths *E. hamata* and *E. fowleri*, which mainly feed on copepods (Terazaki *et al.* 1977, Sullivan 1980, Øresland 1990, Froneman and Pakhomov 1998), and the gonostomatid fishes *C. alba* and *C. pallida*, which both consume small crustaceans, mainly copepods, with the larger *C. pallida* utilising a larger size-fraction of the prey (Hopkins and Sutton 1998). The storage lipids of the chaetognath and fish species contained high amounts of the typical membrane fatty acids 16:0, 20:5(n-3) and 22:6(n-3), and the carnivory marker 18:1(n-9), confirming their carnivorous diet. These feeding modes were also reflected by trophic level positions of the species according to $\delta^{15}N$ values, which were highest for *C. pallida* and lowest for the detritivorous copepod *D. palumbii*. The latter was on

average enriched by 5-7 ‰ compared to $\delta^{15}N$ of surface POM_{susp}. It has been shown that sinking particulate matter can have $\delta^{15}N$ values about 3–4 ‰ higher than that of suspended particulate nitrogen, i.e. phytoplankton, in surface waters due to biological degradation of PON with depth (Michener and Schell 1994, Altabet 1988, Altabet *et al.* 1991, 1999, Voss *et al.* 1996). Taking into account a trophic level fractionation of around 3.4 ‰ (Minagawa and Wada 1984), the $\delta^{15}N$ of this copepod from the deep mesopelagic layer (800-1000 m) would suggest omnivorous feeding on a variety of phytodetritus and heterotrophic remains, described as a typical feeding mode for deep-sea copepods (Gowing and Wishner 1992). The fatty acid compositions of the storage lipids of *D. palumbii* were, however, dominated by the carnivory marker fatty acid 18:1(n-9). High proportions of this fatty acid have been reported previously for bathypelagic copepod species and were interpreted as indicative for a carnivorous /omnivorous feeding behaviour in this group (e.g., Bühring and Christiansen 2001). Since *D. palumbii* has been described as typical suspension feeder (Othsuka *et al.* 1997) and had $\delta^{15}N$ values lower than those in the other mesopelagic zooplanktivores, a strongly carnivorous feeding mode appeared unlikely for this species. Most animals are able to either biosynthesise 18:1(n-9) *de novo* or by chain elongation of 14:0 or 16:0 precursors obtained from the diet to 18:0 and then by desaturation to 18:1(n-9), which is common in carnivorous and omnivorous crustaceous zooplankton (Dalsgaard *et al.* 2003 and references therein). The low proportions of SFA in the storage lipids of *D. palumbii*, despite high proportions of SFA usually present in phytodetrital food sources (Reemtsma *et al.* 1990), might suggest that the observed high amounts of 18:1(n-9) fatty acid in *D. palumbii* were the result of biosynthesis for which dietary saturated 16:0 fatty acid was utilized.

Temporal differences in trophic marker signatures for *D. palumbii* and *E. fowleri* at the deep mesopelagic layer (800-1000 m) were characterized by significantly higher $\delta^{15}N$ values in July compared to April for both species. Observed lower $\delta^{15}N$ values in April might be explained by higher phytoplankton abundance in spring resulting in increased downward flux of sinking organic matter particles of lower $\delta^{15}N$ values. A connection between periods of maximum phytoplankton abundances and particle flux and reduced $\delta^{15}N$ values of sinking particles has been reported previously (Altabet 1989) and the author suggested that increased direct feeding on phytoplankton by the larger epipelagic

zooplankton resulted in a production of sinking particles of lower $\delta^{15}N$ values, which constitute an important food source at the lower mesopelagic layer. Although changes in $\delta^{15}N$ at the base of the food web will become diluted by time averaging in the upper trophic levels (O´Reilly *et al.* 2002), the observed temporal differences were still apparent for the carnivorous *E. fowleri*, although to a smaller extent. The fatty acid proportions and marker ratios of the storage lipids of both species, however, were similar in April and July, possibly due to lipid compositions of faecal pellets being largely altered with respect to the composition of the ingested food (Marty *et al.* 1994, Prahl *et al.* 1984, Harvey *et al.* 1987).

4.2. SPATIAL DIFFERENCES OF BIOCHEMICAL MARKERS AND INDICATIONS OF SEAMOUNT EFFECTS

At Seine Seamount, spatial differences between farfield and seamount locations were analysed for the surveys in April and July. Generally similar $\delta^{15}N$ and $\delta^{13}C$ values for POM_{susp} at all sampling locations for both surveys provided no evidence for seamount-related differences in particulate matter composition. An exception were the significantly lower $\delta^{13}C$ values at the farfield location in July, which might be related to lateral transport of organic matter with a different $\delta^{13}C$ signature to the seamount from the eastern farfield by upwelling filaments. These filaments are associated with the upwelling region off NW Africa, and July has been reported as the time of the year when the upwelling is stronger (Arístegui *et al.* 2009). Seamount-related spatial differences in POM_{susp} compositions were also not clearly apparent in the fatty acid signatures. Fatty acid marker ratios 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) for POM_{susp} were similar for the farfield and seamount locations in July, while in April pronounced differences between the exclusively saturated fatty acid signature at the farfield and summit locations and the phytoplankton marker-dominated signature at the West slope location might indicate highly patchy organic matter compositions rather than a seamount-related effect.

Trophic marker signatures of the epipelagic zooplankton species at Seine Seamount reflected the observed lack of indications for seamount-related differences in POM_{susp} composition. Isotopic values of the epipelagic species were generally similar between farfield and seamount locations with no significant spatial differences. Storage lipids of

epipelagic species, which showed a clear temporal signal of enhanced diatom consumption and herbivory during increased diatom abundance in POM_{susp}, contained similar fatty acid marker ratios at farfield and seamount locations during the surveys in April and July. The exception was *Clausocalanus* spp., which had a markedly elevated carnivory ratio 18:1(n-9)/18:1(n-7) at the summit compared to the farfield location in July. As $\delta^{15}N$ values and, thus trophic levels, of *Clausocalanus* spp. did not differ significantly between locations, higher fatty acid marker ratios in July might reflect the consumption of faecal pellets during summer stratification, which contain large proportions of 18:1(n-9) and might be retained above the summit by local anti-cyclonic current flow (Beckmann and Mohn 2002).

At mesopelagic depths at Seine Seamount, higher trophic level species like the carnivorous chaetognaths and gonostomatid fishes showed considerable variability of isotopic signatures and fatty acid marker ratios, which was more pronounced in April than July, but revealed no seamount-related pattern. The detritivorous copepod *D. palumbii*, in contrast, had significantly higher $\delta^{15}N$ and $\delta^{13}C$ values as well as much higher 16:1(n-7)/16:0 ratios and slightly higher 18:1(n-9)/18:1(n-7) ratios at the farfield compared to the seamount locations in April, which might indicate a faster downward flux of detrital matter at the seamount locations at that time. The lower $\delta^{15}N$ values of *D. palumbii* at the seamount in April suggested feeding on less refractory detritus, as $\delta^{15}N$ generally increases with increased trophic reworking during biological degradation (Michener and Schell 1994, Checkley and Miller 1989). Observed spatial differences in fatty acid marker ratios 16:1(n-7)/16:0 and 18:1(n-9)/18:1(n-7) of *D. palumbii* might be related to a utilisation of dietary saturated 16:0 for the biosynthesis of 18:1(n-9) in this species resulting in low proportions of 16:0 and high proportions of 18:1(n-9), which affect the fatty acid marker ratios (see 4.1. for discussion). The possible influence of biosynthesis on the proportions of marker fatty acids in the storage lipids complicated an interpretation of the fatty acid signatures. It has been speculated that large dietary input of 16:1 fatty acid might damp down endogenous biosynthesis of mono-unsaturates in animals (Sargent and Whittle 1981), which in the context of lower ratios at the seamount locations, might indicate faster downward transport of fresh detritus with higher proportions of 16:1 fatty acid at the seamount. Storage lipid fatty acid proportions of 16:1(n-7), however, were similar for farfield and seamount locations in

April. The spatial differences in biomarker signatures observed in April were not apparent in July suggesting that the assumed accelerated downward transport of detritus was not permanent feature.

At Sedlo Seamount in November, $\delta^{15}N$ values of POM_{susp} were significantly higher at the farfield location compared to the seamount locations and indicated local upwelling of $\delta^{15}N$-enriched deep-water nitrate. Similarly to Seine Seamount, enriched $\delta^{15}N$ values of POM_{susp} at the farfield location were not reflected in the epipelagic zooplankton species, possibly indicating the recent nature of this $\delta^{15}N$-enrichment in POM_{susp}, although the trophic mismatch was not as pronounced (see 4.1. for discussion). Indications for seamount upwelling-related elevated diatom abundances were also not apparent in the fatty acid marker ratio 16:1(n-7)/16:0 of POM_{susp} as values were similar at the seamount and farfield locations.

Epipelagic zooplankton species at Sedlo Seamount had similar values of the ratio 16:1(n-7)/16:0 at all locations and reflected the lack of evidence in POM_{susp} for enhanced diatom abundance. Elevated values of the carnivory ratio 18:1(n-9)/18:1(n-7) for *Clausocalanus* spp. at the summit location might be part of the large variability of this ratio observed at the seamount locations, while no spatial differences of this ratio were apparent for the other species.

At mesopelagic depths at Sedlo Seamount, stable isotope ratios showed no significant difference between farfield and seamount locations for the chaetognath *E. fowleri*, which was the only mesopelagic species sampled at the farfield location. Large spatial differences of fatty acid marker ratios between summit and slope locations were observed for the other mesopelagic species, but indicated no clear spatial pattern. These spatial differences were much larger than those observed for the same species at Seine Seamount and might be the result of patchy organic matter distribution due to the altered current regime in the vicinity of the mesopelagic summit depth of Sedlo Seamount (Bashmachnikov *et al.* 2009, Mohn *et al.* 2009). However, this remains speculative in the absence of farfield samples for the mesopelagic species for comparison.

At both Sedlo and Seine Seamounts, trophic marker analyses of POM_{susp} and selected zooplankton species provided no evidence for altered feeding conditions at the

seamount fuelled by current-induced nutrient-upwelling. This might be the result of the strong variability and intermittent nature of Taylor column generation at these seamounts (see Material and Methods). Prerequisites for the development of enhanced primary and secondary production at a seamount, according to the hypothesis of locally enhanced seamount productivity, are the persistence of local nutrient-upwelling conditions and the retention of enhanced phytoplankton biomass for the time needed for zooplankton generation, i.e. for weeks to months. Zooplankton must also be capable of remaining in the vicinity of the seamounts over similar timescales (Dower and Mackas 1996). The intermittent nature of the Taylor column current regime reported for both seamounts might only allow for short periods of locally enhanced phytoplankton growth and would most likely prevent any development of locally enhanced zooplankton secondary production and biomass. This agrees with concurrent studies of organic matter distribution (Vilas *et al.* 2009) and plankton metabolism (Arístegui *et al.* 2009), which reported only sporadic indications of enhanced primary production at the summit locations. The authors suggested that the two seamounts would act as trapping mechanisms for organic matter rather than increasing primary production significantly. A concurrent study on the zooplankton distribution at Seine and Sedlo Seamounts detected no enhanced zooplankton biomass above the seamount summits (Martin and Christiansen 2009) confirming the lack of evidence for increased secondary production. Furthermore, a model developed to simulate the influence of Taylor column flow on the behaviour of both passive particles and vertically migrating organisms at Great Meteor Seamount (Beckmann and Mohn 2002), suggested a higher retention time for passive particles, but showed no retention of vertically migrating zooplankton.

5. CONCLUSIONS

Stable isotope and fatty acid biomarker analyses provided useful tools to elucidate temporal and spatial differences in the food sources and the diets of epi- and mesopelagic zooplankton species at Seine and Sedlo Seamounts. Temporal differences were characterized in November by a trophic mismatch between elevated $\delta^{15}N$ values of POM_{susp}, indicating recent nutrient upwelling, and uniformly low $\delta^{15}N$ values of epipelagic zooplankton species, suggesting a preceding dominance of ^{15}N-depleted food sources. In April storage lipid fatty acid compositions of epipelagic zooplankton species

clearly reflected the elevated diatom abundance indicated in the total lipids of POM_{susp}. Lower $\delta^{15}N$ values observed in mesopelagic zooplankton species in April compared to July might be related to higher phytoplankton abundance in April resulting in increased flux of sinking organic matter particles with lower $\delta^{15}N$ values. Although temporal differences were clearly apparent in the biomarker signatures of POM_{susp} and the zooplankton species, spatial differences between farfield and seamount locations were comparatively small, or in the case of the mesopelagic species were highly variable with no apparent seamount-related pattern. Trophic marker analyses provided, thus, no evidence for altered feeding conditions at Seine and Sedlo Seamounts fuelled by current-induced nutrient-upwelling as proposed by the hypothesis of locally-enhanced seamount productivity.

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REFERENCES

Altabet MA (1988) Variations in nitrogen isotopic composition between sinking and suspended particles: Implications for nitrogen cycling and particle transformation in the open ocean. Deep-Sea Res. 35: 535-554

Altabet MA, Deuser WG, Honjo S., Stienen S. (1991) Seasonal and depth-related changes in the source of sinking particles in the N. Atlantic. Nature 354: 136–139

Altabet MA, Pilskaln C., Thunell R., Pride C., Sigman D., Chavez F., and Francois R. (1999) The nitrogen isotope biogeochemistry of sinking particles from the margin of the eastern North Pacific. Deep-Sea Res. 46: 655–679

Altabet MA (1989) A time-series study of the vertical structure of nitrogen and particle dynamics in the Sargasso Sea. Limnol. Oceanogr., 34(7), 1185-1201

Arístegui J, Mendonça A, Vilas JC, Espino M, Polo I, Montero MF, Martins A (2009) Plankton metabolic balance at two north Atlantic seamounts. Deep-Sea Research Part II, in press

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods Themisto abyssorum and T. libellula. Polar Biol 25:374–383

Bashmachnikov I, Mohn C, Pelegrí JL, Martins A, Jose F, Machín F, White M (2009) Interaction of Mediterranean water eddies with Sedlo and Seine Seamounts, Subtropical Northeast Atlantic. Deep-Sea Research II, in press

Beckmann A, Mohn C (2002) The upper ocean circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. Ocean Dynamics, 52: 194-204

Bergé, J-P, Barnathan G (2005) Fatty acids from lipids of marine organisms: molecular biodiversity, roles as biomarkers, biologically active compounds, and economical aspects. Adv Biochem Eng Biotechnol. 96:49-125.

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology, 37, 911–917

Boehlert, GW., Genin A (1987) A review of the effects of seamounts on biological processes. In: B. H. Keating, P. Fryer, R. Batiza, G. W. Boehlert (Eds.), Seamounts, Islands and Atolls. Geophysical monograph, vol 43, American Geophysical Union.

Broglio E, Saiz E, Calbet A (2004) Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). Aquat. Microb. Ecol., 35, 65-78

Bühring SI, Christiansen B (2001) Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone? Progress in Oceanography 50, 369-382

Checkley DM, Entzeroth LC (1985) Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. J. Plank. Res. 7: 553-568

Checkley DM Jr., Miller CA (1989) Nitrogen isotope fractionation by oceanic zooplankton, Deep Sea Res., 36: 1449– 1456

Cloern JE, Canuel EA, Harris D (2002) Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnology and Oceanography, 47: 713–729

Christiansen B and Wolff GA (2009) The oceanography, biogeochemistry and ecology of two NE Atlantic seamounts: The OASIS project. Deep-Sea Research II, in press

Christie WW (1982) Esterification of Fatty-Acids in Adipose-Tissue. J. Science Food Agriculture. 33: 809-809

Cushing, DH (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J. Plankton Res., 11: 1–13

Dalerum F, Angerbjörn A (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. Oecologia, 144: 647-658

Dalsgaard, J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225-340

Dam HG, Miller CA, Jonasdottir SH (1993) The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic bloom experiment. Deep-Sea Research Part II 40: 197–212

Davenport SR, Bax NJ (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Sciences, 59: 514-530

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta, 42: 495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta, 45: 341–351

Dower JF, Freeland H, Juniper K (1992) A strong biological response to oceanic flow past Cobb Seamount. Deep-Sea Research, 39: 1139–1145

Dower JF, Mackas DL (1996) ‘‘Seamount effects’’ in the zooplankton community near Cobb Seamount. Deep-Sea Research I, 43: 837– 858

Epp D, Smoot NC (1989) Distribution of seamounts in the North Atlantic. Nature, 337: 254-257

Fedosova RA (1974) Distribution of some copepod species in the vicinity of the underwater Hawaiian Ridge. Oceanology 14: 724-727

Fessenden L, Cowles TJ (1994) Copepod predation on phagotrophic ciliates in Oregon coastal waters. Mar Ecol Prog Ser 107:103–111.

Fraser AJ, Sargent JR, Gamble JC, Seaton DD (1989) Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. Marine Chemistry, 27: 1-18

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry, 226: 497-509

Froneman PW, Pakhomov EA, Perissinotto R, Meaton V (1998) Feeding and predation impact of two chaetognath species, Eukrohnia hamata and Sagitta gazellae, in the vicinity of Marion Island (southern ocean). Marine Biology 131: 95-101

Fry B, Arnold C (1982) Rapid $^{13}C/^{12}C$ turnover during growth of brown shrimp (*Penaeus aztecus*). Oecologia, 54: 200–204

Fry B, and Sherr E (1984) $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27:15-47

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography, 33: 1182–1190

Genin A, Boehlert GW (1985) Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 43: 907– 924

Genin A, Dayton PK, Lonsdale PF, Spiess FN (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322:59–61

Genin A. (2004) Biophysical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems, 50: 2-20

González N, Anadón R, Mouriño B, Fernandez E, Sinha B, Escánez J, Armas DD (2001) The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: The role of mesoscale instabilities. Limnology and Oceanography, 46: 946-952

Gowing MM, Wishner KF (1992) Feeding ecology of benthopelagic zooplankton on an eastern tropical Pacific seamount. Marine Biology, 112: 451–468

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53–61

Hagen W (2000) Lipids. In: R. Harris, P. Wiebe, J. Lenz, H.R. Skjoldal, M. Huntley (Eds). ICES Zooplankton Methodology Manual. Academic Press, San Diego: 113-119

Harvey HR, Eglinton G, O'Hara, Scan CM, Corner E (1987) Biotransformation and assimilation of dietary lipids by Calanus feeding on a dinoflagellate. Geochim. Cosmochim. Acta, 51: 3031-3040

Harding GCH (1974) The food of deep-sea copepods. J. Mar. Biol. Assoc. UK 54:141-155

Harris RP (1982) Comparison of the feeding behaviour of *Calanus* and *Pseudocalanus* in two experimentally manipulated enclosed systems. Journal of the Marine Biological Association of the United Kingdom, 62: 71–91

Head RN, Medina G, Huskin I, Anadón R, Harris RP (2002) Phytoplankton and mesozooplankton distribution and composition during transects of the Azores Subtropical Front. Deep-Sea Research II, 49: 4023–4034

Hesslein RH, Hallard KA, Ramlal P (1993) Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}C$, $\delta^{13}C$, and $\delta^{15}N$. Canadian Journal of Fisheries and Aquatic Sciences, 50: 2071–2076

Hopkins TL, Sutton TT (1998) Midwater fishes and shrimps as competitors in low latitude oligotrophic ecosystems. Marine Ecology Progress Series 164: 37-45

Huskin I, Viesca L, Anadón R (2004) Particle flux in the Subtropical Atlantic near the Azores: influence of mesozooplankton. Journal of Plankton Research, 26: 403–415

Isaacs JD, Schwartzlose RA (1965) Migrant sound scatterers: interaction with the seafloor. Science, 150: 1810–1813

Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. Marine Ecology Progress Series, 287: 251–253

Kattner G, Fricke HSG (1986) Simple gas-liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. Journal of Chromatography, 361: 263-268

Kattner G, Alber C, Graeve M, Schnack-Schiel SB (2003) Fatty acid and alcohol composition of the small polar copepods, Oithona and Oncaea : indication on feeding modes. Polar Biol 26: 666–671

Kinsey ST, Hopkins TL (1994) Trophic strategies of euphausiids in a low-latitude ecosystem. Marine Biology. 118:651-661.

Kiriakoulakis K, White M, Bett BJ, Wolff GA (2004) Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. Deep-Sea Research I, 51:1937-1954

Kiriakoulakis K, Vilas JC, Blackbird SJ, Arístegui J, Wolff GA (2009) Seamounts and organic matter—is there an effect? The case of Sedlo and Seine Seamounts. Part II. Composition of suspended particulate organic matter. Deep-Sea Research II, in press

Kirsch PE, Iverson SJ, Bowen WD, Kerr SR, Ackman RG (1998) Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 55: 1378–1386

Kleppel GS, Frazel D, Pieper RE, Holliday DV (1988) Natural diets of zooplankton off southern California. Mar. Ecol. Prog. Ser. 49: 231-241

Koppelmann R, Böttger-Schnack R, Möbius J, Weikert H (2009) Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. Journal of Plankton Research, 31: 669-686

Koslow JA (1997) Seamounts and the ecology of deep-sea fisheries. American Scientist, 85: 168– 176

Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar Ecol Prog Ser 213:111–125

Lampitt RS, Gamble JC (1982) Diet and respiration of the small planktonic marine copepod *Oithona nana*. Marine Biology, 66: 185–190

Lampitt RS, Wishner KF, Turley CM, Angel MV (1993) Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Mar Biol 116:689–702

Longhurst AR, Williams R (1979) Materials for plankton modelling: Vertical distribution of Atlantic zooplankton in summer. J. Plankton Res. 1: 1-28

Longhurst A. (1995) Seasonal cycles of pelagic production and consumption. Progress in Oceanography: 36, 77–167

Longhurst A. (1998) Ecological Geography of the Sea. Academic Press, San Diego: 398 pp.

MacAvoy SE, Macko SA, Garman GC (2001) Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. Canadian Journal of Fisheries and Aquatic Sciences, 58: 923–932

Martin B, Christiansen B (2009) Distribution of zooplankton biomass at three seamounts in the NE Atlantic. Deep-Sea Research II, (in press).

Marty JC, Nicolas E, Miquel JC, Fowler SW (1994) Particulate fluxes of organic compounds and their relationship to zooplankton fecal pellets in the northwestern Mediterranean Sea. Marine Chemistry 46: 387-405

Matsueda H, Handa N (1986) Vertical flux of hydrocarbons as measured in sediment traps in the eastern North Pacific Ocean. Mar. Chem., 20: 179-195

Mauchline J (1998) The Biology of Calanoid Copepods. Adv. Mar. Biol., 33, 710 pp.

Mayzaud P, Chanut J-P, Ackman RG (1989) Seasonal changes of the biochemical composition of marine particulate matter with special reference to fatty acid and sterols. Mar. Ecol. Prog. Ser. 56: 189-204

Mayzaud P, Virtue P, Albessard E (1999) Seasonal variations in the lipid and fatty acid composition of the euphausiid *Meganyctiphanes norvegica* from the Ligurian Sea. Mar Ecol Prog Ser 186:199–210

Michener RM, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: R.H. Michener, K. Lajtha (Eds). Stable isotopes in ecology and environmental science. Blackwell, Oxford:138–157

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta, 48: 1135–1140

Mohn C, White M,Bashmachnikov IL, Jose F, Pelegrí J-L (2009) Dynamics at an elongated, intermediate depth seamount in the North Atlantic (Sedlo Seamount, 40°12´00 N, 26°14´00 W). Deep-Sea Research II, in press

Montoya JP, Carpenter EJ, Capone DG (2002) Nitrogen-fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol. Oceanogr., 47:1617–1628.

Montoya JP, Holl CM, Zehr JP, Hansen A, Villareal TA, Capone DG (2004) High rates of N2-fixation by unicellular diazotrophs in the oligotrophic Pacific, Nature, 430, 1027–1031

Mouriño B, Fernandez E, Serret P, Harbour D, Sinha B, Pingree R (2001) Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). Oceanologica acta, 24 (2): 1-20

Mullineaux LS, Mills SW (1997) A test of the larval retention hypothesis in seamount-generated flows. Deep-Sea Res I 44:745–770

Najdek M, Puskaric S, Bochdansky AB (1994) Contribution of zooplankton lipids to the flux of the organic matter in the northern Adriatic Sea. Marine Ecology Progress Series, 111: 241–249

Neuer S, Cianca A, Helmke P, Freudenthal T, Davenport R, Meggers H, Michaela, Knoll M, Santana-Casiano JM, González-Davila M, Rueda M-J, Llinás O (2007) Biogeochemistry and hydrography in the eastern subtropical North Atlantic gyre. Results from the European time-series station ESTOC. Progress in Oceanography, 72: 1–29

Ohtsuka S, Böttger-Schnack R, Okada M, Onbé T (1996) In situ feeding habits of Oncaea (Copepoda: Poecilostomatoida) from the upper 250 m of the central Red Sea, with special reference to consumption of appendicularian houses. Bull Plankton Soc Jpn 43:89–105

Ohtsuka S, Soh HY, Nishida S (1997) Evolutionary switching from suspension feeding to carnivory in the calanoid family Heterorhabdidae (Copepoda). Journal of Crustacean Biology, 17 (4): 577-595

O'Reilly CM, Hecky RE, Cohen AS, Plisnier P-D (2002) Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. Limnol. Oceanogr. 47: 306-309

Øresland V (1990) Feeding and predation impact of the chaetognath Eukrohnia hamata in the Gerlache Strait, Antarctic Peninsula. Mar Ecol Prog Ser 63: 201-209

Owens NJP (1987) Natural variations in 15N in the marine environment. In Advances in Marine Biology, 24: 389–451. Academic Press, New York

Parin NV, Mironov AN, Nesis KN (1997) Biology of the Nazca and Sala-y-Gómez submarine ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific ocean: composition and distribution of the fauna, its community and history. Advances in Marine Biology, 32,145-242

Pearre S (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences.Biol. Rev. 78:1-79

Perga ME, Gerdeaux D (2005) ‘Are fish what they eat‘ all year round? Oecologia, 144: 598-606

Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin) - evidence from lipid composition. Marine Biology, 149: 1417-1429

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics, 18: 239-320

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, 83: 703–718

Prahl FG, Eglinton G, Corner EDS, O'Hara SCM, Forsberg TSV (1984) Changes in plant lipids during passage through the gut of *Calanus*. J. Mar. Biol. Assoc. UK,64: 317-334

Rau GH, Hopkins TL, Torres JJ (1991) ^{15}N:^{14}N and ^{13}C:^{12}C in Weddell Sea invertebrates: implications for feeding diversity. Marine Ecology Progress Series, 77: 1–6

Reemtsma T, Haake B, Ittekkot V, Nair RR, Brockmann UH (1990) Downward flux of particulate fatty acids in the central Arabian Sea. Marine Chemistry, 29: 183–202

Rice AL, Billett DSM, Fry J, John AWG, Lampitt RS, Mantoura RFC, Morris RJ (1986) Seasonal deposition of phytodetritus to the deep-sea floor. Proceedings of the Royal Society of Edinburgh, 88: 265–279

Richer de Forges B, Koslow JA, Poore GCB (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405:944–947

Roden GI (1987) Effects of seamounts and seamount chains on ocean circulation and thermohaline structure. In: B.H. Kaeting, P. Fryer, R. Batisa, G.W. Boehlert (Eds). Seamounts, Islands, and Atolls. Geophysical Monograph Series, 43, AGU, Washington D.C.: 335-354

Rogers AD (1994) The Biology of Seamounts. Advances in Marine Biology, 30: 305–349

Sargent JR, Whittle KJ (1981) Lipids and hydrocarbons in the marine food web. London: Academic Press.

Sargent JR, Henderson RJ (1995) Marine (n-3) polyunsaturated fatty acids. In: R.J. Hamilton (Ed). Developments in oils and fats. Blackie Academic and Professional, London: 32-65

Schmidt K, Atkinson A, Petzke K-J, Voss M, Pond DW (2006). Protozoans as a food source for Antarctic krill, *Euphausia superba* - complementary insights from stomach content, fatty acids and stable isotopes. Limnology and Oceanography 51(5): 2409-2427.

Schnetzer A, Steinberg DK (2002) Natural Diets of Vertically Migrating Zooplankton in the Sargasso Sea. Mar Biol, 141(1):89-99

Sieracki ME, Verity PG, Stoecker DK (1993) Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic Spring Bloom. Deep-Sea Research II, 40: 213–225

Silver MW, Bruland KW (1981) Differential feeding and fecal pellet composition of salps and pteropods, and the possible origin of the deep-water flora and olive-green "cells". Mar. Biol. 62:263 273

Skjoldal HR, Wassmann P (1986) Sedimentation of particulate organic matter and silicium during spring and summer in Lindaspollene, West Norway. Mar Ecol Prog Ser 30:49–63

Smith DK, Jordan TH (1988) Seamount statistics in the Pacific Ocean. Journal of Geophysical Research, 93: 2899-2919.

St. John MA, Lund T (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea Cod. Marine Ecology Progress Series, 131, 75-85

Sullivan BK (1980) *In situ* feeding behaviour of *Sagitta elegans* and *Eukrohnia hamata* (Chaetognatha) in relation to the vertical distribution and abundance of prey at ocean station "P". Limnol Oceanogr 25: 317±326

Tanoue E, Hara S (1986) Ecological implications of fecal pellets produced by the Antarctic krill *Euphausia superba* in the Antarctic Ocean. Mar. Biol. 91: 359-369

Teira E, Mouriño B, Marañón E, Péreza V, Pazó MJ, Serreta P, Armas D de, Escánez J, Malcolm E, Woodward S, Fernández E (2005) Variability of chlorophyll and primary production in the Eastern North Atlantic Subtropical Gyre: potential factors affecting phytoplankton activity. Deep-Sea Research I, 52: 569–588

Terazaki M, Marumo R, Fujita Y (1977) Pigments of Meso- and Bathypelagic Chaetognaths. Marine Biology 41: 119-125

Tönnesson K, Tiselius P (2005) Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. Marine Ecology Progress Series 289: 177-190

Tseitlin VB (1985) The energetics of fish populations inhabiting seamounts. *Oceanology,* 25, 237–239

Uda M, Ishino M (1958) Enrichment pattern resulting from eddy systems in relation to fishing grounds. Journal of the Tokyo University of Fisheries, 44: 105-129

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography, 46: 2061–2066

Vilas JC, Arístegui J, Kiriakoulakis K, Wolff GA, Espino M, Polo I, Montero MF, Mendonça A (2009) Seamounts and organic matter – is there an effect? The case of Sedlo and Seine Seamounts; Part 1. Distributions of dissolved and particulate organic matter. Deep-Sea Research Part II, in press

Voss M, Altabet M, Bodungen B v (1996) Stable nitrogen isotopes in sediment trap material as indicator of pelagic zone processes. Deep-Sea Research 43: 33-47

Wada E, Terazaki M, Kobaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on biogeochemical structure of the food web. Deep-Sea Research, 34: 829–841

Wakeham SG, Lee C, Farrington JW, Gagosian RB (1984) Biogeochemistry of particulate organic matter in the oceans: results from sediment trap experiments. Deep-Sea Research, 31: 509–528

Wakeham SG (1995) Lipid biomarkers for heterotrophic alteration of suspended particulate organic matter in oxygenated and anoxic water columns of the ocean. Deep Sea Research Part I: Oceanographic Research Papers, vol. 42, issue 10: 1749-1771

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology, 87: 313-323

Wu C-H, Hwang J-S, Yang J-S (2004) Diets of Three Copepods (Poecilostomatoida) in the Southern Taiwan Strait. Zoological Studies 43(2): 388-392

FEEDING ECOLOGY AND FOOD SOURCES OF SELECTED EPIBENTHIC INVERTEBRATES ON THE SUMMIT PLATEAU OF SEINE SEAMOUNT

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ABSTRACT

Stable isotopes and fatty-acid biomarkers were used to investigate the diets of selected epibenthic invertebrates sampled at 170 m on the summit plateau of Seine Seamount (34°N, 14°W) located in the NE Atlantic. Feeding types represented by the sampled species included suspension feeders, suspension/surface deposit feeders, predators /scavengers and omnivores. $\delta^{15}N$ of the investigated species ranged from 6.17 ‰ for the echinoid *Centrostephanus longispinus* to 12.33 ‰ for the triton *Charonia lampas*. The majority of the epibenthic species occupied intermediate trophic level positions between the 2nd and 3rd trophic level irrespective of feeding type and body size, indicative for a food web dominated by species with opportunistic and omnivorous feeding behaviour. $\delta^{13}C$ values ranged from -19.79 ‰ for a poriferan species to -15.08 ‰ for the asteroid *Luidia ciliaris* and the large range suggested feeding on a variety of differently enriched food sources. High proportions of the phytoplankton marker fatty acids 20:5(n-3) and 22:6(n-3) in the storage lipids of the epibenthic invertebrates and a $\delta^{15}N$ trophic level-enrichment in the range of surface particulate organic matter indicated a close link between the surface phytoplankton production and the benthic food web and rapid deposition of relatively fresh phytodetritus. Suspension feeders and suspension/surface deposit feeders showed the closest link to the pelagic food source as indicated by least enriched stable isotope ratios and by the abundance of phytoplankton marker fatty acids as well as the carnivory marker 18:1(n-9), which was abundant in the total lipids of pelagic heterotrophs. Transfer of essential nutrients from phytoplankton to higher trophic level species via benthic primary consumers was indicated by higher proportions of 20:4(n-6) compared to those species feeding directly from the pelagic food source. Elevated proportions of arachidonic acid 20:4(n-6) in the storage lipids of all epibenthic species compared to trace or low amounts

detected in the total lipids of pelagic organisms suggested a benthic association or origin of this essential fatty acid. Rhodophyta were suggested as possible origin as they are characterised by a high content of arachidonic acid and as some living specimen of coralline algae were recovered from benthic samples. Enriched $\delta^{13}C$ values observed in some epibenthic invertebrates might originate from dietary input of ^{13}C-enriched Rhodophyta. Contribution of Rhodophyta to the organic carbon pool of the benthic community was assumed to be of low quantity, but might be of some qualitative importance as additional source of essential fatty acids.

1. INTRODUCTION

Seamounts have often been described as biologically productive habitats, with dense aggregations of fishes and species-rich benthic communities dominated by long-lived suspension feeders (Genin *et al.* 1986, Rogers 1994, Koslow 1997, Richer de Forges *et al.* 2000, Koslow *et al.* 2001). High levels of endemism have been reported in benthic seamount fauna ranging from 15 % (Wilson and Kaufmann 1987) to potentially up to 34 % for individual seamounts (Richer de Forges *et al.* 2000). Factors influencing the distribution, diversity, and abundance of benthic organisms on seamounts are numerous, including substrate type, summit depth and seamount topography, local hydrographic conditions and geographic location (Genin *et al.* 1986, Boehlert and Genin 1987, Wilson and Kaufmann 1987, Genin *et al.* 1988, Rogers 1994, Mullineaux and Mills 1997, Richer de Forges *et al.* 2000, Beckmann and Mohn 2002). Due to enhanced bottom flows over abrupt topographies causing increased fluxes of suspended organic material (Mohn and Beckmann 2002a,b), benthic seamount communities on hard substrata were typically dominated by corals and other suspension feeders (Genin *et al.* 1986, Wilson and Kaufmann 1987, Rogers 1994). On soft substrata, in contrast, they were reported to consist mainly of mobile, deposit-feeding holothurians and echinoids (Lundsten *et al.* 2009) while infaunal organisms were dominated by polychaetes (Rogers 1994). Infaunal densities appeared to decrease with increasing current strength (Rogers 1994). Deposit feeders were also typical of most of the deep-sea benthos communities (Billett *et al.* 2001, Ginger *et al.* 2001, Wigham *et al.* 2003) and close links with food pulses of surface-derived phytoplankton detritus have been reported for detritivorous echinoderms, including holothurians (Ginger *et al.* 2001, Hudson *et al.* 2004), asteroids (Howell *et al.* 2004), and

echinoids (Féral *et al.* 1990). The complex food web structures on seamounts and their nutritional links to pelagic food supplies as well as the feeding ecology of most seamount species are still poorly understood (e.g. Dower and Perry 2001, Koslow *et al.* 2001, Genin 2004, McClain 2007).

Biochemical markers, such as stable isotopes and fatty acids, have been used extensively in studies of trophic ecology, including marine systems (e.g. Iken *et al.* 2001, 2005, Dalsgaard *et al.* 2003 and references therein). In contrast to gut content analysis, which provides information on recent food ingested by the consumer, biochemical markers provide an analysis of assimilated diet integrated over time (e.g., Davenport and Bax 2002, Dalsgaard *et al.* 2003). Isotopic signatures, i.e. the ratio of the rare heavier isotope to the common lighter isotope, change from prey to predator due to chemical reactions during metabolic processes (Peterson and Fry 1987). This change, termed trophic fractionation, occurs in a predictable way for the different elements and can be used to evaluate carbon sources and trophic position of an organism (e.g. Peterson and Fry 1987, Vander Zanden and Rasmussen 2001, Post 2002). The use of fatty acids biomarkers to trace predator-prey relationships in the ocean is based on the observation that particular fatty acids can only be biosynthesised by certain phytoplankton and macroalgal species and that these fatty acid patterns are transferred conservatively from primary producers to their consumers and among consumers (Dalsgaard *et al.* 2003 and references therein). In contrast to the conservative fatty acid composition of structural lipids (mainly phospholipids) of consumers, which are relatively independent of dietary input, the fatty acid profiles of neutral lipids, which are used for energy storage, are much more variable and more readily influenced by dietary input (Sargent and Henderson 1995). In this study, the fatty acid signature of the neutral lipid fraction was used to investigate the diets of the epibenthic invertebrates studied.

The aim of this study is to elucidate the food sources of selected seamount epibenthic invertebrate species as well as trophic interactions in the benthic food web and nutritional links to the pelagic food web using a stable isotope and fatty acid biomarker approach.

Specific objectives were:

1. to elucidate dietary sources of the epibenthic invertebrates sampled on the summit plateau of Seine Seamount,
2. to identify nutritional links of epibenthic consumers to the primary food source, which was hypothesised to be phytoplankton-derived detritus, and
3. to investigate trophic structure and nutritional pathways of essential nutrients within the benthic food web.

2. MATERIALS AND METHODS

This investigation was part of an interdisciplinary study on North Atlantic seamounts within the framework of the European Project OASIS (OceAnic Seamounts: an Integrated Study) (Christiansen and Wolff 2009). Seine Seamount is located northeast of Madeira (33°50'N - 14°20'W) and is a single summit, cone-shaped seamount which rises from more than 4000 m depth to a summit plateau at ~170 m. (Fig. 1). It is situated within the oligotrophic biogeochemical eastern North Atlantic Subtropical Gyre (NASE) province (Longhurst *et al.* 1995, 1998). Video observation on the summit plateau of Seine Seamount revealed rippled coarse sand-like sediment containing little fine material, indicative of strong bottom current flows, with few outcropping rock. Abundance of megabenthos was generally low and consisted of localised aggregations of polychaetes, sea urchins, and gastropods. On the summit edge, on the other hand, highly localised aggregations of sessile megabenthos were observed along rock edges and ridges (Christiansen, unpublished data).

Sampling. Epibenthic macrofauna was sampled on the summit plateau of Seine Seamount at a water depth of 170-190 m during three field surveys in December 2003 (11 November – 6 December 2003; FS *Meteor*, M60/1), March 2004 (25 March – 8 April; FS *Poseidon*, P309) and May 2005 (14 May – 1 June; FS *Poseidon*, P322) (Fig. 1, Tab. 1). Animals were collected using an epibenthic sledge (December 2003), an ottertrawl (March 2004) and a beamtrawl (May 2005) (see Christiansen *et al.* 2009 for details). For stable isotope and lipid analysis, either whole specimens (polychaetes, ophiuroids) or dissected tissue samples (asteroid arm sections, echinoid gonads, gorgonian stem sections, poriferan tissue)

were taken directly upon recovery of the trawls and stored at -20°C for stable isotope analysis and at -80°C or in liquid nitrogen for lipid analysis.

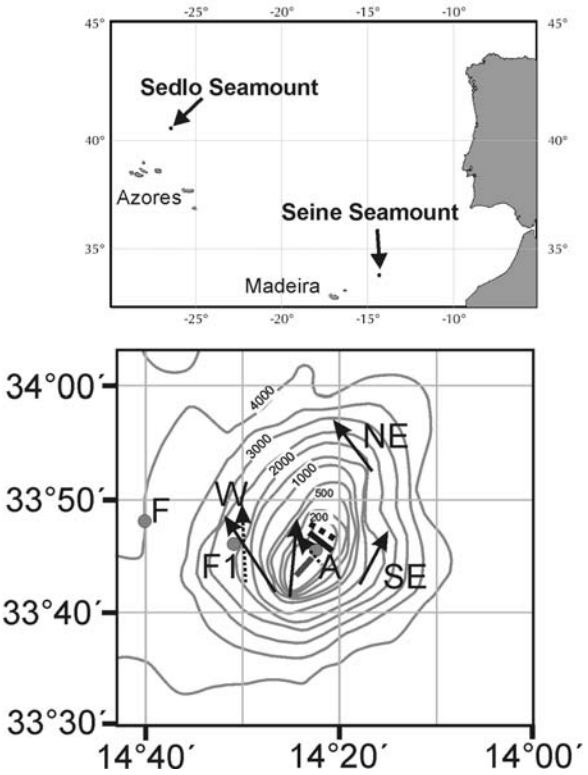


Figure 1.

Location and bathymetry of Seine Seamount. Sampling locations of benthos trawls on the summit plateau of Seine Seamount (Tab. 1) are indicated for December 2003 (broken line), March 2004 (solid line) and May 2005 (solid grey line). POM_{susp} water sample locations (filled circles) are indicated as A for summit, F1 and F for the west slope. MOCNESS zooplankton hauls are given for December 2003 (broken line arrow) and March 2004 (solid line arrow). MOCNESS haul locations are indicated as A for the summit, NE (northeast), SE (southeast), and W (west) for the slope locations.

Samples for suspended particulate organic matter (POM_{susp}), zooplankton and benthopelagic fish were collected at locations above the summit and slopes of Seine Seamount in December 2003 and March 2004 (Fig. 1, Tab. 1). Water samples for stable isotope and lipid analyses of POM_{susp} were collected at 50 m depth using Niskin bottles mounted on a CTD rosette. Prior to filtration, the sampled water was passed through a 300 µm mesh sieve to remove larger zooplankton organisms which would bias the POM_{susp} data. Water for stable isotope (10-20 l per filter) and for lipid (20 l per filter) samples were vacuum filtered immediately on board at low pressure on pre-combusted (450°C; 5 h) GF/C filters (Whatman®; 55 mm diameter; nominal pore size 1.2 µm). All filter samples were wrapped in muffled (450ºC; 5 h) aluminium foil and immediately frozen at -20ºC (stable isotope samples) and -80ºC or in liquid nitrogen (lipid samples) until further analysis.

Zooplankton, micronekton and mesopelagic fishes were sampled using a 1 m^2-Double-MOCNESS (Multiple Open/Closing Net and Environmental Sensing System, Wiebe *et al.* 1985) with a 1 m^2-opening and equipped with 20 dark coloured nets (10 nets at each side)

of 0.333 µm mesh size. In December 2003, a 10 m^2-MOCNESS with a 10 m^2-opening equipped with 6 nets of 1.6 mm mesh size was also used. The nets were sequentially opened and closed at defined depths and depth was controlled by a temperature corrected pressure sensor. Zooplankton samples were taken with stratified oblique hauls starting at the greatest sampling depth and progressing up towards the surface at a ships speed of 2 knots. Sampling depths above the slopes of the seamount covered the upper 600 m to include diel vertically migrating species at their depth range during day hauls. Directly upon recovery of the MOCNESS, specimen for stable isotope and lipid analyses were sorted on board in a temperature controlled laboratory at 4°C or at ambient temperature conditions on ice using a dissecting microscope. Depending on species size, each sample consisted of 1 to 200 individuals. Benthopelagic fishes were taken from the same trawls used for collection of the epibenthic invertebrates and dorsal muscle tissue was dissected for stable isotope and lipid analyses. Stable isotope samples were stored at -20°C and lipid samples at -80°C or in liquid nitrogen until further analyses.

Table 1. Sampling data for epibenthos and benthopelagic fish trawls, MOCNESS zooplankton hauls and CTD-Rosette water sampling for POM_{susp} during 3 surveys in December 2003, March 2004 and May 2005.
Gear labels are as follows: EBS = Epibenthic sledge, OT = Ottertrawl, BT = Beamtrawl, ROS = CTD-Rosette with Niskin bottles, MOC and 10MOC = MOCNESS plankton net, 1 m² and 10 m² opening, respectively.

Gear-Haul	Date	Sampling time (UTC)	Location	Sampling depth (m)	Water depth (m)	Latitude N	Longitude W
Meteor 60/1, December 2003							
EBS-2	04.12.2003	17:33 - 18:30	Summit-A	176-193	176-193	33°45.9	14°21.7
ROS-748	03.12.2003	08:38 - 08:46	Summit-A	50	178	33°46.0	14°22.0
MOC-11	03.12.2003	16:00 - 17:21	Summit-A	50 - 100	190	33°44.7	14°20.9
10MOC-3	03.12.2003	10:09 - 12:33	W slope	300 - 600	1195	33°42.1	14°30.1
Poseidon 309, March 2004							
OT-1	31.03.2004	14:48 - 15:11	Summit-A	166-172	166-172	33°43.2	14°25.1
ROS-18-4	29.03.2004	21:37 - 21:43	Summit-A	50	171	33°46.0	14°21.8
ROS-22-1	30.03.2004	21:20 - 21:32	Wslope-F	50	4008	33°48.0	14°40.1
ROS-28-1	01.04.2004	14:13 - 14:20	Wslope-F1	50	2479	33°46.0	14°30.9
MOC-02	29.03.2004	13:34 - 16:48	Summit-A	50 - 150	174	33°41.4	14°25.5
MOC-03	29.03.2004	23:57 - 02:05	Summit-A	50 - 163	168	33°41.1	14°26.0
MOC-04	01.04.2004	10:36 - 13:20	W slope	200 - 600	1188	33°42.4	14°27.7
MOC-05	01.04.2004	21:04 - 23:16	W slope	50 - 600	1173	33°42.1	14°27.5
MOC-07	03.04.2004	21:25 - 23:54	NE slope	50 - 300	1547	33°51.8	14°16.9
MOC-08	04.04.2004	12:42 - 14:51	NE slope	50 - 600	1595	33°52.0	14°16.9
MOC-09	05.04.2004	22:40 - 00:15	SE slope	50 - 600	1360	33°43.0	14°18.6
MOC-10	06.04.2004	09:57 - 11:09	SE slope	50 - 600	1478	33°43.9	14°17.5
Poseidon 322, May 2005							
BT-2	18.5.2005	11:10 - 12:00	Summit	169-170	169-170	33°43.4	14°24.8

Stable isotope analysis. For analysis of $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures, frozen samples of the epibenthic species as well as POM_{susp}, zooplankton, micronekton, mesopelagic and benthopelagic fish were lyophilised for at least 48 h at -60°C. Isotopic analyses of the POM_{susp} filter samples were performed simultaneously for carbon and nitrogen stable isotopes by elemental analyser/continuous flow isotope ratio mass spectrometry (Thermo-Finnigan Delta$^+$ Advantage Mass Spectrometer / Costech EAS Elemental Analyser) at UCSB/MSI Analytical Laboratory. The analytical error of this method is ≤0.25 ‰ for $\delta^{13}C$ and $\delta^{15}N$.

$\delta^{13}C$ of an organism or tissue is biased by the lipid content as lipids are depleted in ^{13}C compared with proteins and carbohydrates (Peterson and Fry 1987, Wada *et al.* 1987). Lipids of lyophilsed whole organism or tissue samples of epibenthic invertebrates, mesopelagic and benthopelagic fishes were, thus, removed using Soxhlet extraction with a dichloromethane:methanol mixture (DCM:MeOH 2:1, v:v) for 4 - 6 hours (Bligh and Dyer 1959). Afterwards the samples were lyophilised again (48 h) and ground to a homogenous powder using pestle and mortar. Lipids were not removed from zooplankton and micronekton samples to avoid loss of biomass of the often very small sample quantities. Instead, taking C:N as a proxy for lipid content, lipid normalised values of $\delta^{13}C$ were calculated according to equations in Post *et al.* (2007) ($\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$ (Eq. 3)). Since inorganic carbonates tend to be less negative in $\delta^{13}C$ than other body fractions, which would introduce a positive bias in $\delta^{13}C$ measurements, (DeNiro and Epstein 1978, Fry 1988, Rau *et al.* 1991, Cloern *et al.* 2002), carbonates were removed from calcareous epibenthic (asteroids, ophiuroids, gorgonians, porifera) and zooplankton (ostracods, pteropods) samples by adding 1 mol l^{-1} hydrochloric acid (HCl) drop-by-drop to each powdered sample until CO_2 release stopped. To minimise loss of dissolved organic matter, the samples were not rinsed with de-ionised water after the treatment (Jacob *et al.* 2005). The samples were dried at 60°C and ground to homogenous powder again. Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) and C:N analyses of the pulverised animal samples were performed simultaneously with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyser via a THERMO/Finnigan Conflo II- interface at the GeoBio-Center^{LMU} in Munich, Germany. Standard deviation for repeated measurements of lab standard material (peptone) were <0.15 ‰ for nitrogen and carbon. Standard deviations of concentration measurements of

replicates of laboratory standard were <3 % of the concentration analysed. Standards used for nitrogen and carbon stable isotope determination were atmospheric N_2 and Peedee Belemnite (PDB), respectively.

Stable isotope values were expressed in δ-notations as parts per thousand (‰), where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively:

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

The ratio of carbon isotopes ($\delta^{13}C$) changes little (< 1 ‰) between trophic levels and is used to evaluate the sources of carbon for an organism (DeNiro and Epstein 1978, DeNiro and Epstein 1981, Peterson and Fry 1987, Michener and Schell 1994). The ratio of nitrogen stable isotopes ($\delta^{15}N$), on the other hand, is typically enriched by 3-4 ‰ (average 3.4 ‰) relative to its diet and is used to estimate trophic position of a consumer (Minagawa and Wada 1984). In this study, a $\delta^{15}N$ trophic-enrichment factor of 3.4 ‰ per trophic level and mean $\delta^{15}N$ of POM_{susp} as the first trophic level of the pelagic foodweb were used for trophic level estimates.

Lipid analysis. Frozen animal samples and POM_{susp} filters were lyophilised for at least 48 h at -60°C prior to lipid extraction.

Lipids of animal samples were extracted with minor modifications as described by Hagen (2000) based on the method of Folch *et al.* (1957) and Bligh and Dyer (1959) using ultrasonic disruption in a dichloromethane (DCM):methanol (MeOH) (2:1/v:v) mixture and a washing procedure with aqueous KCl solution (0.88%). A known amount of internal standard (nonadecanoic acid) for quantification of fatty acids was added to the sample prior to extraction. For the epibenthic species, lipid classes of the total lipid extracts were separated by solid phase extraction according to the method of Peters *et al.* (2006) using 1 ml glass columns filled with 100 mg SiOH (CHROMABOND®, Macherey-Nagel) on a vacuum manifold. Prior to sample load, the columns were washed with a solvent sequence of acetone, diethylether, and hexane:diethylether-mixtures to remove residues. After column conditioning with 4 ml of hexane, a subsample of the total lipid extract dissolved in hexane was added. The neutral lipid fraction was eluted with 2.5 ml hexane:diethylether (95:5/v:v) and 2.5 ml hexane:diethylether (1:1/v:v). For fatty acid analyses, subsamples of the neutral lipid fractions of the epibenthic species and of the total lipids of zooplankton,

micronekton, mesopelagic and benthopelagic fishes were hydrolysed and fatty acids converted to their methyl ester derivatives (FAME) by adding 250 µl hexane and 1 ml of 3% concentrated sulphuric acid (H_2SO_4) in methanol to the dried extracts. The solution was left to react at 80°C for 4 h. After cooling, 4 ml of aqua bidest. were added, and FAMEs were extracted three times with 2 ml hexane (Kattner and Fricke, 1986). Samples were analysed using a gas chromatograph (Agilent 6890N) equipped with a DB-WAX column (30 m length × 0.32 mm inner diameter, 0.25 µm film thickness) operated with helium as carrier gas (constant flow 2.0 ml min^{-1}). The following oven temperature program was used: 40°C held for 5 min, 40-150°C at 10°C min^{-1}, 150°C held for 5min, 150-220°C at 2°C min^{-1}, 220°C held for 20 min. Samples were injected using a temperature programmed vaporizer injector (Gerstel® CIS3) in solvent vent mode (injection volume 5 µl, injection speed 10 µl s^{-1}, injection temperature -40°C (temperature programm: -40–40°C at 6°C s^{-1} after 0.51 min, 40°C held for 0.1 min, 40-250°C at 12°C s^{-1}, 250°C held for 2.0 min), vent flow 50 ml min^{-1}, vent pressure: 34 kPa, splitless time 0.5-1.5 min, purge flow: 50 ml min^{-1}, split flow: 20 ml min^{-1}). The FAMEs were detected by flame ionisation (FID, detector temperature: 250°C, hydrogen flow: 30 ml min^{-1}, air flow: 350 ml min^{-1}, makeup (N_2) flow: 30 ml min^{-1}) and identified by comparing retention times with those obtained from known standards (Supelco™ 37 Component FAME Mix, single FAME standards: nonadecanoic acid (C19:0), Octadecatetraenoic acid (C18:4n3)) and/or from the literature. Data was processed using Agilent GC ChemStation Software©. Total fatty acids were calculated as the sum of all identified fatty acid from the chromatogram.

Lipid extraction and analyses of the POM_{susp} filter samples were carried out with minor modifications according to Kiriakoulakis *et al.* (2004). The lyophilised filter samples were placed in glass extraction thimbles and a known amount of an internal standard (5α(H)-cholestane) was added. The filters were then extracted (24 h) in a soxhlet apparatus using a dichloromethane (DCM):methanol (MeOH) solvent mixture (2:1, v:v). The solvent extract was evaporated to dryness under vacuum and the residue taken up in a minimum volume of DCM and then passed through anhydrous sodium sulphate into a vial. The solvent was removed by evaporation under nitrogen and an aliquot of the total extract (50%; redissolved in DCM) was transferred to a 5 ml Reacti-Vial with a Teflon screw-cap, evaporated to dryness and transmethylated with 1.5 ml of 10 % methanolic acetyl chloride (10% of redistilled acetyl chloride added very slowly to chilled MeOH; 0°C). The solution

was left to react (40ºC; 12 h; Christie, 1982) in the dark. Subsequently, the sample was evaporated to dryness with a stream of N_2, redissolved in DCM and stored at -20°C prior to GC-MS analysis. GC-MS analyses were performed on the derivatised (*bis*-trimethylsilyltrifluoroacetamide; BSFTA, 1 % TMS; 30-50 μL; 40°C; 0.5 - 1 h), transmethylated extracts using a Trace 2000 Series gas chromatograph fitted with an on-column injector and a fused high-temperature silica column (60 m × 0.25 mm i.d.; 5 %; DB5-HT equivalent; J&W) with helium as the carrier gas (ca. 1.6 ml min^{-1}). A retention gap of deactivated fused silica (1 m × 0.32 mm i.d.) was used at the front of the column. The oven was programmed from 60°C to 170°C at 6°C min^{-1} after 1 minute, then up to 315°C at 2.5°C min^{-1} and held for 10 minutes. The GC column was fed directly into the EI source of a Thermoquest Finnigan TSQ7000 mass spectrometer (ionisation potential 70 eV; source temperature 215°C; trap current 300 μA), operated in Full Data Acquisition mode, (50 - 600 Thompsons cycled every s) and data was processed using Xcalibur software. Compounds were identified either by comparison of their mass spectra and relative retention indices with those available in the literature and/or by comparison with authentic standards. Quantitative data were calculated by comparison of peak area of the internal standard (5α(H)-cholestane spiked onto the filters before extraction) with those of the compounds of interest, using the total ion current chromatogram. The relative response factors of the analytes were determined individually for 36 representative compounds using authentic standards. For analytes without authentic standards, the response factors for similar compounds of the same class and/or similar structure were used. Total fatty acids were calculated as the sum of all identified fatty acid from the chromatogram.

Data analysis. Statistical analyses were performed using the software SPSS. Principal component analysis (PCA) was performed with arc *sine* square root transformed percentage data of relative fatty acid compositions on the correlation matrix, extracting non-rotated components with eigenvalues >1.

3. RESULTS

3.1 STABLE ISOTOPES OF EPIBENTHIC SPECIES AND POTENTIAL FOOD SOURCES

The epibenthic invertebrates studied grouped into 4 feeding types according to literature (Tab. 2). The poriferan and gorgonian species were grouped as suspension feeders, the ophiuroid species *Amphipholis squamata* as suspension/surface deposit feeder, the echinoids *Centrostephanus longispinus* and *Cidaris cidaris* as omnivores, the polychaete *Hyalinoecia tubicola*, the asteroid species *Astropecten irregularis* and *Luidia ciliaris*, the hermit crab *Dardanus arrosor* and the gastropod *Charonia lampas* as predators/scavengers.

Table 2. Mean stable isotope values (± SD) of benthic invertebrates. Feeding type abbreviations are according to literature and refer to suspension feeders (SF), suspension/surface-deposit-feeders (SF/SDF), omnivores (O), and predators/scavengers (P/S), tissue type = sampled tissue type, n = number of individuals sampled.

Species	Sampling period	Feeding type	Tissue type	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Porifera						
Porifera sp. 1	Mar 04	SF[A]	body tissue	1	-19.79	12.32
Porifera sp. 2	Mar 04	SF[A]	body tissue	1	-19.16	11.95
Porifera sp. 3	Mar 04	SF[A]	body tissue	1	-18.12	8.76
Porifera sp. 4	Mar 04	SF[A]	body tissue	1	-18.00	7.96
Cnidaria						
Anthozoa						
Gorgonacea sp.	Mar 04	SF[B]	stem sections	4	-19.35 (0.27)	6.77 (0.20)
Echinodermata						
Ophiuroidea						
Amphipholis squamata	Dec 03	SF/SDF[C]	complete	2	-19.65 (0.10)	7.07 (0.04)
Asteroidea						
Astropecten irregularis	Dec 03	P/S[D]	arm	3	-18.29 (0.50)	8.66 (0.69)
	Mar 04	P/S[D]	arm	1	-19.07	7.92
Luidia ciliaris	Dec 03	P/S[E]	arm	1	-15.08	9.19
	Mar 04	P/S[E]	arm	1	-16.17	8.15
Echinoidea						
Cidaris cidaris	Dec 03	O[F]	gonads	5	-18.54 (0.14)	8.35 (0.51)
Centrostephanus longispinus	Mar 04	O[G]	gonads	3	-17.54 (0.96)	6.79 (0.54)
Annelida						
Polychaeta						
Hyalinoecia tubicola	Dec 03	P/S[H]	complete	10	-18.84 (0.37)	8.16 (0.76)
	Mar 04	P/S[H]	complete	2	-19.48 (0.12)	7.09 (0.83)
Arthropoda						
Malacostraca						
Dardanus arrosor	May 05	P/S[I]	muscle pincer	1	-16.88	10.73
Mollusca						
Gastropoda						
Charonia lampas	May 05	P/S[J]	muscle foot	2	-16.10 (0.35)	12.03 (0.43)

Feeding type source data:
[A] Bergé and Barnathan 2005 and references therein
[B] Coma *et al.* 1994, Ribes *et al.* 1999, 2003, Orejas *et al.* 2003, Rossi *et al.* 2004, Tsounis *et al.* 2006
[C] Warner 1982 and references therein
[D] Christensen 1970, Franz and Worley 1982, Beddingfield and McClintock 1993, de Juan *et al.* 2007
[E] Brun 1972, Riedl 1983, Menge 1982
[F] De Ridder and Lawrence 1982 and references therein
[G] Pawson and Miller 1983
[H] Fauchald and Jumars 1979, Britton and Morton 1994
[I] Hazlett 1981
[J] Riedl 1983

Three species, *H. tubicola*, *A. irregularis* and *L. ciliaris*, were sampled during both surveys in December 2003 and March 2004. The small sample size available did not allow for statistical testing of temporal differences in $\delta^{13}C$ and $\delta^{15}N$ values of the 3 species, but as the observed differences were generally smaller than the species specific variability, stable isotope values of these species were pooled for the two surveys. Mean $\delta^{13}C$ values in March were lower by 0.64 ‰ for *H. tubicola*, 0.78 ‰ for *A. irregularis* and 1.09 ‰ for *L. ciliaris* compared to December. Mean $\delta^{15}N$ values in March were lower by 1.07 ‰ for *H. tubicola*, 0.74 ‰ for *A. irregularis* and 1.04 ‰ for *L. ciliaris* compared to December 2003.

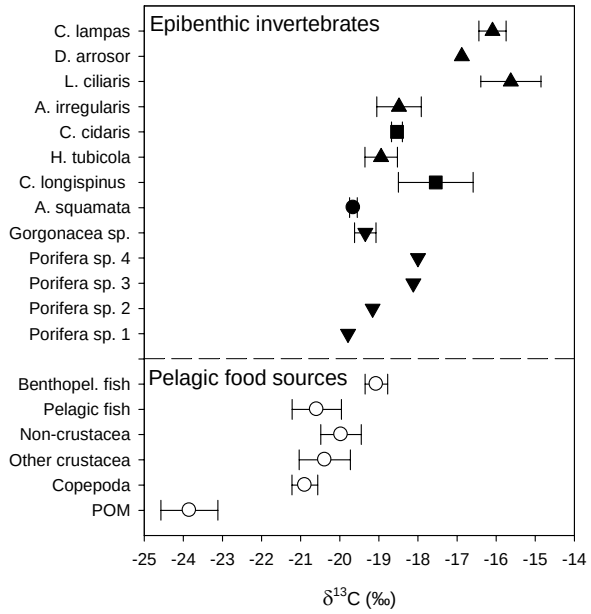


Figure 2.

Mean $\delta^{13}C$ stable isotope values (± SD) of epibenthic invertebrates and potential pelagic and benthopelagic food sources from the 3 surveys of Seine Seamount. Symbols for the epibenthic invertebrates refer to feeding types as given in Tab. 2
▼ = suspension feeders;
● = suspension/surface deposit feeders;
■ = omnivores;
▲ = predators/scavengers.
Mean values of food sources (○) are calculated from mean species values.

Taxonomic labels for food sources: (n = number of samples):
"POM": suspended particulate organic matter n = 12;
"Copepoda" n=6: *Oncaea* spp., *Lucicutia* spp., *Clausocalanus* spp., *Euchaeta* spp., *Pleuromamma xiphias*, *Chirundina streetsi*;
"Other crustacea" n=9: Ostracoda spp., *Stylocheiron* cf. *carinatum*, *Euphausia hemigibba*, *Nematoscelis atlantica*, *Nematoscelis* spp. furcilia, *Thysanoessa* sp. furcilia, *Thysanopoda aequalis*, Mysidacea sp., *Gennades* sp.;
"Non-crustacea" n=6: *Cavolinia inflexa*, *Styliola subula*, *Pterosagitta draco*, *Sagitta* sp., *Sagitta* spp., *Sagitta neodecipiens*;
"Pelagic fish" n=10: Fish eggs, Myctophid sp.1-4 larvae, Myctophid spp.1-4, *Cyclothone alba*;
"Benthopel. fish" = benthopelagic fishes n=2: *Arnoglossus rueppelli*, *Macroramphosus* spp.

$\delta^{13}C$ values of the epibenthic invertebrates ranged from -19.79 ‰ for the poriferan sp. 1 to -15.08 ‰ for the asteroid *L. ciliaris* (Tab. 2). The lowest mean $\delta^{13}C$ values were found for the suspension feeding gorgonian, one poriferan species, and the suspension /surface deposit feeding ophiuroid species (Fig. 2). Suspension feeding poriferan species covered a large range of values with two species showing similar values to the other suspension feeders, while the other two species were more enriched. The opportunistic scavenger polychaete *H. tubicola* had $\delta^{13}C$ values ranging from those of suspension and deposit feeding species to the more enriched values of the omnivore *C. cidaris* and the

predator/scavenger *A. irregularis*, respectively. The omnivorous echinoid *C. longispinus* had the greatest variability in $\delta^{13}C$ values and occupied an intermediate position between the latter two species and the most enriched predators/scavengers *L. ciliaris*, *D. arrosor* and *C. lampas*.

The range of $\delta^{13}C$ values covered by the epibenthic species was twice as large as the range covered by the pelagic species (Fig. 2). The $\delta^{13}C$ values of *C. lampas*, *D. arrosor*, *L. ciliaris* and individuals of *C. longispinus* were noticeably higher compared to those of the other species that occupied the lower 2 ‰ of the total $\delta^{13}C$ range covered by the epibenthic invertebrates. The suspension feeding gorgonian and suspension/surface deposit feeding ophiuroid species were on average about 1.54 ‰ and 1.24 ‰ enriched in $\delta^{13}C$, respectively, compared to copepods. There was a pronounced difference in $\delta^{13}C$ values between POM_{susp}, which was assumed to represent the base of the pelagic food web, and the pelagic and epibenthic species. Compared to POM_{susp}, $\delta^{13}C$ values of the copepods were on average enriched by about 3 ‰ and the gorgonian and ophiuroid species by about 4.5 ‰ and 4.2 ‰, respectively. The demersal flatfish *Arnoglossus rueppelli* and the benthopelagic snipe fish *Macroramphosus* spp. had on average more enriched $\delta^{13}C$ values than pelagic fish species, which consisted mainly of myctophids and gonostomatids.

$\delta^{15}N$ values of the epibenthic invertebrates ranged from 6.17 ‰ for the echinoid *C. longispinus* and to 12.33 ‰ for the gastropod *C. lampas* (Tab. 2). The suspension feeding gorgonian and suspension/surface deposit feeding ophiuroid as well as the omnivorous echinoid *C. longispinus* belonged to the group of species with the lowest $\delta^{15}N$ values and, thus, the lowest trophic level positions of the epibenthic species studied (Fig. 3). The four suspension feeding poriferan species covered a large range of intermediate to high $\delta^{15}N$ values, which separated them from the other suspension feeders. Predators/scavengers such as the asteroids *A. irregularis* and *L. ciliaris*, and the polychaete *H. tubicola* as well as the omnivorous echinoid *C. cidaris* formed a group of species with intermediate $\delta^{15}N$ values. The $\delta^{15}N$ values of the polychaete *H. tubicola* covered a large range and overlapped with those of the lowest trophic group. The third group consisted of the 2 predators/scavengers *D. arrosor* and *C. lampas*, which had the highest $\delta^{15}N$ values and, thus, occupied the highest trophic level positions of the epibenthic species studied.

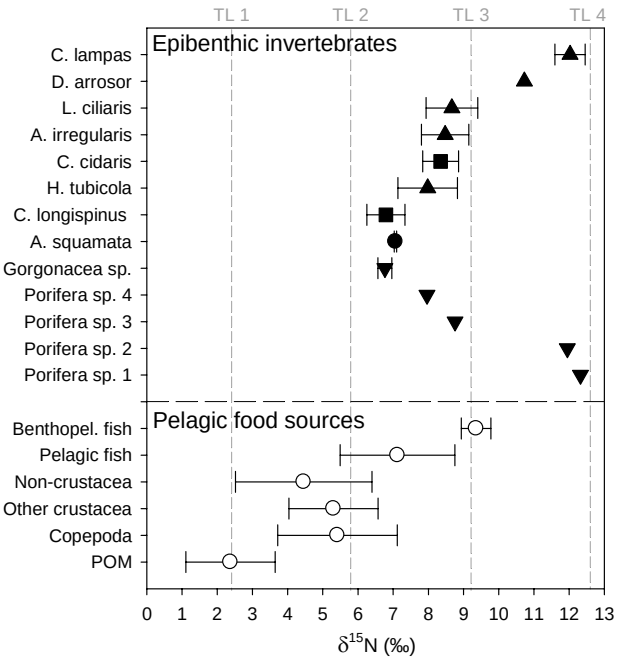


Figure 3.

Mean $\delta^{15}N$ values (± SD) of benthic invertebrates and potential pelagic and benthopelagic food sources from the 3 surveys of Seine Seamount. Trophic levels (TL) were estimated assuming mean $\delta^{15}N$ of POM_{susp} as TL1 and an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level. Symbols for the epibenthic invertebrates refer to feeding types as given in Tab. 2:

▼ = suspension feeders;
● = suspension/surface deposit feeders;
■ = omnivores;
▲ = predators/scavengers.

Mean values of food sources (○) are calculated from mean species values, see Fig. 2 for taxonomic labels.

The $\delta^{15}N$ values of pelagic consumers covered a range of 8.67 ‰, from 0.80 ‰ for ostracod species to 9.47 ‰ for myctophid species. The $\delta^{15}N$ values for POM_{susp} ranged between 0.78 and 4.44 ‰. Assuming mean $\delta^{15}N$ of POM_{susp} as the base of the food web and first trophic level (TL1) and a $\delta^{15}N$ increase of 3.4 ‰ per trophic level, trophic positions of the pelagic species ranged between the 1st and 3rd trophic level and those of the epibenthic invertebrates between the 2nd and 4th trophic level (Fig. 3). The $\delta^{15}N$ values of crustacean and non-crustacean zooplankton ranged in the lower part of the total range, while fish species were positioned in the upper part.

3.2 FATTY ACID MARKER IN EPIBENTHIC SPECIES AND POTENTIAL FOOD SOURCES

Storage lipid fatty acid signatures were analysed for the 11 epibenthic species sampled in December 2003 and March 2004 and showed considerable inter- as well as intra-specific variability (Tab. 3, Fig. 4A). Values for the 3 species sampled during both surveys in December 2003 and March 2004, *H. tubicola*, *A. irregularis* and *L. ciliaris*, were pooled, since temporal differences were generally smaller than the species-specific variability.

Table 3. Fatty acid composition (%) of storage lipids of the epibenthic species sampled on the summit of Seine Seamount during December 2003 and March 2004. Standard deviations are given in parentheses, n = number of samples, tissue types given refer to sampled tissue type.

Fatty acid	Porifera spp.				Gorgonacea sp.	*H. tubicola*		*A. squamata*	*A. irregularis*		*L. ciliaris*		*C. cidaris*	*C. longispinus*
	sp.1	sp.2	sp.3	sp.4										
		Mar 04			Mar 04	Dec 03	Mar 04	Dec 03	Dec 03	Mar 04	Dec 03	Mar 04	Dec 03	Mar 04
	tissue	tissue	tissue	tissue	stem section	complete	complete	complete	arm	arm	gonads	arm	gonads	gonads
	n=1	n=1	n=1	n=1	n=3	n=5	n=2	n=2	n=4	n=1	n=1	n=1	n=5	n=3
Saturates (SFA)														
14:0	1.80	3.17	2.41	1.48	3.56 (0.26)	2.96 (1.56)	5.00 (1.95)	8.17 (4.21)	0.94 (0.18)	2.13	7.85	1.36	6.27 (0.91)	3.71 (1.24)
15:0	1.08	4.38	1.49	0.99	1.20 (0.07)	1.07 (0.15)	1.89 (0.30)	2.52 (0.26)	0.99 (0.16)	1.01	3.19	0.98	3.92 (0.60)	1.60 (0.21)
16:0	13.74	16.30	14.71	5.24	24.22 (1.19)	9.92 (2.37)	14.08 (3.84)	17.07 (1.05)	5.03 (0.88)	7.58	13.35	8.15	18.45 (1.25)	13.42 (1.11)
17:0	12.83	2.70	2.39	0.57	2.17 (0.18)	2.15 (0.50)	2.30 (0.33)	2.24 (0.20)	1.16 (0.23)	1.15	2.16	1.18	1.97 (0.05)	1.26 (0.03)
18:0	5.07	5.06	11.91	4.74	7.41 (0.41)	6.59 (1.95)	5.73 (1.21)	6.25 (0.11)	6.92 (0.97)	6.76	8.77	9.73	5.34 (0.41)	4.37 (0.24)
20:0	0.16	1.24	0.98	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22:0	0.00	0.00	0.00	0.00	0.55 (0.48)	0.86 (0.16)	0.97 (0.77)	0.94 (0.83)	2.44 (0.33)	2.29	0.58	1.49	0.58 (0.19)	1.42 (0.30)
Mono-unsaturates (MUFA)														
16:1(n-7)	4.44	2.65	10.00	5.14	3.52 (0.39)	5.97 (1.25)	8.33 (3.23)	6.00 (2.14)	0.93 (0.22)	1.47	3.50	0.56	5.59 (0.49)	3.45 (0.39)
18:1(n-9)	4.00	9.45	3.96	1.75	11.96 (3.03)	4.58 (1.79)	5.64 (3.26)	7.85 (3.87)	1.65 (0.24)	2.58	2.15	0.81	2.01 (0.23)	2.93 (0.47)
18:1(n-7)	2.89	2.98	6.67	4.30	3.72 (0.57)	4.00 (1.84)	4.57 (1.30)	2.55 (0.18)	2.14 (0.46)	2.84	2.32	1.63	4.16 (0.25)	2.91 (0.53)
20:1(n-11)	0.00	0.00	0.43	0.00	0.00	4.24 (1.54)	3.61 (1.26)	0.00	0.00	0.00	0.00	0.00	2.28 (0.60)	0.00
20:1(n-9)	1.84	4.00	0.68	21.96	6.47 (0.90)	6.68 (1.26)	5.71 (2.30)	10.58 (0.73)	13.93 (4.86)	17.33	24.99	18.24	6.19 (0.65)	15.88 (0.88)
20:1(n-7)	0.46	2.79	2.92	1.56	1.57 (0.23)	1.59 (0.21)	1.75 (0.09)	0.00	1.63 (0.77)	1.60	0.00	0.00	2.88 (0.49)	3.00 (0.38)
22:1(n-11)	0.00	0.00	0.00	0.00	0.83 (0.14)	0.87 (0.35)	0.92 (0.24)	1.67 (0.81)	1.38 (0.73)	1.07	1.89	0.66	0.00	0.41 (0.03)
22:1(n-9)	0.00	1.96	1.27	0.13	1.04 (0.26)	1.81 (0.47)	1.40 (0.22)	1.49 (0.66)	0.73 (0.29)	0.96	0.93	0.23	6.01 (1.07)	1.17 (0.19)
22:1(n-7)	4.80	1.08	2.83	4.10	2.67 (0.13)	0.00	0.00	1.03 (0.84)	0.00	0.00	0.00	0.00	0.83 (0.27)	0.36 (0.04)
24:1	6.55	15.92	0.86	26.86	3.11 (0.17)	2.12 (1.27)	2.35 (1.77)	5.10 (2.37)	1.33 (0.98)	2.25	2.01	0.58	1.62 (0.70)	1.00 (0.30)
Poly-unsaturates (PUFA)														
18:2(n-6)	1.10	2.15	0.54	0.36	1.04 (0.15)	1.35 (0.12)	0.95 (0.02)	1.22 (0.37)	0.48 (0.12)	0.76	0.20	0.45	0.61 (0.13)	0.54 (0.23)
18:3(n-6)	0.63	1.14	0.63	0.19	0.00	0.00	0.00	1.22 (1.23)	0.29 (0.09)	0.00	0.00	0.00	0.00	0.00
18:3(n-3)	0.00	0.00	0.00	0.00	0.91 (0.09)	1.27 (0.21)	1.11 (0.20)	1.23 (0.55)	0.09 (0.18)	0.73	0.00	0.00	0.77 (0.10)	1.11 (0.12)
18:4(n-3)	1.26	2.05	0.80	0.10	1.07 (0.16)	0.37 (0.19)	0.40 (0.05)	2.23 (1.05)	0.54 (0.15)	0.75	0.35	0.26	0.70 (0.07)	0.52 (0.19)
18:5(n-3)	0.47	0.28	0.32	0.07	0.45 (0.30)	1.10 (0.13)	0.77 (0.13)	0.00	1.58 (0.95)	2.51	0.33	2.83	0.00	0.00
20:2(n-6)	1.89	1.35	1.08	15.94	1.54 (0.19)	4.54 (0.23)	3.92 (0.56)	2.18 (1.03)	3.36 (0.69)	2.01	1.55	1.15	2.40 (0.37)	7.06 (1.06)
20:3(n-6)	1.06	0.38	0.36	0.19	0.48 (0.26)	0.89 (0.53)	0.68 (0.12)	0.20 (0.28)	0.00	0.00	0.00	0.00	0.48 (0.23)	0.45 (0.09)
20:4(n-6)	9.68	2.62	7.93	0.63	4.61 (2.83)	11.51 (4.19)	8.63 (5.08)	4.23 (1.63)	24.56 (3.21)	17.23	9.98	30.45	9.28 (2.12)	13.51 (0.52)
20:3(n-3)	0.00	0.00	0.00	0.24	0.00	0.55 (0.25)	0.39 (0.22)	0.39 (0.54)	0.72 (0.21)	0.81	0.49	0.23	0.65 (0.10)	0.36 (0.03)
20:4(n-3)	1.60	0.73	0.36	0.39	0.79 (0.19)	0.51 (0.38)	0.41 (0.14)	0.29 (0.41)	0.00	0.00	0.41	0.20	0.42 (0.17)	0.55 (0.09)
20:5(n-3)	7.19	5.92	19.91	0.87	10.25 (1.50)	12.47 (5.88)	8.83 (8.18)	6.19 (0.48)	18.20 (3.63)	14.69	9.33	16.44	3.29 (0.33)	8.05 (0.83)
22:2	0.00	0.00	0.00	0.00	0.31 (0.17)	1.17 (0.65)	0.72 (0.07)	0.00	0.00	0.00	0.00	0.00	0.61 (0.34)	0.63 (0.16)
22:6(n-3)/24:0	15.18	9.18	3.53	1.64	4.25 (0.12)	8.13 (0.83)	7.70 (2.95)	6.50 (2.78)	7.74 (2.29)	8.45	2.59	1.81	12.41 (4.02)	10.22 (1.28)
∑ minor FA	0.3	0.5	1.0	0.4	0.3	0.7	1.3	0.7	1.2	1.0	1.1	0.6	0.3	0.1
∑ SFA	34.86	33.25	34.44	13.17	39.33 (1.16)	24.20 (3.41)	31.07 (5.61)	37.70 (4.74)	18.60 (2.09)	21.93	36.98	23.46	36.78 (1.52)	25.91 (2.28)
∑ MUFA	25.07	40.94	30.09	66.18	34.98 (4.84)	31.95 (7.95)	34.42 (11.0)	36.43 (2.19)	23.82 (3.92)	30.13	37.78	22.72	31.60 (2.42)	31.10 (1.42)
∑ PUFA	40.07	25.80	35.47	20.64	25.69 (4.92)	43.85 (9.05)	34.51 (16.7)	25.87 (6.94)	57.58 (5.89)	47.94	25.24	53.82	31.62 (1.96)	42.99 (3.49)

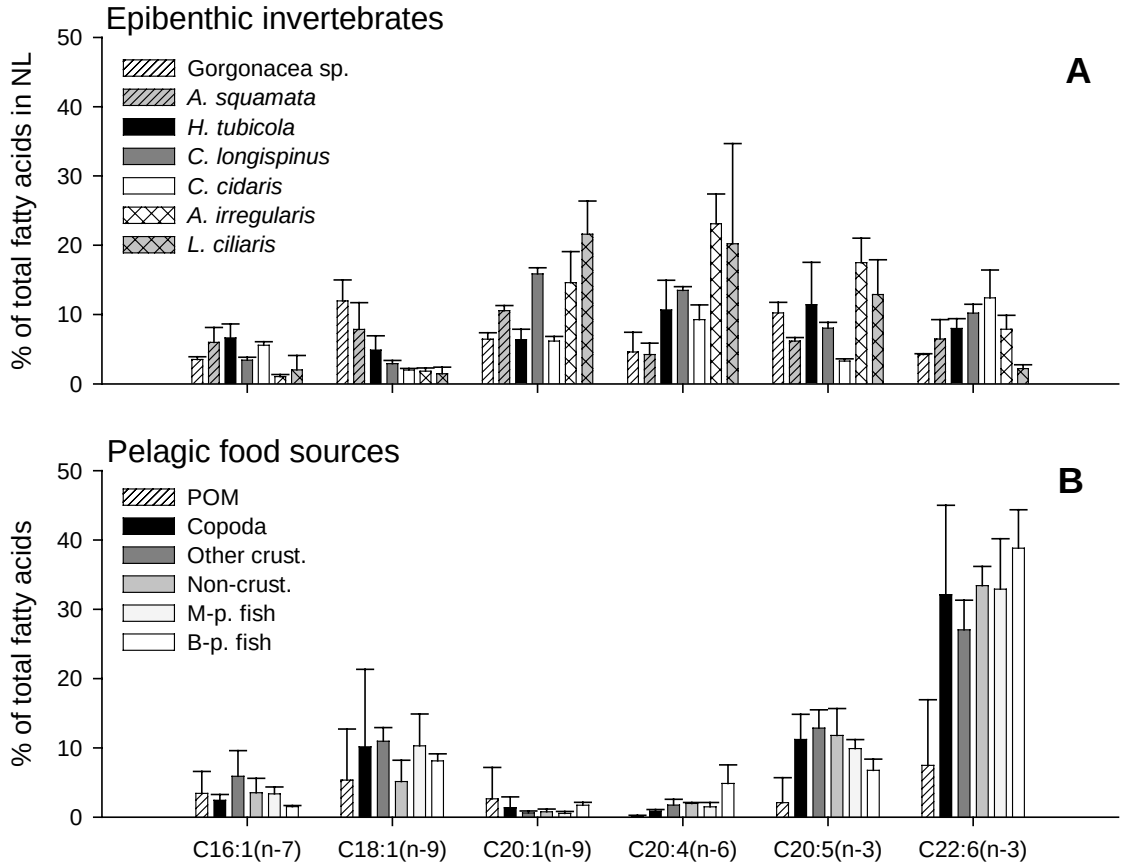
minor FA = sum of fatty acids with max proportions < 1% of total fatty acids in all species (SFAs: 12:0,13:0, 21:0, 23:0; MUFAs: 14:1, 15:1, 17:1)

Saturated fatty acids (SFAs) dominated the storage lipids of the suspension feeding gorgonian and suspension/surface deposit feeding *A. squamata* and of the omnivorous echinoid *C. cidaris* (Tab. 3). Storage lipids of the predators/scavengers, except for the gonad tissue sample of *L. ciliaris*, as well as the omnivorous echinoid C. *longispinus* were dominated by poly-unsaturated fatty acids (PUFAs). Poriferan species were characterised by rather unique fatty acid profiles, which were quite different from those of the other suspension feeders and differed also largely within this taxonomic group. Mono-unsaturated fatty acids (MUFAs) were dominant in 2 of the poriferan species while PUFAs were dominant in the other two species.

The most abundant SFAs in the storage lipids of the epibenthic species (Tab. 3), although to a varying degree, were 14:0, 16:0 and 18:0, with 16:0 dominating. MUFAs in the echinoderm species were dominated by 20:1(n-9), which was, except for 2 poriferan species, also present in considerable proportions in the other species. The ophiuroid *A. squamata* was distinguished from the other echinoderms by higher proportions of the fatty acid 18:1(n-9) that were similar to those of the suspension feeding gorgonian, which had the highest proportion of this fatty acid together with one of the poriferan species (sp.2). The polychaetes and the poriferan species 1 and 3 contained intermediate proportions of this fatty acid. Considerable proportions of the fatty acid 16:1(n-7) were present in the polychaete *H. tubicola* as well as in the ophiuroid *A. squamata*, the echinoderm *C. cidaris* and the poriferan species 3. Poriferan MUFAs were, except for species 3, dominated by 24:1. The most abundant PUFAs in all species were 20:4(n-6), 20:5(n-3) and 22:6(n-3), except for the poriferan species 4, but their proportions varied considerably between species. The highest proportions of 20:4(n-6) and 20:5(n-3) were detected for the two predatory asteroid species and the lowest proportions of 20:4(n-6) for the suspension feeding gorgonian, the suspension/surface deposit feeding ophiuroid and the two poriferan species 2 and 4. The echinoderm *C. cidaris* was characterised by the lowest proportions of 20:5(n-3) and the highest proportions of 22:6(n-3), except for poriferan sp. 4 with lower 20:5(n-3) proportions and poriferan sp. 1 with higher 22:6(n-3) proportions. Odd-number fatty acids were present in relatively low proportions in all species, dominated by 15:0 and 17:0.

Relative contributions of the most abundant unsaturated fatty acids in the storage lipids of the epibenthic invertebrate species (Fig. 4A) and the total lipids of potential pelagic food

sources (Fig. 4B) revealed similarities as well as pronounced differences between pelagic and epibenthic taxa as well as between taxonomic groups. Fatty acid profiles of the poriferan species were not included in Figure 4 as their fatty acid profiles differed strongly from those of the other epibenthic species (Tab. 3).



Taxonomic labels for food sources (B) (n= number of samples):
"POM" = suspended particulate organic matter N = 3;
"Copepoda" n=18: *Oncaea* spp., *Lucicutia* spp., *Clausocalanus* spp., *Euchaeta* spp., *Pleuromamma xiphias*;
"Other crust." = Other crustacea n=6: Ostracoda spp., Mysidacea sp., *Euphausia hemigibba*;
"Non-crust." = Non-crustacea n=5: *Cavolinia inflexa*, Chaetognath spp.;
"M-p. fish" = mesopelagic fishes n=9: fisheggs, *Notoscopelus resplendens* larvae, *Hygophum hygomi* larvae, Myctophid sp.1-2, *Cyclothone alba*;
"B-p. fish" = benthopelagic fishes n=10: *Arnoglossus rueppelli*, *Macroramphosus* spp.

Figure 4. Proportions of the most abundant unsaturated fatty acids in (A) the storage lipids (NL=neutral lipids) of the epibenthic invertebrates, excluding poriferan species, and (B) the total lipids of potential pelagic and benthopelagic food sources for the epibenthic invertebrates at Seine Seamount. Values represent overall means (± SD) from the 3 surveys. Overall means of the food source taxonomic groups were calculated from mean species values.

Proportions of the abundant unsaturated fatty acids in POM_{susp} were characterised by a large variability and lower proportions of PUFAs compared to the pelagic taxa and the benthopelagic fishes (Fig. 4 B). Despite considerable within-group variability of the fatty acid proportions of the pelagic and the benthopelagic fish groups, mean fatty acid proportions were relatively similar between these groups. Fatty acids of these taxa were

dominated by 22:6(n-3) with substantial contributions of 20:5(n-3), 18:1(n-9) and, to a lesser degree, of 16:1(n-7). The fatty acids 20:1(n-9) and 20:4(n-6) were present only in small or trace amounts in the pelagic groups, while the benthopelagic fish had noticeably higher 20:4(n-6) proportions.

In the storage lipids of the epibenthic invertebrates (Fig. 4A), the proportions of these abundant fatty acids varied considerably between species, but storage lipid compositions of all species were characterised by higher proportions of 20:1(n-9) and 20:4(n-6) and lower proportions of 22:6(n-3) compared to those in the total lipids of pelagic and benthopelagic taxa. Proportions of 18:1(n-9) were also considerably lower in the epibenthic species compared to the pelagic taxa, with the exception of the gorgonian, the ophiuroid and the polychaete species, which had proportions similar to those of pelagic and benthopelagic taxa. Proportions of 20:5(n-3) and 16:1(n-7) in epibenthic species were in the range of those in pelagic species and benthopelagic fishes.

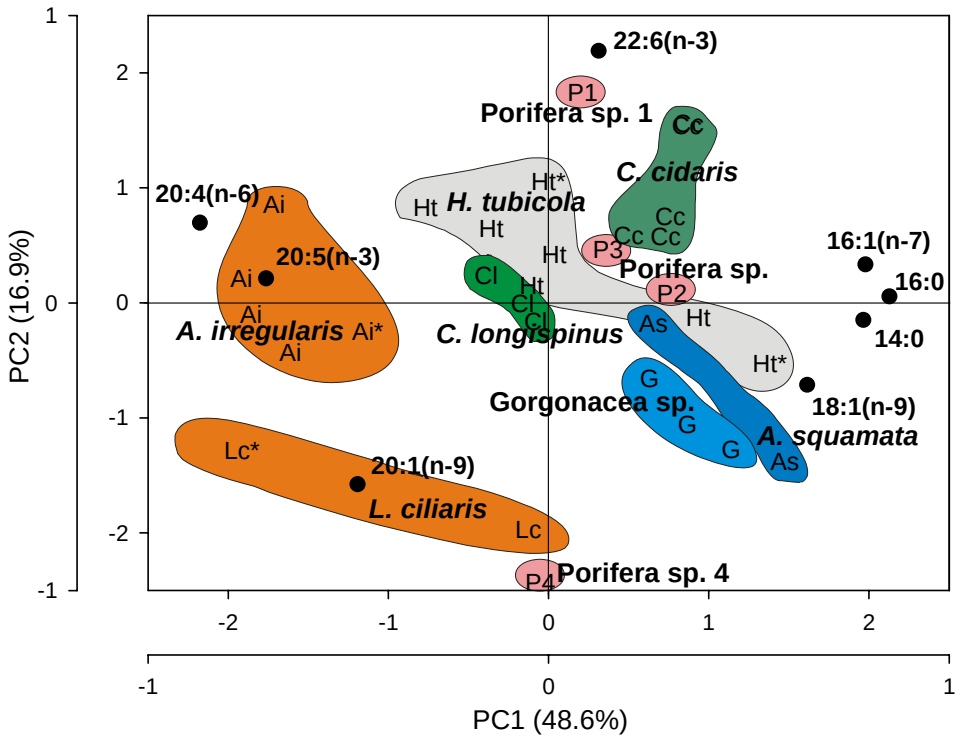


Figure 5. Principal component analysis on the relative fatty acid composition of storage lipids of the epibenthic invertebrates on Seine Seamount. Species labels with an asterisk (*) refer to specimen sampled in March 2004, all other were sampled in December 2003; filled circles = fatty acids; scales were adjusted to combine plots: scales of principal components (PC) refer to sample plot, scale of variables ranges from -1 to +1 for both PCs. Proportion of variance accounted for by each PC is given in brackets.

Principal component analysis (PCA) on the 8 most abundant fatty acids of the storage lipids of the epibenthic invertebrates extracted three components with eigenvalues >1 of which the major two explained 66 % of the variance (Fig. 5). PCA clearly distinguished the different species based on their relative fatty acid compositions, although some marginal overlapping occurred and mainly involved the opportunistic polychaete *H. tubicola*. PC1, which explained 49 % of the variance, separated species mainly due to either higher proportions of the fatty acids 20:4(n-6), 20:5(n-3) and 20:1(n-9), like the two asteroids *A. irregularis* and *L. ciliaris*, and some individuals of the polychaete *H. tubicola*, or due to higher proportions of 16:0, 14:0, 16:1(n-7) and 18:1(n-9), like the gorgonian species, the ophiuroid *A. squamata*, the echinoid *C. cidaris* and individuals of *H. tubicola*. PC2 separated the asteroid *L. ciliaris* due to higher amounts of 20:1(n-9), *C. cidaris* due to higher amounts of 22:6(n-3) and, as was more apparent on PC3, the gorgonian species due to higher amounts of 18:1(n-9) from other species. The echinoid *C. longispinus* took a central position in the plot, due to intermediate proportions of the fatty acids plotted. Poriferan species were largely separated from each other. While species 1 and 4 were separated along PC2 due to high values of 22:6(n-3) and 20:1(n-9), respectively, species 2 was separated along PC1 due to high values of 16:0 and 18:1(n-9), and species 3 took a central position due to high proportions of all the fatty acids separating along PC1 and PC2.

4. DISCUSSION

The epibenthic invertebrates sampled on the summit plateau of Seine Seamount are mainly opportunistic organisms which typically inhabit the upper continental slope/upper bathyal zone and have a cosmopolitan or Mediterranean-Atlantic and Western African distribution, including the Azores (Beck *et al.* 2005, Gillet and Dauvin 2000, 2003). Wilson and Kaufmann (1987) concluded in a review that seamount communities were similar to those found on nearby continental shelves.

4.1 FEEDING ECOLOGY OF EPIBENTHIC SPECIES

Gorgonians are passive suspension feeders, which may feed opportunistically on a heterogeneous diet including a broad range of plankton size-classes from nanoeukaryotes (~3.8 μm) to copepods (700 μm) with particles >100 μm dominating (Coma *et al.* 1994,

Ribes *et al.* 1999, 2003, Orejas *et al.* 2003, Rossi *et al.* 2004). Detrital particulate organic matter as well as crustacean fragments and copepods have been identified as important food sources in polyp guts, while invertebrate eggs and phytoplankton were less important (Tsounis *et al.* 2006). The tall whip-like gorgonian species analysed in this study conformed to this general pattern according to stable isotopic and fatty acid biomarker data. Storage lipids of the gorgonian species in this study were, next to the saturated fatty acid 16:0, dominated by the diatom marker fatty acids 16:1(n-7) and 20:5(n-3), the 22:6(n-3) fatty acid, which is abundant in dinoflagellates, as well as the carnivory marker fatty acid 18:1(n-9) (e.g., Dalsgaard *et al.* 2003, and references therein). The presence of substantial amounts of phytoplankton marker fatty acids and the relatively low concentration of bacterial markers, such as the odd-numbered fatty acids 15:0 and 17:0 (Dalsgaard *et al.* 2003, and references therein) suggests that the gorgonian fed on relatively fresh phytodetritus. The high proportion of the carnivory marker 18:1(n-9), which is abundant in pelagic heterotrophs, indicates that a part of the diet may also be covered carnivorously, e.g. on small pelagic zooplankton. Dietary input from a benthic source was suggested by enhanced proportions of 20:4(n-6) and might imply feeding on resuspended benthic meiofauna (Sherwood *et al.* 2005), as this fatty acid was notably more abundant in epibenthic species compared to pelagic zooplankton (see 4.2.2 for discussion).

Mean $\delta^{15}N$ of the gorgonian species was enriched by 4.4 ‰ compared to mean POM_{susp} at the surface. Assuming a $\delta^{15}N$-enrichment of 3.4 ‰ per trophic level (Minagawa and Wada 1984) and taking into account that POM_{susp} included autotrophic as well as heterotrophic components, the gorgonian $\delta^{15}N$ values indicated relatively fresh POM_{susp} as the main food source. The "fresh" character of POM_{susp} on the seamount summit was further supported by a concurrent study on POM_{susp} quality (Kiriakoulakis *et al.* 2009), which reported a low $\delta^{15}N$-enrichment of ~2 ‰ in POM_{susp} between the surface and close to the summit at 160 m depth, indicating little heterotrophic reworking (Checkley and Miller 1989).

Marine sponges are active suspension feeders and since they are the most primitive multi-cellular animals, they contain special structural features in their cell membranes and their lipids are one of the richest sources of unusual fatty acids (Bergé and Barnathan 2005). They can be associated with bacteria (Bergé and Barnathan 2005 and references therein) and diatoms (Bavestrello *et al.* 2000; Cerrano *et al.* 2000, 2004a,b). The fatty acid and stable isotope signatures of the poriferan species in this study were markedly different

from those of the other suspension feeders. Poriferan sp.1, for example, had the second highest $\delta^{15}N$ of all epibenthic species investigated and contained high levels of the bacterial fatty acid 17:0 and the potential benthic marker 20:4(n-6). This combination of trophic markers might indicate feeding on highly refractory organic matter or association with resuspended benthic bacteria. Poriferan sp.3, on the other hand, was separated from other suspension feeders by high amounts of diatom marker fatty acids, indicating a feeding preference for this phytoplankton group, together with high proportions of 20:4(n-6) and a relatively enriched $\delta^{15}N$ value, possibly due to feeding on refractory benthic material.

The fatty acid compositions of the echinoderm species studied were generally consistent with that of shallow- and deep-water echinoderms. Echinoderms are characterized by relatively low amounts of 18:1, with various moieties of 20:1 being the major monoenoic fatty acids, and relatively high proportions of 20:4(n-6) and 20:5(n-3) together with lower percentages of 22:6(n-3) and low levels of bacterially derived branched-chain and odd-number fatty acids (e.g. Takagi *et al.* 1980, Sargent *et al.* 1983, Howell *et al.* 2003). The high proportions of 20:1(n-9) in the echinoderm species observed in this study may be due to their potential capability to synthesise *de novo* various moieties of 20:1 including 20:1(n-9) (Takagi *et al.* 1980, Sargent *et al.* 1983).

The ophiuroid *A. squamata* is a deposit feeder collecting particles with its tube feet, and a suspension feeder via trapping detritus in mucus. Stomach contents were reported to include a variety of items such as unicellular algae, small gastropods, foraminiferans and amphipod limbs (Warner 1982). The fatty acid signature of the ophiuroid species contained similar amounts of the diatom markers 16:1(n-7) and 20:5(n-3) and the dinoflagellate markers 22:6(n-3) and 18:4(n-3) indicating dietary uptake of both phytoplankton groups. The relatively low amount of the bacterial biomarker fatty acids 15:0 and 17:0 suggest feeding on rather fresh detritus. Like the suspension feeding gorgonian species, this species contained also markedly elevated amounts of the carnivory marker 18:1(n-9) indicating a partially carnivorous diet of mainly pelagic origin, while proportions of the assumed benthic marker 20:4(n-6) were comparably low (see 4.2.2 for discussion). Low $\delta^{13}C$ and $\delta^{15}N$ values compared to the other epibenthic species confirmed the species´ trophic position as being predominantly a primary consumer of fresh detritus.

Regular echinoids are generally assumed to be opportunistic feeders and their omnivorous feeding mode includes herbivorous feeding on littoral plants and/or algae, deposit feeding, scavenging and feeding on small invertebrates and encrusting organisms (De Ridder and Lawrence 1982, Pawson and Miller 1983, Jacob *et al.* 2003). The diet of *Centrostephanus longispinus* varies according to the habitat occupied, and may consist of large proportions of plants, algae or seaweed, with a preference for leafy red algae, or of a varied diet of small invertebrates, encrusting organisms, and drift algae (Pawson and Miller 1983). Storage lipids of this species on Seine Seamount contained considerable amounts of the fatty acid 20:4(n-6), which is characteristic for Rhodophyta (Dembitsky 1991, Dalsgaard *et al.* 2003) and might suggest a macroalgal contribution to the diet (see 4.2.2 for discussion). The phytoplankton markers 20:5(n-3) and 22:6(n-3) were the next most abundant PUFAs and suggested surface deposit feeding on fresh diatom and dinoflagellate-derived phytodetritus. The low amounts of the pelagic carnivory marker 18:1 (n-9) further implied little importance of zooplankton in the diet. A trophic status as primary consumer was also supported by the low $\delta^{15}N$ values for *C. longispinus*, which were similar to those for the suspension feeding gorgonian species and the surface deposit feeding ophiuroid *A. squamata*. The food source marker $\delta^{13}C$ was more enriched for *C. longispinus* than for the latter two species and suggested a mixed diet of fresh phytoplankton derived food and of a more enriched $\delta^{13}C$ source such as red algae, considering the low amount of bacterial marker fatty acids present (see 4.2.2 for discussion).

Little is known about the feeding habits of cidaroids, which include several deep-sea species (Tyler and Gage 1984). They have been described as deposit feeders and scavengers as well as predators of sponges and other sessile taxa, such as hydroids and bryozoans (De Ridder and Lawrence 1982). Due to morphological constraints they appeared not to consume diatoms, in contrast to other sympatrically occurring echinoid families (Jacob *et al.* 2003). This observation was confirmed by the fatty acid signature of *C. cidaris,* which contained the lowest proportion of the diatom marker 20:5(n-3) and the highest proportion of the dinoflagellate marker 22:6(n-3) of all epibenthic invertebrates studied. The storage lipids were dominated by saturated fatty acids, which are abundant in phytodetritus (Reemtsma *et al.* 1990), and also contained elevated proportions of odd-chain fatty acid bacterial markers suggesting feeding on dinoflagellate-derived phytodetritus. Slightly more enriched $\delta^{15}N$ values compared to other deposit feeders, e.g.

the ophiuroid species, might be explained by feeding also at lower depths, where detritus is more refractory, and/or by feeding on benthic primary consumers as suggested by literature and by moderate amounts of the assumed benthic marker fatty acid 20:4(n-6).

Both of the asteroid species studied are predominantly predatory. *Astropecten irregularis* has been described as a potentially important primary predator on the benthos, while *Luidia ciliaris* might also be a secondary and tertiary carnivore (Menge 1982). The diet of the burrowing starfish *A. irregularis* was reported to include infaunal molluscs, mainly gastropods and bivalves, while polychaetes, larger crustaceans, fish and carrion only constituted a small proportion of the diet (Christensen 1970, Franz and Worley 1982, Beddingfield and McClintock 1993, de Juan *et al.* 2007). *L. ciliaris* is a predator on other echinoderms, including echinoids and asteroids (Brun 1972, Riedl 1983). The $\delta^{15}N$ signature of both species revealed, however, only slightly higher values for *L. ciliaris*. This agreed with the <1 ‰ difference between these two species observed by Jennings *et al.* (2002) for a North Sea study site (8.2 and 9.0 ‰ for *A. irregularis* and *L. ciliaris*, respectively) and suggested that both species fed mainly as primary predators. The $\delta^{13}C$ values of the 2 species indicated some degree of separation regarding their food sources. The $\delta^{13}C$ values for *A. irregularis* were closer to those of pelagic primary consumers and indicated feeding on benthic primary consumers, which consumed pelagic food sources. The $\delta^{13}C$ values for *L. ciliaris* were the most enriched of all epibenthic species studied and suggested feeding on benthic consumers which utilised a more enriched benthic food source, possibly derived from enriched sediment-dwelling microorganisms or from macroalgae. Fatty acid signatures of both species contained the highest proportion of the potential benthic food source marker 20:4(n-6) and confirmed their reliance on the benthic food web (see 4.2.2 for discussion). The high proportions of this fatty acid observed in the asteroids might also be due to its selective retention in the storage lipids. The ability of echinoderms to accumulate high proportions of 20:4(n-6) has been reported previously (Takagi *et al.* 1980).

The motile tube-carrying polychaete *Hyalinoecia tubicola* is generally regarded as opportunistic scavenger feeding on a large range of marine carrion (Fauchald and Jumars 1979, Britton and Morton 1994). This cosmopolitan species occurred in great abundance on the summit plateau of Seine Seamount (Beck *et al.* 2005) and has been reported as a common and often abundant (sometimes dominant) polychaete species on seamounts of

the southern Azores (Gillet and Dauvin 2000, 2003). Fatty acid and $\delta^{15}N$ stable isotope signatures of these polychaetes were characterised by the highest variability observed in all epibenthic species and confirmed the opportunistic feeding behaviour of this scavenger. The polychaetes contained relatively high proportions of phytoplankton marker fatty acids, although feeding on phytodetritus was not reported for this species in literature. The mean proportions of the carnivory marker 18:1(n-9) as well as the potentially benthic derived 20:4(n-6) fatty acids were intermediate between those of the more pelagic feeding gorgonian and ophiuroid species and those of the benthic feeding predatory asteroids. Their presence indicated that the phytoplankton fatty acids might be derived through scavenging on pelagic metazoan sources, containing 18:1(n-9), and benthic primary consumers with elevated levels of 20:4(n-6). Principal component analysis of the storage lipid fatty acids supported the opportunistic feeding mode of this species, which appeared to use pelagic as well as benthic food sources in varying proportions. Stable isotope ranges also confirmed this intermediate position between the more pelagic food source-associated species, i.e. the gorgonian and ophiuroid species, and the other species which consumed higher proportions of benthic-derived food.

Most hermit crabs are opportunistic feeders. Observed feeding types included deposit feeders, scavengers, predators and mesograzers, and food items reported consisted of organic debris, macroalgae with associated fauna, small invertebrates and carrion (Benvenuto *et al.* 2003). *Dardanus arrosor* is a scavenger on dead shells and fishes, but is also able to catch crabs and other living animals (Hazlett 1981). The $\delta^{15}N$ value of *D. arrosor* indicated an intermediate trophic level position between the predatory asteroid species and the top predatory gastropod *C. lampas* and confirmed a dietary input from a range of primary and secondary consumers. Similarly intermediate $\delta^{13}C$ values suggested feeding on benthic as well as pelagic feeding prey.

The gastropod *Charonia lampas* is an active predator reported to feed on other molluscs and asteroids (Riedl 1983). The $\delta^{15}N$ values for this species were the highest of all species investigated and indicated the two predatory asteroid species as potential prey. The enriched $\delta^{13}C$ values of *C. lampas* were similar to those of its potential prey *L. ciliaris* and suggested feeding on benthic food web-related prey with enriched $\delta^{13}C$ values.

4.2 FOOD SOURCES OF THE EPIBENTHIC INVERTEBRATES

4.2.1 NUTRITIONAL LINK TO THE PHYTOPLANKTON

The limit of the photic zone in the Seine Seamount area was estimated to be at a depth of 130-150 m and extended algal growth on the summit plateau at around 170 m depth was, thus, unlikely (Beck *et al.* 2005). Benthic communities on Seine Seamount were expected to depend either on phytodetritus or heterotrophic prey as a food source. High amounts of poly-unsaturated phytoplankton marker fatty acids observed in the storage lipids of the studied epibenthic invertebrates support the assumption of phytodetritus being the main direct or indirect nutritional source for the benthic seamount fauna. These n-3 and n-6 PUFAs are biosynthesised *de novo* by phytoplankton and are essential dietary components of marine animals needed for growth, survival and successful reproduction (e.g. Dalsgaard *et al.* 2003, Kattner *et al.* 2007). They can usually not be synthesised by these animals and must be obtained from algal food (Dalsgaard *et al.* 2003, Klein Breteler *et al.* 2004).

The suspension feeding gorgonian species and the suspension/surface deposit feeding ophiuroid *A. squamata* were most closely linked to the pelagic food source. The fatty acid signatures of their storage lipids indicated feeding on fresh phytodetritus. Phytodetritus is known to degrade rapidly during descent from near-surface waters and, as polyunsaturated fatty acids are labile compounds, they are useful as indicators of the degree of "freshness" of organic matter (e.g. Wakeham *et al.* 1984). Saturated fatty acids are less labile and therefore degrade less rapidly (Wakeham *et al.* 1984, Rice *et al.* 1986) and phytodetritus is characterised by high proportions of saturated fatty acids, which are dominated by 16:0 (Reemtsma *et al.* 1990). The supply of rather fresh phytoplankton to the surface of the seamount summit implies a fast downward transport of epipelagic organic matter. Kiriakoulakis *et al.* (2009), who concurrently investigated POM_{susp} quality, reported relatively fresh POM_{susp} at the summit depth. The authors observed a few meters above the seamount summit a similar lipid composition, in particular regarding relative PUFA contents, compared to surface water samples at 50 m depth, although lipid concentrations were lower by up to an order of magnitude. The “fresh” character of POM_{susp} was also reflected in the comparably small $\delta^{15}N$-enrichment of ~2 ‰ in POM_{susp} from surface to summit samples (Kiriakoulakis *et al.* 2009). The rapid deposition of surface organic matter was most likely related to the shallow depth of the seamount summit plateau, but might

also be temporally enhanced by Taylor column-related downwelling (Mullineaux and Mills 1997, Beckmann and Mohn 2002).

Besides direct feeding on fresh detritus, zooplankton appeared to be an important food source for the suspension feeding gorgonian species and the suspension/surface deposit feeding ophiuroid *A. squamata*, as indicated by the high proportions of the pelagic carnivory marker 18:1(n-9) in their storage lipids. Zooplankton might, thus, be an important nutritional link for the transfer of essential fatty acids between phytoplankton and epibenthic suspension feeders.

The epibenthic omnivores and predators/scavengers studied were characterised by higher proportions of 20:4(n-6) in their storage lipids indicating their stronger association to benthic versus pelagic food sources (see 4.2.2 for discussion). Nevertheless, these species contained high proportions of phytoplankton markers. For the omnivorous echinoid species, these fatty acids might be directly derived from the phytodetrital part of their diet. For the carnivorous asteroid and polychaete species, these phytoplankton marker fatty acids would have to be transferred via their primarily benthic prey. Benthic primary consumers, thus, play an important role as nutritional link between the phytoplankton-derived food source and the benthic food web and for the transfer of essential fatty acids to higher trophic levels in the benthos.

4.2.2 Indications for a benthic primary food source

Arachidonic acid (20:4(n-6)) is an essential dietary fatty acid and must be assimilated from primary producers, as it cannot be biosynthesised *de novo* by consumers (e.g. Dalsgaard *et al.* 2003). It is an important component of cell membranes (Sargent and Falk-Petersen 1981) and is involved in intracellular and intercellular signalling (Leitz 1994).

Compared to POM_{susp} with only trace amounts of this fatty acid present and to the small proportions contained in the pelagic species, most epibenthic consumers were substantially enriched in 20:4(n-6). Principal component analysis confirmed the association of 20:4(n-6) with benthic-derived food, as the first principal component, which explained 48.6 % of the variance, reflected a benthic to pelagic feeding axis.

A possible explanation for the elevated levels of 20:4(n-6) observed in the benthos-associated species might be the existence of an additional benthic primary source of arachidonic acid other than phytoplankton. Several different sources for arachidonic acid have been suggested in the literature and these include macroalgae, especially Rhodophyta (Takagi *et al.* 1980, Pettitt *et al.* 1989, Khotimchenko *et al.* 1990, Dembitsky *et al.* 1991, Dalsgaard *et al.* 2003), sediment dwelling micro-organisms such as protozoans and microeukaryotes (Bell and Sargent 1985, Fullarton *et al.* 1995), and certain diatom species (Dunstan *et al.* 1994). Evidence for the presence of a benthic primary source was found in the catches of the benthic hauls from the summit plateau, which contained a few living coralline algae. Rhodophyta are characterised by high proportions of 20:4(n-6) (Pettitt *et al.* 1989, Khotimchenko *et al.* 1990, Dembitsky *et al.* 1991, Dalsgaard *et al.* 2003) often in combination with high proportions of 20:5(n-3) (Pettitt *et al.* 1989, Dembitsky *et al.* 1991), which was the other abundant PUFA in the storage lipids of the epibenthic species studied. High proportions of these PUFAs might thus originate from or were supplemented by dietary input from Rhodophyta.

The $\delta^{13}C$ values reported for Rhodophyta species were generally enriched compared to phytoplankton with values mainly around -17 ‰, although large ranges from -13 to -35 ‰ were observed (Moncreiff and Sullivan 2001, Behringer and Butler 2006, Jaschinski *et al.* 2008). Benthic diatoms were reported with $\delta^{13}C$ stable isotope values ranging from about -14 to -17 ‰ (Kang *et al.* 2003, Riera and Hubas 2003). In this study, elevated $\delta^{13}C$ values were observed in epibenthic invertebrate consumers such as the omnivorous echinoid *C. longispinus*, which has a feeding preference for red algae, and for a group of predators/scavengers including the asteroid *L. ciliaris*, the hermit crab *D. arrosor* and the gastropod *C. lampas*, which feed on a range of benthic prey that may be enriched in their $\delta^{13}C$ values due to their use of the macroalgal food source.

An alternative or additional explanation for the high concentrations of 20:4(n-6) as well as 20:5(n-3) encountered in the epibenthic invertebrates might be selective retention of these essential fatty acids in the storage lipids. The ability to accumulate high proportions of 20:4(n-6) has been reported previously for echinoderms (Takagi *et al.* 1980, Sargent *et al.* 1983) and storage may be an adaptation to help overcome limitation of these essential fatty acids (Müller-Navarra 2008).

Considering the low light levels and the low abundance of living macroalgal specimen encountered on the summit plateau, the quantitative contribution of Rhodophyta to the organic carbon pool of the benthic community is expected to be negligible. Their qualitative contribution regarding a sufficient supply of dietary essential fatty acids for benthic consumers, on the other hand, might be of some importance. However, without direct measurements of macroalgal specimen as well as sediment and infaunal primary consumers, the assumption of Rhodophyta as a benthic primary food source and their potential nutritional contribution to the benthic food web on the summit of Seine Seamount remains tentative.

4.3 TROPHIC LEVEL AND IMPLICATIONS FOR THE BENTHIC FOOD WEB STRUCTURE

The epibenthic invertebrate species on the summit plateau of Seine Seamount were mainly opportunistic feeders which were able to utilise a wide range of benthic and/or pelagic food sources. Their $\delta^{15}N$ values covered a range equivalent to about 2 trophic levels, but most species occupied intermediate trophic level positions between the 2nd and 3rd trophic level irrespective of body size. The dominance of intermediate trophic level positions has been described previously as characteristic for food webs with predominantly omnivorous consumers (France *et al.* 1998, Marguillier 1997). The lack of a relationship between trophic position and body size across all taxa has been observed for diverse food webs, which are characterised by a broad range of primary consumer body sizes (Layman *et al.* 2005).

Based on $\delta^{15}N$ values, the epibenthic invertebrate species separated into 3 groups, excluding poriferan species. The first group was composed of the suspension feeding gorgonian species, the suspension/surface deposit feeding ophiuroid *A. squamata* and the omnivorous echinoid *C. longispinus* and was characterised by the lowest $\delta^{15}N$ values observed. According to trophic level enrichment, these $\delta^{15}N$ values suggested direct feeding on fresh phytodetritus, with some carnivorous feeding on primary consumers, and were confirmed by fatty acid biomarkers and $\delta^{13}C$ values.

The suspension feeding poriferan species were excluded from this group as they yielded curiously enriched $\delta^{15}N$ values, which placed 2 of the species on the same trophic level as the predatory gastropod *C. lampas*. These extremely high $\delta^{15}N$ values in poriferan species have been observed before and have been related to indiscriminate filtering of a variety of

suspended and sinking particulate material potentially including bacteria and their exudates (Iken *et al.* 2001, Nyssen *et al.* 2002, Mincks *et al.* 2008).

Species of the second group were enriched by approximately half a trophic level compared to the first group according to their average $\delta^{15}N$ values. The group consisted of opportunistic predators/scavengers, which covered a broad range of body sizes like the 2 asteroid species *A. irregularis* and *L. ciliaris* and the polychaete *H. tubicola* as well as the omnivorous echinoid *C. cidaris*. Their $\delta^{15}N$ values suggested primary consumers as their main food source and they appear to be closely linked to the pelagic food source with relatively fresh phytodetritus as base of the benthic food web.

The top predator *C. lampas* belonged to the third group and is known to prey on other echinoderm species, especially asteroids. $\delta^{15}N$ values were enriched by 1 trophic level compared to its potential prey in the second group and, thus, confirmed this feeding behaviour. The hermit crab *D. arrosor*, an opportunistic scavenger/predator, also belonged to this group and its $\delta^{15}N$ value, which was approximately intermediate to the second group and *C. lampas*, may include species from both of the other groups as potential prey, which is in accordance with its opportunistic feeding behaviour.

5. CONCLUSIONS

Analyses of stable isotope signatures and fatty acid composition of the storage lipids of epibenthic consumers and the total lipids of potential pelagic food sources proved useful tools to elucidate the dietary sources of selected epibenthic invertebrate species from the summit plateau of Seine Seamount. The majority of the epibenthic species occupied intermediate trophic level positions, which reflected a predominantly opportunistic feeding behaviour. High amounts of phytoplankton marker fatty acids and $\delta^{15}N$-enrichment in the range of surface particulate organic matter indicated close coupling between the surface phytoplankton production and the benthic food web through rapid deposition of relatively fresh phytodetritus. Essential nutrients were transferred via pelagic and benthic consumers to higher trophic levels. The contribution of a benthic primary source, presumably Rhodophyta, remained tentative and probably of low quantity, but might be of some importance as additional source of essential fatty acids.

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REFERENCES

Bavestrello G, Arillo A, Calcinai B, Cattaneo-Vietti R, Cerrano C, Gaino E, Penna A, Sarà M (2000) Parasitic diatoms inside Antarctic sponges. Biol. Bull. 198, 29–33

Beck T, Metzger T, Freiwald A (2005) *BIAS: Biodiversity Inventorial Atlas of Macrobenthic Seamount Animals*. OASIS, Hamburg: 118 pp.

Beckmann A, Mohn C (2002) The upper ocean circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. Ocean Dynamics, 52: 194-204

Beddingfield S, McClintock J (1993) Feeding behaviour of the sea star *Astropecten articulatus* (Echinodermata: Asteroidea): an evaluation of energy-efficient foraging in a soft-bottom predator. Marine Biology 115, 669–676

Behringer DC, Butler IV MJ (2006) Stable isotope analysis of production and trophic relationships in a tropical marine hard-bottom community. Oecologia 148: 334-341

Bell MV, Sargent JR (1985) Fatty acid analyses of phosphoglycerides from tissues of the clam *Chlamys islandica* (Muller) and the starfish *Ctenodiscus crispatus* (Retzius) from Balsfjorden, northern Norway. J Exp Mar Biol Ecol 87:31–40

Benvenuto C, Sartoni G, Gherardi F (2003) Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore. Journal of the Marine Biological Association of the UK, 83:3:457-461

Bergé, J-P, Barnathan G (2005) Fatty acids from lipids of marine organisms: molecular biodiversity, roles as biomarkers, biologically active compounds, and economical aspects. Adv Biochem Eng Biotechnol. 96:49-125

Billett DSM, Bett BJ, Rice AL, Thurston MH, Galéron J, Sibuet M, Wolff GA (2001) Long-term change in the megabenthos of the Porcupine Abyssal Plain (NE Atlantic). Progress in Oceanography, 50, 325-348

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology, 37, 911–917

Boehlert GW, Genin A (1987) A review of the effects of seamounts on biological processes. In: B. H. Keating, P. Fryer, R. Batiza, G. W. Boehlert (Eds.), Seamounts, Islands and Atolls. Geophysical monograph, vol 43, American Geophysical Union

Britton JC, Morton B (1994) Marine carrion and scavengers. Oceanography and Marine Biology: an Annual Review 32: 369-434

Brun E (1972) Food and feeding habits of *Luidia ciliaris* (Echinodermata: Asteroidea). J. Mar. Biol. Assoc. UK 1972; 52: 225–236

Cerrano C, Arillo A, Bavestrello G, Calcinai B, Cattaneo-Vietti R, Penna A, Sarà M, Totti C (2000) Diatom invasion in the Antarctic hexactinellid sponge *Scolymastra joubini*. Polar Biol. 23, 441–444

Cerrano C, Calcinai B, Cucchiari E, Di Camillo C, Totti C, Bavestrello G (2004a) The diversity of relationships between Antarctic sponges and diatoms: the case of *Mycale acerat*a (Porifera, Demospongiae). Polar Biol. 27, 231–237

Cerrano C, Calcinai B, Cucchiari E, Di Camillo C, Nigro M, Regoli F, Saragrave A, Schiaparelli S, Totti C, Bavestrello G (2004b) Are diatoms a food source for Antarctic sponges? Chem. Ecol. 20, 57–64

Checkley DM Jr., Miller CA (1989) Nitrogen isotope fractionation by oceanic zooplankton, Deep Sea Res., 36: 1449– 1456

Christensen A (1970) Feeding biology of the sea-star *Astropecten irregularis*. Ophelia 8, 1–134

Christiansen B, Martin B, Hirch S (2009)The benthopelagic fish fauna on the summit of Seine seamount, NE Atlantic: composition, population structure and diets. *Deep-Sea Research II*, in press

Christiansen B and Wolff GA (2009) The oceanography, biogeochemistry and ecology of two NE Atlantic seamounts: The OASIS project. Deep-Sea Research II, in press

Christie WW (1982) Esterification of Fatty-Acids in Adipose-Tissue. J.Science FoodAgriculture. 33:809-809

Cloern JE, Canuel EA, Harris D (2002) Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. Limnology and Oceanography, 47: 713–729

Coma R, Gili JM, Zabala M, Riera T (1994) Feeding and prey capture cycles in the aposymbiotic gorgonian Paramuricea clavata Mar Ecol Prog Ser 115:257–270

Dalsgaard, J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225-340

Davenport SR, Bax NJ (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Sciences, 59: 514-530

de Juan S, Cartes JE, Demestre M (2007) Effects of commercial trawling activities in the diet of the flat fish *Citharus linguatula* (Osteichthyes: Pleuronectiformes) and the starfish *Astropecten irregularis* (Echinodermata: Asteroidea). Journal of Experimental Marine Biology and Ecology 349: 152–169

Dembitsky VM, Pechenkina-Shubina EE, Rozentsvet OA (1991) Glycolipids and fatty acids of some sea weeds and marine grasses from the Black Sea. Phytochemistry, 30(7): 2279-2283

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta, 42: 495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta, 45: 341–351

De Ridder C, Lawrence JM (1982) Food and feeding mechanisms: Echinoidea. In: Jangoux M, Lawrence JM (eds) Echinoderm nutrition. Balkema, Rotterdam, pp 57–115

Dower J.F., Perry R.I. (2001) High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific. Fisheries Oceanography, 10: 268–274

Dunstan GA, Volkman JK, Barrett SM, Leroi JM, Jeffrey SW (1994) Essential polyunsaturated fatty acids from 14 species of diatom (Bacillariophyceae). Phytochem 35:155–161

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanographv and Marine Biology: an Annual Review 17: 193-284

Féral JP, Ferrand JG, Guille A (1990) Macrobenthic physiological responses to environmental fluctuations : the reproductive cycle and enzymatic polymorphism of a eurybathic sea-urchin on the northwestern Mediterranean shelf and slope. Continental Shelf Research, 10(9-11): 1147-1155

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry, 226: 497-509

France R, Chandler M, Peters R (1998) Mapping trophic continua of benthic food webs: body size-δ^{15}N relationships. Marine Ecology Progress Series, 174: 301–306

Franz D, Worley E (1982) Seasonal variability of prey in the stomachs of *Astropecten americanus* (Echinodermata: Asteroidea) from off Sourthern New England, USA. Estuarine, Coastal and Shelf Science 14, 355–368

Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography, 33: 1182–1190

Fullarton JG, Dando PR, Sargent JR, Southward AJ, Southward EC (1995) Fatty acids of hydrothermal vent *Ridgeia piscesae* and inshore bivalves containing symbiotic bacteria. J Mar Biol Assoc UK 75:455–468

Genin A, Dayton PK, Lonsdale PF, Spiess FN (1986) Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322:59–61

Genin A, Haury L, Greenblatt P (1988) Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep Sea Research, 35: 151-175

Genin A (2004) Biophysical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems, 50: 2-20

Gillet P, Dauvin J-C (2000) Polychaetes from the Atlantic Seamounts of the southern Azores: biogeographical distribution and reproductive patterns. Journal of the Marine Biological Association of the United Kingdom, 80: 3651-3661

Gillet P, Dauvin J-C (2003) Polychaetes from the Irving, Meteor and Plato seamounts, North Atlantic ocean: origin and geographical relationships. J. Mar. Biol. Ass. U.K., 83: 49-53

Ginger ML, Billett DSM, Mackenzie KL, Kiriakoulakis K, Neto RR, Boardman DK, Santos VLCS, Horsfall IM, Wolff GA (2001) Organic matter assimilation and selective feeding by holothurians in the deep sea: some observations and comments. Progress in Oceanography, 50: 407-422

Hazlett BA (1981). The behavioral ecology of hermit crabs. Annual Review of Ecology and Systematics, 12, 1-22

Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty acid biomarker approach. Mar Ecol Prog Ser 255: 193–206

Howell KL, Billett DSM, Tyler PA, Davidson R (2004) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a pigment biomarker approach. Marine Ecology Progress Series, 266: 103–110

Hudson IR., Pond DW, Billett DSM, Tyler PA, Lampitt RS, Wolff GA (2004) Temporal variations in fatty acid composition of deep-sea holothurians: Evidence of bentho-pelagic coupling. Marine Ecology Progress Series, 281: 109-120

Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Progress in Oceanography, 50: 383–405

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biology, 28, 238–249

Jacob U, Terpstra S, Brey T (2003) High-Antarctic regular sea urchins – the role of depth and feeding in niche separation. Polar Biol 26: 99–104

Jacob U, Mintenbeck K, Brey T, Knust R, Beyer K (2005) Stable isotope food web studies: a case for standardized sample treatment. Marine Ecology Progress Series, 287: 251–253

Jaschinski S, Brepohl DC, Sommer U (2008) Carbon sources and trophic structure in an eelgrass (*Zostera marina* L.) bed based on stable isotope and fatty acid analyses. Marine Ecology Progress Series, 358: 103-114

Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2002) Linking size-based and trophic analyses of benthic community structure. Mar. Ecol. Prog. Ser. 226: 77–85

Kang CK, Kim JB, Lee KS, Lee PY, Hong JS (2003) Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. Mar. Ecol. Progr. Ser. 259: 79-92

Kattner G, Fricke HSG (1986) Simple gas-liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. Journal of Chromatography, 361: 263-268

Kattner G, Hagen W, Lee RF, Campbell R, Deibel D, Falk-Petersen S, Graeve M, Hansen BW, Hirche H-J, Jónasdóttir S, Madsen ML, Mayzaud P, Müller-Navarra D, Nichols PD, Paffenhöfer G-A, Pond D, Saito H, Stübing D, Virtue P (2007) Perspectives on marine zooplankton lipids, Canadian Journal of Fisheries and Aquatic Sciences. 64(11): 1628-1639

Khotimchenko SV, Vaskovsky VE, Przhemenetskaya VF (1990) Distribution of eicosapentaenoic and arachidonic acids in different species of *Gracilaria*. Phytochemistry, 30(1): 207-209

Kiriakoulakis K, White M, Bett BJ, Wolff GA (2004) Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. Deep-Sea Research I, 51:1937-1954

Kiriakoulakis K, Vilas JC, Blackbird SJ, Arístegui J, Wolff GA (2009) Seamounts and organic matter—is there an effect? The case of Sedlo and Seine Seamounts. Part II. Composition of suspended particulate organic matter. Deep-Sea Research II, in press

Klein-Breteler WCM., Koski M, Rampen S (2004) Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by marine ciliate. – Mar. Ecol. Progr. Ser. 274: 199–208

Koslow JA (1997) Seamounts and the ecology of deep-sea fisheries. American Scientist, 85: 168– 176

Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar Ecol Prog Ser 213:111–125

Layman CA, Winemiller KO, Arrington DA, Jepson DB (2005) Body size and trophic position in a diverse food web. Ecology, 86: 2530–2535

Leitz T, H Beck, Stephan M, Lehma WD, de Petrocellis L, di Marzo V (1994) Possible Involvement of Arachidonic Acid and Eicosanoids in Metamorphic Events in *Hydractinia echinata* (Coelenterata; Hydrozoa). The Journal of Experimental Zoology 269:422-431

Longhurst A (1995) Seasonal cycles of pelagic production and consumption. Progress in Oceanography: 36, 77–167

Longhurst A (1998) Ecological Geography of the Sea. Academic Press, San Diego: 398 pp.

Lundsten L, Barry JP, Caillet GM, Clague DA, DeVogelaere AP, Geller JB (2009) Benthic Invertebrate Communities on Three Seamounts off Southern and Central California,USA. Mar Ecol Prog Ser.374:23-32

Marguillier S, van der Velde G, Dehairs F, Hemminga MA, Rajagopal S (1997) Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}C$ and $\delta^{15}N$. Marine Ecology Progress Series, 151: 115–121

McClain CR (2007) Is seamount biogeography island biogeography? J Biogeogr 34:2001–2008

Menge BA (1982) Effects of feeding on the environment: Asteroidea, in: Jangoux, M.; Lawrence, J.M. (Ed.). Echinoderm nutrition. pp. 521-551

Michener RM, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: R.H. Michener, K. Lajtha (Eds). Stable isotopes in ecology and environmental science. Blackwell, Oxford:138-157

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta, 48: 1135–1140

Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by delta-13C and delta-15N analysis. Deep-Sea Research II 55: 2502-2514

Moncreiff CA, Sullivan MJ (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analysis. Mar Ecol Prog Ser 215:93–106

Müller-Navarra D (2008) Food Web Paradigms: The Biochemical View on Trophic Interactions. International Review of Hydrobiology 93:4-5, 489-505

Mullineaux LS, Mills SW (1997) A test of the larval retention hypothesis in seamount-generated flows. Deep-Sea Res I 44:745–770

Mohn C, Beckmann A (2002a) Numerical studies on flow amplification at an isolated shelf break bank, with application to Porcupine Bank. Cont. Shelf Res., 22, 1325-1338

Mohn C, Beckmann A (2002b) The upper ocean circulation at Great MeteorSeamount. Part I: Structure of density and flow fields. Ocean Dyn., 52: 179-193

Nyssen F, Brey T, Lepoint G, Bouquegneau J-M, DeBroyer C, Dauby P (2002) A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods. Polar Biology 25: 280–287

Orejas C, Gili JM, Arntz W (2003) Role of small-plankton communities in the diet of 2 Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.). Mar Ecol Prog Ser 250:105–116

Pawson DL, Miller JE (1983) Systematics and ecology of the sea-urchin Genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and Eastern Pacific Oceans. Smithsonian Contributions to the Marine Sciences 20: 1-15

Peters J, Renz J, van Beusekom J, Boersma M, Hagen W (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin) - evidence from lipid composition. Marine Biology, 149: 1417-1429

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics, 18: 239-320

Pettitt TR, Jones AL, Harwood JL (1989) Lipids of the marine red algae, *Chondrus crispus* and *Polysiphonia lanosa*. Phytochemistry, 28 (2): 399-405

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, 83: 703–718

Post DM, Arrington DA, Layman CA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, 152: 179-189

Rau GH, Hopkins TL, Torres JJ (1991) ^{15}N:^{14}N and ^{13}C:^{12}C in Weddell Sea invertebrates: implications for feeding diversity. Marine Ecology Progress Series, 77: 1–6

Reemtsma T, Haake B, Ittekkot V, Nair RR, Brockmann UH (1990) Downward flux of particulate fatty acids in the central Arabian Sea. Marine Chemistry, 29: 183–202

Ribes M, Coma R, Gili JM (1999) Heterogenous feeding in benthic suspension feeders: the natural diet and grazing rate of the temperate gorgonian *Paramuricea clavata* (Cnidaria: Octocorallia) over a year cycle. Mar Ecol Prog Ser 183:125–137

Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa*. Mar Ecol Prog Ser 254:141–150

Rice AL, Billett DSM, Fry J, John AWG, Lampitt RS, Mantoura RFC, Morris RJ (1986) Seasonal deposition of phytodetritus to the deep-sea floor. Proceedings of the Royal Society of Edinburgh, 88: 265–279

Richer de Forges B, Koslow JA, Poore GCB (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405:944–947

Riedl R (1983) Fauna und Flora des Mittelmeeres. 3.Auflage, Parey Verlag, Hamburg, Berlin

Riera P, Hubas C (2003) Trophic ecology of nematodes from various microhabitats of the Roscoff Aber Bay (France): importance of stranded macroalgae evidenced by δ13C and δ15N. Mar. Ecol. Prog. Ser., 260: 151-159

Rogers AD (1994) The Biology of Seamounts. Advances in Marine Biology, 30: 305–349

Rossi S, Ribes M, Coma R, Gili JM (2004) Temporal variability in zooplankton prey capture rate of the passive suspension feeder *Leptogorgia sarmentosa* (Cnidaria: Octocorallia), a case study. Mar Biol 144:89–99

Sargent JR, Falk-Petersen S (1981) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid-winter. Mar. Biol. 62, 131-137

Sargent JR, Falk-Petersen IB, Calder AG (1983) Fatty acid compositions of neutral glycerides from the ovaries of the asteroids *Ctenodiscus crispatus*, *Asterias lincki* and *Pteraster militaris* from Balsfjorden, northern Norway. Mar Biol 72:257–264

Sargent JR, Henderson RJ (1995) Marine (n-3) polyunsaturated fatty acids. In: R.J. Hamilton (Ed). Developments in oils and fats. Blackie Academic and Professional, London: 32-65

Sherwood OA, Heikoop JM, Scott DB, Risk MJ, Guilderson TP, McKinney RA (2005) Stable isotopic composition of deep-sea gorgonian corals *Primnoa* spp.: a new archive of surface processes. Marine Ecology Progress Series, 301: 135-148

Takagi T, Eaton CA, Ackman RG (1980) Distribution of fatty acids in lipids of the common atlantic sea urchin *Strongylocentrotus droebachiensis*. Can J Fish Aquat Sci 37:195–202

Tsounis G, Rossi S, Laudien J, Bramanti L, Fernández N, Gili J-M, Arntz W (2005) Diet and seasonal prey capture rates in the Mediterranean red coral (*Corallum rubrum* L.), Marine Biology, 149(2): 313-325

Tyler PA, Gage JD (1984) Seasonal reproduction of *Echinus afinis* (Echinodermata: Echinoidea) from the Rockall Trough, northeast Atlantic Ocean. Deep-Sea Res. 31: 387-402.

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography, 46: 2061–2066

Wada E, Terazaki M, Kobaya Y, Nemoto T (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on biogeochemical structure of the food web. Deep-Sea Research, 34: 829–841

Wakeham SG, Lee C, Farrington JW, Gagosian RB (1984) Biogeochemistry of particulate organic matter in the oceans: results from sediment trap experiments. Deep-Sea Research, 31: 509–528

Warner G (1982). Food and feeding mechanisms: Ophiuroidea. in Jangoux M, Lawrence JM (Ed.): Echinoderm nutrition. AA Balkema: Rotterdam, pp. 161-181

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Marine Biology, 87: 313-323

Wigham BD, Tyler PA, Billett DSM (2003) Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter? Journal of the Marine Biological Association of the United Kingdom 83 (1): 175-188

Wilson RR, Kaufmann RS (1987) Seamount biota and biogeography. In: Keating BH, et al. (1987) Seamounts, Islands, and Atolls. Washington: American Geophysical Union. pp 227–237

FOOD SOURCES AND TROPHIC INTERACTIONS OF BENTHOPELAGIC FISH SPECIES ON THE SUMMIT PLATEAU OF SEINE SEAMOUNT, NE ATLANTIC

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ABSTRACT

Several hypotheses have been developed to explain the trophic mechanisms that support the often large benthopelagic fish stocks at seamounts. The present study investigated the diets, nutritional pathways and trophic interactions of benthopelagic fish species on the summit plateau of Seine Seamount (34°N, 14°W, NE Atlantic, summit depth: 170 m) particularly with regard to these hypotheses. A combined approach of gut content, stable isotopes and fatty-acid biomarker analyses was employed. Fish species included zooplanktivores, benthivores, piscivores and species with mixed crustacean/ cephalopod/ fish diets. The dominance of pelagic prey in the guts of zooplanktivorous species, stable isotope enrichments in the range of pelagic prey items, high proportions of phytoplankton and zooplankton marker fatty acids in the storage lipids of the benthopelagic fishes and the similarity with fatty acid signatures of pelagic prey all suggested a strong reliance on pelagic prey and a close coupling between the pelagic food source and the benthopelagic fish fauna. Elevated levels of arachidonic acid in a benthivorous species indicated a minor dietary contribution of rhodophyta to the benthopelagic community. The lack of larger diel vertically migrating taxa in the guts of the benthopelagic fishes suggested current-driven horizontal fluxes of non- or weakly-migrating zooplankton as main food supply to the resident fish fauna. Habitat- and prey-related resource partitioning among zooplanktivorous fish species and ontogenetic stages were indicated by differences in gut contents, stable isotopes and storage lipid fatty acid signatures. The benthopelagic fishes studied occupied intermediate trophic level positions between the 3rd and 4th trophic level despite differences in body size and feeding mode and indicated a food web composed of predominantly omnivorous consumers.

PROBLEM

Seamounts are often inhabited by large standing stocks of resident benthopelagic fish species such as rockfishes (*Sebastes* spp.), sablefish (*Anoplopoma fimbria*), pelagic armourhead (*Pseudopentaceros wheeleri*), alfonsin (*Beryx* spp.) and orange roughy (*Hoplostethus atlanticus*) (Isaacs & Schwartzlose 1965, Uchida & Tagami 1984, Rogers 1994, Koslow 1997, Koslow *et al.* 2000, Clark 2001, Dower & Perry 2001). Aggregations of pelagic fishes such as sharks, rays, tuna and swordfish have also been frequently observed in the vicinity of seamounts (Yasui 1986, Klimley *et al.* 2005). The association of such commercially valuable fish species with seamounts resulted in the development of a seamount trawling and long lining fisheries over the past fifty years which is exploiting seamount habitats and the waters overlying them throughout the world's oceans (Clark 1999, Koslow *et al.* 2000). Exploitation of the seamount-associated fish community has stimulated scientific interest in the trophic mechanisms supporting fish production at seamounts. Several hypotheses have been developed to explain the supply of sufficient energy to sustain fish aggregations at seamounts despite the often impoverished nutritional conditions of the ambient oceanic regions. These hypotheses are based on interactions between seamounts and the surrounding open ocean current regimes that influence local hydrographic conditions (Roden 1987, Gonzales *et al*. 2001). The hypothesis of enhanced local *in situ* productivity proposed a seamount-induced local increase in primary production due to a combination of local nutrient-upwelling and particle-retention by Taylor columns which would promote local secondary production that could sustain resident fish populations (Uda & Ishino 1958). Taylor columns are the formation of an anti-cyclonic circulation cell trapped at the seamount summit region (e.g. Beckmann & Mohn 2002). Although upwelling and elevated chlorophyll concentrations related to Taylor column formation have been observed above a number of seamounts (Genin & Boehlert 1985, Dower *et al*. 1992, Dower & Mackas 1996, Mouriño *et al*. 2001), support for local enhancement of secondary production remained weak (Uda & Ishino 1958, Genin & Boehlert 1985) and appeared insufficient to sustain the aggregations of fishes observed in the vicinity of seamounts (Tseitlin 1985, Koslow 1997). The sound-scattering layer interception hypothesis (Isaacs & Schwartzlose 1965) proposed the presence of increased food supply to the seamount fauna due to topographic blockage and trapping of the vertically migrating fauna of the sound-scattering layer during descend. This mechanism has been

suggested to provide sufficient prey to maintain fish aggregations at seamounts (Rogers 1994, Parin *et al.* 1997, Koslow 1997, Genin 2004) and was supported by studies of the gut contents of rockfishes (Genin *et al.* 1988) and pelagic armourheads (Seki & Somerton, 1994) that contained vertical migrators as dominant prey. It has further been suggested that the resident seamount fauna is sustained by the enhanced flux of prey organisms past the seamounts from adjacent oceanic regions due to the amplification of near-bottom flows (Tseitlin 1985, Genin *et al.* 1988, Koslow 1997, Genin 2004). Increased food supply might also result from behavioural responses of zooplankton to vertical water mass movement caused by topographic interaction with ocean currents, when zooplankton swim vertically in order to maintain their depth and become locally aggregated (Genin 2004).

Gut content analyses provide information on recent feeding and types of prey ingested by a consumer, but might underestimate the importance of rapidly digested prey (e.g., MacDonald et al. 1982). In contrast to gut content analyses, biochemical markers provide an analysis of assimilated diet integrated over time (e.g., Davenport & Bax 2002, Dalsgaard *et al.* 2003). Biochemical markers, such as stable isotopes and fatty acids, have been used extensively in studies of trophic ecology, including marine systems (e.g. Iken *et al.* 2001, 2005, Davenport & Bax 2002, Dalsgaard *et al.* 2003 and references therein, Iverson *et al.* 2004). Isotopic signatures, i.e. the ratio of the rare heavier isotope to the common lighter isotope, change from prey to predator due to chemical reactions during metabolic processes (Peterson & Fry 1987). This change, termed trophic fractionation, occurs in a predictable way for the different elements and can be used to evaluate carbon sources and trophic position of an organism (e.g. Peterson & Fry 1987, Vander Zanden & Rasmussen 2001, Post 2002). The use of fatty acids biomarkers to trace predator-prey relationships in the ocean is based on the observation that particular fatty acids can only be biosynthesised by certain phytoplankton and macroalgal species and that these fatty acid patterns are transferred conservatively from primary producers to their consumers and among consumers (Dalsgaard *et al.* 2003 and references therein). In contrast to the conservative fatty acid composition of structural lipids (mainly phospholipids) of consumers, which are relatively independent of dietary input, the fatty acid profiles of neutral lipids, which are used for energy storage, are much more variable and more readily influenced by dietary

input (Sargent & Henderson 1995). In this study, the fatty acid signature of the neutral lipid fraction was used to investigate the diets of the benthopelagic fish species studied.

The aim of this study was to investigate the food sources, nutritional pathways and trophic interactions of the benthopelagic fish fauna on the summit plateau of Seine Seamount using the combined approach of gut content and biochemical marker analyses. Specific objectives were:

1. to identify the dietary sources of the resident fishes on the summit plateau of Seine Seamount,
2. to elucidate the nutritional link sustaining the benthopelagic fish community with special respect to the sound scattering layer interception hypothesis as mechanism of enhanced food supply, and
3. to investigate the trophic structure and interactions of the benthopelagic fish community.

STUDY AREA

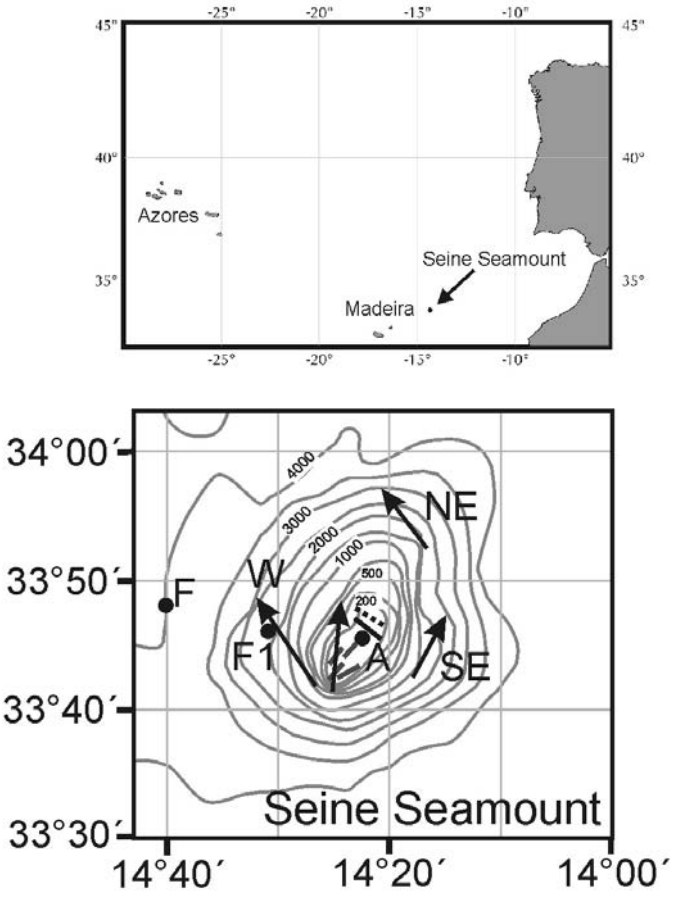

Figure 1.

Location and bathymetry of Seine Seamount. Sampling locations of fish trawls are indicated for December 2003 (broken line), March 2004 (solid line) and May 2005 (solid grey line). POM_{susp} water sample locations (filled circles) are indicated as A for summit, F1 and F for the west slope. MOCNESS zooplankton hauls during the survey in March 2004 are given as arrows and haul locations are indicated as A for the summit, NE (northeast), SE (southeast), and W (west) for the slope locations.

Seine Seamount is located northeast of Madeira (33°50'N - 14°20'W) within the oligotrophic regime of the eastern North Atlantic Subtropical Gyre (NASE) biogeochemical province as defined by Longhurst (1995, 1998) (Fig. 1). It is a single summit, cone-shaped seamount which rises from more than 4000 m depth to a summit plateau at ~170 m. The summit plateau is dominated by coarse biogenic sediments with ripple marks, indicative of strong bottom current flows, with few outcropping rocks (Christiansen, unpublished data).

MATERIAL AND METHODS

Benthopelagic fish species were sampled on the summit plateau of Seine Seamount at a water depth of 170-190 m during three field surveys in December 2003 (11 November – 6 December 2003; FS *Meteor*, M60/1), March 2004 (25 March – 8 April; FS *Poseidon*, P309) and May 2005 (14 May – 1 June; FS *Poseidon*, P322) (Fig. 1, Tab. 1). Animals were collected using an epibenthic sledge (December 2003), an ottertrawl with a 45-feet footrope length (March 2004) and an 80-feet footrope length (May 2005) and a 2 m-beamtrawl (May 2005).

Tissue samples of the dorsal muscle of benthopelagic fish species were dissected for both stable isotope and lipid analysis directly upon recovery of the trawls. Stable isotope samples were stored at -20°C and lipid samples at -80°C or in liquid nitrogen until biochemical analyses. Fish species caught during the survey in May 2005 were frozen whole at -20°C and muscle tissue samples were dissected from the frozen specimen after return to the home-laboratory. Stomachs of *T. picturatus* were dissected on board and stored individually in 4% borax-buffered formaldehyde-seawater solution. Guts of the other tissue-sampled individuals were dissected after arrival at the home-laboratory. Like the remaining catch of the surveys in December 2003 and March 2004, the tissue-sampled individuals were preserved in 4% borax-buffered formaldehyde-seawater solution after their total length was determined. Additional muscle tissue samples for stable isotope analysis were dissected from formalin-preserved specimen at the home-laboratory for selected, previously sampled species concurrently with reference samples from individuals that had been tissue-sampled prior to preservation.

Table 1. Sampling data for benthopelagic fish trawls at Seine Seamount during 3 surveys in December 2003, March 2004 and May 2005. MOCNESS hauls for zooplankton sampling and CTD-Rosette water sampling for POM_{susp} were carried out during the survey in March 2004.

Gear-Haul	Date	Sampling time (UTC)	Location	Sampling depth (m)	Water depth (m)	Latitude N	Longitude W
Meteor 60/1, December 2003							
EBS-2	04.12.2003	17:33 - 18:30	Summit-A	176-193	176-193	33°45.9	14°21.7
Poseidon 309, March 2004							
OT45-1	31.03.2004	14:48 - 15:11	Summit-A	166-172	166-172	33°43.2	14°25.1
ROS-18-4	29.03.2004	21:37 - 21:43	Summit-A	50	171	33°46.0	14°21.8
ROS-22-1	30.03.2004	21:20 - 21:32	Wslope-F	50	4008	33°48.0	14°40.1
ROS-28-1	01.04.2004	14:13 - 14:20	Wslope-F1	50	2479	33°46.0	14°30.9
MOC-02	29.03.2004	13:34 - 16:48	Summit-A	50 - 150	174	33°41.4	14°25.5
MOC-03	29.03.2004	23:57 - 02:05	Summit-A	50 - 163	168	33°41.1	14°26.0
MOC-04	01.04.2004	10:36 - 13:20	W slope	200 - 600	1188	33°42.4	14°27.7
MOC-05	01.04.2004	21:04 - 23:16	W slope	50 - 600	1173	33°42.1	14°27.5
MOC-07	03.04.2004	21:25 - 23:54	NE slope	50 - 300	1547	33°51.8	14°16.9
MOC-08	04.04.2004	12:42 - 14:51	NE slope	50 - 600	1595	33°52.0	14°16.9
MOC-09	05.04.2004	22:40 - 00:15	SE slope	50 - 600	1360	33°43.0	14°18.6
MOC-10	06.04.2004	09:57 - 11:09	SE slope	50 - 600	1478	33°43.9	14°17.5
Poseidon 322, May 2005							
OT80-1	15.05.2005	14:53 - 15:43	Summit	170-174	170-174	33°42.6	14°24.7
BT-1	17.05.2005	15:40 - 16:30	Summit	172-173	172-173	33°42.1	14°24.7
BT-2	18.05.2005	11:10 - 12:00	Summit	169-170	169-170	33°43.4	14°24.8
OT80-2	18.05.2005	13:42 - 14:38	Summit	165-168	165-168	33°44.5	14°24.0

Samples for suspended particulate organic matter (POM_{susp}) and zooplankton were collected during the survey in March 2004 at locations above the summit and slopes of Seine Seamount (Fig. 1, Tab. 1). Water samples for stable isotope analyses of POM_{susp} were collected at 50 m depth using Niskin bottles mounted on a CTD rosette. Prior to filtration, the sampled water was passed through a 300 µm mesh-size sieve to remove larger zooplankton organisms that would bias the POM_{susp} data. Water samples (10 l per filter) were vacuum filtered immediately on board at low pressure on pre-combusted (450°C; 5 h) GF/C filters (Whatman®; 55 mm diameter; nominal pore size 1.2). All filter samples were wrapped in muffled (450ºC; 5 h) aluminium foil and immediately frozen at -20ºC until further analysis.

Zooplankton, micronekton and mesopelagic fishes were sampled using a 1 m^2-Double-MOCNESS (Multiple Open/Closing Net and Environmental Sensing System, Wiebe *et al.* 1985) with a 1 m^2-opening and equipped with 20 dark coloured nets of 0.333 µm mesh size. The nets were sequentially opened and closed at defined depths and depth was controlled by a temperature corrected pressure sensor. Zooplankton samples were

taken with stratified oblique hauls starting at the greatest sampling depth and progressing up towards the surface at a towing speed of 2 knots. Sampling depths above the slopes of the seamount ranged from 50 – 600 m to include diel vertically migrating species at their depth range during day hauls. Directly upon recovery of the MOCNESS, specimen for stable isotope and lipid analyses of selected species were sorted on board using a dissecting microscope. Depending on species size, each sample consisted of 1 to 200 individuals. Stable isotope samples were stored at -20°C and lipid samples in liquid nitrogen until further analyses.

For diet analyses, guts of benthopelagic fish species were dissected from those individuals that had been tissue-sampled for stable isotope and lipid analyses. All food items were identified to the lowest taxonomic level possible using a dissecting microscope and prey size was measured. Due to the progressed digestion state, most prey items could not be identified to species or genus level. The percentage frequency of occurrence (%FO) and percentage contribution to the total number of prey (%N) were determined for each prey group. The lengths of benthic polychaetes represent minimum size as individuals were fragmented and fragment size was used.

For the analysis of carbon and nitrogen isotopic ratios ($\delta^{13}C$ and $\delta^{15}N$), frozen samples were lyophilised for at least 48 h at -60°C. Isotopic compositions of the POM_{susp} filter samples were then measured with a Thermo-Finnigan Delta^{+} Advantage Mass Spectrometer with a Costech EAS Elemental Analyser at UCSB/MSI Analytical Laboratory (analytical error ≤0.25 ‰). Tissue samples of benthopelagic and mesopelagic fishes were treated prior to isotopic analysis to remove lipids, because lipids are depleted in ^{13}C and differences in lipid content can bias $\delta^{13}C$ values (Peterson & Fry 1987, Wada *et al.* 1987). Lipids of lyophilised tissue samples were removed using Soxhlet extraction with a dichloromethane:methanol mixture (DCM:MeOH 2:1, v:v) for 4-6 hours (Bligh & Dyer 1959). Afterwards the samples were lyophilised again (48 h) and ground to a homogenous powder using pestle and mortar. Lipids of zooplankton and micronekton samples were not removed to avoid loss of biomass of the often very small sample quantities. Instead, taking C:N as a proxy for lipid content, lipid-normalised values of $\delta^{13}C$ were calculated according to equations in Post *et al.* (2007) ($\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$ (Eq. 3)). Inorganic carbonates, which would introduce a positive bias in $\delta^{13}C$ measurements as they tend to be less negative in $\delta^{13}C$

than other body fractions (DeNiro & Epstein 1978, Fry 1988, Rau *et al.* 1991, Cloern *et al.* 2002), were removed from calcareous zooplankton samples (ostracods, pteropods) by adding 1 mol l^{-1} hydrochloric acid (HCl) drop-by-drop to each powdered sample until CO_2 release stopped (Jacob *et al.* 2005). The samples were dried at 60°C and ground to homogenous powder again. Stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) and C:N analyses of the pulverised animal samples were performed simultaneously with a THERMO/Finnigan MAT Delta plus isotope ratio mass spectrometer, coupled to a THERMO NA 2500 elemental analyser via a THERMO/Finnigan Conflo II- interface at the GeoBio-Center^{LMU} in Munich, Germany (analytical error <0.15 ‰). Standards used for nitrogen and carbon stable isotope determination were atmospheric N_2 and Peedee Belemnite (PDB), respectively.

Stable isotope values were expressed in δ-notations as parts per thousand (‰), where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively:

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

The ratio of carbon isotopes ($\delta^{13}C$) changes little (< 1 ‰) between trophic levels and is used to evaluate the sources of carbon for an organism (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987, Michener & Schell 1994). The ratio of nitrogen stable isotopes ($\delta^{15}N$), on the other hand, is typically enriched by 3-4 ‰ (average 3.4 ‰) relative to its diet and is used to estimate trophic position of a consumer (Minagawa & Wada 1984). In this study, trophic levels (TL) were estimated using mean $\delta^{15}N$ values of POM_{susp} as baseline of the first trophic level (TL1) and an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level.

Additional muscle tissue samples for stable isotope analysis were taken from four benthopelagic fish species from formalin-preserved specimen (Tab. 2). Preservation of fish samples with formalin has been reported to cause a decrease in $\delta^{13}C$ values and, to a smaller extent, an increase in $\delta^{15}N$. The reported changes were of small magnitude and directionally uniform which allowed for a correction of the bias prior to interpreting the data (Bosley & Wainright 1999, Kaehler & Pakhomov 2001, Arrington & Winemiller 2002, Sarakinos *et al.* 2002, Koppelmann *et al.* 2009). In this study, reference specimen, which had been sampled prior to formalin preservation and were re-sampled together

with the additional formalin-preserved specimen, were used to account for possible preservation effects. Differences in $\delta^{13}C$ and $\delta^{15}N$ signatures of frozen and formalin-preserved muscle tissue samples from the same individuals were significant for all species and juvenile stages ($P<0.05$; paired *t*-test) except for $\delta^{15}N$ values of adult *Macroramphosus* spp. and juvenile *Centracanthus cirrus* (Tab. 2). Formalin preservation resulted in a slight increase of $\delta^{15}N$ values (0.24 to 0.43 ‰) and a decrease of $\delta^{13}C$ values (1.31 to 1.54 ‰), which were in the range of values reported in other studies (see references above). Stable isotope values of formalin-preserved samples were corrected for the significant preservation effects by adding ($\delta^{13}C$) or subtracting ($\delta^{15}N$) the species- and stage-specific mean deviations prior to data analysis (Tab. 2).

Table 2. Comparison of sample preservation effects on isotopic values (mean ± SD) of fish muscle tissue. Mean $\delta^{15}N$ and $\delta^{13}C$ values of samples from the same individuals preserved frozen (-20°C) and in 4% borax-buffered formaldehyde-seawater solution are listed with mean preservation-related isotopic differences (Δ). Preservation-related differences in isotopic values were tested for significance using a paired *t*-test with significance levels of ** $P<0.01$, * $P<0.05$ and NS = not significant.

Species	n	$\delta^{15}N$ (‰)				$\delta^{13}C$ (‰)			
		frozen	formalin	Δ	*P*	frozen	formalin	Δ	*P*
Macroramphosus spp.	5	9.57 (0.33)	9.70 (0.46)	0.12 (0.17)	NS	-19.31 (0.10)	-20.61 (0.09)	-1.31 (0.12)	**
Capros aper	6	9.09 (0.41)	9.33 (0.37)	0.24 (0.15)	*	-19.25 (0.44)	-20.59 (0.45)	-1.35 (0.33)	*
Centracanthus cirrus	3	9.37 (0.26)	9.80 (0.20)	0.43 (0.08)	*	-18.75 (0.22)	-20.29 (0.05)	-1.54 (0.17)	**
C. cirrus juv.	3	8.50 (0.58)	8.74 (0.81)	0.24 (0.23)	NS	-20.05 (0.47)	-21.52 (0.32)	-1.47 (0.18)	**
Anthias anthias	3	9.80 (0.11)	10.22 (0.10)	0.42 (0.03)	**	-18.77 (0.21)	-20.26 (0.11)	-1.49 (0.14)	**

Prior to lipid extraction for fatty acid biomarker analyses, frozen fish and zooplankton samples were lyophilised for at least 48 h. Lipids were extracted with minor modifications as described by Hagen (2000) based on the method of Folch *et al.* (1957) and Bligh & Dyer (1959) using ultrasonic disruption in a dichloromethane (DCM):methanol (MeOH) (2:1/v:v) mixture and a washing procedure with aqueous KCl solution (0.88%). A known amount of internal standard (nonadecanoic acid) for quantification of fatty acids was added to the sample prior to extraction. Total lipid extracts of the benthopelagic fish species were separated into lipid classes by solid phase extraction using 1 ml glass columns filled with 100 mg SiOH (CHROMABOND®, Macherey-Nagel) on a vacuum manifold according to the method of Peters *et al.* (2006). Prior to sample load, the columns were washed with a solvent sequence of acetone, diethylether, and hexane:diethylether-mixtures to remove residues. After column conditioning with 4 ml of hexane, a subsample of the total lipid extract

dissolved in hexane was added. The neutral lipid fraction was eluted with 2.5 ml hexane:diethylether (95:5/v:v) and 2.5 ml hexane:diethylether (1:1/v:v).

Fatty acid analyses were performed on subsamples of the neutral lipid fractions of the benthopelagic fish species and on subsamples of the total lipids of zooplankton samples. Lipid extracts were hydrolysed and fatty acids converted to their methyl ester derivatives (FAME) by adding 250 µl hexane and 1 ml of 3% concentrated sulphuric acid (H_2SO_4) in methanol to the dried extracts. The solution was left to react at 80°C for 4 h. After cooling, 4 ml of bi-distilled water were added, and FAMEs were extracted three times with 2 ml hexane (Kattner & Fricke, 1986). Samples were analysed using a gas chromatograph (Agilent 6890N) equipped with a DB-WAX column (30 m length × 0.32 mm inner diameter, 0.25 µm film thickness) operated with helium as carrier gas (constant flow 2.0 ml min^{-1}). The following oven temperature program was used: 40°C held for 5 min, 40-150°C at 10°C min^{-1}, 150°C held for 5min, 150-220°C at 2°C min^{-1}, 220°C held for 20 min. Samples were injected using a temperature programmed vaporiser injector (Gerstel® CIS3) in solvent vent mode (injection volume 5 µl, injection speed 10 µl s^{-1}, injection temperature -40°C (temperature program: -40–40°C at 6°C s^{-1} after 0.51 min, 40°C held for 0.1 min, 40-250°C at 12°C s^{-1}, 250°C held for 2.0 min), vent flow 50 ml min^{-1}, vent pressure: 34 kPa, splitless time 0.5-1.5 min, purge flow: 50 ml min^{-1}, split flow: 20 ml min^{-1}). The FAMEs were detected by flame ionisation (FID, detector temperature: 250°C, hydrogen flow: 30 ml min^{-1}, air flow: 350 ml min^{-1}, makeup (N_2) flow: 30 ml min^{-1}) and identified by comparing retention times with those obtained from known standards (Supelco™ 37 Component FAME Mix, single FAME standards: nonadecanoic acid (19:0), Octadecatetraenoic acid (18:4(n-3)) and/or from the literature. Data was processed using Agilent GC ChemStation Software©. Total fatty acids were calculated as the sum of all identified fatty acids from the chromatogram.

All statistical analyses were performed using the software SPSS. Normal distribution of the data was checked using the Shapiro-Wilk-test and homogeneity of variances using the Levene-test. Preservation-related effects on isotopic values were tested for significance using a paired *t*-test. A Student's T-test was used to test temporal differences in stable isotope signatures of benthopelagic fish species. Species- and stage-specific differences in $\delta^{13}C$ and $\delta^{15}N$ between zooplanktivorous fish species

sampled during the survey in March 2004 were tested using a non-parametric Kruskal-Wallis test followed by a Dunnet T3 *post-hoc* comparison test. The Spearman-Rank-Order Correlation coefficient (r_S) was used to analyse the correlation between the total length of individual benthopelagic fishes and their $\delta^{15}N$ signature. For identification of coherences between variables, principal component analysis (PCA) of the most abundant fatty acids in the storage lipids of benthopelagic fishes was performed with arc *sine* square root transformed percentage data of relative fatty acid compositions on the correlation matrix, extracting non-rotated components with eigenvalues >1.

RESULTS

The ten benthopelagic fish species sampled for trophic analyses covered a size range from 6.5 to 146 cm and belonged to 4 feeding types, according to literature, which included benthivores, primarily zooplanktivores, primarily piscivores and species with mixed crustacean/cephalopod/fish diets (Tab. 3).

Table 3. Sample data summary of benthopelagic fish species collected on the summit plateau of Seine Seamount during surveys in December 2003, March 2004 and May 2005. Feeding type abbreviations are according to literature (1 - 9) and refer to B = benthivore, Z = predominantly zooplanktivore, P = predominantly piscivore, M = mixed crustacean/cephalopod/fish diet. Total fish length (cm) is given as mean with ranges. juv. = juvenile, n_{Gut} = number of fish guts used for gut content analysis, n_{SI} = number of individuals sampled for stable isotope analysis, n_{Lip} = number of individuals sampled for lipid analysis. Feeding type source data: (1) Whitehead *et al.* 1986, (2) Halpern & Floeter 2008, (3) Fock *et al.* 2002a, (4) Matthiesen *et al.* 2003, (5) Lopes *et al.* 2006, (6) FishBase 2009, (7) Morato *et al.* 1999, (8) O'Sullivan *et al.* 2004, (9) Ehrich 1974.

Order	Family	Species	Sampling period	Feeding type	Total length mean (ranges)	n_{Gut}	n_{SI}	n_{Lip}
Pleuronectiformes	Bothidae	*Arnoglossus rueppelli*	Dec 03	B[1, 2]	11.8 (10.5-14.5)	6	3	3
Syngnathiformes	Centriscidae	*Macroramphosus* spp.	Dec 03	Z[1, 3, 4, 5]	11.4 (11.0-11.7)	3	3	3
		Macroramphosus spp.	Mar 04		12.5 (11.0-14.0)	16	22	5
		Macroramphosus spp. juv.	Mar 04		7.3 (6.5-8.0)	6	2	2
Zeiformes	Caproidae	*Capros aper*	Mar 04	Z[1, 3, 5]	11.6 (9.0-14.5)	20	20	5
Perciformes	Serranidae	*Anthias anthias*	Mar 04	Z[1]	18.5 (16.0-20.0)	6	10	3
	Centracanthidae	*Centracanthus cirrus*	Mar 04	Z[2]	19.4 (18.5-20.0)	6	10	2
		C. cirrus juv.	Mar 04		8.0 (7.5-8.5)	6	8	3
	Carangidae	*Trachurus picturatus*	Mar 04	M[1, 9]	38.5 (37.0-41.0)	4	4	4
		Trachurus picturatus	May 05		38.7 (38.0-39.5)	-	3	3
Scorpaeniformes	Scorpaenidae	*Pontinus kuhlii*	May 05	M[6]	25.1 (19.0-32.5)	-	6	-
Anguilliformes	Congridae	*Conger conger*	May 05	P[7, 8]	122 (104-146)	-	4	-
Scopeliformes	Aulopidae	*Aulopus filamentosus*	May 05	M[6]	38.5 (36.0-41.0)	-	2	-
Torpediformes	Torpedinidae	*Torpedo nobiliana*	May 05	P[1]	69.5 (52.0-87.0)	-	2	-

GUT CONTENTS OF BENTHOPELAGIC FISH SPECIES

Gut contents of 6 of the most abundant fish species caught on the summit plateau of Seine Seamount in December 2003 and March 2004 were analysed for their prey composition and a total of 36 prey categories in 73 fish guts were found, representing 4316 total prey items (Tab. 4).

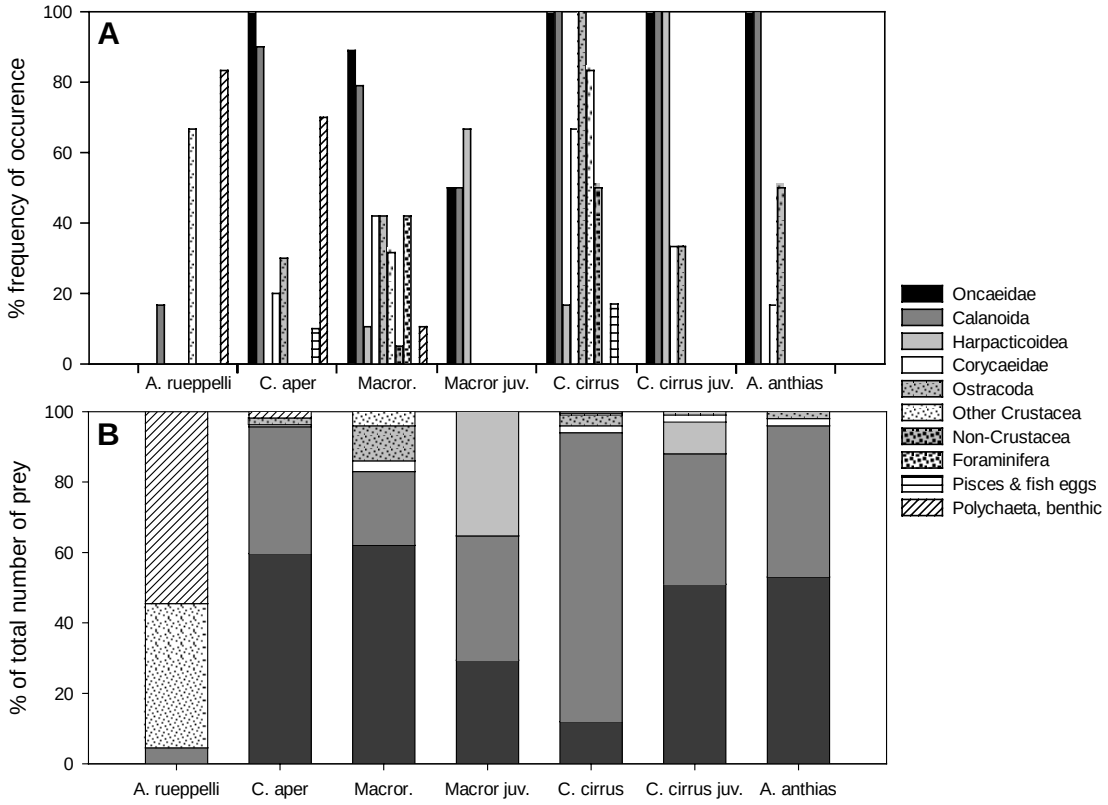

Figure 2. Prey consumed by benthopelagic fish species as (A) percentage frequency of occurrence (%FO) and (B) percentage of total number of prey (%N) during surveys in December 2003 and March 2004. Values refer to Table 4. Foraminifera were not included in calculations of relative abundance (%N). Macror. = *Macroramphosus* spp.

Regarding frequency of occurrence (FO) and total abundance (N) of prey, the gut contents of the benthivorous flatfish *A. rueppelli* were dominated by benthic polychaetes (N: 55 %, FO: 83 %) and non-copepod crustaceans (N: 41 %, FO: 67 %) such as mysids, decapods and unidentified crustacean pieces in a size range of 2-15 mm (Tab. 4, Fig. 2A,B).

Stomach contents of the blue jack mackerel *T. picturatus*, which feeds on a mixed diet of crustaceans, cephalopods and fish according to literature, consisted exclusively of fish remains, mainly juvenile *Macroramphosus* spp. (Tab. 4).

Table 4. Prey consumed by benthopelagic fish species as percentage frequency of occurrence (%FO) and percentage of total number of prey (%N) for specimen caught in December 2003 and March 2004. Total numbers of fish guts analysed and total number of prey items are given at the bottom of the appropriate columns (Totals). [A] = sampled in December 2003, [B] = sampled on both surveys, all others sampled in March 2004, [C] = not included in calculations of %N, n.q. = not quantified.

Prey category	Prey size range (mm)	*A. rueppelli* [A]		*C. aper*		*Macroramphosus* spp. adult [B]		*Macroramphosus* spp. juvenile		*C. cirrus* adult		*C. cirrus* juvenile		*A. anthias*		*T. picturatus*	
		%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N
Crustacea																	
Copepoda																	
Oncaeidae	1-1.5			100	59.6	89	62.2	50	29.4	100	12.3	100	51.4	100	52.9		
Corycaeidae	1-2			20	0.6	42	2.7			67	1.6	33	1.6	17	2.2		
Sapphirinidae	1-2					5	0.5										
Harpacticoidea	1					11	0.3	67	35.3	17	0.0	100	8.8				
Oithonidae	1			5	0.1					17	0.1						
Calanoida																	
Unident. Calanoida	1-4			90	34.3	53	11.0	50	35.3	100	61.3	100	37.1	100	37.9		
Candacia sp.	2-4			20	0.7	16	0.7			67	0.5			17	0.6		
Pleuromamma sp.	1-2	17	4.5	5	0.1	16	0.5			83	1.1						
Euchaeta sp.	1.5-2.5			5	0.2	5	0.2			83	1.0						
Lucicutia sp.	1.5-2			5	0.2	5	0.5			100	3.6						
Clausocalanus sp.	1-1.2					21	5.9			100	13.2			17	4.1		
Rhincalanus nasutus	3-4			15	0.4	5	0.2			100	0.5						
Nannocalanus sp.	2.1-2.5					11	1.3			50	0.2						
Neocalanus sp.	2									17	0.2						
Temora sp.	2					5	0.2										
Aetideidae	1.8-2									50	0.2						
Scoletrichidae	2									33	0.4						
Ostracoda	0.5-1.5			30	1.9	42	9.7			100	2.6	33	1.0	50	2.2		
Mysidacea	7-10	50	13.6			11	1.0										
Euphausiacea, Furc. & Calyp.	1-4.5					5	2.0			83	0.6						
Decapoda	2-10	17	9.1							17	0.0						
Amphipoda	4					5	0.2			17	0.0						
Unident. Crustacea pieces		67	18.2			5	0.3										
Foraminifera																	
Unident. Foram. fragments [C]	0.5-1					42	n.q.										
Mollusca																	
Gastropoda, pelagic	1-2					5	0.3										
Chaetognatha																	
Unident. Chaetognatha	4-6									17	0.1						
Annelida																	
Polychaeta, pelagic	ca. 3									50	0.4						
Polychaeta, benthic	ca. 6-20	83	54.5	70	1.7	11	0.3										
Pisces																	
Macroramphosus spp. juv.	60-75															75	100
Fish eggs	1									17	0.0						
Fish scales [C]				10												25	
Miscellaneous [C]																	
Shell fragments		17				5											
Echinoderm remains						5											
Sand grains		17				5											
Totals		6	22	20	805	19	598	6	17	6	2158	6	385	6	314	4	17

In the guts of the 4 zooplanktivorous species examined (Tab. 4, Fig. 2A,B), prey items of 1-2 mm size contributed 96-100 % of total prey abundance irrespective of differences in predator size. Smallest maximum prey sizes were observed for juveniles of *Macroramphosus* spp. and *C. cirrus* (both 2 mm). Copepods were the dominant prey in the guts of all zooplanktivores (N: 86-100%, FO: 89-100 %) with oncaeid and calanoid copepods constituting the dominant taxonomic groups. Oncaeids were generally more abundant (N: 51-62 %) than calanoids (N: 20-43 %), except for the more pelagic-living *C. cirrus*, which was characterised by the highest total abundance of calanoids (N: 82 %) and the lowest total abundance of oncaeids (N: 12 %). Similar abundances of oncaeids (N: 29 %) and calanoids (N: 35 %) were observed for juveniles of *Macroramphosus*. Corycaeid copepods were frequently present in low numbers in the guts of all species (FO: 17-67 %; N: 0.6-2.6 %). The majority of calanoid copepods remained unidentified (54-94%) due to the advanced digestion stage of gut contents. *Clausocalanus* spp. was the most abundant (10-29 %) of those 11 taxa identified to a lower taxonomic level, except for *C. aper*, where this taxa was not identified. Individuals of the diel vertically migrating *Pleuromamma* spp. were occasionally present in the gut contents although in low frequency and abundance. Non-copepod crustacean prey items consisted mainly of ostracods, which were frequently present in all species (FO: 30-100 %) although in low abundances (N: < 3 %), except for *Macroramphosus* spp. (N: 10%). Other crustacean taxa, like euphausiid furcilia and calyptopis larvae, mysids, decapods and amphipods, were only present in *C. cirrus* and *Macroramphosus* spp. in low abundances (0.6 and 3.5 %, respectively). Only these two species also contained occasionally and in low abundances (N: < 1 %) non-crustacean invertebrate prey items, like chaetognaths and pelagic polychaetes and gastropods. Foraminiferans occurred only in the guts of *Macroramphosus* spp., where they were present in nearly half of the guts (FO: 42 %) with a total abundance of 96 individuals and numerous fragments. Fish scales were found in 2 individuals of *C. aper*, while only one fish egg was found in a gut of *C. cirrus*. Prey items of benthic origin were only present in the guts of *C. aper* and *Macroramphosus* spp. and consisted of fragmented benthic polychaetes. While the frequency and total abundance of this prey item was relatively low in *Macroramphosus* spp. (FO: 11 %; N: 0.3 %), it was a frequent prey item for *C. aper* (FO: 70%), although with low total abundance (N: 1.7%). Prey diversity regarding taxonomic groups was highest for *Macroramphosus* spp. and *C.*

cirrus and included for both species the widest range of pelagic taxa and for *Macroramphosus* spp. additionally benthic prey. The lowest prey diversity in adult zooplanktivores was found for *A. anthias*, with ostracods as the only non-copepod prey item.

Ontogenetic differences in the gut contents were apparent for juveniles of *Macroramphosus* spp. and *C. cirrus*, although results for *Macroramphosus* spp. juveniles need to be treated with caution due to the low total number of prey items present in the guts. Prey size was smaller and prey diversity lower for juvenile specimen compared to their adult congeners. The dominance of either oncaeid and calanoid copepods in the guts differed also markedly, as *Macroramphosus* spp. juveniles contained a lower number of oncaeids and a higher number of calanoids than the adults, while this pattern was reversed for *C. cirrus* juveniles and adults. The importance of harpacticoid copepods was higher in juveniles than adults regarding both frequency of occurrence and abundance.

STABLE ISOTOPE ANALYSIS OF BENTHOPELAGIC FISH SPECIES AND POTENTIAL PREY

The $\delta^{13}C$ values covered by the 10 benthopelagic fish species ranged from -20.83 to -16.75 ‰ with lowest values for juveniles of zooplanktivorous species and highest values for the piscivorous *T. nobiliana* (Tab. 5, Fig. 3). Irrespective of feeding mode, the other species concentrated within 1.5 ‰ (-19.71 to -18.17 ‰) of the total $\delta^{13}C$ range. An increase of $\delta^{13}C$ with body size was indicated by a significant positive correlation between $\delta^{13}C$ value and total length of individuals of the benthopelagic fishes studied (r_S = 0.819, P<0.01, n = 99). Zooplanktivorous fish species sampled during the survey in March 2004 were tested for species- and stage-specific differences in their $\delta^{13}C$ values (Tab. 6). Juveniles of *Macroramphosus* spp. and *C. cirrus* had on average lower $\delta^{13}C$ values than their adult congeners (0.58 ‰ and 1.50 ‰, respectively) and values of *C. cirrus* juveniles differed significantly not only from the adults but also from the other zooplanktivorous species (Tab. 6). Sample size for *Macroramphosus* spp. juveniles was too small to allow statistical testing. Among the adult zooplanktivores, $\delta^{13}C$ values differed significantly between but not among the slightly smaller-sized species *Macroramphosus* spp. and *C. aper* with lower $\delta^{13}C$ values and the larger-sized *A. anthias* and *C. cirrus* (Tab. 6).

Table 5. Means (± SD) and ranges of $\delta^{13}C$ and $\delta^{15}N$ signatures of benthopelagic fish species collected on the summit plateau of Seine Seamount during surveys in December 2003, March 2004 and May 2005. Species that include samples corrected for formalin preservation effects are marked with (A) when both $\delta^{13}C$ and $\delta^{15}N$ were corrected, and with (B) when only $\delta^{13}C$ values were corrected (see methods for details), n = number of individuals sampled.

Species	Sampling period	n	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
			Mean ± SD	Range	Mean ± SD	Range
Arnoglossus rueppelli	Dec 03	3	-18.86 ± 0.11	-18.94 to -18.73	9.06 ± 0.03	9.04 to 9.09
Macroramphosus spp.	Dec 03	3	-19.21 ± 0.39	-19.55 to -18.78	9.79 ± 0.21	9.62 to 10.03
Macroramphosus spp. [B]	Mar 04	22	-19.41 ± 0.17	-19.71 to -19.11	9.54 ± 0.27	8.88 to 10.00
Macroramphosus spp. juv.	Mar 04	2	-19.99 ± 0.11	-20.06 to -19.91	7.68 ± 0.10	7.61 to 7.75
Capros aper [A]	Mar 04	20	-19.34 ± 0.29	-19.70 to -18.62	9.01 ± 0.43	8.29 to 9.81
Anthias anthias [A]	Mar 04	10	-18.87 ± 0.15	-19.12 to -18.63	9.69 ± 0.17	9.39 to 9.91
Centracanthus cirrus [A]	Mar 04	10	-18.75 ± 0.19	-19.00 to -18.39	9.48 ± 0.17	9.13 to 9.77
C. cirrus juv. [B]	Mar 04	8	-20.25 ± 0.38	-20.83 to -19.52	8.51 ± 0.61	7.66 to 9.46
Trachurus picturatus	Mar 04	4	-18.41 ± 0.13	-18.50 to -18.23	10.38 ± 0.14	10.24 to 10.52
Trachurus picturatus	May 05	3	-19.02 ± 0.21	-19.22 to -18.80	9.79 ± 0.70	9.12 to 10.51
Pontinus kuhlii	May 05	6	-18.73 ± 0.16	-18.88 to -18.46	10.26 ± 0.46	9.68 to 10.82
Aulopus filamentosus	May 05	2	-19.00 ± 0.08	-19.05 to -18.94	10.75 ± 0.30	10.54 to 10.96
Torpedo nobiliana	May 05	2	-16.99 ± 0.34	-17.23 to -16.75	10.61 ± 0.25	10.43 to 10.79
Conger conger	May 05	4	-18.41 ± 0.21	-18.61 to -18.17	11.27 ± 0.35	10.79 to 11.55

Adult zooplanktivores had on average about 1.5 to 2 ‰ higher $\delta^{13}C$ values than their major prey, when the average $\delta^{13}C$ value of copepod taxa (-20.91 ‰) was used for comparison (Fig. 3). A similar increase in $\delta^{13}C$ of 1.6 ‰ was observed between *T. picturatus* and its main prey *Macroramphosus* juveniles in April 2004, according to gut contents (Fig. 3).

Table 6. Results of statistical comparison (expressed as *P*-values) of species- and stage-specific differences in $\delta^{15}N$ and $\delta^{13}C$ of zooplanktivorous fish species caught during the survey in March 2004 (Kruskal-Wallis test followed by a Dunnet T3 *post-hoc* comparison). NS = not significant

$\delta^{15}N$ and $\delta^{13}C$ of zooplanktivorous fish:
Kruskall-Wallis test: $P < 0.001$
Dunnet T3 *post-hoc* comparisons:

		C. aper	*C. cirrus*	*C. cirrus* juv.	*Macror.* spp.
A. anthias	$\delta^{15}N$	<0.001	NS	0.006	NS
	$\delta^{13}C$	<0.001	NS	<0.001	<0.001
C. aper	$\delta^{15}N$		0.003	NS	<0.001
	$\delta^{13}C$		<0.001	<0.001	NS
C. cirrus	$\delta^{15}N$			0.021	NS
	$\delta^{13}C$			<0.001	<0.001
C. cirrus juv.	$\delta^{15}N$				0.014
	$\delta^{13}C$				0.003

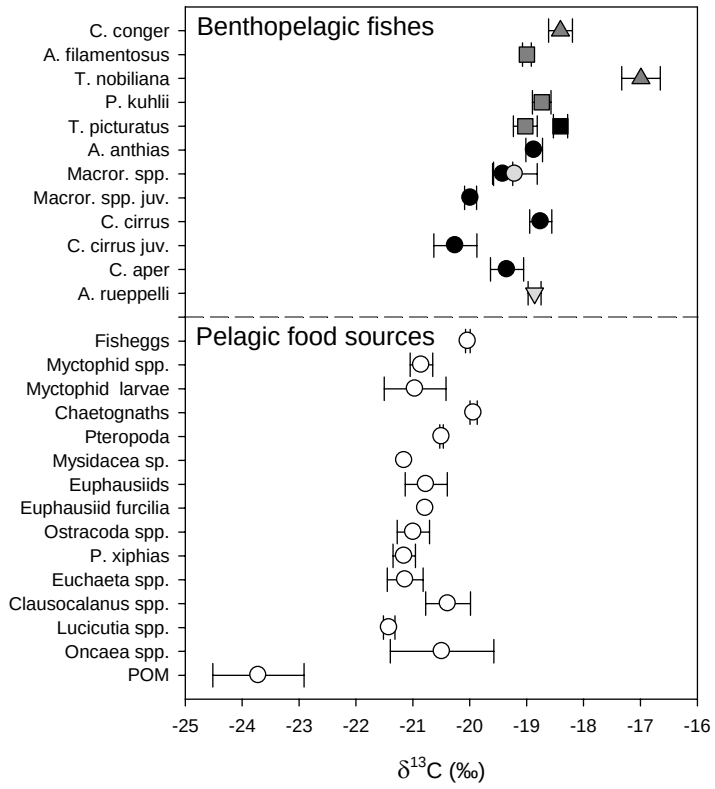

Figure 3.

Mean $\delta^{13}C$ stable isotope values (± SD) of benthopelagic fish species and potential pelagic food sources. Fish species sampled during the 3 surveys are marked according to sampling time: light grey = December 2003, black = March 2004 and dark grey = May 2005. Symbols for the benthopelagic fish species refer to feeding types given in Table 3:

▼ = benthivore
● = zooplanktivore;
▲ = predominantly piscivore
■ = mixed crustacean/cephalopod /fish diet

Mean values of food sources (○) were determined from samples collected in March 2004 and taxonomic labels are described below.

Taxonomic labels for food sources: (n = number of samples, individuals per sample in brackets):
"POM": suspended particulate organic matter n=9
Copepoda: *Oncaea* spp. n=3 (50-108), *Lucicutia* spp. n=5 (68-100), *Clausocalanus* spp. n=3 (62-127), *Euchaeta* spp. n=3 (86-100), *Pleuromamma xiphias* n=3 (50-65)
Ostracoda spp. n=2 (100-102)
"Euphausiid furcilia": *Nematoscelis* spp. furcilia n=1 (1-20)
"Euphausiids" are given as mean of species mean (n=4): *Euphausia hemigibba* n=4 (1-2), *Nematoscelis atlantica* n=3 (1-2), *Thysanoessa* sp. n=1 (3), *Thysanopoda aequalis* n=2 (1-3)
Mysidacea sp. n=1 (1)
"Pteropoda": *Cavolinia inflexa* n=1 (30), *Styliola subula* n=1 (38)
"Chaetognaths": *Eukrohnia hamata* n=1 (17), *Sagitta* spp. n=1 (16), *Sagitta neodecipiens* n=1 (11)
Pisces: Myctophid spp. larvae n=4 (1-2), Myctophid spp. n=3 (muscle tissue), Fish eggs n=3 (20-22)

The $\delta^{15}N$ values of the benthopelagic fishes covered a range of 3.94 ‰ corresponding to just over one trophic level according to a trophic level enrichment of 3.4 ‰. Values ranged from 7.61 ‰ for juvenile *Macroramphosus* spp. to 11.55 ‰ for *C. conger* (Tab. 5, Fig. 4). Zooplanktivores and the benthivorous flatfish *A. rueppelli* had generally lower mean $\delta^{15}N$ values than species with piscivorous or mixed crustacean/cephalopod /fish diets (Fig. 4). A significant positive correlation between $\delta^{15}N$ values and total length of individuals of the benthopelagic fishes studied (r_S = 0.678, P<0.01, n = 99) suggested some influence of body size on trophic level position. Among zooplanktivores, juveniles of *Macroramphosus* spp. and *C. cirrus* had the lowest and adults of *C. cirrus*, *Macroramphosus* spp. and *A. anthias* the highest mean $\delta^{15}N$ values. *Capros aper* took an intermediate trophic position between juvenile and adult

zooplanktivores with mean $\delta^{15}N$ values similar to those of the benthivorous flatfish *A. rueppelli*. Juveniles of *Macroramphosus* spp. and *C. cirrus* had on average lower $\delta^{15}N$ values compared to their adult congeners (1.86 and 0.97 ‰, respectively) and $\delta^{15}N$ values of *C. cirrus* juveniles were significantly different from their adult congeners and all other zooplanktivores, except for *C. aper* (Tab. 6). The $\delta^{15}N$ values of *C. aper* differed significantly from those of the other 3 adult zooplanktivorous species, *C. cirrus*, *Macroramphosus* spp. and *A. anthias*, which had similar mean $\delta^{15}N$ values (P>0.05, Tab. 6).

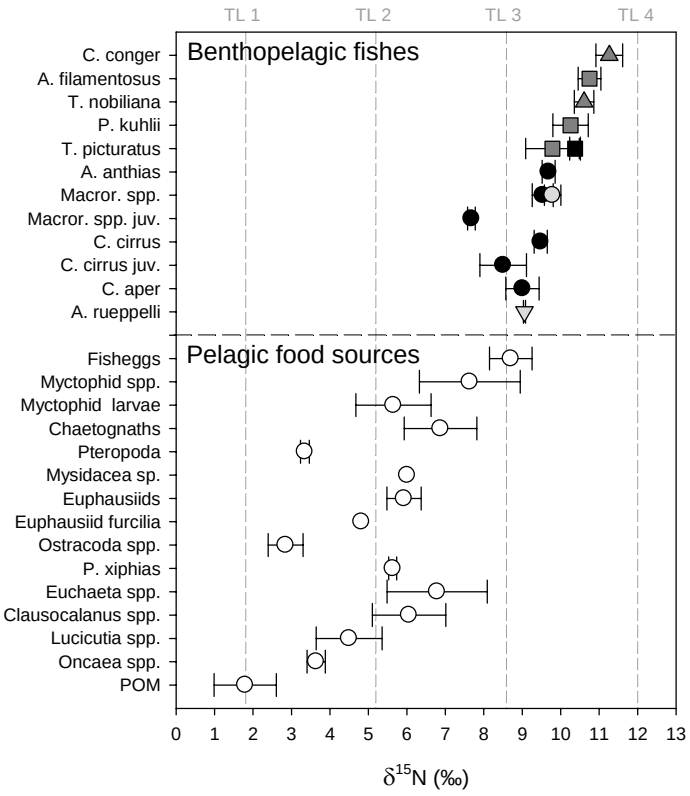

Figure 4.

Mean $\delta^{15}N$ stable isotope values (± SD) of benthopelagic fish species and potential pelagic food sources. Trophic levels (TL) were estimated using mean $\delta^{15}N$ values of POM_{susp} as baseline (TL1) and an increase in $\delta^{15}N$ of 3.4 ‰ per trophic level. Fish species sampled during the 3 surveys are marked according to sampling time: light grey = December 2003, black = March 2004 and dark grey = May 2005. Symbols for the benthopelagic fish species refer to feeding types given in Table 3:
▼ = benthivore
● = zooplanktivore;
▲ = predominantly piscivore
■ = mixed crustacean/cephalopod /fish diet
Mean values of food sources (○) were determined from samples collected in March 2004 and taxonomic labels are described in Figure 3.

Assuming $\delta^{15}N$ values of POM_{susp} as the first trophic level, all benthopelagic fish species belonged to the third trophic level, except for the juvenile zooplanktivores that were positioned on a high second trophic level comparable to myctophids (Fig. 4). Potential pelagic food items for the zooplanktivores, according to gut contents, covered mainly the first two trophic levels with a total range of 6.78 ‰. Ostracods had the lowest and fish eggs the highest $\delta^{15}N$ values (Fig. 4). Copepod taxa, which constituted the dominant prey item for all zooplanktivores according to gut contents, covered nearly

the total range of $\delta^{15}N$ values for potential prey items. Oncaeids were positioned on the lower end of the range, while calanoid taxa covered the whole range with mostly higher $\delta^{15}N$ values than oncaeids. $\delta^{15}N$ values of non-copepod potential prey items like euphausiids, mysids, pteropods, chaetognaths and myctophid larvae fell within the range of copepod values with the exception of lower values for ostracods and some higher values for myctophids and fish eggs. A mean $\delta^{15}N$ trophic level enrichment of 2.70 ‰ was observed between the piscivorous *T. picturatus* and its main prey juvenile *Macroramphosus* in April 2004, according to gut contents.

Temporal differences in stable isotope signatures were tested for *Macroramphosus* spp. and *T. picturatus*. No significant differences were detected for $\delta^{13}C$ and $\delta^{15}N$ values of *Macroramphosus* spp. between the December 2003 and March 2004 surveys ($P>0.05$, T-test), while temporal differences for *T. picturatus* between samples from March 2004 and May 2005 were significant for $\delta^{13}C$ ($P<0.05$, T-test) with a 0.61 ‰ higher mean value in March 2004, but not for $\delta^{15}N$ ($P>0.05$, T-test).

FATTY ACID ANALYSIS OF BENTHOPELAGIC FISH SPECIES AND POTENTIAL PREY

Fatty acids in the storage lipids of the 6 benthopelagic fish species sampled in December 2003, March 2004 and May 2005 (Tab. 7) were dominated by poly-unsaturated fatty acids (PUFAs) which accounted for 40 – 48 % of total fatty acids, except for adult *C. cirrus* (32 % PUFAs) and juvenile *Macroramphosus* spp. (35 % PUFAs) for which saturated fatty acids (SFAs) were the major fraction (both 37 % of total fatty acids). For all other species SFAs were the second largest fraction ranging from 30 to 37 % of total fatty acids. Mono-unsaturated fatty acids (MUFAs) represented the lowest proportion in all species (21 – 31 % of total fatty acids).

Fatty acid profiles of all species were dominated by the SFAs 16:0 and 18:0 and the unsaturated phytoplankton marker fatty acids 22:6(n-3) and 20:5(n-3) as well as the marker fatty acid for carnivory in zooplankton 18:1(n-9), which together accounted for 67 - 80 % of total fatty acids of the neutral lipid fraction (Tab. 7). Inter- and intra-specific variability of the most abundant fatty acids were highest for 22:6(n-3) and generally much less pronounced for the other fatty acids, except for the exceptionally high and variable proportions of 20:4(n-6) in the storage lipids of *A. rueppelli* (Tab. 7, Fig. 5A).

Table 7. Fatty acid composition (mean % of total fatty acids and SD) of storage lipids of benthopelagic fish species sampled on the summit plateau of Seine Seamount during December 2003, March 2004 and May 2005. n = number of samples.

Fatty acids	*A. rueppelli*	*C. aper*	*Macroramph osus* spp.			*A. anthias*	*C. cirrus*		*T. picturatus*	
			adult		juvenile		adult	juvenile		
	Dec 03	Mar 04	Dec 03	Mar 04	Mar 04	Mar 04	Mar 04	Mar 04	Mar 04	May 05
	n=3	n=5	n=3	n=4	n=2	n=3	n=2	n=3	n=4	n=3
Saturates (SFA)										
14:0	2.72 (1.24)	2.23 (1.45)	2.48 (1.97)	2.42 (0.94)	4.33 (0.54)	3.12 (0.63)	5.42 (0.66)	2.74 (1.00)	1.13 (0.57)	1.29 (0.55)
15:0	1.25 (0.50)	0.66 (0.08)	1.13 (0.66)	0.52 (0.13)	0.75 (0.08)	0.85 (0.09)	1.02 (0.08)	0.75 (0.14)	0.37 (0.07)	0.51 (0.08)
16:0	19.16 (4.36)	21.76 (0.96)	21.88 (1.52)	19.78 (1.84)	23.50 (1.59)	23.79 (0.39)	22.15 (1.26)	26.66 (2.53)	19.14 (0.91)	20.11 (1.08)
17:0	1.53 (0.59)	0.99 (0.07)	1.18 (0.53)	0.85 (0.15)	0.86 (0.07)	1.19 (0.10)	1.27 (0.08)	1.23 (0.16)	0.70 (0.05)	0.82 (0.06)
18:0	9.34 (1.93)	6.64 (0.64)	8.98 (2.71)	7.35 (0.38)	7.08 (0.71)	6.05 (0.06)	6.81 (2.22)	5.34 (0.88)	7.99 (0.65)	7.14 (0.42)
Mono-unsaturates (MUFA)										
16:1(n-7)	2.67 (0.88)	2.88 (1.12)	3.20 (1.72)	2.22 (0.61)	4.34 (0.23)	3.83 (0.51)	5.83 (0.30)	4.17 (2.11)	1.39 (0.49)	1.86 (0.63)
18:1(n-9)	8.70 (3.20)	10.13 (3.44)	12.39 (1.33)	11.24 (1.72)	14.84 (1.44)	11.79 (1.34)	14.34 (0.58)	12.44 (2.31)	11.96 (3.50)	12.22 (3.74)
18:1(n-7)	1.76 (0.50)	2.28 (0.18)	2.18 (0.23)	1.46 (0.27)	2.04 (0.05)	2.23 (0.17)	1.97 (0.36)	2.32 (0.85)	2.11 (0.12)	2.15 (0.07)
20:1(n-11)	3.34 (3.93)	0.16 (0.04)	0.64 (0.73)	0.23 (0.15)	0.12 (0.03)	0.24 (0.04)	0.27 (0.08)	0.15 (0.07)	0.00	0.00
20:1(n-9)	2.44 (1.15)	2.06 (1.33)	2.82 (1.93)	3.77 (0.96)	3.55 (0.07)	1.13 (0.29)	2.67 (0.48)	0.53 (0.06)	3.66 (1.61)	1.72 (0.39)
20:1(n-7)	1.16 (0.36)	0.30 (0.10)	0.64 (0.48)	0.18 (0.09)	0.15 (0.00)	0.28 (0.06)	0.33 (0.02)	0.12 (0.03)	0.16 (0.05)	0.20 (0.08)
22:1(n-11)	0.59 (0.36)	0.51 (0.39)	0.15 (0.05)	0.27 (0.11)	0.97 (0.30)	0.25 (0.09)	2.16 (0.83)	0.21 (0.23)	0.28 (0.12)	0.58 (0.29)
22:1(n-9)	0.80 (0.59)	0.74 (0.49)	0.54 (0.31)	0.45 (0.10)	0.25 (0.12)	0.39 (0.11)	0.89 (0.37)	0.23 (0.06)	0.43 (0.17)	0.17 (0.02)
24:1	1.20 (0.55)	2.30 (0.58)	0.73 (0.32)	2.26 (0.35)	1.49 (0.05)	1.89 (0.08)	2.17 (0.16)	1.95 (0.58)	2.86 (0.32)	2.00 (0.20)
Poly-unsaturates (PUFA)										
18:2(n-6)	0.82 (0.23)	0.86 (0.11)	1.08 (0.50)	0.78 (0.10)	1.32 (0.05)	1.01 (0.02)	1.00 (0.07)	1.35 (0.33)	1.03 (0.13)	1.26 (0.14)
18:3(n-3)	0.56 (0.15)	0.44 (0.08)	0.57 (0.28)	0.40 (0.07)	1.06 (0.02)	0.62 (0.06)	0.81 (0.09)	0.88 (0.31)	0.33 (0.14)	0.68 (0.20)
18:4(n-3)	0.63 (0.15)	0.40 (0.14)	0.70 (0.43)	0.43 (0.12)	1.76 (0.02)	0.39 (0.08)	1.07 (0.13)	1.87 (0.89)	0.27 (0.15)	0.58 (0.28)
20:2(n-6)	0.83 (0.44)	0.39 (0.06)	0.85 (0.50)	0.39 (0.19)	0.41 (0.02)	0.33 (0.03)	0.35 (0.01)	0.23 (0.07)	0.40 (0.16)	0.55 (0.02)
20:4(n-6)	8.48 (7.44)	2.74 (0.66)	3.25 (1.25)	1.45 (0.42)	0.63 (0.05)	2.15 (0.43)	1.20 (0.16)	0.80 (0.18)	2.50 (0.59)	2.19 (0.25)
20:4(n-3)	0.54 (0.13)	0.66 (0.08)	0.42 (0.38)	0.54 (0.13)	1.31 (0.03)	1.02 (0.16)	1.03 (0.13)	1.47 (0.39)	0.59 (0.14)	0.98 (0.16)
20:5(n-3)	7.49 (3.21)	5.40 (0.69)	4.95 (0.69)	5.40 (0.83)	7.46 (0.41)	4.81 (0.20)	5.95 (0.95)	7.94 (1.22)	3.72 (0.56)	5.57 (0.85)
22:6(n-3)/24:0	22.20 (7.58)	34.40 (7.11)	26.62 (7.50)	36.17 (5.43)	20.04 (2.17)	31.32 (4.04)	19.47 (0.38)	25.20 (9.34)	37.59 (4.72)	35.39 (6.06)
∑ minor FA [A]	1.81	1.05	2.61	1.45	1.73	1.30	1.82	1.42	1.40	2.02
∑ SFA	34.40 (2.92)	32.33 (0.91)	36.46 (0.32)	31.26 (2.15)	36.81 (1.51)	35.13 (1.12)	36.78 (0.12)	36.76 (2.74)	29.72 (0.47)	30.73 (0.35)
∑ MUFA	22.68 (2.11)	21.55 (7.22)	23.62 (4.04)	22.27 (3.47)	28.01 (1.17)	22.32 (2.62)	31.11 (0.64)	22.41 (5.06)	23.07 (5.70)	21.15 (4.91)
∑ PUFA	42.91 (4.84)	46.12 (7.84)	39.92 (4.34)	46.48 (5.44)	35.18 (2.68)	42.55 (3.74)	32.11 (0.76)	40.83 (7.72)	47.21 (5.63)	48.12 (5.18)

[A] minor fatty acids (<1% of total FA in all individuals) are given as sum of mean SFAs (12:0, 13:0, 20:0, 21:0, 22:0, 23:0), MUFAs (14:1, 15:1, 17:1, 22:1(n-7)) and PUFAs (18:3(n-6), 18:5(n-3), 20:3(n-6), 20:3(n-3), 22:2)

Temporal differences in fatty acid composition between individuals of *Macroramphosus* spp. sampled in December 2003 and March 2004 and individuals of *T. picturatus* sampled in March 2004 and May 2005 were generally small and within ranges of species-specific variability, except for a lower proportion of 22:6(n-3) in *Macroramphosus* specimen sampled in December 2003 (Tab. 7).

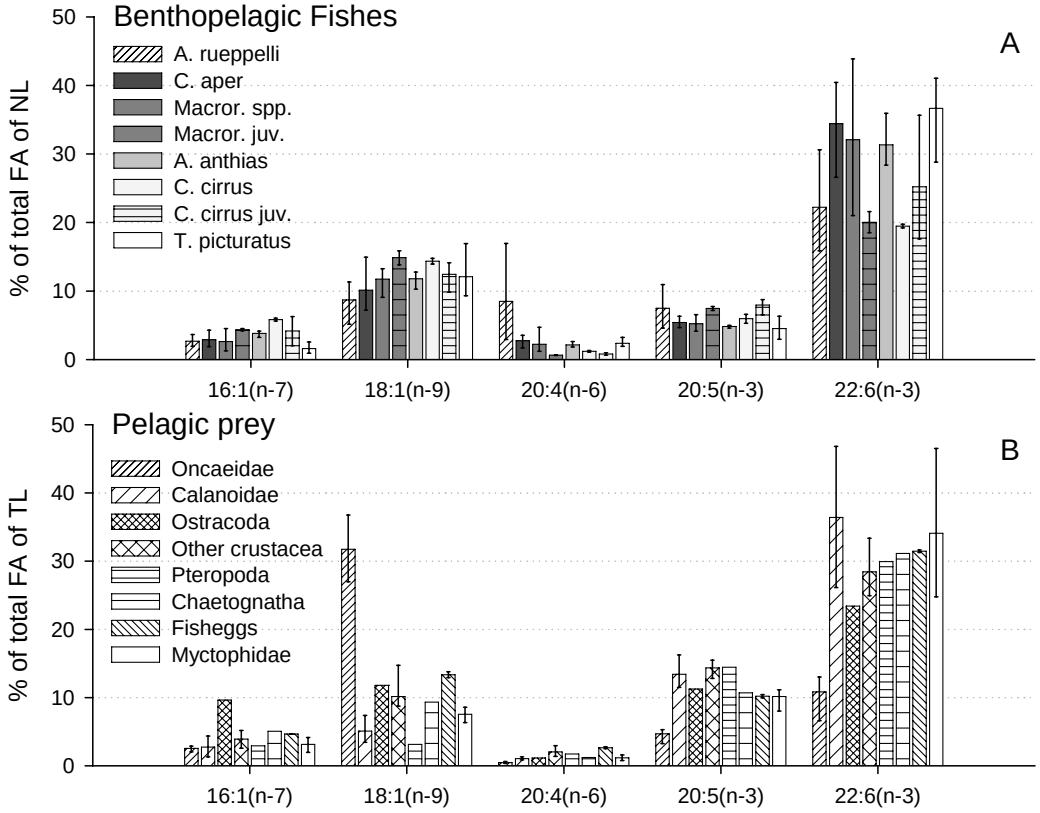

Figure 5. Proportions of the most abundant unsaturated fatty acids (FA) in (A) the total storage lipids (NL=neutral lipids) of the benthopelagic fish species, and (B) the total lipids (TL) of potential pelagic prey taxa for the benthopelagic fishes on Seine Seamount. Values for benthopelagic fish species and stages are presented as means and ranges from the 3 surveys. Mean values and ranges of potential pelagic prey taxa were determined from samples collected in March 2004 and taxonomic labels are described below.

Despite the high degree of similarity in fatty acid composition of the storage lipids between the fish species studied, some differences between feeding types, species and ontogenetic stages were apparent. The storage lipids of the crustacean/cephalopod/fish-feeder *T. picturatus* were characterised by high proportions of the dinoflagellate marker fatty acid 22:6(n-3) and low proportions of 16:1(n-7) and 14:0, which are abundant fatty acids in diatoms. The benthivorous flatfish *A. rueppelli* contained the highest mean proportion of 20:4(n-6) of all species, although with a large variability among

individuals, and among the lowest mean proportions of 18:1(n-9) and 22:6(n-3). Species- and stage-specific differences in storage lipid fatty acid signatures of the zooplanktivores were generally of low magnitude. Among adult zooplanktivores, the more pelagic-living *C. cirrus* separated most clearly from the other 3 near-bottom species by the lowest mean proportion of 22:6(n-3) as well as the assumed benthic marker fatty acid 20:4(n-6) and high mean proportions of the diatom marker fatty acids 20:5(n-3), 16:1(n-7) and 14:0 and the carnivorous zooplankton marker fatty acid 18:1(n-9), although these differences were of a low magnitude. Adults of the other 3 species had similar mean proportions for the most abundant fatty acids. Ontogenetic differences in storage lipid fatty acid composition between juveniles and adults of *C. cirrus* were small, while they were pronounced for juveniles and adults of *Macroramphosus* spp. Fatty acid proportions in the *Macroramphosus* juveniles were quite similar to those of the more pelagic-living *C. cirrus*, i.e. with low proportions of 22:6(n-3) and 20:4(n-6) and high proportions of the diatom and carnivorous zooplankton marker fatty acids.

The fatty acid signatures of the total lipids of potential pelagic prey sampled above the summit of Seine Seamount in March 2004 were largely similar among the different taxonomic groups, except for oncaeid copepods, which differed markedly in mean proportions of nearly all of the abundant fatty acids (Fig. 5B). These differences in relative fatty acid composition were characterised by strongly elevated proportions of 18:1(n-9) and reduced proportions of 22:6(n-3) and 20:5(n-3) in oncaeid copepods and were most pronounced compared to calanoid copepods.

The total lipid fatty acid signatures of the most abundant fatty acids of potential pelagic prey showed a high degree of similarity to those in the storage lipids of the benthopelagic fish species (Fig. 5A,B). Proportions of the fatty acid 20:4(n-6), which were elevated in the flatfish species, were similarly low in the pelagic taxa as in the other fish species.

Oncaeid and calanoid copepods constituted the dominant prey items in the gut contents of zooplanktivorous fish species, but species-specific differences in their proportions were not detectable in storage lipid fatty acid signatures of the zooplanktivores. For example, the gut contents of adult *C. cirrus* were dominated by calanoid copepods, while those of the near-bottom species were dominated by oncaeid copepods. Despite the dominance of oncaeid copepods in the gut contents of near-bottom species, the

storage lipid fatty acid signatures of these species were characterised by higher proportions of 22:6(n-3) and similar proportions of 18:1(n-9) compared to those in the storage lipids of adult *C. cirrus*, contrary to the expected lower proportions of 22:6(n-3) and higher proportions of 18:1(n-9).

The storage lipids of the blue jack mackerel *T. picturatus* were characterised by high proportions of the fatty acid 22:6(n-3), despite low proportions of this fatty acid in the total lipids of *Macroramphosus* spp. juveniles (26 % of total fatty acids, data not plotted), its main prey according to gut content analysis (Fig. 5A,B).

Although benthic prey dominated the gut contents of the benthivorous flatfish *A. rueppelli* proportions of the abundant storage lipid fatty acids were generally similar to those in the total lipids of the pelagic organisms, except for the markedly elevated proportions of the fatty acid 20:4(n-6) (Fig. 5A,B).

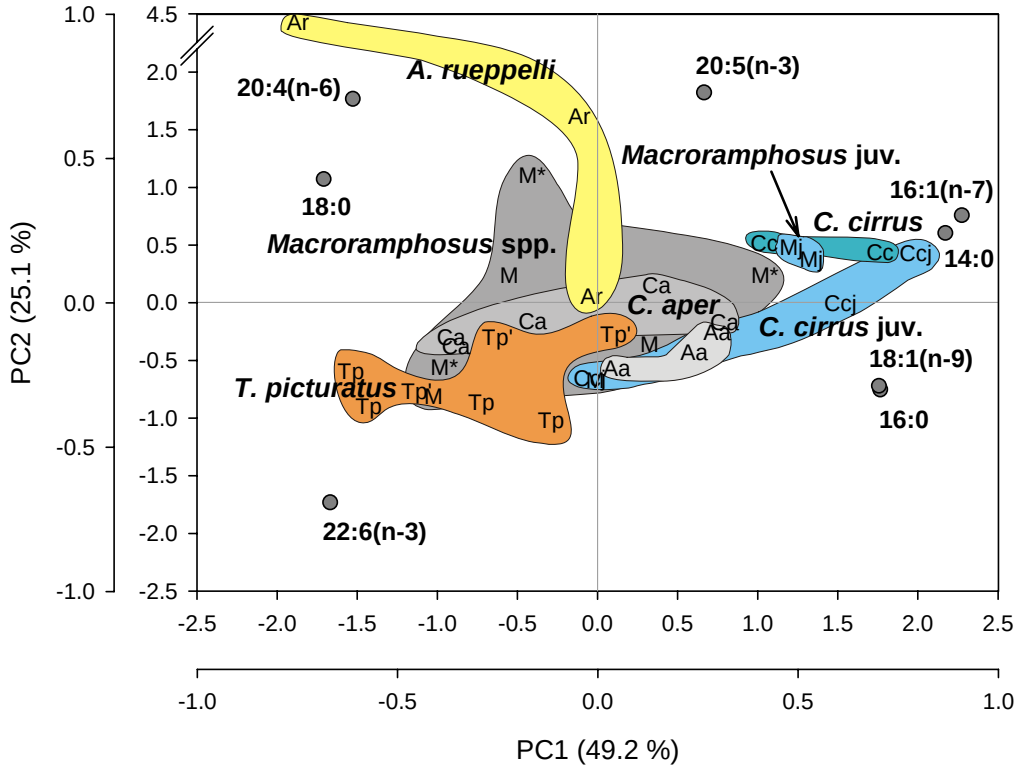

Figure 6. Principal component analysis on the relative fatty acid compositions of the most abundant fatty acids in the storage lipids of the benthopelagic fish species on Seine Seamount sampled in December 2003, March 2004 and May 2005. Species labels with an asterisk (*) refer to specimen sampled in December 2003, with an apostrophe (') refer to specimen sampled in May 2005, all other specimen were sampled in March 2004; filled circles = fatty acids; scales were adjusted to combine plots: scales of principal components (PC) refer to sample plot, scale of variables ranges from -1 to +1 for both PCs. Proportion of variance accounted for by each PC is given in brackets.

Principal component analysis (PCA) on the eight most abundant storage lipid fatty acids of the benthopelagic fish species extracted three components with eigenvalues >1 of which the major two explain 74 % of the variance (Fig. 6). Despite a considerable overlap in fatty acid composition, some degree of separation between species and stages was apparent.

PC1, which explained 49% of the variance, separated species with higher proportions of 22:6(n-3), 20:4(n-6) and 18:0, like *T. picturatus*, most individuals of *C. aper* and adult *Macroramphosus* spp. as well as one individual of *A. rueppelli*, from species with higher proportions of 14:0, 16:0, 16:1(n-7) and 18:1(n-9), like adult and juvenile *C. cirrus*, juveniles of *Macroramphosus* spp., *A. anthias* and individuals of adult *Macroramphosus* spp. and *C. aper*. PC2, which explained 25% of the variance, separated individuals of the benthivorous *A. rueppelli* and one adult *Macroramphosus* spp. due to higher amounts of 20:4(n-6) and 20:5(n-3) as well as to a lesser extent juveniles *Macroramphosus* spp. and adults of *C. cirrus* due to higher amounts of 20:5(n-3) from individuals of *T. picturatus* with higher amounts of 22:6(n-3).

Species and stages separated, thus, either due to higher proportions of epipelagic marker fatty acids, like 16:1(n-7) and 14:0, which are abundant in diatoms, and 16:0 and 18:1(n-9) which are abundant in carnivorous zooplankton, or due to higher proportions of the assumed benthic marker fatty acid 20:4(n-6) and the dinoflagellate marker and dominant membrane fatty acid 22:6(n-3).

DISCUSSION

NUTRITIONAL LINKS TO THE BENTHOPELAGIC FISH FAUNA

The benthopelagic fish fauna on the summit plateau of Seine Seamount was dominated by the snipe fish *Macroramphosus* spp., with *C. aper*, *C. cirrus* and *A. anthias* being the next most abundant species (Christiansen *et al.*, 2009). The dominance of zooplanktivorous species and their gut contents, which consisted mainly of pelagic copepods, suggested a strong reliance of the fish community on pelagic food sources. The storage lipid fatty acid signatures of the benthopelagic fishes studied showed a high degree of similarity among species as well as with the fatty acid signatures determined for the total lipids of potential pelagic prey taxa and supported a close coupling between the pelagic food source and the benthopelagic fish fauna irrespective of the feeding

mode. The close nutritional link to the epipelagic phytoplankton production was further apparent from high proportions of diatom marker fatty acids like 16:1(n-7) and 20:5(n-3), the dinoflagellate marker fatty acid 22:6(n-3) and the marker fatty acid for carnivory in zooplankton 18:1(n-9) (e.g. Dalsgaard *et al.* and references therein), which characterised the storage lipid fatty acid composition of the fishes. As indicated by gut content analysis, the nutritional link to the benthopelagic fish community ran either via pelagic prey to zooplanktivorous fish species, which in turn were preyed upon by piscivorous species like *T. picturatus* and *C. conger*, or via the phytodetritus-dependent benthic food web utilised by benthivorous fish species like the flatfish *A. rueppelli*.

Stable isotope analysis also confirmed a close link to the pelagic food source. The $\delta^{15}N$ values of zooplanktivorous fish were in the range of the average enrichment per trophic level suggested by literature (Minagawa and Wada 1984, Vander Zanden & Rasmussen 2001, Post 2002), although exact determination was not possible due to the large range of $\delta^{15}N$ values covered by the potential prey. The average trophic level enrichment of $\delta^{13}C$ values between zooplanktivorous fishes and their potential prey ranged between 1.5 and 2 ‰ and was thus slightly higher than the generally proposed <1 ‰ trophic level increase (DeNiro & Epstein 1978, DeNiro & Epstein 1981, Peterson & Fry 1987, Michener & Schell 1994). The slightly higher trophic level enrichment might be due, on one hand, to the large range of $\delta^{13}C$ values covered by the potential prey, but might also be influenced by preservation effects in fish samples and by lipid content in zooplankton samples despite correction of $\delta^{13}C$ values, although similar trophic level differences were observed in studies from shelf areas (Davenport & Bax 2002, Bode *et al*. 2004).

Predominantly benthic food sources were utilised by the benthivorous flatfish *A. rueppelli* and presumably resulted in elevated proportions of the fatty acid 20:4(n-6). The variability of 20:4(n-6) proportions observed among individuals of *A. rueppelli* suggested, however, some degree of individual specialisation. High proportions of this fatty acid were also present in the storage lipids of epibenthic invertebrate species studied concomitantly on Seine Seamount summit (Hirch, unpublished data). In a study of Dunstan *et al.* (1988), high levels of 20:4(n-6) were characteristic for fish species feeding from a benthic-derived food source, like a benthivorous shark species, which had assimilated presumably macroalgal-derived 20:4(n-6) via predation on sea urchin

and snails, while fish species that relied on a microalgal-based food web had the lowest concentrations of 20:4(n-6).

The arachidonic acid 20:4(n-6) must be assimilated from primary producers, as it cannot be biosynthesised *de novo* by consumers (e.g. Dalsgaard *et al.* 2003). Possible sources include macroalgae, especially Rhodophyta, which are characterised by high proportions of this fatty acid (Pettitt *et al.* 1989, Khotimchenko *et al.* 1990, Dembitsky *et al.* 1991, Dalsgaard *et al.* 2003). Evidence for the presence of living coralline red algae on the summit plateau of Seine Seamount was discovered among the predominantly dead corallinacean gravels recovered during the survey in May 2005 (Beck *et al.* 2005) and indicated the existence of a benthic primary food source. Regarding the low light levels and low abundance of living macroalgal specimen encountered on the summit plateau as well as the absence of living herbivorous gastropods in the summit samples (Beck *et al.* 2005), the quantitative contribution of Rhodophyta to the organic carbon pool of the benthopelagic community is expected to be negligible. Their qualitative contribution regarding a sufficient supply of the dietary essential fatty acid 20:4(n-6) for benthic and benthopelagic consumers might, however, be of some importance.

The sound-scattering layer interception hypothesis proposed by Isaacs & Schwartzlose (1965) suggests the presence of an increased food supply to the seamount fauna due to topographic blockage of diel vertical migrators during descend and would explain the observed close link between the pelagic food source and the benthopelagic fish community. This hypothesis predicts a maximal supply of diel vertical migrators for seamounts at intermediate depths, i.e. with summits just below the photic layer (Genin 2004). As the summit plateau of Seine Seamount at about 170 m is situated just below the photic layer (about 130-150 m; Beck *et al.* 2005), the resident benthopelagic fish fauna was expected to receive additional food supply through the trapping of diel vertical migrators. Studies on the summit plateau of Great Meteor Seamount (subtropical NE Atlantic, summit depth: ~280 m), reported of high daytime abundances of vertically migrating zooplankton taxa, mostly larger than 0.5 cm, close to the bottom of the plateau (Martin & Nellen 2004) and of a distribution and diel behaviour of the benthopelagic fish assemblage most likely explained by a food supply through the topographic blockage mechanism (Fock *et al.* 2002a,b). Gut contents of the

zooplanktivorous fish species examined in this study did, however, not support major nutritional augmentation through the topographic blockage mechanism as they contained hardly any diel vertically migrating zooplankton taxa. Instead, small, presumably non- or weakly-migrating copepods (<0.5 cm) dominated the gut contents of the zooplanktivores. Zooplankton distribution concurrently investigated by Martin & Christiansen (2009) at Seine Seamount revealed a near absence of larger diel vertically migrating zooplankton (>0.5 cm) above the summit, which were present in considerable numbers above the slopes of Seine Seamount and at open ocean reference sites, and reported a predominance of small (<0.5 cm) non-vertically migrating copepods. Gut contents of the zooplanktivores thus reflected, to a large extent, prey availability rather then prey selection according to the size-composition of the zooplankton community above the summit plateau. Regarding this absence of zooplankton aggregations on the summit plateau of Seine Seamount, the resident benthopelagic fish fauna appeared to be predominantly sustained by current-driven horizontal fluxes of planktonic food (Genin 2004), which might be enhanced due to the amplification of near-bottom flows over seamounts (Mohn & Beckmann 2002a,b). The lower zooplankton biomass above the seamount summit reported by Martin & Christiansen (2009) might further indicate a reduced food supply to resident zooplanktivorous fish and could be a cause for the lack of enhanced fish standing stocks on the summit plateau reported from trawl surveys by Christiansen *et al.* (2009). Longline surveys of the benthopelagic fish assemblages conducted on Seine Seamount did not show clear enhancement of standing stocks either, when compared to similar depths on the Madeira and Azores islands slopes (Menezes, 2009).

RESOURCE PARTITIONING AMONG ZOOPLANKTIVORES

Considerable dietary overlap among the benthopelagic zooplanktivorous fishes was indicated by similarities in gut contents, fatty acid signatures of the storage lipids and trophic levels occupied. Nevertheless, some degree of resource partitioning regarding feeding habitats utilised, prey selection and diversity and ontogenetic separation were apparent and precluded competitive exclusion.

Resource partitioning through vertical habitat differences were suggested by differences in gut contents and fatty acid signatures. The zooplanktivorous fish species belonged

either to the near-bottom ichthyocenosis, assigned to species which generally stay within a few metres to the bottom, like *Macroramphosus* spp., *C. aper* and *A. anthias* (Pakhorukov 2008), or were grouped as pelagic fish species which occur in the water column above seamount tops like *C. cirrus* and juveniles of *Macroramphosus* spp. (Ehrich 1974, Kukuev 2004, Pakhorukov 2008). Vertical habitat differences of the adult zooplanktivorous fishes might be the cause of observed differences in prey compositions in the gut contents. Oncaeid copepods constituted the dominant prey group of the 3 near-bottom species *Macroramphosus* spp., *C. aper* and *A. anthias* while calanoid copepods were the dominant prey of the more pelagic-living *C. cirrus*. Higher proportions of oncaeid copepods in the guts of the near-bottom species might suggest positive selection for this taxa and mirror higher abundances below 100m as observed in the water column above the summit of Seine Seamount in one of the day haul samples, although calanoids remained dominant (Martin 2008). Habitat-derived differences in prey composition were also indicated in the fatty acid composition of the storage lipids of the zooplanktivores. Principal component analysis separated the more pelagic-living juveniles and adults of *C. cirrus* and juveniles of *Macroramphosus* spp. from the near-bottom dwelling adult *Macroramphosus* spp., *C. aper* and *A. anthias* by higher amounts of phytoplankton (16:1(n-7), 20:5(n-3), 22:6(n-3)) and zooplankton (18:1(n-9)) marker fatty acids and lower amounts of the presumably benthos-associated fatty acid 20:4(n-6) (e.g. Dalsgaard *et al.* and references therein). These differences in marker fatty acid composition might be due to a higher concentration of phytoplankton and higher abundance of herbivorous copepods in the epipelagic feeding habitat, which is presumably utilised by the more pelagic-living species and stages. Habitat-dependent resource utilisation was also reported for the dominant benthopelagic fishes of the Great Meteor Seamount fish community, *Zenopsis conchifer*, *Macroramphosus* spp., *Antigonia capros* and *Capros aper*, and suggested sufficient resource partitioning among species to avoid competitive exclusion (Fock *et al.* 2002a).

Species-specific differences in the range of prey items utilised were also apparent in the gut contents of the zooplanktivorous fish species and might further reduce competitive exclusion. Among the 3 near-bottom species, only *A. anthias* fed exclusively on pelagic prey, while *C. aper* and to a lesser extent *Macroramphosus* spp. also utilised benthic-derived food, like benthic polychaetes. Additionally, gut contents of *Macroramphosus*

spp. also contained the largest variety of pelagic crustacean and non-crustacean prey taxa. The ability to utilise a large range of food sources is typical for species with opportunistic feeding behaviour. The high diversity of prey items observed for *Macroramphosus* spp. might partly reflect the lack of separation between the two still disputed morphotypes or species *M. scolopax* (Linnaeus, 1758), which is a predominantly benthic feeder and *M. gracilis* (Lowe, 1839), which is a pelagic feeder (e.g. Matthiessen *et al.* 2003). Ehrich (1976, 1986) claimed that the genus is monotypic and is represented by *M. scolopax* with the slender form changing to the deep-bodied one during ontogeny, while other studies considered both species valid and found substantial differences between them in morphology, larval development and feeding habitats (Matthiessen *et al.* 2003; Miyazaki *et al.* 2004; Marques *et al.* 2005; Bilecenoglu 2006). In a recent study, Robalo *et al.* (2009) found no genetic differences between individuals considered to belong to both species as well as the intermediate forms and suggested that in the north-eastern Atlantic *M. scolopax* represents a single species with different interbreeding morphotypes. The low frequency and abundance of benthic prey found in the guts of *Macroramphosus* spp. in this study suggested that the majority of individuals investigated belonged to the pelagic feeding morphotype or species. Prey items of *Macroramphosus* spp. identified in this study were similar to those reported from other areas. Small copepods, predominantly *Temora* spp., also dominated the diets of *M. gracilis* on the Portuguese coast and copepods were reported as main prey of the *M. gracilis*–type in the Atlantic Moroccan coast and Australian coast (Lopes *et al.* 2006 and references therein). On Great Meteor Seamount, the *M. gracilis*–type fed also mainly on small prey items like ostracods, calanoid copepods, pteropods and foraminifers, while the benthic feeding-type additionally fed on decapods and polychaetes (Matthiessen *et al.* 2003). The diets of *C. aper* observed in this study were also similar to those reported from the Portuguese coast (Lopes *et al.* 2006) and on Great Meteor Seamount (Fock *et al.* 2002a) where they were dominated by copepods, while in a study from the southern coast of Portugal euphausiids and hyperiid amphipods associated with the deep scattering layers constituted the major prey (Santos & Borges 2001) and demonstrated the capacity of this species to also utilise larger pelagic prey items. In studies, which analysed the diets of co-occurring *Macroramphosus* spp. and *C. aper* (Fock *et al.* 2002a, Lopes *et al.* 2006), sufficient

resource partitioning through pronounced differences in prey choice were observed between the species.

Avoidance of intra-specific competition for resources through ontogenetic differences in habitat and prey choice was observed for juveniles and adults of *Macroramphosus* spp. and *C. cirrus*. Competition between early life stages and adults of *Macroramphosus* spp. is avoided by extended pelagic life stages of the juveniles remote from seamounts. Pelagic life stages of *Macroramphosus* spp. up to a size of 50 mm were reported from oceanic surface waters before they descended into greater depth to settle closer to the bottom (Ehrich 1974, Badcock & Merrett 1976, Miyazaki *et al.* 2004). *Macroramphosus* spp. juveniles in this study had an average size of about 70 mm and likely represented an early phase of settlement onto the seamount. The stronger phytoplanktonic signal in the fatty acid signature of their storage lipids compared to the adults suggested a more pelagic feeding habitat of the juveniles and indicated a prolonged post-settlement resource partitioning through vertical habitat separation from adult congeners at the seamount.

Analysis of gut contents revealed marked differences in prey selection between juveniles and adult congeners of both *Macroramphosus* spp. and *C. cirrus* and were characterised by a lower prey size and prey diversity as well as higher proportions of harpacticoid copepods for juveniles. As juveniles of both species were of similar size and substantially smaller than their adults, these differences are to a large extent size-related. An ontogenetic increase of both the maximum prey size and the variety of prey types in the diet has been reported for a number of larval and juvenile marine fishes (e.g. Anderson 1994 and references therein). Higher proportions of harpacticoid copepods in the gut contents of juveniles might also indicate a positive selection for this group by the juvenile fishes as zooplankton composition above the summit of Seine Seamount showed low abundances of harpacticoid copepods (<1 % of total copepod abundance) compared to calanoid and oncaeid copepods (Martin 2008). Abundances of harpacticoid copepods might, however, be underestimated, as their small size and slim body shape might have prevented a quantitative catch. Gut contents of *Macroramphosus* spp. juveniles also need to be treated with caution due to the low number of prey items they contained.

Stable isotope signatures supported the existence of ontogenetic differences in the diet. Juveniles of both species had markedly, in the case of *C. cirrus*, significantly lower $\delta^{15}N$ and $\delta^{13}C$ values than their adult congeners. These lower trophic level positions might be explained by juveniles feeding on a larger proportion of smaller-sized and presumably more herbivorous copepod species (Turner 2004) and was supported by a higher dietary proportion of harpacticoid copepods, which are predominantly herbivorous (O´Neil *et al.* 1996, De Troch *et al.* 2006, Caramujo *et al.* 2008).

The higher taxonomic resolution of species-specific differences in gut contents were not reflected in the fatty acid and stable isotope signatures of the zooplanktivorous fishes. For example, the gut contents of adult *C. cirrus* were dominated by calanoid copepods, while those of near-bottom species were dominated by oncaeid copepods. Oncaeid copepods were characterised by lower $\delta^{15}N$ values as well as high proportions of the fatty acid 18:1(n-9) and low proportions of the fatty acid 22:6(n-3). Despite the dominance of calanoid copepods in the gut contents of *C. cirrus* adults, $\delta^{15}N$ values and proportions of 18:1(n-9) in the storage lipids were similar to species with oncaeid-dominated gut contents while proportions of 22:6(n-3) were even lower. This lack of a higher taxonomic resolution of the biochemical markers might in case of the stable isotope signatures be due to the large ranges of $\delta^{15}N$ values covered by the prey organisms, while the high degree of similarity in the fatty acid composition of total lipids among the different prey taxa prevented a higher taxonomic resolution in the fatty acid signature of the storage lipids of the zooplanktivorous fishes.

The fatty acid composition of fish tissues is not only determined by dietary input but is also influenced by differences in species-specific and individual metabolic activity. These metabolic activities include *de novo* biosynthesis of short-chain SFA and MUFA, selective uptake and "direct" incorporation of dietary fatty acids and uptake and modification of dietary fatty acids prior to incorporation as well as increased mobilization of energy stores during growth, reproduction and starvation (e.g. Dalsgaard *et al.* 2003 and references therein). *Centracanthus cirrus* has been reported to be a summer spawner (Tortonese 1986) and the low proportion of 22:6(n-3) in the storage lipids might be the result of selective mobilization for reproduction. This fatty acid is essential for the development of the embryo (e.g., Watanabe 1993) and high proportions have been observed in eggs (Watanabe 1993) and gonads (Tocher &

Sargent 1984) of marine fish species. Similarly, lower proportions of 22:6(n-3) have been observed in individuals of *Macroramphosus* spp. in December 2003 as compared to March 2004 (Tab. 7) and probably also coincided with gonad maturation in December as spawning of this species starts in January/February in the Azores region (Ehrich 1974, Sobrinho-Gonçalves & Isidro 2001). Low mean proportions of 22:6(n-3) were also observed for juveniles of both *C. cirrus* and *Macroramphosus* spp. and might be due to selective utilization during growth rather than to dietary differences. The essential fatty acid 22:6(n-3) is an important structural component of biomembranes (Sargent & Henderson 1986; Tande & Henderson 1988) and might be utilised by the growing juvenile for the formation of cellular membranes resulting in preferential incorporation into the polar membrane lipid fraction and the observed reduced proportions in the storage lipids.

Further causes for differences between gut contents and biomarkers are that gut contents represent only a "snapshot" of recently ingested prey and might vary considerably according to short term changes in prey availability caused by patchy distribution (e.g., Wiebe 1970). Biochemical markers provide information on assimilated diet integrated over time (Fry 2006). The rate at which changes in the food source are reflected in the biomarker signature of an organism varies depending on its turnover time, which is influenced mainly by growth, but also by general metabolic maintenance (Fry & Arnold, 1982; Hesslein *et al.*, 1993, MacAvoy *et al.*, 2001) and the tissue type analysed (Dalerum & Angerbjörn 2005). This time lag in equilibration to changes in the food source may take several days to several months for stable isotopes (Dalerum & Angerbjörn 2005, Perga & Gerdeaux 2005) and several days to several weeks for fatty acid signatures (St.John 1996, Fraser *et al.* 1989, Kirsch 1998) and may result in a lack of correspondence between gut contents and biochemical markers.

TROPHIC STRUCTURE OF THE BENTHOPELAGIC FISH COMMUNITY

The trophic structure of the studied benthopelagic fish species was characterised by an increase of trophic level from juvenile zooplanktivores, which occupied the lowest trophic position, to adult zooplanktivores and the benthivorous flatfish to those species with mixed fish, cephalopod and larger crustacean diet or a predominantly piscivore diet. These trophic relationships confirmed results from gut content analysis and diet

data from literature. A significant positive correlation between size and $\delta^{15}N$ values of the individual fishes indicated an influence of size on the trophic position occupied. This is partly explained by ontogenetic diet shifts and partly by the fact that predators are typically larger than their prey and thus trophic position often increases with body size within a given food web (France *et al.* 1998, Jennings *et al.* 2001, Jennings & Mackinson 2003), although complex food webs without relationship between trophic position and body size have also been described (Layman *et al.* 2005). In this study, sizes and $\delta^{15}N$ values of prey and predators increased from suspended particulate organic matter consumed by copepods to copepod-consuming zooplanktivores which in turn were consumed by *T. picturatus*, according to gut contents, and by *C. conger* according to literature (Morato *et al.* 1999, O'Sullivan *et al.* 2004). A verification of a $\delta^{15}N$ increase of about 3.4 ‰ per trophic level, as suggested by Minagawa & Wada (1984), proved difficult as the different benthopelagic fish species fed on a range of trophic levels. Potential prey items of the zooplanktivores determined from gut contents covered nearly 2 trophic levels. *T. picturatus* was enriched by 2.70 ‰ to *Macroramphosus* spp. juveniles, its main prey according to stomach contents, but is also known to feed on lower trophic level crustaceans (Smith-Vaniz 1986) so that this value might be the result of a mixed diet. The same is true for the predominantly piscivorous top predator *C. conger*, which was reported to feed mainly on *Capros aper* and *Macroramphosus scolopax* in the Azores region (Morato *et al.* 1999), but in this study $\delta^{15}N$ was only enriched by just over 2 ‰ compared to these species. Trophic level enrichments of less than 3 ‰ observed in other studies were explained by significant omnivory within the food web and resulted in the dominance of intermediate trophic level positions (France *et al.* 1998, Marguillier *et al.* 1997). A dominance of intermediate trophic level positions was also apparent for the benthopelagic fish species in this study, which occupied positions between the 3rd and 4th trophic level irrespective of differences in size and feeding type, and indicated a food web composed of predominantly omnivorous consumers.

CONCLUSIONS

The combination of gut content, stable isotope and storage lipid fatty acid analyses provided a useful tool for studying food sources and trophic interactions of the

benthopelagic fish fauna on the summit plateau of Seine Seamount (Fig. 7). All methods indicated a close nutritional link between the benthopelagic fish community and pelagic food sources, while benthic contributions to the diet were small. Habitat- and prey - related resource partitioning among zooplanktivorous species and ontogenetic stages were apparent and presumably reduced inter- and intra-specific competition in a resident community composed of predominantly omnivorous fish species. The dominance of small non- or weakly-migrating copepods and lack of larger diel vertically migrating taxa in the gut contents of the benthopelagic zooplanktivores suggested that current-driven horizontal fluxes of planktonic food were the main mechanism of food supply to the resident fish community. The gut contents reflected the absence of larger and more mobile pelagic species in the water column above the seamount summit (Martin and Christiansen 2009) and emphasised the importance of interactions between seamount-altered ocean currents and local zooplankton stocks in determining the mechanisms of food supply and the food quantity available to the resident fish fauna.

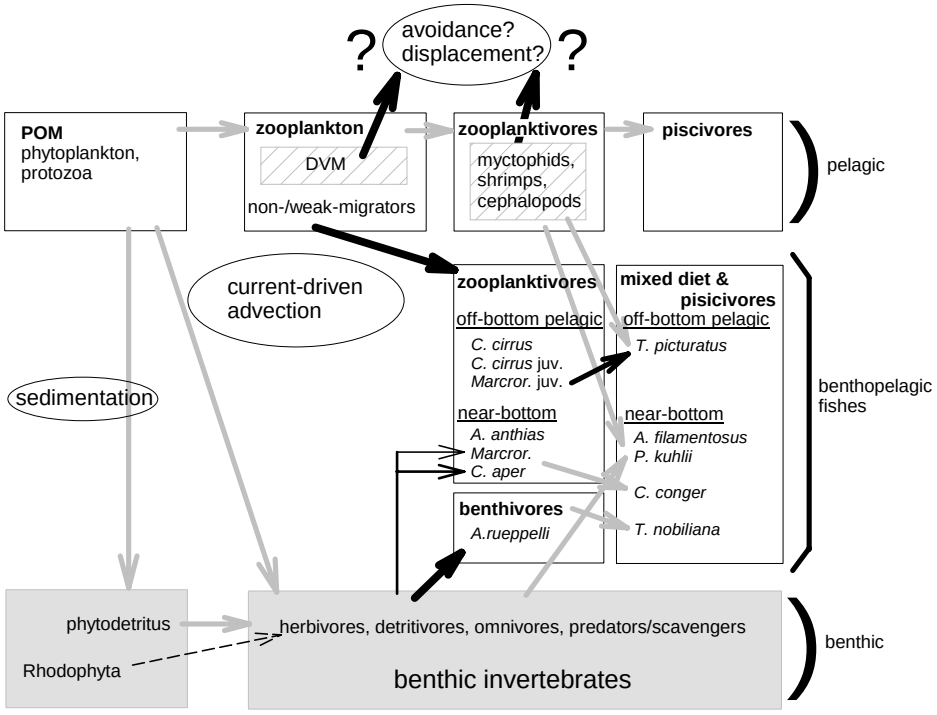

Figure 7. Simplified trophic pathways from pelagic and benthic food sources to the benthopelagic fish fauna on the summit plateau of Seine Seamount. Pathways observed in this study are indicated with black arrows. More important pathways are indicated by thick lines and minor ones by thin or broken lines. Investigated fish species are listed with regard to their vertical habitat. Trophic links taken from literature are indicated by grey arrows. Assumed transport mechanisms that supply pelagic food sources (POM, zooplankton) to the seamount fauna or that might explain the lack of diel vertical migrators (DVM, indicated by shaded boxes) in the overlying water column are also given.

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REFERENCES

Anderson J.T. (1994) Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. *Marine Ecology Progress Series,* **104**, 211-226.

Arrington D.A., Winemiller K.O. (2002) Preservation effects on stable isotope analysis of fish muscle. *Transactions of the American Fisheries Society*, **131**, 337–342.

Badcock J., Merrett N.R. (1976) Midwater Fishes in the eastern North Atlantic–I. Vertical distribution and associated biology in 30°N, 23°W, with development notes on certain myctophids. *Progress in Oceanography*, **7**, 3–58.

Beck, T., Metzger T., Freiwald A. (2005) *BIAS: Biodiversity Inventorial Atlas of Macrobenthic Seamount Animals*. OASIS, Hamburg: 118 pp.

Beckmann A., Mohn C. (2002) The upper ocean circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. *Ocean Dynamics*, **52**, 194-204.

Bilecenoglu M (2006) Status of the genus *Macroramphosus* (Syngnathiformes:Centriscidae) in the eastern Mediterranean Sea. *Zootaxa*, **1273**, 55–64.

Bligh E.G., Dyer W.J. (1959) A rapid method of total lipid extraction and purification. *Canadian Journal of Biochemistry and Physiology*, **37**, 911–917.

Bode A., Alvarez-Ossorio M.T., Carrera P., Lorenzo J. (2004) Reconstruction of trophic pathways between plankton and the North Iberian sardine (*Sardina pilchardus*) using stable isotopes. *Scientia Marina*, **68**, 165-178.

Bosley K.L., Wainright S.C. (1999) Effects of preservatives and acidification on the stable isotope ratios (^{15}N:^{14}N, ^{13}C:^{12}C) of two species of marine animals. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2181–2185.

Caramujo M.J., Boschker H.T.S., Admiraal W. (2008) Fatty acid profiles of algae mark the development and composition of harpacticoid copepods. *Freshwater Biology*, **53**, 77–90.

Clark M.R. (1999) Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. *Oceanologica Acta*, **22**(6), 593–602.

Clark M.R. (2001) Are deepwater fisheries sustainable?—the example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research*, **51**, 123–135.

Cloern J.E., Canuel E.A., Harris D. (2002) Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology and Oceanography*, **47**, 713–729.

Christiansen B., Martin B., Hirch S. (2009).The benthopelagic fish fauna on the summit of Seine seamount, NE Atlantic: composition, population structure and diets. *Deep-Sea Research II*, (in press).

Dalerum F., Angerbjörn A. (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*, **144**, 647-658.

Dalsgaard, J., St. John M., Kattner G., Müller-Navarra D, Hagen W. (2003). Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology*, **46**, 225-340.

Davenport S.R., Bax N.J. (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 514-530.

Dembitsky V.M., Pechenkina-Shubina E.E., Rozentsvet O.A. (1991) Glycolipids and fatty acids of some sea weeds and marine grasses from the Black Sea. *Phytochemistry*, **30**(7), 2279-2283.

DeNiro M.J., Epstein S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, **42**, 495–506.

DeNiro M.J., Epstein S. (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, **45**, 341–351.

De Troch M., Chepurnov V., Gheerardyn H., Vanreusel A., Ólafsson E. (2006) Is diatom size selection by harpacticoid copepods related to grazer body size? *Journal of Experimental Marine Biology and Ecology*, **332**, 1– 11.

Dower J.F., Freeland H., Juniper K. (1992) A strong biological response to oceanic flow past Cobb Seamount. *Deep-Sea Research*, **39**, 1139–1145.

Dower J.F., Mackas D.L. (1996) ''Seamount effects'' in the zooplankton community near Cobb Seamount. *Deep-Sea Research I*, **43**, 837– 858.

Dower J.F., Perry R.I. (2001) High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific. *Fisheries Oceanography*, **10**, 268–274.

Dunstan, G.A., Sinclair A. J., O´Dea K., Naughton J. M. (1988) The lipid content and fatty acid composition of various marine species from southern Australian coastal waters. *Comparative Biochemistry and Physiology*, **91B**, 165-169.

Ehrich S. (1974) Die Fische der großen Meteorbank. Ph.D. Thesis, Universität Kiel, 1-213.

Ehrich S. (1976) Zur Taxonomie, Ökologie und Wachstum von *Macroramphosus scolopax* (Linnaeus, 1758) (Pisces, Syngnathiformes) aus dem subtropischen Nordostatlantik. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, **24**, 251-266.

Ehrich S. (1986) Macroramphosidae. In: P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (Eds). *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris. Vol 2.: 627.

FishBase (2009). Froese, R. and D. Pauly (Editors). World Wide Web electronic publication: www.fishbase.org, version (06/2009).

Fock H.O., Matthiessen B., Zidowitz H., von Westernhagen H. (2002a) Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. *Marine Ecology Progress Series*, **244**, 219–233.

Fock H.O., Uiblein F., Köster F., von Westernhagen H. (2002b) Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic) sampled by different trawls. *Marine Biology*, **141**, 185–199.

Folch J., Lees M., Sloane-Stanley G.H. (1957) A simple method for isolation and purification of total lipids from animal tissues. J*ournal of Biological Chemistry*, **226**, 497-509.

France R., Chandler M., Peters R. (1998) Mapping trophic continua of benthic food webs: body size-$\delta^{15}N$ relationships. *Marine Ecology Progress Series*, **174**, 301–306.

Fraser A.J., Sargent J.R., Gamble J.C., Seaton D.D. (1989) Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. *Marine Chemistry*, **27**, 1-18.

Fry B., Arnold C. (1982) Rapid $^{13}C/^{12}C$ turnover during growth of brown shrimp (*Penaeus aztecus*). *Oecologia*, **54**, 200–204.

Fry B. (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*, **33**, 1182–1190.

Fry B. (2006) *Stable Isotope Ecology*. Springer Verlag, New York, USA.

Genin A., Boehlert G.W. (1985) Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. *Journal of Marine Research*, **43**, 907– 924.

Genin A., Haury L., Greenblatt P. (1988) Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. *Deep Sea Research*, **35**, 151-175.

Genin A. (2004) Biophysical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, **50**, 2-20.

González N., Anadón R., Mouriño B., Fernandez E., Sinha B., Escánez J., Armas D.D. (2001) The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: The role of mesoscale instabilities. *Limnology and Oceanography*, **46**, 946-952.

Hagen W. (2000) Lipids. In: R. Harris, P. Wiebe, J. Lenz, H.R. Skjoldal, M. Huntley (Eds). *ICES Zooplankton Methodology Manual*. Academic Press, San Diego: 113-119.

Halpern B.S., Floeter S.R. (2008) Functional diversity responses to changing species richness in reef fish communities. *Marine Ecology Progress Series*, **364**, 147–156.

Hesslein R.H., Hallard K.A., Ramlal P. (1993) Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}C$, $\delta^{13}C$, and $\delta^{15}N$. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2071–2076.

Iken K., Brey T., Wand U., Voigt J., Junghans P. (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Progress in Oceanography*, **50**, 383–405.

Iken K., Bluhm B.A., Gradinger R. (2005) Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. *Polar Biology*, **28**, 238–249.

Isaacs J.D., Schwartzlose R.A. (1965) Migrant sound scatterers: interaction with the seafloor. *Science*, **150**, 1810–1813.

Iverson S.J., Field C., Bowen W.D., Blanchard W. (2004) Quantitative fatty acid signature analysis: a new method of estimating predator diets. *Ecological Monographs*, **74**(2), 211–235.

Jacob U., Mintenbeck K., Brey T., Knust R., Beyer K. (2005) Stable isotope food web studies: a case for standardized sample treatment. *Marine Ecology Progress Series*, **287**, 251–253.

Jennings S., Pinnegar J.K., Polunin N.V.C., Boon T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934–944.

Jennings S., Mackinson S. (2003) Abundance–body mass relationships in size-structured food webs. *Ecology Letters*, **6**, 971–974.

Kaehler S., Pakhomov E.A. (2001) Effects of storage and preservation on the $\delta^{13}C$ and $\delta^{15}N$ signatures of selected marine organisms. *Marine Ecology Progress Series*, **219**, 299–304.

Kattner G., Fricke H.S.G. (1986) Simple gas-liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. *Journal of Chromatography*, **361**, 263-268.

Khotimchenko S.V., Vaskovsky V.E. and Przhemenetskaya V.F. (1990) Distribution of eicosapentaenoic and arachidonic acids in different species of *Gracilaria*. *Phytochemistry*, **30**(1), 207-209.

Kirsch P.E., Iverson S.J., Bowen W.D., Kerr S.R., Ackman R.G. (1998) Dietary effects on the fatty acid signature of whole Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1378–1386.

Klimley A.P., Richert J.E., Jorgensen S.J. (2005) The Home of Blue Water Fish. *American Scientist*, **93**, 42-49.

Koppelmann R., Böttger-Schnack R., Möbius J., Weikert H. (2009) Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. *Journal of Plankton Research*, **31**, 669-686.

Koslow J.A. (1996) Energetic and life-history patterns of deepsea benthic, benthopelagic and seamount-associated fish. *Journal of Fish Biology*, **49**(Suppl A), 54-74.

Koslow J.A. (1997) Seamounts and the ecology of deep-sea fisheries. *American Scientist*, **85**, 168– 176.

Koslow J.A., Boehlert G.W., Gordon J.D.M., Haedrich R.L., Lorance P., Parin N. (2000) The impact of fishing on continental slope and deep-sea ecosystems. *ICES Journal of Marine Science*, **57**, 548-557.

Kukuev E.I. (2004) Ichthyofauna research on underwater mountain within the North-Atlantic ridge and adjacant areas. *Archive of Fishery and Marine Research*, **51**, 215–232.

Layman C.A., Winemiller K.O., Arrington D.A., Jepson D.B. (2005) Body size and trophic position in a diverse food web. *Ecology*, **86**, 2530–2535.

Longhurst A. (1995) Seasonal cycles of pelagic production and consumption. *Progress in Oceanography*, **36**, 77–167.

Longhurst A. (1998) *Ecological Geography of the Sea*. Academic Press, San Diego: 398 pp.

Lopes M., Murta A.G., Cabral H.N. (2006) Discrimination of snipefish *Macroramphosus* species and boarfish *Capros aper* morphotypes through multivariate analysis of body shape. *Helgoland Marine Research*, **60**, 18-24.

MacAvoy S.E., Macko S.A., Garman G.C. (2001) Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 923–932.

MacDonald J.S., Waiwood K.G., and Green R.H. (1982) Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and American plaice (*Hippoglossoides platessoides*). *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 651–659.

Marguillier S., van der Velde G., Dehairs F., Hemminga M.A., Rajagopal S. (1997) Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}C$ and $\delta^{15}N$. *Marine Ecology Progress Series*, **151**, 115–121.

Marques V., Chaves C., Morais A., Cardador F., Stratoudakis Y. (2005) Distribution and abundance of snipefish (*Macroramphosus* spp.) off Portugal (1998–2003). *Scientia Marina*, **69**, 563–576.

Martin B., Nellen W. (2004) Composition and distribution of zooplankton at the Great Meteor Seamount (subtropical North-east Atlantic). *Archive of Fishery and Marine Research*, **51** (1-3), 89-100.

Martin B. (2008) Der Einfluss von Seebergen auf Zooplanktongemeinschaften. Ph.D. Thesis, Universität Hamburg, 1-139.

Martin B., Christiansen B. (2009) Distribution of zooplankton biomass at three seamounts in the NE Atlantic. *Deep-Sea Research II*, (in press).

Matthiessen B., Fock H.O., von Westernhagen H. (2003) Evidence for two sympatric species of snipefishes *Macroramphosus* spp. (Syngnathiformes, Centriscidae) on Great Meteor Seamount. *Helgoland Marine Research*, **57**, 63-72.

Menezes G.M., Rosa A., Melo O., Pinho M.R. (2009) Demersal fish assemblages off the Seine and Sedlo seamounts (northeast Atlantic). *Deep-Sea Research II*, (in press).

Michener R.M., Schell D.M. (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: R.H. Michener, K. Lajtha (Eds). *Stable isotopes in ecology and environmental science*. Blackwell, Oxford:138–157.

Minagawa M., Wada E. (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. *Geochimica et Cosmochimica Acta*, **48**, 1135–1140.

Miyazaki E., Sasaki K., Mitani T., Ishida M., Uehara S. (2004) The occurrence of two species of *Macroramphosus* (Gasterosteiformes: Macroramphosidae) in Japan: morphological and ecological observations on larvae, juveniles, and adults. *Ichthyological Research*, **51**, 256–262.

Mohn C., Beckmann A. (2002a) Numerical studies on flow amplification at an isolated shelf break bank, with application to Porcupine Bank. *Continental Shelf Research*, *22*, 1325-1338.

Mohn C., Beckmann A. (2002b) The upper ocean circulation at Great Meteor Seamount. Part I: Structure of density and flow fields. *Ocean* Dynamics, 52, 179-193.

Morato T., Sola E., Gros M.P., Menezes G. (1999) Diets of forkbeard (*Phycis phycis*) and conger eel (*Conger conger*) off the Azores during spring of 1996 and 1997. *Arquipelago. Life and Marine Sciences*, **17A**, 51-64.

Mouriño B., Fernandez E., Serret P., Harbour D., Sinha B., Pingree R. (2001) Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). *Oceanologica acta*, **24** (2), 1-20.

O'Neil J.M., Metzler P.M., Glibert P.M. (1996) Ingestion of $^{15}N_2$-1abelled Trichodesmium spp. and ammonium regeneration by the harpacticoid copepod *Macrosetella gracilis*. *Marine Biology*, **125**, 89-96.

O'Sullivan S., Moriarity C., Davenport J. (2004) Analysis of the stomach contents of the European conger eel *Conger conger* in Irish waters. *Journal of the Marine Biological Association of the United Kingdom*, **84(4)**, 823-826.

Pakhorukov N.P. (2008) Visual Observations of Fish from Seamounts of the Southern Azores Region (the Atlantic Ocean). *Journal of Ichthyology*, **48** (1), 114–123.

Parin N.V., Mironov A.N., Nesis K.N. (1997) Biology of the Nazca and Sala-y-Gómez submarine ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific ocean: composition and distribution of the fauna, its community and history. *Advances in Marine Biology*, **32**,145-242.

Perga M.E., Gerdeaux D. (2005) 'Are fish what they eat' all year round? *Oecologia*, **144**, 598-606.

Peters J., Renz J., van Beusekom J., Boersma M., Hagen W. (2006) Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin) - evidence from lipid composition. *Marine Biology*, **149**, 1417-1429.

Peterson B.J., Fry B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 239-320.

Pettitt T.R., Jones A.L., Harwood J.L. (1989) Lipids of the marine red algae, *Chondrus crispus* and *Polysiphonia lanosa*. *Phytochemistry*, **28** (2), 399-405.

Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.

Post D.M., Arrington D.A., Layman C.A., Takimoto G., Quattrochi J., Montaña C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, **152**, 179-189.

Rau G.H., Hopkins T.L., Torres J.J. (1991) ^{15}N:^{14}N and ^{13}C:^{12}C in Weddell Sea invertebrates: implications for feeding diversity. *Marine Ecology Progress Series*, **77**, 1–6.

Robalo J.I., Sousa-Santos C., Cabral H., Castilho R., Almada V.C. (2009) Genetic evidence fails to discriminate between *Macroramphosus gracilis* Lowe 1839 and *Macroramphosus scolopax* Linnaeus 1758 in Portuguese waters. *Marine Biology*, (in press).

Roden G.I. (1987) Effects of seamounts and seamount chains on ocean circulation and thermohaline structure. In: B.H. Kaeting, P. Fryer, R. Batisa, G.W. Boehlert (Eds). *Seamounts, Islands, and Atolls*. Geophysical Monograph Series, 43, AGU, Washington D.C.: 335-354.

Rogers A.D. (1994) The Biology of Seamounts. *Advances in Marine Biology*, **30**, 305–349.

Santos J., Borges T. (2001) Trophic relationships in deep-water fish communities off Algarve, Portugal. *Fisheries Research*, **51**, 337-341.

Sarakinos H.C., Johnson M.L., Vander Zanden M.J. (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. *Canadian Journal of Zoology*, **80**, 381–387.

Sargent J.R., Henderson R.J. (1986) Lipids. In: E.D.S. Corner, S. O´Hara (Eds). *Biological chemistry of marine copepods.* University Press, Oxford: 59-108.

Sargent J.R., Henderson R.J. (1995) Marine (n-3) polyunsaturated fatty acids. In: R.J. Hamilton (Ed). *Developments in oils and fats*. Blackie Academic and Professional, London: 32-65.

Seki M.P., Somerton D.A. (1994) Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Southeast Hancock Seamount. *Environmental Biology of Fishes*, **39**, 73–84.

Smith-Vaniz W.F. (1986) Carangidae. In: P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (Eds). *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris. Vol. 2: 815-844.

Sobrinho-Gonçalves L., Isisdro E. (2001) Fish larvae and zooplankton biomass around Faial Island (Azores archipelago). A preliminary study of species occurrence and relative abundance. *Arquipélago. Life and Marine Sciences*, **18A**, 35-52.

St. John M.A., Lund T. (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea Cod. *Marine Ecology Progress Series*, **131**, 75-85.

Tande K.S., Henderson R.J. (1988) Lipid composition of copepodite stages and adult females of *Calanus glacialis* in Arctic waters of the Barents Sea. *Polar Biology*, **8**, 333-339.

Tocher D.R., Sargent J.R. (1984) Analyses of lipids and fatty acids in ripe roes of some northwest European marine fish. *Lipids*, **19**, 492-499.

Tortonese E. (1986) Centracanthidae. In: P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (Eds). *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO, Paris. Vol. 2: 908-911.

Tseitlin V.B. (1985) The energetics of fish populations inhabiting seamounts. *Oceanology*, **25**, 237–239.

Turner J.T. (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zoological Studies*, **43**(2), 255-266.

Uchida R.N., Tagami D.T. (1984) Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. *Marine Fisheries Review*, **2**, 1– 17.

Uda M., Ishino M. (1958) Enrichment pattern resulting from eddy systems in relation to fishing grounds. *Journal of the Tokyo University of Fisheries*, **44**, 105-129.

Vander Zanden M.J., Rasmussen, J.B. (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography*, **46**, 2061–2066.

Wada E., Terazaki M., Kobaya Y., Nemoto T. (1987) ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on biogeochemical structure of the food web. *Deep-Sea Research*, **34**, 829–841.

Watanabe T. (1993) Importance of Docosahexaenoic Acid in Marine Larval Fish. *Journal of the World Aquaculture Society*, **24**(2), 152-161.

Whitehead P.J.P., Bauchot M.-L., Hureau J.-C., Nielsen J., Tortonese E. (Eds) (1986) *Fishes of the North-eastern Atlantic and the Mediterranean.* UNESCO, Paris. Vols. I-III: 1473 pp.

Wiebe P.H. (1970) Small-scale spatial distribution in oceanic zooplankton. *Limnology and Oceanography*, **15**, 205-217.

Wiebe P.H., Morton A.W., Bradley A.M., Backus R.H., Craddock J.E., Barber V., Cowles T.J., Flierl G.R. (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Marine Biology*, **87**, 313-323.

Yasui M. (1986) Albacore, *Thunnus alalunga*, pole-and-line fishery around the Emperor Seamounts. In: R. N. Uchida, S. Hayasi, G.W. Boehlert (Eds). *Environment and resources of seamounts in the North Pacific*. NOAA Technical Report NMFS 43: 37-40.

THE BENTHOPELAGIC FISH FAUNA ON THE SUMMIT OF SEINE SEAMOUNT, NE ATLANTIC: COMPOSITION, POPULATION STRUCTURE AND DIETS

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ABSTRACT

Benthopelagic fishes were sampled during three cruises to Seine Seamount, NE Atlantic, using bottom trawls and an epibenthic sledge. A total of 16 fish species were caught on the summit plateau of the seamount at 160-180 m depth, belonging to 15 different families. Four species were common to all types of trawls, whereas the other species were found only in part of the catches. Most fishes caught were small species and typical for shelf and seamount communities. The most abundant fish was the snipefish, *Macroramphosus* spp., which was important also in terms of biomass. The population structure (size classes and length/weight relationships) of the 5 most abundant species (*Macroramphosus* spp., *Capros aper*, *Anthias anthias*, *Callanthias ruber*, and *Centracanthus cirrus)* shows that usually two or three size classes, probably representing age groups (year classes), were present, and that growth rates were high. A stomach content analysis of these fishes revealed a predominance of pelagic prey, mainly small copepods. No indications for a seamount effect in terms of enhanced biomass or topographic blockage were found.

1. INTRODUCTION

Seamounts are often regarded as areas of enhanced biodiversity and productivity in the higher trophic levels, as compared to the surrounding ocean. This has, for a few decades, drawn the attention of fishermen who found high abundances of commercially valuable fish species at many seamounts (Koslow, 1997). The reasons for the fish aggregations at seamounts are still not clear. Hypotheses include that seamounts are a "meeting point" of usually dispersed fish stocks, for example to aggregate for spawning, or that an enhanced food supply caused by special current conditions is the basis for locally maintaining large fish stocks. The topographic blockage hypothesis suggests that benthopelagic fish benefit from vertically migrating zooplankton and mikronekton and thus link these compartments of the ecosystem with the higher trophic levels (Isaacs and Schwartzlose, 1965; Genin, 2004).

Although information on commercial fish stocks is available for many seamounts, the knowledge about the smaller benthopelagic fish as their potential food basis is still poor. The most comprehensive study in the north Atlantic was made at Great Meteor Seamount, where fishes were sampled on the summit plateau during cruises in 1967 and 1970 and again in 1998 (Ehrich, 1977; Fock *et al.*, 2002a; Fock *et al.*, 2002b). The fish fauna of this seamount comprised mainly typical shelf species with faunal relationships to the NW African shelf, the European shelf and the Macaronesian islands (Ehrich, 1977).

In the framework of the OASIS project fishes were collected at Seine Seamount using two approaches: On the one hand, longline sets were employed to collect fish of potentially commercial value (see Menezes *et al.*, 2009). In this study, we used different types of bottom trawls to catch those fish which are not readily sampled by baited longlines.

2. MATERIAL AND METHODS

Benthopelagic fishes were sampled on the summit of Seine Seamount, NE Atlantic. This seamount lies ca 180 km northeast of Madeira. It has a near-circular shape and rises from more than 4000 m to a summit plateau at 160-180 m (Figure 1). The almost plane summit plateau has an elliptical shape and is about 15 km long and 7 km wide; the

area above the 200 m contour is ca 50 km^2. Seafloor photographs show that it is covered in most places by coarse-grained sediment with only a few organisms and Lebensspuren visible. In some places flat rocks protrude a few centimeters above the sedimentary surface.

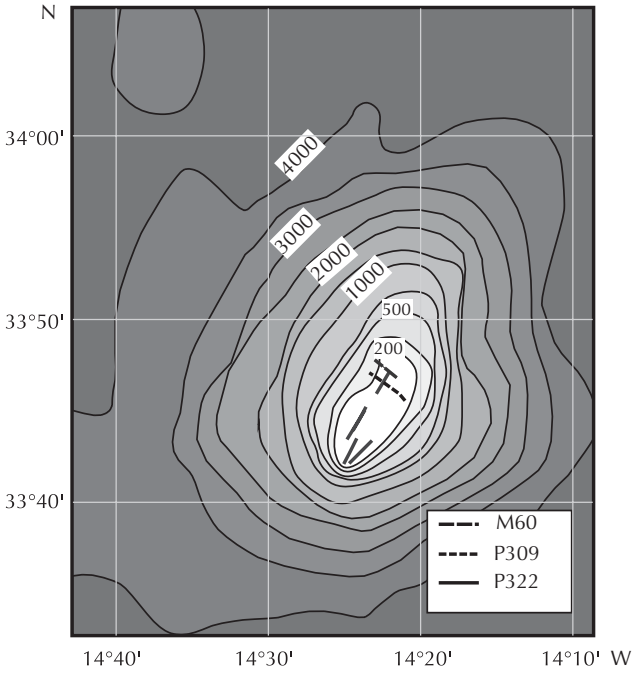

Figure 1.

Bathymetry of Seine Seamount with tracks of trawls.

Fishes were collected on three cruises to Seine Seamount using different types of trawls. The tow statistics for all trawl hauls are summarized in Table 1.

Table 1. Haul data.

Cruise	M60/1	P309	P322	P322	P322	P322
Gear/haul	EBS	OT45	OT80/1	BT2/1	BT2/2	OT80/2
Date	4.12.2003	31.3.2004	15.5.2005	17.5.2005	18.5.2005	18.5.2005
Start position	33°45.9'N 014°21.7'W	33°43.2'N 014°25.1'W	33°42.6'N 014°24.7'W	33°42.1'N 014°24.7'W	33°43.4'N 014°24.8'W	33°44.5'N 014°24.0'W
End position	33°46.8'N 014°23.2'W	33°44.4'N 014°24.8'W	33°43.5'N 014°24.2'W	33°43.4'N 014°23.2'W	33°45.0'N 014°23.7'W	33°45.2'N 014°23.6'W
Depth range	176-193 m	166-172 m	170-174 m	172-173 m	169-170 m	165-168 m
Tow distance /m	2850	2270	1680	1940	1390	1420
Width swept/m	2	8.6	14	2	2	14
Area swept /ha		1.95	2.35	0.39	0.28	1.99

During cruise Meteor 60/1, one haul with an epibenthic sledge was performed on the summit plateau of Seine Seamount at a water depth of 170-180 m. The epibenthic sledge was equipped with a 500 µm suprabenthic net and a 5 mm epibenthic net. Both nets opened only at bottom contact. Tow duration was ca 30 min. The tow track is

shown in Figure 1. After recovery of the sledge, the lower part of the epibenthic net showed signs of abrasure indicating that the sledge was towed partly over rocky areas; however, the catch was not affected.

During cruise Poseidon 309, an otter trawl was successfully employed on the summit plateau of Seine Seamount. We used a Marinovitch otter trawl with a foot rope length of 45 feet (ca 15 m) and an estimated net opening of 8.6 m (Merrett and Marshall, 1981). The mesh size was 44 mm in the front part and 37 mm in the intermediate part and in the codend, with a 13 mm inner liner in the codend. The trawl was towed for ca 25 min (estimated bottom time) at a speed of 2.5 knots (tow track see Figure 1). The mud rollers and the foot rope were damaged during the haul, also showing that rocky areas are present on the summit plateau. However, since the net was largely undamaged, an effect on the catch appears unlikely.

Finally, on cruise Poseidon 322 we made two hauls each with an otter trawl and a beam trawl, both towed at 2.5-3 kn for ca 20 min. The otter trawl had a foot rope length of 80 ft (about 27 m) and a mesh of 30 mm in the codend. The horizontal net opening was estimated as 14 m. The 2 m beam trawl was equipped with a 6 mm mesh net. The tow tracks are shown in Figure 1.

Epibenthic megafauna and benthopelagic fauna from the epibenthic sledge were separately fixed in buffered formaldehyde. A subsample of specimens or tissue from various taxa was frozen at -80 °C for trophic analyses. In the laboratory, the preserved specimens were weighed, measured and sexed.

The catches from the otter trawls and beam trawls (P309 and P322) were sorted on board, and for each species the total weight was measured. Length measurements were made either on all specimens or, if numbers were too high, on a representative subsample. A few sample specimens were fixed in ethanol for genetic analyses. Tissue samples were frozen at -80 °C for isotopic and lipid analyses. The remainder was fixed in buffered formaldehyde. In the laboratory, the identification of fishes was verified, and the preserved fishes (Meteor 60/1 and Poseidon 309 only) were weighed, measured and sexed individually. Stomachs were taken for diet analyses. The stomach contents of a subsample of the three most abundant species (Poseidon 309 only, 12-24 specimens each) were identified to the lowest taxon possible.

3. RESULTS

3.1 CATCH COMPOSITION AND BIOMASS

A total of about 3200 fishes were collected in all 6 hauls, representing 16 fish species belonging to 15 different families (Table 2). The number of fishes caught differed greatly between the hauls, ranging from 16 to about 2200. The most abundant fish in all trawls was the snipefish, *Macroramphosus* sp(p), making up 37-89 % of all specimens. At several NE Atlantic seamounts, two morphological types of this fish were found, *M. scolopax* and *M. gracilis*, which may represent different species (Ehrich, 1974; Matthiessen, 2001; Matthiessen, 2003; Lopes *et al.*, 2006). The distinction of these two types in the Seine Seamount material is not quite clear; according to the position of the spike, most of the fishes belong to the *gracilis* type or an intermediary form. On the other hand, a histogram of the ratios spike length/standard length shows a bimodal shape which may indicate that two distinct types exist (Figure 2). In the following, we will, for practical reasons, consider *M. scolopax/gracilis* one species, but acknowledging that it may in fact represent two species.

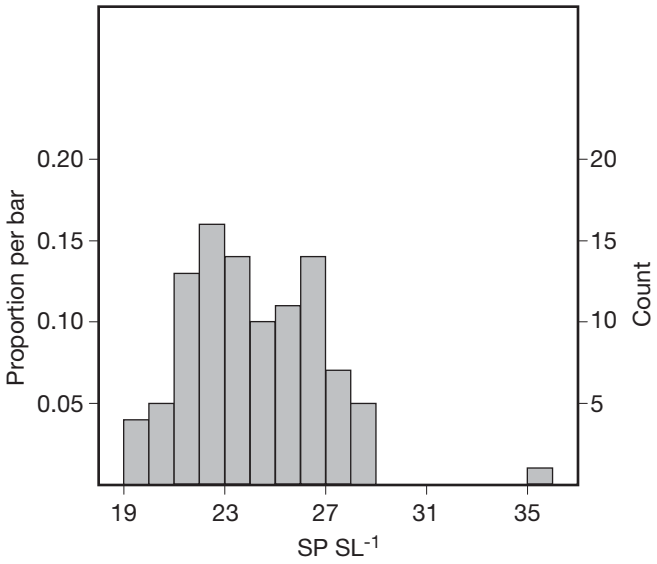

Figure 2.

Macroramphosus sp(p). Histogram of the ratio spike length/standard length.

The number of species per haul ranged from 5 to 10; the highest species numbers were collected with the large otter trawl and the epibenthic sledge. Four fish species were common to all trawl types. Two species were found only in both types of otter trawls, one species in both the beam trawl and epibenthic sledge, and one species only in the otter trawl and beam trawl used on P322. The remaining species occurred in only one type of trawl (Table 2).

Table 2. Catch composition of benthopelagic fishes.

Order	Family	Species	Dec 03 Meteor EBS 2m	Mar 04 Pos OT 45ft	May 05 Pos OT 80ft	May 05 Pos OT 80ft	May 05 Pos BT 2m	May 05 Pos BT 2m	Sum
Rajiformes	Rajidae	*Raja c.f. maderensis*					1		1
Torpediformes	Torpedinidae	*Torpedo nobiliana*			2				2
Perciformes	Labridae	*Lappanella fasciata*	2						2
Perciformes	Centracanthidae	*Centracanthus cirrus*		107	24	2			133
Perciformes	Carangidae	*Trachurus picturatus*		6	1	2			9
Perciformes	Serranidae	*Anthias anthias*	4	58	9	16		1	88
Perciformes	Callanthiidae	*Callanthias ruber*	12	31					43
Scopeliformes	Aulopidae	*Aulopus filamentosus*			1				1
Scorpaeniformes	Scorpaenidae	*Pontinus kuhlii*	1		3		2	1	7
Zeiformes	Caproidae	*Capros aper*	2	44	49	28	4	7	134
Zeiformes	Zeidae	*Zenopsis conchifer*			1				1
Pleuronectiformes	Bothidae	*Arnoglossus rueppeli*	12				3	14	29
Anguilliformes	Congridae	*Gnathophis mystax*	1						1
Anguilliformes	Congridae	*Conger conger*			2	1		1	4
Gadiformes	Moridae	*Gadella maraldi*	3						3
Syngnathiformes	Centriscidae	*Macroramphosus gracilis/scolopax*	33	2000[a]	610	84	6	76	2809
		Sum	70	2246	702	133	16	100	3267
		No species	9	6	10	6	5	6	16
		total biomass/ kg	n.a.	45.6	33.6	8.6	1.4	3.6	92.8
		No/ ind ha^{-1}	123	1150	279	62	41	360	
		biomass/ kg ha^{-1}		23.4	13.4	4.0	3.6	13.0	

[a] Estimated from total catch weight and mean individual biomass

Figure 3 presents the catch composition in terms of wet weight for all hauls except the epibenthic sledge haul performed on cruise M60/1, where no weight measurements of freshly collected fish were made.

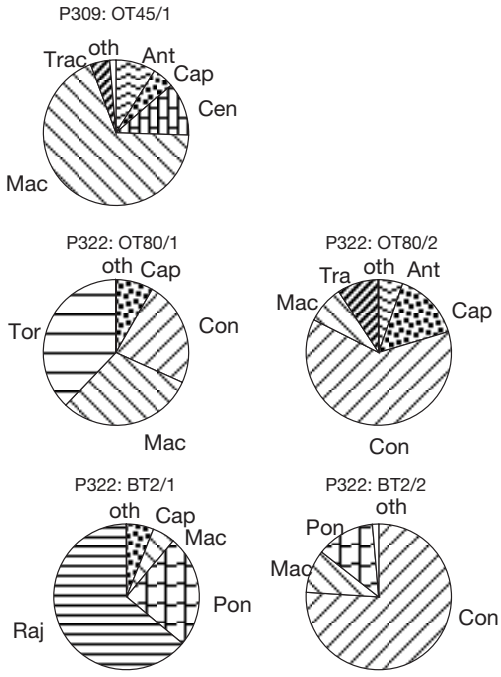

Figure 3.

Catch composition in terms of biomass (wet weight.
Ant: *Anthias anthias* and *Callanthias ruber*;
Cap: *Capros aper*;
Cen: *Centracanthus cirrus*;
Con: *Conger conger*;
Mac: *Macroramphosus* sp(p).;
Pon: *Pontinus kuhlii*;
Raj: *Raja maderensis*;
Tor: *Torpedo nobliliana*;
Tra: *Trachurus picturatus*

The catch composition differs considerable between the five hauls. On cruise P309, only small species were caught with the 45 ft otter trawl. The predominating species was *Macroramphosus* sp(p), making up 70 % of the total catch of 45 kg. *Centracanthus cirrus* followed with 12 %, *Anthias anthias* and *Callanthias ruber* combined with 9 %. All other species contributed less than 5 % to the total catch.

In the two hauls of the 80 ft otter trawl on cruise Poseidon 322, a few large specimens made up a large part of the total biomass. In haul OT80/1, two specimens of the ray *Torpedo nobiliana* and two conger eels formed more than half of the biomass. *Macroramphosus* sp(p) contributed 28 %, and *Capros aper* 8 %. In haul OT80/2, one *Conger conger* was caught (62 % of the biomass), *Macroramphosus* reached only 8 %, *Capros* 15 %, and *Anthias/Callanthias* 5 %. The total catch in haul OT80/2 (8.1 kg) was much smaller than in haul OT80/1 (34 kg).

The catches of the two beam trawl hauls on cruise P322 were also dominated, in terms of biomass, by a few large specimens. In haul BT2/1, the catch was very small (1.4 kg) and comprised one ray (*Raja maderensis*) which made up 64 % of the biomass, a few *Macroramphosus* sp(p). (5 %), *Pontinus kuhlii* (25 %) and *Capros aper* (6 %). In haul BT2/2, one *Conger conger* (76 %) outweighed all other fishes, only *Macroramphosus* sp(p). (13 %) and *Pontinus kuhlii* (10 %) contributing more than 5 % to the total catch of 3.6 kg.

A rough estimate of fish abundance and biomass on the summit plateau of Seine Seamount, based on the trawl catches and using the haul data in Table 1, gives a range from 41-1200 ind ha^{-1} and 4-23 kg ha^{-1}, respectively. Large differences occurred even between identical gear types: 62 vs. 280 ind ha^{-1} and 13 vs. 4 kg ha^{-1} in the two 80 ft otter trawl hauls, 41 vs. 360 ind ha^{-1} and 13 vs. 4 kg ha^{-1} in the two beam trawl hauls.

3.2 SIZE CLASSES AND LENGTH/WEIGHT RELATIONSHIPS

3.2.1 *MACRORAMPHOSUS* SP(P).

A random subsample of 108 individuals from cruise P309 (OT45) and all 33 specimens from cruise M60/1 (EBS) were used for the following analysis; these measurements are based on preserved material. The P322 (OT80 and BT) data are based on shipboard

measurement of fresh material, using all 76 specimens from the beam trawls and a random subsample of 236 from the otter trawls.

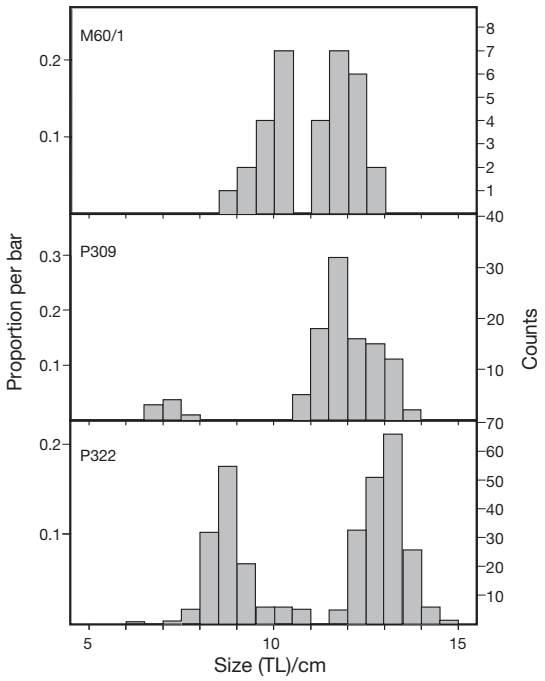

Figure 4.

Size spectra of *Macroramphosus* sp(p)., based on total length.

Figure 4 presents histograms of *Macroramphosus* size classes (total length) for all cruises and gear types. The large size group in the range of 11 to 15 cm appears to be common for all cruises, but with generally higher length values on P322 (mode=13 cm) as compared to P309 and M60/6 (mode=11.5 cm). A second, smaller size group is also present in all samples, but its length range differs between the cruises. In the P309 (OT45) sample, this group comprises only small juveniles (<8 cm). These were not present on M60/1, where the smaller of the two size groups was made up of adults in the range of 8.5-10.5 cm. The length spectrum of the smaller size group in the P322 samples is rather broad, ranging from 6-10.5 cm and including juveniles, but being distinctly smaller than in the M60/1 sample.

The data from M60/1 and P309 were used also to plot body weight versus total length (Figure 5). In the plot, three distinct size clusters show up, corresponding to the three size groups described above in the histograms. If the data from M60/1 and P309 (only adults) are plotted separately, the resulting regression curves differ and indicate a better body condition, in terms of the ratio weight/length, in late autumn than in early spring. A test on the homogeneity of slopes and a subsequent analysis of covariance show that the slopes of the two regression curves do not differ (p=0.643), but that the weight

relative to the length in fact is significantly higher in the late autumn than in the early spring samples ($p<0.001$).

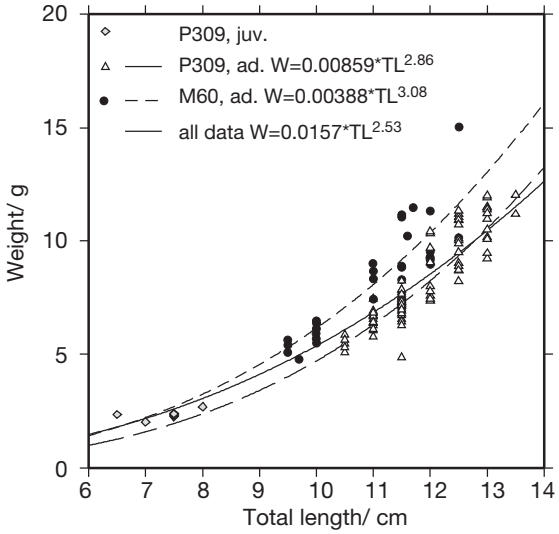

Figure 5.

Length/weight plot of *Macroramphosus* sp(p)., based on total length and wet weight.

3.2.2 *CAPROS APER*

A total of 44 specimens from cruise P309 (preserved specimens) and 39 specimens from cruise P322 (otter trawl and beam trawl, fresh) were analysed. *Capros aper* covered a size range from 4.5 to 14.5 cm. The histogram of total lengths shows a total of three distinct size groups (Figure 6), only the largest of which was found on both cruises. The smallest size group was only sampled on P322 in the beam trawl, and the medium size group only in the otter trawl on P309.

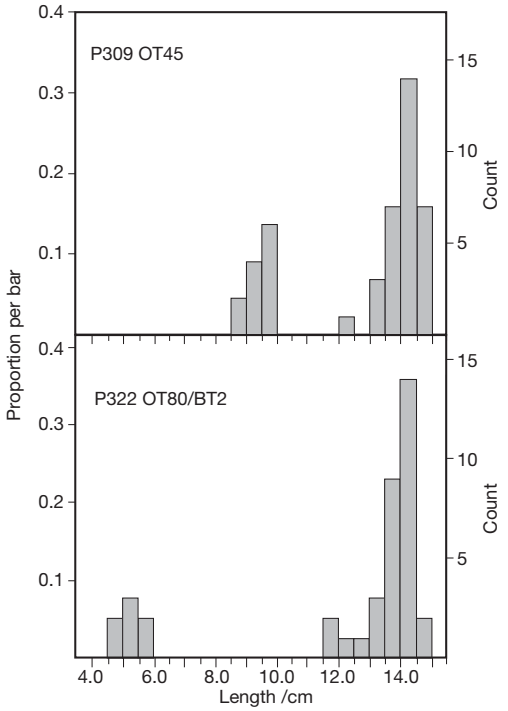

Figure 6.

Size spectra of *Capros aper*, based on total length.

3.2.3 *ANTHIAS ANTHIAS* AND *CALLANTHIAS RUBER*

A total of 61 *A. anthias* and a total of 31 *C. ruber* were caught with the 45 ft otter trawl on cruise P309. The size distribution of *A. anthias* (Figure 7) indicates two or three size classes; however, the separation of the peaks is not very clear.

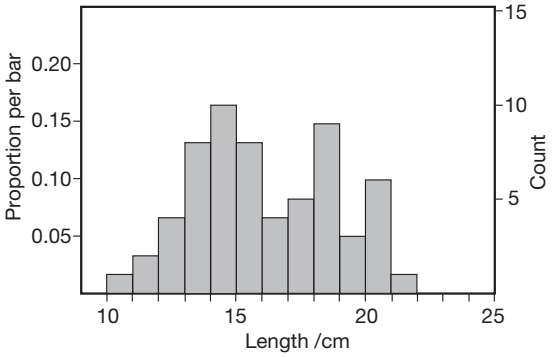

Figure 7.

Size spectra of *Anthias anthias*, based on total length.

C. ruber has the same size range as *A. anthias*, but the size distribution is skewed to the larger size classes and cut off at the right-hand side (Figure 8).

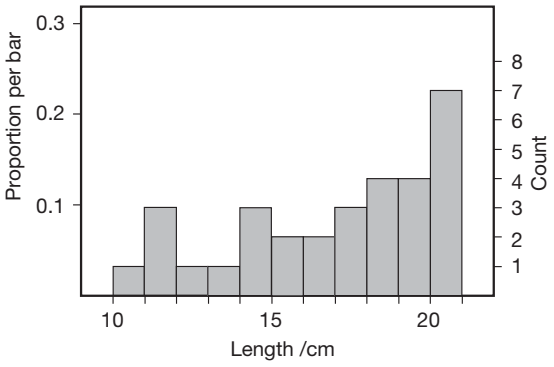

Figure 8.

Size spectra of *Callanthias ruber*, based on total length.

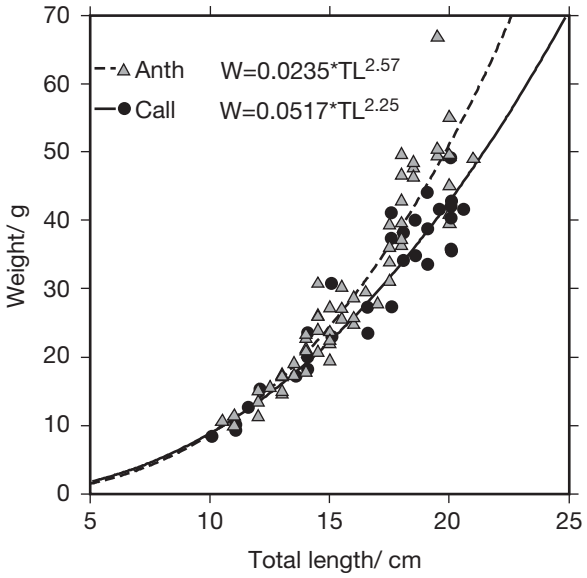

Figure 9.

Length/weight plot of *Anthias anthias* and *Callanthias ruber*, based on total length and wet weight.

The length/weight regressions for both species is shown in Figure 9 . A test on homogeneity of slopes reveals that the slopes of both regressions differ significantly ($p<0.05$), being higher in *A. anthias*.

3.2.4 *CENTRACANTHUS CIRRUS*

This species was the second most abundant fish in the Poseidon 309 sample with 107 specimens, but only 26 specimens were caught in the otter trawls on P322. *Centracanthus cirrus* was completely absent in the epibenthic sledge and beam trawls, respectively.

The size of *Centracanthus cirrus* ranged from 7 to 21 cm. Three clear size groups can be distinguished in the P309 samples, separated by conspicious gaps (Figure 10). During cruise P322 only one size group was caught in the range 9-13 cm. This is larger than the smallest size group in the P309 samples but considerably smaller than the medium size group.

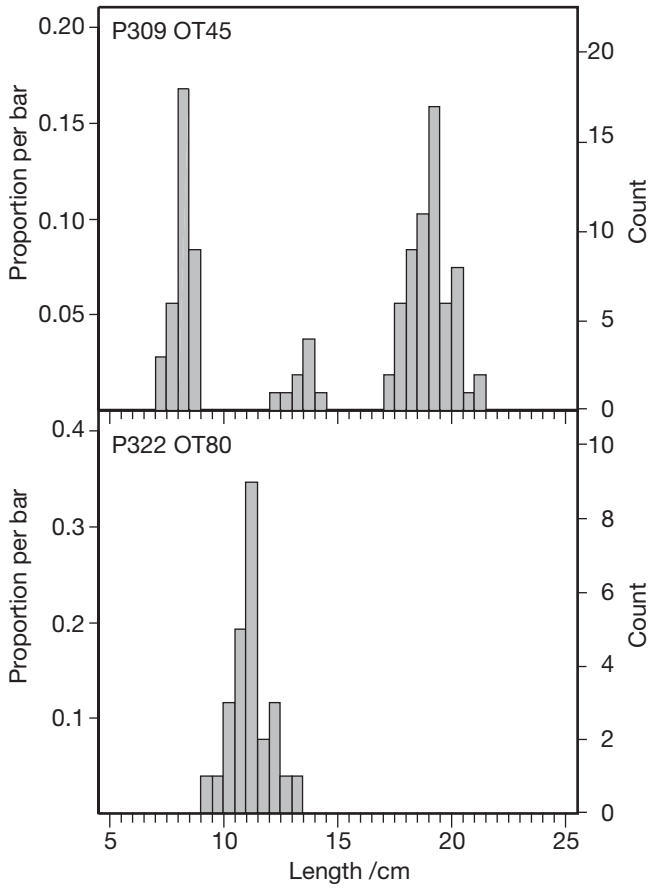

Figure 10.

Size spectra of *Centracanthus cirrus*, based on total length.

The three size groups of the P309 samples also show up in the plot of weight versus total length (Figure 11). The slope of the regression (3.13) indicates an isometric or slightly positive allometric growth.

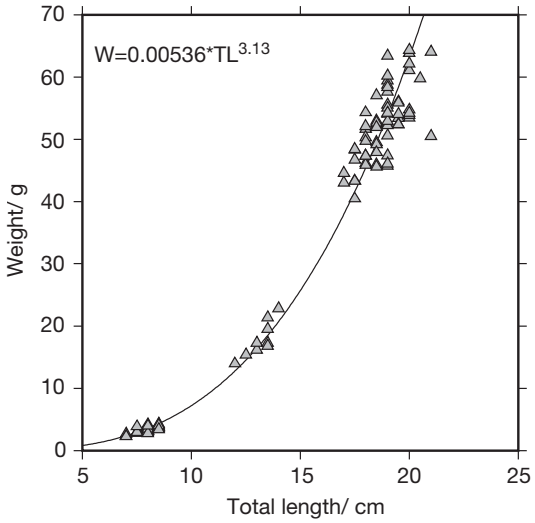

Figure 11.

Length/weight plot of *Centracanthus cirrus*, based on total length and wet weight

3.3 DIETS

Stomach and gut contents were analysed for the three most abundant species, *Macroramphosus* sp(p). (24 specimens, size groups 7-8.5 cm and 11-14 cm), *Capros aper* (20 specimens, size groups 9-9.5 cm and 13-14.5 cm), and *Centracanthus cirrus (*12 specimens, size groups 7.5-8.5 cm and 18.5-20 cm). Although copepods were numerically the predominant food items in the three fish species, making up on average 76-96 % of all prey organisms, some differences in the food composition showed up between the species, but no indications of differences between the size classes within the species were observed. Figure 12 presents the average proportions of different food items found in the stomachs.

Macroramphosus fed mainly on oncaeid copepods, which made up more than half of the prey items in their stomachs. A variety of other groups were also present, but only calanoids were consumed in considerable numbers (23 %). In addition we found small numbers of harpacticoids and corycaeids among the copepods; other crustaceans included ostracods, mysids and non-identified crustacean parts. Foraminifera were frequently found in the stomachs, and also a few polychaetes were observed.

Centracanthus fed mainly on copepods, but with a higher proportion of calanoids (58 %) than oncaeids (33 %). Harpacticoids formed 5 % of all prey. Other prey organisms included ostracods, mysids, polychaetes and chaetognaths.

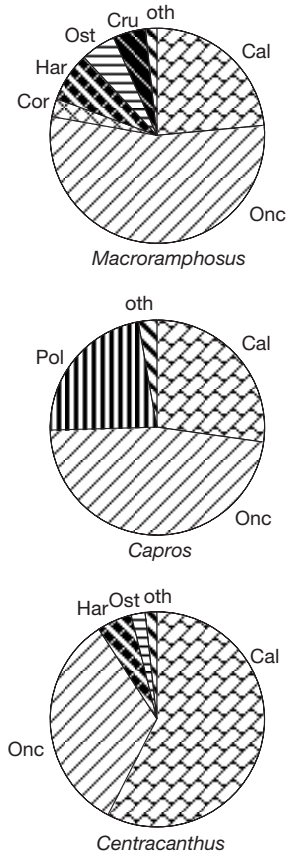

Figure 12.

Composition of fish stomach contents. Top: *Macroramphosus* sp(p).; middle: *Capros aper*; bottom: *Centracanthus cirrus*. Cal: calanoids; Cor: corycaeids; Har: harpacticoids; Onc: oncaeids; Ost: ostracods; Cru: other crustaceans.

By contrast to the species above which almost exclusively fed on crustaceans, polychaetes were an important part of the diet in *Capros*, averaging 23 % of all prey items. However, again oncaeids were the most abundant food organisms in the stomachs (47 %), followed by calanoids with 27 %. Corycaeids, ostracods and non-identified crustaceans were also found, but in low numbers.

4. DISCUSSION

4.1 COMPOSITION AND BIOMASS

On three cruises a total of 6 hauls with different trawl types were made on the summit plateau of Seine Seamount to sample invertebrates and benthopelagic fish. The fish collected comprise typical seamount and shelf epibenthopelagic species with faunal

connections to the south European and African shelfs (Ehrich, 1977; Kukuev, 2004). No endemic species were found.

The total species number of 16 appears to be low in comparison to other studies from seamount locations in the eastern Atlantic; however, differences in sampling effort have to be taken into account. Ehrich (1977) used a variety of gear to sample the fish fauna on the summit plateau of the Great Meteor Seamount, which is about 30times the area of the Seine Seamount summit plateau, during two cruises in 1967 and 1970 . Despite the higher sampling effort of 20 and 22 tows, respectively, the total number of fishes caught in these studies were lower than in the Seine study, but the number of species (34 and 28, respectively) was about twice as high. A total of 33 species were caught in 1998 at the same seamount, involving 14 tows with a 170 ft Engel bottom trawl (Fock *et al.*, 2002a). Reviewing data sets from several cruises, Kukuev (2004) reports that the ichthyocene of the tops and upper slopes of seamounts to the south of the Azores (Atlantis, Plato, Hyères, Great Meteor, Irving) is represented by 28 species; however, in surveys at individual seamounts involving 2-11 tows the number of species caught was often comparable to or even less than ours (Arkhipov *et al.*, 2004).

A longline survey at Seine Seamount revealed a total species number of 41 (Menezes *et al.*, 2009), which included catches made down to 2000 m depth. Only 5 species were common in both the longline and the trawl surveys. Although the total species number appears not to be exceptionally high, the relatively large number of families found indicates a higher genetic diversity than expected from species number alone. The 41 species caught with longlines at Seine belong to 24 families; the 16 species trawled on the Seine Seamount summit even split up in 15 families.

Besides sampling effort, gear selection is certainly one important reason for the observed differences in species numbers, as was already shown in the statistical study of Fock *et al.* (2002a). E.g., *Centracanthus* and *Trachurus*, which are not closely linked to the bottom, but are more pelagic species, were only caught in the otter trawls which are assumed to have a much higher opening than the beam trawl (the EBS has a closing mechanism). The small flatfish *Arnoglossus rueppili* was only found in beam trawl and EBS catches, which may be due to the tickler chains and the close bottom contact of these trawl types, whereas the mudrollers used on the footrope of the 45 ft otter trawl

might have led the net over the fish. *Arnoglossus* was also seen frequently on bottom photographs from the top of Seine Seamount.

Large fish like the rays *Torpedo nobiliana* and *Raja maderensis* and the eel *Conger conger* were only caught on cruise P322. The reasons for this are not clear; net selection may play a role, but, considering the low sampling effort, the catches may be just coincidental due to a low abundance and probably patchiness of these species. Generally, the high variability between the hauls not only for the rare species, and even using the same gear, may indicate a patchy distribution of the fish. In bottom photographs of the Seine Seamount summit plateau (unpublished), groups of fish were frequently seen in association with shallow rocky features.

The total fish biomass on the summit plateau, as estimated from the trawl catches, showed a high variation between the tows, and has to be used with some caution. In comparison to shelf sea areas the range found appears to be very low and resembles values rather found at bathyal depths of the deep-sea plains. E.g., the same type of 45 ft otter trawl as used on cruise P309 was also employed in several deep-sea studies. The biomass range of 4-23 $kgha^{-1}$ found on the Seine summit plateau is in the same order of magnitude as that estimated for the Iceland Basin at ca 3000 m depth (11 $kgha^{-1}$, Martin and Christiansen, 1997). The data from this survey do not support the hypothesis of enhanced benthopelagic fish stocks, at least for the summit plateau of Seine Seamount; however, we cannot exclude the possibility that fish stocks have declined due to commercial fishing. During our surveys we observed a few fishing vessels (longliners), and a lost fishing net was seen on a video from the summit (Brian Bett, pers. comm.)

4.2 SIZE DISTRIBUTION

Our catches of *Macroramphosus* spp. covered a size range of 62-145 mm, which is considerably smaller than the spectrum of 90-179 mm described by Matthiessen (2001) for fishes from the Great Meteor Seamount (GSM). She found a mono-modal spectrum which broadly corresponds to our larger size group (but including larger specimens than our samples), whereas our smaller size group seems to be missing in her samples. We cannot exclude that the different sampling gears may be responsible for this shift in the size spectrum; however, although the trawl used at GSM was considerably larger than

our trawls, the mesh size in the codend (10 mm) was smaller than in our otter trawls (13 and 30 mm, respectively).

Two size groups were present in all samples from Seine Seamount, but differences in their position showed up between cruises. Whereas the larger size group was very similar in cruises P309 and M60/1, it was shifted to the right in cruise P322. This can probably be attributed to the difference between preserved and fresh material. Fixation in formaldehyde and other agents results in significant shrinkage of fishes (e.g., Moku *et al.*, 2004). The modes of the smaller size group, however, are very different in the samples and range from 70 mm to 100 mm. If we arrange the modes on a timescale, we can see increasing modal sizes in the smaller group from March (P309, mode=72.5 mm) over May (P322, mode=85.5 mm) to December (M60/1, mode=102.5mm). Although part of this may be attributed to the difference between preserved (March and December) and fresh material (May), or to different gear selectivity, we assume that the smaller size groups may represent the same age group, but at different seasons, and hence the differences in length can be attributed to growth: the smallest specimens were caught in early spring and may grow to a medium size in late autum.

Length/weight relationships are only available for the M60/1 and P309 samples. The significant difference in the ratio of body weight to length indicates that the body condition of the fishes were better in late autumn than in early spring when probably less food was available, or when spawning had just occurred.

Capros aper also shows two size groups each in the P309 and P322 samples, but while the larger group is very similar for both cruises, the smaller group differs considerably and may in fact represent two age groups, although the absence of the medium group in the P322 sample contradicts this. All size groups are separated by conspicuous gaps which was also reported by Ehrich (1971). If the modes represent age groups, this would mean a high growth rate and obviously a short life span.

No clear size groups could be distinguished in *Anthias anthias* and *Callanthias ruber*; however, the sample size was very small. *Centracanthus cirrus*, which was only caught by the otter trawls, has three very distinct size groups with broad gaps inbetween in the P309 sample, pointing to a high growth rate; but in the catch from P322 only one group was found, which lies between the small and the medium group in the other sample.

Again, the difference between measurements of fresh or preserved material could be responsible for the difference in mean size between samples, or it can be attributed to growth between March and May, if the group caught on cruise P322 corresponds to the smallest size group found on cruise P309.

4.3 DIETS

Copepods were the most important prey organisms for the 3 fish species studied in this survey, and some preliminary results indicate that his holds for two further species, *Anthias anthias* and *Callanthias ruber*. The stomach contents basically reflect the composition of the zooplankton community found over the summit plateau of Seine Seamount, where small copepods were the predominating group in the zooplankton catches (Martin and Christiansen, in prep).

Although all species studied appear to be mainly zooplanktivorous, some differences show up in their preferred prey. Oncaeid copepods were the main prey in *Macroramphosus* and in *Capros*, which on the other hand was the only species with a significant proportion of non-crustacean food. Oncaeid copepods were abundant in the zooplankton catches above the summit of Seine Seamount, but they were usually outnumbered by calanoids (Martin & Christiansen, in prep.). The predominance of this group as prey type in *Macroramphosus* and *Capros*, and probably also in *Anthias* and *Callanthias*, may indicate that these species feed very close to the bottom where the proportion of oncaeids may be higher, or that they may actively select for oncaeids. *Centracanthus* on the other hand, which is supposed to be a more pelagic species, fed mainly on calanoids.

Macroramphosus is reported to have two different feeding types, one preferring benthic prey (b-type), the other pelagic prey (p-type), with a less abundant intermediate (p/b-type) form (Ehrich, 1974; Ehrich, 1977; Clarke, 1984; Matthiessen, 2001). In an extensive study of the diets of *Macroramphosus* from the Great Meteor Seamount, Matthiessen (2001) found that most fishes were of the pelagic prey type feeding mainly on copepods and ostracods. The food of the b-type was more diverse, including mainly benthic crustaceans, molluscs and polychaetes. Only the p-type was found in our study.

4.4 CONCLUSIONS

The trawl catches on the summit plateau of Seine Seamount show that the seamount has an effect on the composition of the benthopelagic fish community, in that the shallow parts of the seamount offer a suitable environment within an otherwise inaccessible oceanic region for species which are typical for seamounts or the continental shelfs. The diversity of the seamount benthopelagic fish fauna appears to be low, as compared to other seamounts in the NE Atlantic, but the rather low sampling effort and methodological constraints may be responsible for an underestimation of species number. The differences between the trawl types and the comparison with the longline catches stress the importance of applying a variety of different methods to minimize the effect of gear selection on the diversity. With the exception of the conger eel, the fishes caught were of no commercial interest. Most species were small and short-lived with 2 or 3 age groups in the samples.

On the other hand, a seamount effect could be observed neither in terms of enhanced stocks of benthopelagic fish nor in a topographic blockage, at least for the summit region. The standing stock of fish is in the order of magnitude which can be found at the bathyal depths of higher latitudes. Although the overall productivity in the region of Seine Seamount is certainly lower than further to the north, we would have expected a much higher biomass than usually is typical for the deep sea. However, the decreased zooplankton biomass above the seamount summit with a nearly total absence of larger, migrating groups like euphausiids (Martin and Christiansen, in prep) indicates that the food supply for planktivorous fish is even lower than in the surrounding ocean. The composition of the stomach contents, with a strong predominance of small, non-migrating copepods, shows that the benthopelagic fish are not responsible for the absence of the larger vertical migrators above Seine Seamount.

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REFERENCES

Arkhipov, A.G., Kozlov, D.A., Sirota, A.A., Shnar, V.N., 2004. Structure of waters and distribution of fish at different ontogenetic stages around seamounts of the Central-Eastern Atlantic Ocean. Archive of Fishery and Marine Research 51, 201–214.

Clarke, T.A., 1984. Diet and morphological variations in snipefishes, presently recognized as *Macroramphosus scolopax*, from southeast Australia: evidence for two sexually dimorphic species. Copeia 3, 595-608.

Ehrich, S. (1971). "Fischfauna und Fischnahrung der Großen Meteorbank," Diplomarbeit, Christian-Albrechts-Universität zu Kiel, Kiel.

Ehrich, S. (1974). "Die Fische der Großen Meteorbank. Eine Untersuchung des Biotops Große Meteorbank aus ichthyologischer Sicht.," Dissertation, Christian-Albrechts-Universität zu Kiel, Kiel.

Ehrich, S., 1977. Die Fischfauna der Großen Meteorbank. Meteor Forschungsergebnisse, Reihe D 25, 1-23.

Fock, H., Uiblein, F., Köster, F., Westernhagen, H.v., 2002a. Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. Marine Biology 141, 185-199.

Fock, H.O., Matthiessen, B., Zidowitz, H., von Westernhagen, H., 2002b. Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Marine Ecology Progress Series 244, 219-233.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems 50, 3-20.

Isaacs, J.D., Schwartzlose, R.A., 1965. Migrant sound scatterers:interaction with the seafloor. Science 150, 1810-1813.

Koslow, J.A., 1997. Seamounts and the Ecology of Deep-Sea Fisheries. American Scientist 85, 168-176.

Kukuev, E.I., 2004. Ichthyofauna research on underwater mountain within the North-Atlantic ridge and adjacant areas. Archive of Fishery and Marine Research 51, 215–232.

Lopes, M., Murta, A.G., Cabral, H.N., 2006. Discrimination of snipefish *Macroramphosus* species and boarfish *Capros aper* morphotypes through multivariate analysis of body shape. Helgoland Marine Research 60, 18-24.

Martin, B., Christiansen, B., 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the northeast Atlantic. Deep-Sea Research 44, 541-558.

Martin, B., Christiansen, B., in prep. Distribution of zooplankton biomass around seamounts in the NE Atlantic.

Matthiessen, B. (2001). "Nahrungsökologie von *Macroamphosus scolopax* (Linnaeus, 1758) (Pisces) auf der Großen Meteorbank unter Berücksichtigung der Populationsstruktur.," Diplomarbeit, Universität Hamburg, Hamburg.

Matthiessen, B., 2003. Evidence for two sympatric species of snipefishes *Macroamphosus* spp. (Syngnathiformes) on Great Meteor Seamount. Helgoland Marine Research 57, 63-72.

Menezes, G.M., Rosa, A., Melo, O., Pinho, M.R., 2009. Demersal fish assemblages off the Seine and Sedlo seamounts from longline surveys (Northeast Atlantic).

Merrett, N.R., Marshall, N.B., 1981. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°-27°N). Progress in Oceanography 9, 185-244.

Moku, M., Mori, K., Watanabe, Y., 2004. Shrinkage in the body length of myctophid fish (*Diaphus* slender-type spp.) larvae with various preservatives. Copeia 2004, 647-651.

GENERAL DISCUSSION

TEMPORAL AND SEAMOUNT-RELATED DIFFERENCES IN ZOOPLANKTON TROPHIC INTERACTIONS AND RESPIRATION RATES

The mesozooplankton communities of subtropical and tropical oligotrophic oceans are characterised by a high species diversity, which is dominated by omnivorous copepods (Paffenhöfer *et al.* 2006 and references therein). For example, a study on copepod species composition in an oceanic location south of the investigated seamounts near the Canary Islands reported 212 calanoid species in the upper 1000 m (Roe 1972).

Zooplankton species selected for trophic analysis in chapter III were mainly omnivores and carnivores, but also included herbivores and detritivores according to storage lipid fatty acid composition and trophic positions determined from $\delta^{15}N$ values. Using POM_{susp} as isotopic baseline of the pelagic food web and assuming a $\delta^{15}N$ enrichment of 3.4 ‰ per trophic level (Minagawa and Wada 1984), epipelagic zooplankton species ranged within the first 2 trophic levels and the mesopelagic detritivorous and carnivorous species ranged within the 2nd and 3rd trophic level. Trophic positions of the species generally increased with increasing degree of carnivory. A mismatch of trophic markers was observed for 2 copepod species, which contained strongly elevated proportions of the carnivory marker fatty acid 18:1(n-9) compared to other carnivores, concurrent with relatively low $\delta^{15}N$ values contradicting a carnivorous feeding mode. However, the carnivory marker fatty acid 18:1(n-9) is also abundant in zooplankton-derived organic matter (e.g., faecal pellets; Tanoue and Hara 1986, Matsueda *et al.* 1986, Najdek *et al.* 1994) and might also be biosynthesised by heterotrophic crustaceous zooplankton (Hagen and Auel 2001, Dalsgaard *et al.* 2003). Storage lipid fatty acid signatures of the epipelagic poecilostomatoid copepod *Oncaea* spp. were similar to those reported for faecal pellets and suggested coprophagy as a possible dietary source of 18:1(n-9). In the mesopelagic copepod *D. palumbii*, high proportions of 18:1(n-9) were concurrent with low proportions of saturated fatty acids and suggested utilisation of the latter for biosynthesis of 18:1(n-9).

Trophic markers indicated pronounced temporal differences in POM_{susp} compositions and zooplankton diets at Seine Seamount and temporal differences were also apparent in the respiration rates of the zooplankton community. In November, the time of deep winter mixing of the upper ocean layer in the region (Bashmachnikov *et al.* 2009), $\delta^{15}N$ values revealed a pronounced trophic mismatch, which was characterised by higher $\delta^{15}N$ values for POM_{susp} than for the epipelagic zooplankton species. This trophic mismatch in $\delta^{15}N$ was probably the result of a time lag in isotopic equilibration of zooplankton species to isotopic changes in the food source and has been previously reported for aquatic ecosystems (O´Reilly *et al.* 2002). Elevated $\delta^{15}N$ values of POM_{susp} indicated recent upwelling of ^{15}N-enriched deep-water nitrate (e.g. Montoya *et al*. 2002), while uniformly low $\delta^{15}N$ values of epipelagic omnivorous and herbivorous zooplankton species suggested a temporal dietary shift towards similar lower trophic level food sources. This shift might be due to a more herbivorous feeding mode during preceding conditions of elevated phytoplankton abundance. For the carnivorous chaetognath *Sagitta* spp., the trophic shift towards lower $\delta^{15}N$ values more likely reflected a shift in the isotopic baseline of the food web rather than more herbivorous feeding. The ability of omnivorous species to shift towards a more herbivorous diet during periods of increased phytoplankton abundance, especially during bloom conditions, has been reported for a number of copepod and euphausiid species (Fessenden and Cowles 1994, Schnetzer and Steinberg 2002). The strong signal of the isotopic marker was, however, not reflected in the fatty acid composition of POM_{susp} or the zooplankton species. Total lipids of POM_{susp} showed a strong heterotrophic character, consisting of high amounts of saturated and mono-unsaturated fatty acids, possibly indicative of a period of low phytoplankton growth (Mayzaud *et al.* 1989). The storage lipids of the epipelagic zooplankton species contained no elevated proportions of phytoplankton marker fatty acids that would support a higher degree of herbivory and, thus, might represent a more recent dietary signal in the storage lipid composition of the zooplankton, which is likely to react faster to dietary shifts than the isotopic signal determined for whole organisms.

Trophic marker fatty acids, on the other hand, indicated elevated diatom abundance in the POM_{susp} composition in April compared to surveys in November and July, and these were generally reflected in the storage lipids of the epipelagic zooplankton species.

Elevated proportions of the diatom marker fatty acids were probably the result of preceding bloom conditions, although flagellate markers still dominated POM_{susp} and zooplankton lipids, and stable isotope signatures indicated no trophic shift, but instead were similar in April and July. In chapter II, lower zooplankton respiration rates in April compared to July (November was not sampled) concurrent with higher zooplankton standing stock biomass supported preceding bloom conditions at Seine Seamount as suggested by elevated diatom marker fatty acids. Late winter blooms resulting in maximum mesozooplankton biomass in March compared to the summer months have been reported previously for the region (Head *et al*. 2002, Hernández-León *et al*. 2004, Huskin *et al*. 2004). The lower zooplankton respiration rates in April might be the result of a post-bloom low food situation, which was supported by higher phaeopigment to chlorophyll *a* ratios observed in April compared to July (Kiriakoulakis *et al.* 2009), but might also be the result of higher proportions of smaller zooplankton with higher respiration rates during stratified summer conditions, as respiration rates increase with decreasing body mass (Hernández-León and Ikeda 2005, Ikeda *et al*. 2001). At Sedlo Seamount, temporal differences in zooplankton community respiration were generally characterised by lower respiration rates and higher standing stocks in November compared to July (April was not sampled) and might, similar to Seine Seamount in April, indicate low food conditions after a period of slightly elevated phytoplankton abundances due to surface cooling- or wind-driven vertical diffusion of nutrients from below the mixed layer. Trophic marker signatures of POM_{susp} and selected zooplankton species were only analysed for November and did not provide an indication of substantially elevated phytoplankton abundance compared to Seine Seamount.

At mesopelagic depths, temporal differences in $\delta^{15}N$ values were observed for copepod and chaetognath species from the 800-1000 m depth layer and were characterised by lower $\delta^{15}N$ values in April compared to July. Observed lower $\delta^{15}N$ values in April might be related to the spring bloom that resulted in increased downward flux of sinking organic matter particles with lower $\delta^{15}N$ values. A connection between periods of maximum phytoplankton abundance and particle flux and reduced $\delta^{15}N$ values of sinking particles has been reported previously (Altabet 1989) and the author suggested that increased direct feeding on phytoplankton by the larger epipelagic zooplankton

resulted in a production of sinking particles of lower $\delta^{15}N$ values. Temporal differences in isotopic signature were not reflected in the storage lipid fatty acid composition of the copepod and chaetognath species. In the case of the detritivorous copepod species this might be due to the effect of biosynthesis on the storage lipid composition and to the observation that the lipid composition of faecal pellets, as a potential food source, might be largely altered compared to the food ingested by the epipelagic organisms (e.g., Marty *et al.* 1994). Regarding the fatty acid composition of the carnivorous chaetognath, the bloom signal probably became diluted along the food chain. Respiration rates of the zooplankton community at the same depth layer were similar in April and July and did not support higher food fluxes to the deep mesopelagic community in April.

In contrast to the pronounced temporal differences, spatial differences of trophic marker signatures between farfield and seamount locations of the two seamounts were generally small for POM_{susp} and epipelagic zooplankton species, and highly variable with no clear pattern for the mesopelagic species, and indicated no seamount-related influence on POM_{susp} composition or zooplankton diets (chapter III). Locally elevated zooplankton respiration rates were occasionally observed at the seamount locations compared to the farfield locations at both seamounts. This increase of respiration rates was, however, of low magnitude compared to the temporal variability and was not supported by locally higher zooplankton standing stocks. Instead, a persistent pattern of reduced zooplankton biomass observed above the summit location of Seine Seamount resulted in a local reduction of respiratory carbon demand of the zooplankton community (chapter II). POM_{susp} composition as well as zooplankton diets, respiration rates and standing stocks provided, thus, no evidence for the development of local diatom blooms due to nutrient-upwelling, or for enhanced phytoplankton biomass available to the zooplankton community above Seine and Sedlo Seamounts.

TROPHIC INTERACTIONS OF THE RESIDENT FAUNA ON THE SUMMIT PLATEAU OF SEINE SEAMOUNT

The benthopelagic fish and epipelagic invertebrate fauna collected simultaneously on the summit plateau of Seine Seamount (chapters IV,V,VI) comprised typical seamount and continental shelf species that have a cosmopolitan or Mediterranean-Atlantic and

Western African distribution, including the Azores (Beck *et al.* 2005, Ehrich 1977, Gillet and Dauvin 2000, 2003, Kukuev 2004).

Feeding types of the epibenthic invertebrate species studied included suspension feeders, suspension/surface deposit feeders, predators/scavengers and omnivores (chapter IV). The benthopelagic fish fauna was dominated by zooplanktivorous species (chapters V,VI). Other feeding types included in the trophic analyses were benthivores, piscivores and species with mixed crustacean/cephalopod/fish diets (chapter V).

Trophic marker and gut content analyses indicated that the resident seamount fauna was closely linked to pelagic food sources (chapters IV,V). For the epibenthic invertebrates, a close nutritional link to surface suspended particulate organic matter (POM_{susp}) was apparent from fatty acid trophic markers and $\delta^{15}N$ values. The trophic marker signatures suggested the transfer of essential nutrients from phytoplankton to epibenthic invertebrates either directly by suspension or deposit feeding or indirectly via predation on detritivorous benthic primary consumers (chapter IV). The nutritional link was supported by similarities in marker fatty acid signatures between the total lipids of POM_{susp} and the storage lipids of the epibenthic invertebrates, and by the trophic level enrichments of the epibenthic invertebrates compared to $\delta^{15}N$ values of POM_{susp}. Pelagic versus benthic feeding of the epibenthic invertebrate species was indicated by differences in fatty acid trophic marker signatures. Direct utilisation of pelagic-derived food sources resulted in higher proportions of the pelagic zooplankton marker fatty acid 18:1(n-9) in the storage lipids. Utilisation of POM_{susp} via predation on benthic consumers was indicated by high proportions of the fatty acids 20:1(n-9) and 20:4(n-6) in the storage lipids of the epibenthic invertebrates, which were present in low or trace amounts in the pelagic food sources. While 20:1(n-9) has been reported as typical for and possibly biosynthesised by echinoderms (Takagi *et al.* 1980, Sargent *et al.* 1983), the latter is an essential dietary fatty acid that must be assimilated from primary producers as it cannot be biosynthesised *de novo* by consumers (e.g. Dalsgaard *et al.* 2003). Rhodophytes were suggested as possible source, as they are characterised by high proportions of arachidonic acid 20:4(n-6), and a few living specimen of coralline red algae were observed in the benthic hauls during this study. Predominantly pelagic feeding species, like suspension feeding gorgonian and ophiuroid species, thus contained generally higher proportions of the pelagic zooplankton marker fatty acid

18:1(n-9) and lower proportions of the presumably benthic marker fatty acid 20:4(n-6) compared to benthic feeding species, like the predatory asteroids and omnivorous echinoids.

For the benthopelagic fishes, gut content and trophic marker analyses indicated a close link to the pelagic food sources mainly through direct feeding on pelagic prey (chapter V). Gut contents of the zooplanktivorous species were dominated by small, non- or weakly migrating copepods, while benthic contributions to the diets were small. Trophic marker signatures confirmed gut contents as assimilated food. The $\delta^{15}N$ values of zooplanktivorous fish species were enriched by about 1 trophic level compared to their potential pelagic prey, and the storage lipid fatty acid signatures of the benthopelagic fishes were similar to the total lipid fatty acid signatures of the potential zooplankton prey. Elevated levels of arachidonic acid (20:4(n-6)) in a benthivorous flatfish species indicated feeding on benthic primary consumers and a possible dietary contribution of rhodophyta to the benthopelagic community, as has been observed for the epibenthic invertebrates. Differences in 20:4(n-6) concentrations related to feeding on benthic macroalgal- versus pelagic microalgal-derived food sources have previously been reported in a study of Dunstan *et al.* (1988), which revealed higher proportions of this fatty acid in fish species associated with the benthic food web.

The epibenthic invertebrate and benthopelagic fish fauna occupied trophic positions between the 2nd and 4th trophic level, assuming POM_{susp} as trophic baseline and a $\delta^{15}N$-enrichment of 3.4 ‰ per trophic level (Minagawa and Wada 1984). Most of the epibenthic invertebrates occupied intermediate trophic level positions between the 2nd and 3rd trophic levels, confirming the close nutritional link to surface POM_{susp}. Suspension and surface deposit feeders generally occupied the lowest trophic positions. Exceptions were the poriferan taxa with large differences in their marker fatty acid proportions and $\delta^{15}N$ values compared to other suspension feeders. Possible reasons for these differences are indiscriminate filtering of particulate material, potentially including bacteria and their exudates (e.g., Mincks *et al.* 2008), or symbioses with bacteria or diatoms (e.g., Bergé and Barnathan 2005). The epibenthic invertebrate predators/scavengers concentrated on slightly higher intermediate trophic positions suggesting the reliance on benthic primary consumers, as indicated by elevated levels of 20:4(n-6) in their storage lipids. The highest trophic position, around the 4th trophic

level, was occupied by a predatory gastropod species, with $\delta^{15}N$ values enriched by 1 trophic level compared to its potential prey, the asteroid species. The predominance of similar intermediate trophic level positions observed for the epibenthic invertebrate species indicated a dominance of opportunistic omnivorous species. This trophic structure was even more pronounced for the benthopelagic fishes.

The benthopelagic fish species occurred along a continuum of intermediate trophic positions between the 3rd and 4th trophic levels rather than at discrete trophic levels. These trophic continua are characteristic for complex food webs consisting of omnivorous species that feed from different trophic levels. Trophic positions within these food webs have been reported to increase with body size as feeding hierarchies are often determined by size-related predation (France *et al.* 1998, Jennings *et al.* 2001, Jennings and Mackinson 2003), although complex food webs without a relationship between trophic position and body size have also been described (Layman *et al.* 2005). A significant positive correlation between size and $\delta^{15}N$ values of individual benthopelagic fishes in this study supported the influence of size on the trophic position occupied by the species. Trophic positions increased from small juvenile zooplanktivores to adult zooplanktivores and the benthivorous flatfish and then to species with mixed fish or predominantly piscivore diet, with the largest species, *C. conger*, occupying the highest trophic position. Utilisation of prey from different trophic levels was apparent for zooplanktivorous species. These contained zooplankton prey in their guts, which covered a $\delta^{15}N$ range equivalent to 2 trophic levels. Feeding from different trophic levels was also suggested for predominantly piscivorous species, which were less than 1 trophic level enriched compared to the $\delta^{15}N$ values of their potential or actual prey.

Despite considerable dietary overlap among the benthopelagic zooplanktivorous fishes, differences in gut contents, storage lipid fatty acid signatures and trophic levels occupied indicated some degree of resource partitioning regarding feeding habitats, prey selection and ontogenetic separation. Habitat, prey and time have been proposed as the most important environmental niche dimensions for niche differentiation between species (Schoener 1974). Resource partitioning through niche separation can reduce competition and promote co-existence of species (e.g. Hayward and McGowan 1979, Hopkins and Sutton 1998). Resource partitioning through vertical habitat differences of

the zooplanktivores studied in chapter V was suggested by higher proportions of oncaeid copepods in the gut contents of the 3 near-bottom species compared to the more pelagic living species *C. cirrus*, which consumed higher proportions of calanoid copepods. Fatty acid signatures of the more pelagic-living species and stages contained also higher amounts of phytoplankton and zooplankton marker fatty acids and lower amounts of the benthos-associated fatty acid 20:4(n-6). Vertical habitat differences of the zooplanktivorous fish species were confirmed by studies on the distribution of fish species at seamounts (Ehrich 1974, Kukuev 2004, Pakhorukov 2008). Species-specific differences in prey choice and diversity were apparent in the gut contents of the zooplanktivorous fishes and included feeding on different proportions of crustacean and non-crustacean pelagic prey and the utilisation of benthic-derived food sources, like benthic polychaetes. Sufficient resource partitioning through pronounced differences in prey choice between zooplanktivores have been previously reported for species co-occurring on seamounts (Fock *et al.* 2002) and in coastal regions (Lopes *et al.* 2006). Avoidance of intra-specific competition for dietary resources between ontogenetic stages was observed for juveniles and adults of *Macroramphosus* spp. and *C. cirrus* in this study and included differences in feeding habitat and prey choice. Early life stages and adults of *Macroramphosus* spp. are separated by extended pelagic life stages of the juveniles remote from seamounts (Ehrich 1974, Badcock and Merrett 1976, Miyazaki *et al.* 2004). At the seamount, differences in size- and species-specific prey selection between juveniles and adult congeners of both *Macroramphosus* spp. and *C. cirrus* presumably reduced dietary competition and were confirmed by lower $\delta^{15}N$ values of the juveniles of both species compared to their adult congeners. These lower trophic level positions might be explained by juveniles feeding on a larger proportion of smaller-sized and presumably more herbivorous copepod species (Turner 2004), as indicated by gut contents.

The close link observed between the epibenthic invertebrate fauna and surface POM_{susp} was most likely related to the shallow depth of the summit plateau of Seine Seamount (~170 m), but the rapid deposition of detritus might be temporally enhanced by Taylor column-related downwelling (Mullineaux and Mills 1997, Beckmann and Mohn 2002). A concurrent study of organic matter distribution and quality reported higher concentrations of suspended particulate organic carbon and higher proportions of labile

poly-unsaturated fatty acids a few meters above Seine summit compared to other sampling locations at similar depths and suggested retention and rapid downward transport of organic matter as possible explanation (Kiriakoulakis *et al.* 2009).

The lack of larger diel vertically migrating taxa in the gut contents of zooplanktivorous fish species suggested that topographic blockage of diel vertical migrators during descend, according to the sound-scattering layer interception hypothesis (Isaacs and Schwartzlose 1965), did not contribute to the food supply of the benthopelagic fish fauna. The gut contents, instead, reflected the absence of larger and more mobile pelagic species in the water column above the seamount summit (Martin and Christiansen 2009), indicating lower food concentrations above the summit plateau compared to the surrounding ocean. Benthopelagic fish abundances reported for trawl surveys on the summit plateau (chapter VI) as well as longline surveys conducted on Seine Seamount (Menezes *et al.* 2009) indicated no enhanced fish standing stocks. The resident benthopelagic fish fauna on the summit plateau of Seine Seamount appeared, thus, to be predominantly sustained by current-driven horizontal fluxes of non- or weakly-migrating zooplankton advected from the surrounding ocean.

CONCLUSIONS

Fatty acid and stable isotope trophic markers indicated considerable temporal variability in POM_{susp} composition and the diets and trophic positions of zooplankton species. Spatial differences, on the other hand, were small and did not indicate local seamount-related changes in feeding conditions at the two seamounts. Elevated zooplankton respiration rates were occasionally observed at the seamounts, but were of lower magnitude than temporal variability and gave also no clear indications for persistently enhanced feeding conditions for local zooplankton standing stocks compared to the surrounding ocean. The lack of seamount-related changes in POM_{susp} compositions as well as zooplankton diets, respiration rates and standing stocks provided no support for the development of local diatom blooms due to nutrient-upwelling or for enhanced autochthonous food sources available to the zooplankton community above Seine and Sedlo Seamounts, according to the hypothesis of locally-enhanced seamount productivity. However, it cannot be ruled out that enhanced pelagic production occurred, but was advected into the surrounding ocean.

The present study revealed a close link between pelagic food sources and the epibenthic and benthopelagic fauna on the summit plateau of Seine Seamount. The major nutritional pathway to the benthopelagic fish fauna appeared to be the direct feeding on pelagic zooplankton prey. Epibenthic invertebrate species were closely linked to surface particulate organic matter either directly by suspension or surface deposit feeding or by predation on detritivorous benthic primary consumers. The presence of arachidonic acid in the storage lipids of benthivorous species suggested a possible contribution of rhodophytes as benthic primary food source. The fish and invertebrate species occurred along continua of intermediate trophic positions indicative of a food web consisting predominantly of opportunistic species that feed from different trophic levels. Resource partitioning observed between the zooplanktivorous fish species presumably reduced dietary competition and promoted co-existence of the species.

The lack of larger diel vertically migrating taxa in the gut contents of zooplanktivorous species suggested that the topographic blockage of diel vertical migrators, according to the sound-scattering layer interception hypothesis, was not an important mechanism of food supply to the benthopelagic fish fauna. Instead, the resident benthopelagic fish fauna on the summit plateau of Seine Seamount appeared to be predominantly sustained by current-driven horizontal fluxes of non- or weakly-migrating zooplankton advected from the surrounding ocean. The close link of the epibenthic invertebrate fauna to surface organic matter suggested rapid deposition of fresh detritus due to the shallow depth of the seamount summit plateau (~170 m), which might be temporally exhilarated by Taylor column-related downwelling.

PERSPECTIVES

The present study provided new insights into the temporal and spatial variability of diets, trophic positions and respiration rates of zooplankton in the vicinity of seamounts and elucidated nutritional pathways to the resident epibenthopelagic fauna on the summit plateau of Seine Seamount. Nonetheless, new questions and major gaps emerged from this study and will now be outlined.

The remote location, difficult terrain and great depth range of oceanic seamounts impose major constraints on the temporal and spatial sampling resolution. The surveys

conducted during this study focussed the sampling effort on locations close to the seamounts resulting in a lower sampling effort at the open ocean reference locations, which were assumed not to be affected by the seamounts. Future sampling would benefit from a more equal sampling of seamount and reference locations by providing a better estimate of the general background variability of parameters in the surrounding ocean as a base on which possible seamount-related changes can be assessed.

This study revealed considerable temporal variability in trophic marker signatures of particulate organic matter and zooplankton species as well as zooplankton community respiration rates, despite much less pronounced seasonality in subtropical regions compared to higher latitudes. A higher temporal resolution in future studies would contribute to a better understanding of the temporal variability present in the trophic regime of the pelagic food web and, concurrent with sampling of the resident benthic and benthopelagic seamount fauna, could identify possible temporal difference in the seamount food web related to changes in the supply of pelagic food sources.

Lipid storage in zooplankton from lower latitude oligotrophic oceans is generally small and unimportant, because of the high metabolic turnover and the continuous feeding (Lee *et al.* 2006, Kattner *et al.* 2007). I could demonstrate in this thesis, that trophic signals were clearly apparent in the zooplankton species from subtropical oligotrophic regions, when storage lipids were analysed separately from structural lipids. The concept of fatty acid trophic markers was originally established for herbivorous epipelagic copepods, and validation of these markers for subtropical and tropical species, which are primarily omnivorous or carnivorous, is scarce or lacking (e.g. Dalsgaard *et al.* 2003, Lee *et al.* 2006). In the oligotrophic regions larger-sized phytoplankton, which can be directly consumed by mesozooplankton, constitutes only a minor proportion of the autotrophic biomass, and protistan microzooplankton may contribute significantly to mesozooplankton nutrition (Stoecker and Capuzzo, 1990; Klein Breteler *et al.* 1999, Broglio *et al.* 2004). Heterotrophic protists feed on bacteria as well as on nano- and picophytoplankton (Sherr and Sherr 1994) and thus play an important role as trophic intermediaries between the microbial and the classical food webs. Despite the importance of heterotrophic protists, relative little is known about fatty acid marker signatures of their potential food sources or the integration and modification of these signatures and possible “upgrading” through biosynthesis of

essential fatty acids by the protists during transfer to higher trophic level consumers. Further research on the validation of marker fatty acids associated with the microbial loop and of small-sized phytoplankton groups, as well as on their modification by protistan microzooplankton and their transfer to higher trophic levels would contribute substantially to the identification of food sources and pathways of energy and nutrient flow through pelagic as well as phytodetritus-based benthic food webs.

REFERENCES

Altabet MA (1989) A time-series study of the vertical structure of nitrogen and particle dynamics in the Sargasso Sea. Limnol. Oceanogr., 34(7): 1185-1201

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374–383

Badcock J, Merrett NR (1976) Midwater Fishes in the eastern North Atlantic–I. Vertical distribution and associated biology in 30°N, 23°W, with development notes on certain myctophids. Progress in Oceanography, 7: 3–58

Bashmachnikov I, Mohn C, Pelegrí JL, Martins A, Jose F, Machín F, White M (2009) Interaction of Mediterranean water eddies with Sedlo and Seine Seamounts, Subtropical Northeast Atlantic. Deep-Sea Research II, in press

Beck T, Metzger T, Freiwald A (2005) *BIAS: Biodiversity Inventorial Atlas of Macrobenthic Seamount Animals*. OASIS, Hamburg: 118 pp.

Beckmann A, Mohn C (2002) The upper ocean circulation at Great Meteor Seamount. Part II: Retention potential of the seamount induced circulation. Ocean Dynamics, 52: 194-204

Bergé,J-P, Barnathan G (2005) Fatty acids from lipids of marine organisms: molecular biodiversity, roles as biomarkers, biologically active compounds, and economical aspects. Adv Biochem Eng Biotechnol. 96:49-125

Broglio E, Saiz E, Calbet A (2004) Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). Aquat. Microb. Ecol., 35, 65-78

Clark MR (1999) Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. Oceanologica Acta, 22(6): 593–602

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225-340

Davenport SR, Bax NJ (2002) A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Sciences, 59: 514-530

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta, 42: 495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta, 45: 341–351

Dower JF, Freeland H, Juniper K (1992) A strong biological response to oceanic flow past Cobb Seamount. Deep-Sea Research, 39: 1139–1145

Dower JF, Mackas DL (1996) ‘‘Seamount effects’’ in the zooplankton community near Cobb Seamount. Deep-Sea Research I, 43: 837– 858

Dunstan GA, Sinclair AJ, O´Dea K, Naughton JM (1988) The lipid content and fatty acid composition of various marine species from southern Australian coastal waters. Comparative Biochemistry and Physiology, 91B: 165-169

Ehrich S (1974) Die Fische der großen Meteorbank. Ph.D. Thesis, Universität Kiel, 1-213

Ehrich S (1977) Die Fischfauna der Großen Meteorbank. Meteor Forschergeb Reihe D Biol 25:1–23

Epp D, Smoot NC (1989) Distribution of seamounts in the North Atlantic. Nature, 337: 254-257

Fessenden L, Cowles TJ (1994) Copepod predation on phagotrophic ciliates in Oregon coastal waters. Mar Ecol Prog Ser 107:103–111

Fock HO, Matthiessen B, Zidowitz H, von Westernhagen H (2002) Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. Marine Ecology Progress Series, 244: 219–233

France R, Chandler M, Peters R (1998) Mapping trophic continua of benthic food webs: body size-δ^{15}N relationships. Marine Ecology Progress Series, 174: 301–306

Genin A, Boehlert GW (1985) Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 43: 907– 924

Genin A, Haury L, Greenblatt P (1988) Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep Sea Research, 35: 151-175

Genin A (2004) Biophysical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems, 50: 2-20

Gillet P, Dauvin J-C (2003) Polychaetes from the Irving, Meteor and Plato seamounts,

North Atlantic ocean: origin and geographical relationships. J. Mar. Biol. Ass. U.K., 83: 49-53

Gillet P, Dauvin J-C (2000) Polychaetes from the Atlantic Seamounts of the southern Azores: biogeographical distribution and reproductive patterns. Journal of the Marine Biological Association of the United Kingdom, 80: 3651-3661

Giorgio P.A. del, Williams P.J.B. (2005) Respiration in aquatic ecosystems. Oxford University Press, New York, 315pp.

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53–61

Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313–326

Hayward TL, McGowan JA (1979) Pattern and structure in an oceanic zooplankton community. American Zoologist 19: 1045-1055

Head RN, Medina G, Huskin I, Anadón R, Harris RP (2002) Phytoplankton and mesozooplankton distribution and composition during transects of the Azores Subtropical Front. Deep-Sea Research II, 49: 4023–4034

Hernández-León S, Gómez M (1996) Factors affecting the Respiration/ETS ratio in marine zooplankton. J. Plankton Res., 18: 239–255

Hernández-León S, Almeida C, Gómez M, Torres S, Montero I, Portillo-Hahnefeld A (2001) Zooplankton biomass and indices of feeding and metabolism in island-generated eddies around Gran Canaria. J. Mar. Syst., 30: 51–66

Hernández-León S, Almeida C, Bécognée P, Yebra L, Arístegui J (2004) Zooplankton biomass and indices of grazing and metabolism during a late winter bloom in subtropical waters. Mar. Biol., 145: 1191-1200

Hernández-León S, Ikeda T (2005) Zooplankton respiration. In: del Giorgio PA, Williams PJB (Eds.), Respiration in aquatic ecosystems. Oxford University Press, pp. 57-82

Hopkins TL, Sutton TT (1998) Midwater fishes and shrimps as competitors in low latitude oligotrophic ecosystems. Marine Ecology Progress Series 164: 37-45

Huskin I, Viesca L, Anadón R (2004) Particle flux in the Subtropical Atlantic near the Azores: influence of mesozooplankton. Journal of Plankton Research, 26: 403–415

Ikeda T, Torres JJ, Hernández-León S, Geiger SP (2000) Metabolism. In RP Harris, P H Wiebe, J Lenz, HR Skjoldal, M Huntley (Eds.), ICES Zooplankton Methodology Manual. Academic Press, San Diego, pp. 455–532

Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. Mar. Biol., 139: 587–596

Isaacs JD, Schwartzlose RA (1965) Migrant sound scatterers: interaction with the seafloor. Science, 150: 1810–1813

Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology, 70: 934–944

Jennings S, Mackinson S (2003) Abundance–body mass relationships in size-structured food webs. Ecology Letters, 6: 971–974

Kattner G, Hagen W, Lee RF, Campbell R, Deibel D, Falk-Petersen S, Graeve M, Hansen BW, Hirche H-J, Jónasdóttir S, Madsen ML, Mayzaud P, Müller-Navarra D, Nichols PD, Paffenhöfer G-A, Pond D, Saito H, Stübing D, Virtue P (2007) Perspectives on marine zooplankton lipids, Canadian Journal of Fisheries and Aquatic Sciences. 64(11): 1628-1639

King FD, Packard TT (1975a) Respiration and the activity of the respiratory electron transport system in marine zooplankton. Limnol. Oceanogr., 20: 849-854

King FD, Packard TT (1975b) The effect of hydrostatic pressure on respiratory electron transport system activity in marine zooplankton. Deep-Sea Research, 22: 99–105

Kiørboe T, Møhlenberg F, Hamburger K (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. Mar. Ecol. Prog. Ser., 26: 85–97

Kiriakoulakis K, Vilas JC, Blackbird SJ, Arístegui J, Wolff GA (2009) Seamounts and organic matter—is there an effect? The case of Sedlo and Seine Seamounts. Part II. Composition of suspended particulate organic matter. Deep-Sea Research II, in press

Klein-Breteler WCM, Schogt N, Baas M, Schouten S, Kraay GW (1999) Trophic upgrading of food quality by protozoan enhancing copepod growth: role of essential lipids. Mar. Biol. 135: 191–198

Klimley AP, Richert JE, Jorgensen SJ (2005) The Home of Blue Water Fish. American Scientist, 93: 42-49

Koslow JA (1996) Energetic and life-history patterns of deepsea benthic, benthopelagic and seamount-associated fish. Journal of Fish Biology, 49(Suppl A): 54-74

Koslow JA (1997) Seamounts and the ecology of deep-sea fisheries. American Scientist, 85: 168– 176

Koslow JA, Boehlert GW, Gordon JDM, Haedrich RL, Lorance P, Parin N (2000) The impact of fishing on continental slope and deep-sea ecosystems. ICES Journal of Marine Science, 57: 548-557

Koslow JA, Gowlett-Holmes K, Lowry JK, O'Hara T, Poore GCB (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. Mar Ecol Prog Ser 213:111–125

Kukuev EI (2004) Ichthyofauna research on underwater mountain within the North-Atlantic ridge and adjacant areas. Archive of Fishery and Marine Research, 51: 215–232

Kunze E, Toole JM (1997) Tidally driven vorticity, diurnal shear and turbulence at Fieberling Guyot. J. Phys. Oceanogr. 27: 2663-2693

Lampert W (1986) Response of the respiratory rate of *Daphnia magna* to changing food conditions. Oecologia, 70: 495-501

Layman CA, Winemiller KO, Arrington DA, Jepson DB (2005) Body size and trophic position in a diverse food web. Ecology, 86: 2530–2535

Lee RF, HagenW, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307: 273–306

Lopes M, Murta AG, Cabral HN (2006) Discrimination of snipefish *Macroramphosus* species and boarfish *Capros aper* morphotypes through multivariate analysis of body shape. Helgoland Marine Research, 60: 18-24

Martin B, Christiansen B (2009) Distribution of zooplankton biomass at three seamounts in the NE Atlantic. Deep-Sea Research II, in press

Marty JC, Nicolas E, Miquel JC, Fowler SW (1994) Particulate fluxes of organic compounds and their relationship to zooplankton fecal pellets in the northwestern Mediterranean Sea. Marine Chemistry 46: 387-405

Matsueda H, Handa N (1986) Vertical flux of hydrocarbons as measured in sediment traps in the eastern North Pacific Ocean. Mar. Chem., 20: 179-195

Mayzaud P, Chanut J-P, Ackman RG (1989) Seasonal changes of the biochemical composition of marine particulate matter with special reference to fatty acid and sterols. Mar. Ecol. Prog. Ser. 56: 189-204

McClain CR (2007) Is seamount biogeography island biogeography? J Biogeogr 34:2001–2008

McClain CR, Lundsten L, Ream M, Barry J, DeVogelaere A (2009) Endemicity, Biogeography, Composition, and Community Structure On a Northeast Pacific Seamount. PLoS ONE 4(1): e4141.

Menard HW (1964) Marine Geology of the Pacific. McGraw Hill, New York.

Menezes GM, Rosa A, Melo O, Pinho MR (2009) Demersal fish assemblages off the Seine and Sedlo seamounts (northeast Atlantic). Deep-Sea Research II, in press

Michener RM, Schell DM (1994) Stable isotope ratios as tracers in marine aquatic food webs. In: R.H. Michener, K. Lajtha (Eds). Stable isotopes in ecology and environmental science. Blackwell, Oxford:138–157

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica et Cosmochimica Acta, 48: 1135–1140

Mincks SL, Smith CR, Jeffreys RM, Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by delta-13C and delta-15N analysis. Deep-Sea Research II 55: 2502-2514

Miyazaki E, Sasaki K, Mitani T, Ishida M, Uehara S (2004) The occurrence of two species of *Macroramphosus* (Gasterosteiformes: Macroramphosidae) in Japan: morphological and ecological observations on larvae, juveniles, and adults. Ichthyological Research, 51: 256–262

Montoya JP, Carpenter EJ, Capone DG (2002) Nitrogen-fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol. Oceanogr., 47:1617–1628

Mouriño B, Fernandez E, Serret P, Harbour D, Sinha B, Pingree R (2001) Variability and seasonality of physical and biological fields at the Great Meteor Tablemount (subtropical NE Atlantic). Oceanologica acta, 24 (2): 1-20

Mullineaux LS, Mills SW (1997) A test of the larval retention hypothesis in seamount-generated flows. Deep-Sea Res I 44:745–770

Najdek M, Puskaric S, Bochdansky AB (1994) Contribution of zooplankton lipids to the flux of the organic matter in the northern Adriatic Sea. Marine Ecology Progress Series, 111: 241–249

O'Reilly CM, Hecky RE, Cohen AS, Plisnier P-D (2002) Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. Limnol. Oceanogr. 47: 306-309

Owens TG and FD King (1975) The measurement of respiratory electron transport system activity in marine zooplankton. Mar. Biol., 30: 27–36

Packard TT (1985) Measurement of electron transport activity of marine microplankton. Advances in Aquatic Microbiology, 3: 207-261

Paffenhöfer G-A, Mazzocchi MG, Tzeng MW (2006) Living on the edge: feeding of subtropical open ocean copepods. Marine Ecology 27: 99–108

Pakhorukov NP (2008) Visual Observations of Fish from Seamounts of the Southern Azores Region (the Atlantic Ocean). Journal of Ichthyology, 48 (1): 114–123

Parin NV, Mironov AN, Nesis KN (1997) Biology of the Nazca and Sala-y-Gómez submarine ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific ocean: composition and distribution of the fauna, its community and history. Advances in Marine Biology, 32: 145-242

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics, 18: 239-320

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, 83: 703–718

Richer de Forges B, Koslow JA, Poore GCB (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. Nature 405:944–947

Roden GI (1987) Effects of seamounts and seamount chains on ocean circulation and thermohaline structure. In: B.H. Kaeting, P. Fryer, R. Batisa, G.W. Boehlert (Eds). Seamounts, Islands, and Atolls. Geophysical Monograph Series, 43, AGU, Washington D.C.: 335-354

Roe HSJ (1972) The vertical distributions and diurnal migrations of calanoid copepods collected on the SOND cruise, 1965, I. The total population and general discussion. J. Mar. Biol. Assoc. UK, 52: 277-314

Rogers AD (1994) The Biology of Seamounts. Advances in Marine Biology, 30: 305–349

Sargent JR, Falk-Petersen IB, Calder AG (1983) Fatty acid compositions of neutral glycerides from the ovaries of the asteroids *Ctenodiscus crispatus*, *Asterias lincki* and *Pteraster militaris* from Balsfjorden, northern Norway. Mar Biol 72:257–264

Sargent JR, Henderson RJ (1995) Marine (n-3) polyunsaturated fatty acids. In: R.J. Hamilton (Ed). Developments in oils and fats. Blackie Academic and Professional, London: 32-65

Schalk PH (1990) Biological activity in the Antarctic zooplankton community. Polar Biol. 10:405–411

Schmidt K, Atkinson A, Petzke K-J, Voss M, Pond DW (2006). Protozoans as a food source for Antarctic krill, *Euphausia superba* - complementary insights from stomach content, fatty acids and stable isotopes. Limnology and Oceanography 51(5): 2409-2427

Schmoker C,Hernández-León S (2003) The effect of food on the respiration rates of *Daphnia magna* using a flow-through system. Sci. Mar., 67 (3): 361-365

Schnetzer A, Steinberg DK (2002) Natural Diets of Vertically Migrating Zooplankton in the Sargasso Sea. Mar Biol, 141(1):89-99

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27-39

Seki MP, Somerton DA (1994) Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Southeast Hancock Seamount. Environmental Biology of Fishes, 39: 73–84

Sherr EB, Sherr BF (1994) Bacterivory and herbivory: Key roles of phagotrophic protists in pelagic food webs. Microb. Ecol. 28: 223–235

St. John MA, Lund T (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea Cod. Marine Ecology Progress Series, 131, 75-85

Stoecker DK, Capuzzo J (1990) Predation on Protozoa: its importance to zooplankton. J Plankton Res 12:891–908

Takagi T, Eaton CA, Ackman RG (1980) Distribution of fatty acids in lipids of the common atlantic sea urchin *Strongylocentrotus droebachiensis*. Can J Fish Aquat Sci 37:195–202

Tanoue E, Hara S (1986) Ecological implications of fecal pellets produced by the Antarctic krill *Euphausia superba* in the Antarctic Ocean. Mar. Biol. 91: 359-369

Thor P (2000) Relationship between specific dynamic action and protein deposition in calanoid copepods. J. Exp. Mar. Biol. Ecol., 245: 171–182

Tseitlin VB (1985) The energetics of fish populations inhabiting seamounts. Oceanology, 25, 237–239

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies, 43(2): 255-266

Uda M, Ishino M (1958) Enrichment pattern resulting from eddy systems in relation to fishing grounds. Journal of the Tokyo University of Fisheries, 44: 105-129

Vander Zanden MJ, Rasmussen JB (2001) Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: Implications for aquatic food web studies. Limnology and Oceanography, 46: 2061–2066

Wessel P (1997) Sizes and Ages of Seamounts Using Remote Sensing: Implications for Intraplate VolcanismSeamount ecosystems. Science 277: 802-805

Wilson RR, Kaufmann RS (1987) Seamount biota and biogeography. In: Keating BH, et al. (1987) Seamounts, Islands, and Atolls. Washington: American Geophysical Union. pp 227–237

INDIVIDUAL SCIENTIFIC CONTRIBUTIONS TO THE MULTIPLE-AUTHOR MANUSCRIPTS

The following five manuscripts are included in the chapters of this thesis and below I have outlined my contributions to the manuscripts. Laboratories and equipment were provided by the Institute for Hydrobiology and Fisheries Science (Prof. Dr. St.John) at the University of Hamburg. This research was part of the OASIS (OceAnic Seamounts: an Integrated Study) project, which was funded by the European Commission under the Fifth Framework Programme (contract EVK3-CT-2002-00073-OASIS).

Chapter II

Hirch S., Martin B. and Christiansen B.

Zooplankton metabolism and carbon demand at two seamounts in the NE Atlantic

I was involved in the sampling and performed the laboratory analysis (electron transfer system (ETS) activity) and the data analysis. B. Martin provided the biomass data for the zooplankton standing stock. The manuscript was written by myself under the supervision of B. Christiansen. The manuscript is published in Deep-Sea Research II 56 (2009) 2656–2670 [doi:10.1016/j.dsr2.2008.12.033].

Chapter III

Hirch S., Kiriakoulakis K., Koppelmann R., Peters J. and Christiansen B.

Food sources and diets of zooplankton at two seamounts in the NE Atlantic: Are there seamount effects?

I developed the concept of this study and conducted the sampling and analysis of samples, including extraction of lipids, determination of fatty acid composition and preparation of the stable isotope samples for measurement, as well as evaluation of the data. Stable isotopes were measured at the GeoBio-Center of the Ludwig-Maximilians-Universität in Munich and at the MSI Analytical Laboratory of the University of California Santa Barbara, USA. Lipid extraction of the filter samples and GC-MS analysis of the lipid extracts were performed at the Department of Earth and Ocean Sciences of the University of Liverpool, U.K. under the supervision of K. Kiriakoulakis. J. Peters contributed important methodological advice on the separation of lipid classes. R. Koppelmann provided valuable comments to the manuscript. The manuscript was

written by myself under the supervision of B. Christiansen. The manuscript will shortly be submitted to Marine Ecology Progress Series.

Chapter IV

Hirch S., Kiriakoulakis K. and Christiansen B.

Feeding ecology and food sources of selected epibenthic invertebrates on the summit plateau of Seine Seamount

I developed the concept of this study and conducted the sampling, lipid analysis, stable isotope sample preparation and evaluation of the data. Stable isotopes were measured at the GeoBio-Center in Munich and at the MSI Analytical Laboratory of the University of California Santa Barbara. Lipid extraction of the particulate organic matter filter samples and GC-MS analysis of the lipid extracts were performed at the University of Liverpool, U.K. under the supervision of K. Kiriakoulakis. The manuscript was written by myself under the supervision of B. Christiansen. The manuscript is planned for submission to the Journal of the Marine Biological Association of the United Kingdom.

Chapter V

Hirch S. and Christiansen B.

Food sources and trophic interactions of benthopelagic fish species on the summit plateau of Seine Seamount, NE Atlantic

I developed the concept of this study and conducted the sampling, lipid analysis, stable isotope sample preparation and evaluation of the data. Stable isotopes were measured at the GeoBio-Center in Munich. I performed the gut content analysis with the assistance of K. Philipps-Bussau. The manuscript was written by myself under the supervision of B. Christiansen. It was submitted to Marine Biology and is now in revision.

Chapter VI

Christiansen B., Martin B. and Hirch S.

The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: Composition, population structure and diets

I was involved in the taxonomic identification and biometric measurements of the fish species and performed the gut content analysis with the assistance of K. Philipps-Bussau. The manuscript is published in Deep-Sea Research II 56 (2009) 2705–2712 [doi:10.1016/j.dsr2.2008.12.032].

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