Der Einfluss von Seebergen auf Zooplanktongemeinschaften

Dissertation

zur Erlangung des Doktorgrades
des Departments Biologie
der Universität Hamburg

vorgelegt von
Bettina Martin

Hamburg, Oktober 2008

Genehmigt vom Department Biologie
der Fakultät für Mathematik, Informatik und Naturwissenschaften
an der Universität Hamburg
auf Antrag von Professor Dr. C. MÖLLMANN
Weiterer Gutachter der Dissertation:
Herr Professor Dr. M. ST. JOHN
Tag der Disputation: 21. November 2008

Hamburg, den 07. November 2008

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Hamburg October 6th 2008

English Language Evaluation of the Ph.D. thesis of Bettina Martin

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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.

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Zusammenfassung

Ozeanische Seeberge sind in den letzten Jahrzehnten zunehmend in den Blickpunkt wissenschaftlicher Forschung gerückt. Gründe dafür sind Berichte über Fischreichtum, hohe Diversität der Fauna und eine erhöhte Anzahl an endemischen Arten an Seebergen. Es wird dabei angenommen, dass Seebergökosysteme besonders empfindlich auf die Ausbeutung durch Fischerei reagieren. Diese Berichte beziehen sich in den meisten Fällen auf Beobachtungen an pazifischen Seebergen; über atlantische Seeberge liegen bisher nur wenige Informationen vor. Die Steuermechanismen dieser Ökosysteme sind bisher weitgehend ungeklärt. Weder ist die Grundlage der Nahrungsnetze nachgewiesen, noch sind der Einfluss von Höhe, Form und geographischer Lage der Berge auf die ansässige Fauna genauer untersucht. Das Zooplankton, insbesondere Copepoden, nimmt eine Schlüsselrolle in allen marinen Nahrungsnetzen ein. In der vorgelegten Arbeit werden die Verteilung und Zusammensetzung des Zooplanktons an Seebergen mit der im freien Ozean verglichen, um den Einfluss der Topographie auf diese Faunengruppe und ihre Rolle im Seebergökosystem zu untersuchen. Dafür wurden vier Seeberge im Nordost-Atlantik beprobt und die Biomasse, Abundanz und taxonomische Zusammensetzung des Zooplanktons an verschiedenen Lokationen an den Bergen und ozeanischen Referenzstationen untersucht. Ausserdem wurde anhand von Fängen benthopelagischer Fische an einem der Berge deren Zusammensetzung, Altersstruktur und Nahrung untersucht, um mögliche Räuber-Beutebeziehungen aufzuklären. Anhand biochemischer Untersuchungen wurde die Hypothese von lokal erhöhter Produktion geprüft. An keinem der Berge konnte eine Akkumulation des Zooplanktons festgestellt werden, im Gegenteil waren die Bestände über den Gipfeln der flachen Berge verglichen mit den Hängen und dem offenen Wasser deutlich reduziert. Diese Reduzierung betraf insbesondere die größeren Größenklassen. Die Untersuchung der Stoffwechselraten des Zooplanktons ergab ebenfalls keinen deutlichen Nachweis lokal erhöhter Produktion an den Seebergen. Auch die Bestände der benthopelagischen Fischfauna waren nicht erhöht und entsprachen denen aus bathyalen Tiefen höherer Breiten. Die möglichen Gründe für diese Ergebnisse werden in den vorgelegten Publikationen diskutiert.

Einführung

Geologie

Seeberge sind meist kegelförmige und steil aufragende untermeerische Geländeformationen mit elliptischer oder kreisförmiger Basis, die sich über die Tiefseeebenen der Weltmeere erheben. Nach der Definition von Menard (1964) haben sie eine Höhe von mindestens 1000 m. Sie sind in unterschiedlich dichter Verteilung in allen Ozeanbecken zu finden (Wessel, 2007). Erhebungen zwischen 500 und 1000 m werden ‚knolls' genannt, unter 500 m ‚hills' (US Board of Geographic Names, 1981). An diese Definition wird sich allerdings in wissenschaftlichen Veröffentlichungen nicht immer gehalten, häufig werden als Seeberge alle Erhebungen über den Tiefseeboden bezeichnet, unabhängig von ihrer Höhe (Epp & Smoot, 1989).

Die meisten Seeberge sind vulkanischen Ursprungs, entstanden entweder an den Spreizungszonen mittelozeanischer Rücken, an Subduktionszonen oder über Magmaherden, so genannten *hot spots*, auf ozeanischen Platten (Wilson, 1963; Epp & Smoot, 1989). Letztere bilden oft Ketten, da die tektonische Platte sich langsam über die Magmaherde (mantle plumes) schiebt.

Obwohl nur wenige Seeberge genau auf ihr Alter datiert sind, so ist doch das Alter des sie formenden Meeresbodens in aller Regel erforscht. Beim Auseinanderdriften der ozeanischen Platten wird durch vulkanische Aktivität an den ozeanischen Rücken fortwährend neuer Meeresboden gebildet, der, wenn die ozeanische Platte auf eine Kontinentalplatte trifft, in der Regel an dieser Subduktionszone unter die Kontinentalplatte geschoben und eingeschmolzen wird. Die ozeanischen Platten befinden sich daher in steter Erneuerung. Der älteste Meeresboden wird auf ca. 200 Millionen Jahre geschätzt, ein großer Teil ist erst ca 80 Millionen Jahre alt und damit sind die auf ihm entstandenen Seeberge, verglichen mit den Kontinentalplatten, geologisch gesehen noch jung. Da die Berge auf bereits bestehendem Meeresboden entstehen, ergibt sich eine obere Altersgrenze. Weiterhin kann man bei Seebergketten, die sich durch die Bewegung der Platten über *hotspots* hinweg gebildet haben, über Modellberechnungen der Plattenbewegung auf ihr ungefähres Alter schließen. Der jüngste Berg ist dem Magmaherd am nächsten (Koppers *et al*., 2001; Kroenke *et al*., 2004). Statistische Studien haben ergeben, dass kleine Seeberge sich meist auf jungen und dünnen ozeanischen Krusten bilden, während sich die größten Seeberge auf alter Lithosphäre erheben (Epp, 1984; Wessel, 2001).

Geschichte der Seebergforschung

Die Existenz dieser untermeerischen Berge war Seefahrern, Fischern, Kaufleuten und Entdeckungsreisenden indirekt seit Jahrhunderten bekannt: Sie bemerkten sie als Orte veränderter Strömung, erhöhten Fisch- und Seevogelaufkommens und durch die vermehrte Anwesenheit von Walen.

Die genauere Erforschung von Seebergen fällt mit der Entwicklung des Lotens zusammen. Sir James Clark Ross wird die erste korrekte Vermessung der Tiefsee zugesprochen, die er 1840 während seiner *Erebus* und *Terror* Expedition im Südatlantik durchgeführt hat, und bei der eine Tiefe von 4434 m ermittelt wurde (Deacon, 1971; Schlee, 1973). Am Ende des 19. Jahrhunderts begannen die ersten systematischen kartographischen Erfassungen des Kontinentalschelfs und der angrenzenden ozeanischen Gebiete. Seeberge wurden zu dieser Zeit nicht als weit verbreitete geologische Erscheinungen angesehen, sondern als Anomalien in einer ansonsten flachen Tiefseelandschaft. Die *Josephine Bank* im Nordatlantik westlich von Portugal war wahrscheinlich die erste als Seeberg erkannte Formation. Sie wurde während einer Reise der schwedischen Corvette *Josephin*e im Jahre 1869 entdeckt. Auf der Bank wurden Proben mit Dredgen und Netzen genommen. Aus den Expeditionsberichten geht hervor, dass die ausgeführten Probennahmen von Benthos und Plankton reiche Fänge ergaben, ausserdem wurde eine erhöhte Anzahl von Seevögeln festgestellt (Ankarcrona, 1969).

Anfang des 20. Jahrhunderts revolutionierte das Echolot die Kartierung des Meeresbodens. Die Methode gewann nach dem 2. Weltkrieg durch den technischen Fortschritt auf diesem Gebiet sehr an Genauigkeit. Die erste untermeerische Erhebung, die offiziell, vom US Board on Geographic Names (1938), den Namen Seeberg erhielt, war 1938 der *Davidson Seamount*. Die Bezeichnung „Seeberg“ wurde jedoch erst 1941 von Murray als “large isolated elevation characteristically of conical form“ genauer definiert. Menard (1964) spezifizierte später die Größe eines Seebergs auf mindestens 1000 m Höhe. Heute, im Zeitalter der Satelliten-Erkundung, schätzt man die Zahl der ozeanischen Seeberge, die mindestens 1000 m hoch sind, auf 70.000 bis 100.000, von denen 15.000 auf Grund von Schiffslotungen identifiziert sind (Wessel, 2001); die Zahl von Erhebungen >100 m dürfte mehr als 1.000.000 betragen. Von den großen Seebergen (>1000 m) befindet mehr als die Hälfte im Pazifik (Wessel, 2001).

Physikalische Ozeanographie

Dass ozeanische Rücken und Plateaus die Zirkulation des Wassers in den Ozeanen beeinflussen, z.B. durch Veränderungen der Strömungsrichtung oder das Verhindern der Mischung von Tiefenwasser mit wärmerem Wasser aus höheren Schichten, ist seit längerem bekannt. Der

Einfluss kleinerer Hindernisse, wie der von Seebergen, wurde erst in jüngerer Zeit genauer untersucht. So ist z. B. die Durchmischung des Oberflächenwassers in der Umgebung eines flachen, d.h. oberflächennahen, Seebergs deutlich verstärkt gegenüber Gebieten über ungestörten Tiefseeebenen.

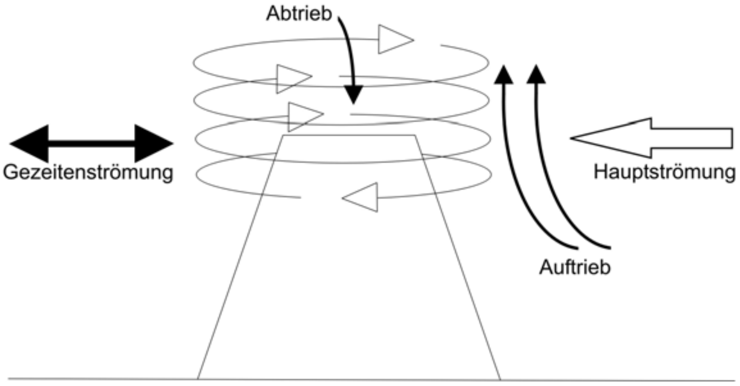

Abbildung 1: Strömungsmuster an einem Seeberg, die zur Ausbildung einer Taylorsäule führen.

Am Seeberg selbst kann Auftrieb entstehen, und es können, abhängig von der Stärke der generellen ozeanischen Strömung, die auf den Seeberg trifft, in diesem Gebiet den Berg umkreisende Strömungen mit höheren Strömungsgeschwindigkeiten als denen des umgebenden Wasserkörpers angetrieben werden (siehe Abb. 1). Diese ringförmigen Strömungen verlaufen, bedingt durch die Coriolis Kraft, auf der nördlichen Hemisphäre rechtsdrehend, auf der Südhalbkugel linksdrehend. Durch Gezeiten können die Ringströmungen verstärkt werden, in Äquatornähe ist diese Gezeitenresonanz schwächer als in höheren Breiten. Je nachdem, ob die Ringströmung die Wasseroberfläche erreicht oder vom Oberflächenregime abgekoppelt ist, wird sie als Taylorsäule oder Taylorkappe bezeichnet (Chapman & Haidvogel, 1992). Direkt über dem Seeberg kommt es dabei zu Abtrieb (Rogers, 1994), an den Rändern der Ringströmung zu Auftrieb.

Seeberg Ökosystem

Zwar ist der Fischreichtum an vielen Seebergen dokumentiert (Hubbs, 1959; Genin *et al.*, 1988; Boehlert & Seki, 1984; Boehlert, 1988), doch die Herkunft der Nahrungsgrundlage für die hohen Bestände von Fisch und anderen Zooplanktivoren ist bisher nicht befriedigend erklärt. Zur Erklärung für die z.T. reichen Fischpopulationen wurden in der modernen wissenschaftlichen Literatur mehrere Hypothesen herangezogen:

1. Der Auftrieb von kälterem, nährstoffreichen Wasser an Seebergen, deren Gipfel bzw. die über dem Gipfel entstandene Taylorsäule in die photische Zone reicht, kann die Primärproduktion

und weitergehend die Sekundärproduktion von autochthonem Plankton lokal erhöhen (siehe Abb. 1; Dower *et al.*, 1992; Boehlert & Genin, 1987; Genin & Boehlert, 1985; Lophukin, 1986; Tseytlin, 1985; Voronina & Timonin, 1986), welches die Nahrungsgrundlage für die Bestände der ansässigen Räuber bildet.

2. Durch den ‚trapping effect' wird ozeanisches Zooplankton, das tägliche Vertikalwanderungen durchführt, beim morgendlichen Abstieg von einem Seeberg blockiert, sofern dieser mit seinem Gipfel in die Reichweite der Tagestiefe der Organismen ragt. Daraufhin wird dieses so ‚gefangene' Plankton die Beute von Fischen und planktivorem Benthos (siehe Abb. 2; Genin *et al.*, 1988; Rogers, 1994).

3. Es wird vermutet, dass Taylorkappen und –säulen Organismen und Partikel für eine längere Zeit über dem Berg zurückhalten können (Beckmann & Mohn, 2002; Boehlert & Mundy, 1993; Mullineux & Mills, 1997; Dower & Perry, 2001). Dadurch wird einerseits allochthones Plankton über dem Berg festgehalten und andererseits die Verdriftung von Eiern und Larven der ansässigen Fauna vom Berg fort verringert.

4. Die ‚feed-rest' Hypothese postuliert, dass planktivore Fische einerseits von einem erhöhten Nahrungsangebot profitieren, das durch die von der Topographie verstärkten Strömungen herangetragen wird. Andererseits bietet der Seeberg leewärts strömungsberuhigte Gebiete, die die Tiere während Ruhephasen aufsuchen können (Genin, 2004).

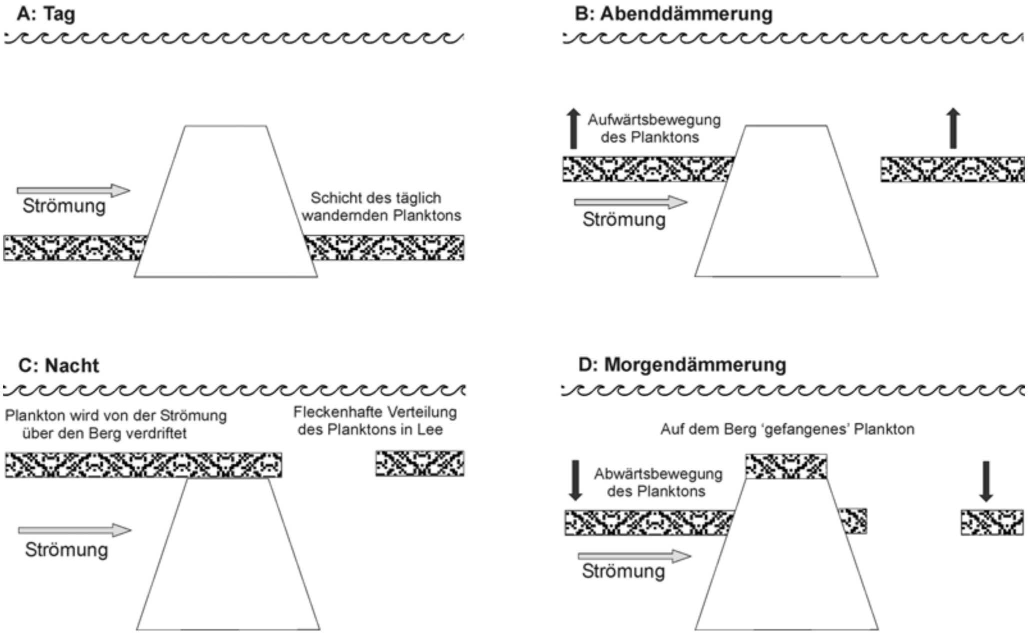

Abbildung 2: Täglich wanderndes Zooplankton an einem Seeberg (nach Rogers 1994).

Zusätzlich zu dem häufig auftretenden Fischreichtum wurde bei Untersuchungen an pazifischen und atlantischen Seebergen eine große Artenvielfalt und ein hohes Aufkommen endemischer Arten bei Benthosorganismen festgestellt (Richer de Forges *et al.*, 2000; George & Schminke, 2002; Gad, 2004). Die lokale Diversität wird aber auch durch pelagische Besucher wie Cephalopoden, Schildkröten, Fische und Meeressäuger weiter erhöht. Hohe Seeberge gelten zudem als ‚stepping stones' für die Verbreitung von Schelfarten. Auf welche Seeberge Eigenschaften wie erhöhter Endemismus und verstärkte Diversität zutreffen, und durch welche Komponenten, wie Strömung, Nährstoffreichtum, Beschaffenheit des Substrats und erhöhtes Nahrungsangebot aus dem offenen Ozean, das Ökosystem am Berg gesteuert wird, ist noch weitgehend unbekannt. Der Klärung dieser Fragen wurde seit den 90er Jahren erhöhte Aufmerksamkeit zuteil.

Ein weiterer Grund für den Bedarf an Untersuchungen ist die zunehmende Ausbeutung der Fischbestände an Seebergen sowie die Erwägung, vorhandene mineralische Rohstoffe wie Kupfer, Mangan und Kobalt zu erschließen. Schon jetzt kann der destruktive Einfluss der Fischerei auf das Benthos und die Fischpopulationen an häufig frequentierten Bergen festgestellt werden (Grigg, 1986; Clark & Koslow, 2007; Clark *et al.*, 2007). Da sich viele der ansässigen Tierarten durch Langlebigkeit, langsames Wachstum und späte Geschlechtsreife auszeichnen, sind ihre Bestände besonders anfällig für den Eingriff durch den Menschen (Grigg, 1986;, Boehlert & Sasaki, 1988; Boehlert & Mundy, 1993). Um ein schonendes Management der Seebergfischerei und den Schutz der wahrscheinlich besonders empfindlichen Seeberg-Ökosysteme zu gewährleisten, ist eine genauere Kenntnis ihrer Funktionsweisen und Steuermechanismen notwendig.

Vorgelegte Arbeiten

Die vorgelegten Arbeiten sollen dazu beitragen, die Nahrungsnetze an Seebergen näher zu beleuchten und die Mechanismen zu klären, die die Seeberg-Ökosysteme beeinflussen. Es galt dabei, die im vorigen Abschnitt erläuterten Hypothesen zur Erklärung des erhöhten Räuberaufkommens zu prüfen. Der Schwerpunkt lag dabei auf der Rolle des Zooplanktons an den Bergen. Dafür wurden Studien zur Biomasse, Verteilung und Artenzusammensetzung des Zooplanktons sowie potentieller Räuber an verschiedenen nordatlantischen Seebergen dokumentiert. Zudem wurde die Frage untersucht, ob die Stoffwechselraten des Zooplanktons (potentielle Respirationsraten und Kohlenstoffbedarf) die Theorie einer erhöhten lokalen Produktivität stützen. Da die untersuchten Berge (Abb. 3) sich in Höhe, Ausdehnung und geographischer Lage unterscheiden, wurde versucht, die Einflüsse dieser Faktoren auf das jeweilige Ökosystem herauszuarbeiten.

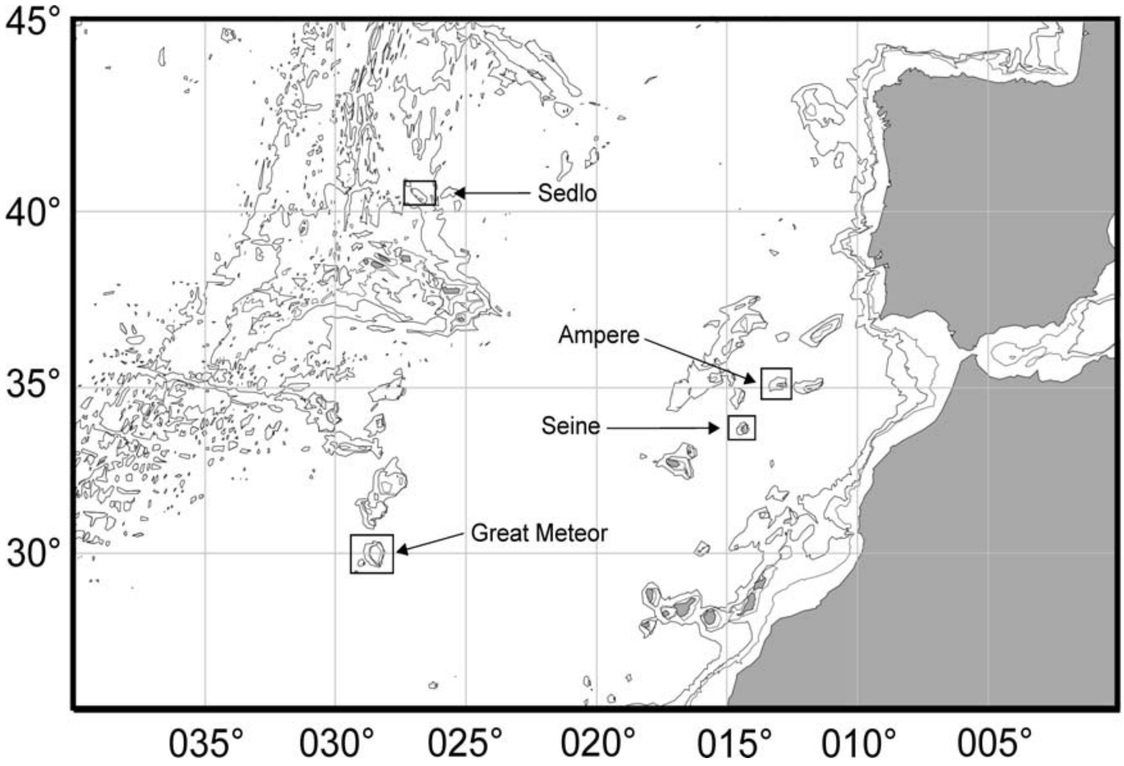

Abbildung 3: Lage der untersuchten Seeberge im Nordatlantik.

Manuskript Nr. 1 ‘Composition and distribution of zooplankton at the Great Meteor Seamount, subtropical Northeast Atlantic’ erschien 2004 im *Archive of Fishery and Marine Research* und beschreibt die Ergebnisse planktologischer Untersuchungen an der Großen Meteorbank. Im Jahre 1998 fand eine Expedition zu diesem westlich der Cap Verden gelegenen Seeberg statt. Der Seeberg ragt aus 4400 m Tiefe bis in ca 300 m unter dem Wasserspiegel auf. Sein Plateau erstreckt sich über ca 1500 km². Die Arbeit wertet die dort mit einem Longhurst-Hardy-Planktonrekorder (Longhurst *et al*., 1966) gesammelten Zooplanktonfänge aus. Es wurden die Biomassen und die Zusammensetzung des Planktons an verschiedenen Stationen zu verschiedenen Tageszeiten über dem Plateau und den Hängen des Berges verglichen.

Die Manuskripte Nr. 2, 3 und 4 sind eingereicht, begutachtet und von den Gasteditoren akzeptiert, und werden in Kürze in einem Sammelband der Zeitschrift *Deep Sea Research* veröffentlicht.

Manuskript Nr. 2 ‘Distribution of zooplankton biomass at three seamounts in the NE Atlantic’ dokumentiert die Ergebnisse verschiedener Expeditionen zum Seine Seamount und Ampère Seamount, beide nördlich von Madeira gelegen, sowie zum Sedlo Seamount nördlich der Azoren. Die Gipfel der Berge reichen 750 m (Sedlo), 160 m (Seine) bzw. 55 m (Ampère) unter den Meeresspiegel. Die Fänge wurden mit einem MOCNESS (Multiple opening and Closing Net and Environmental Sensing System, Wiebe *et al.*, 1985) durchgeführt. Es wurde die Verteilung der Zooplanktonbiomasse zu verschiedenen Tageszeiten über den Gipfeln, den Hängen und an ozeanischen Referenzstationen analysiert.

Manuskript Nr. 3 ‘The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: Composition, population structure and diets’ behandelt die Zusammensetzung der bodennahen Fischfauna am Seine Seamount sowie deren Nahrung. Es wurden die Artzusammensetzung, Populationsstruktur und Mageninhalte von bodennahen Fischen analysiert, die während dreier Reisen zum Seine Seamount gefangen worden waren.

Manuskript Nr. 4 ‘Zooplankton metabolism and carbon demand at two seamounts in the NE Atlantic’ untersucht die Stoffwechselraten des Zooplanktons am Seine und Sedlo Seamount und ozeanischen Referenzstationen auf Grundlage der ETS (electron transfer system) Aktivitäten im Hinblick auf eine lokal erhöhte Produktion an den Bergen.

Manuskript Nr. 5 ‘Distribution and community composition of zooplankton at three seamounts in the NE Atlantic’ behandelt die Zusammensetzung und Verteilung des Zooplanktons an den Seebergen Sedlo, Ampère und Seine. Dabei wurden die Zooplanktongemeinschaften an den verschiedenen Bergen sowie die Fänge von den Gipfeln mit denen am Hang und an ozeanischen Referenzstationen der jeweiligen Berge in Bezug auf Häufigkeiten und taxonomische Zusammensetzung verglichen. Desgleichen wurde die Tiefenverteilung bestimmter taxonomischer Gruppen und Arten an den drei untersuchten Bergen und an den verschiedenen Probengebieten der jeweiligen Berge miteinander verglichen.

Archive of Fishery
and Marine Research

Composition and distribution of zooplankton at the Great Meteor Seamount, subtropical North-east Atlantic

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Abstract

During an expedition in September 1998 zooplankton was sampled over the plateau and on the slope of the Great Meteor Seamount, using a Longhurst-Hardy Plankton Recorder. Sound scattering layers were observed with the ship's 33 kHz echo sounder. Higher biomass and a slightly different composition of zooplankton groups were found on the upstream side of the seamount compared to its downstream side. The abundance of copepod exoskeletons was higher on the seamount plateau than in its vicinity. Strongly vertically migrating plankton groups like copepods of the genus *Pleuromamma* and euphausiids were found in high abundances at daytime close to the bottom of the plateau and constituted the main component of the relatively high biomass. The latter group most likely formed the scattering layer found at this station. The distribution of zooplankton in the vicinity of the seamount is probably influenced by both predation and the flow regime influenced by the irregular bottom topography.

Kurzfassung

Zusammensetzung und Verteilung von Zooplankton bei der Grossen Meteorbank, subtropischer Nordostatlantik

Während einer Expedition zur Grossen Meteorbank im September 1998 wurden Zooplanktonfänge über dem Plateau und dem Hang des Tafelbergs mit einem Longhurst-Hardy-Plankton-Recorder durchgeführt und parallel dazu das mit einer Frequenz von 33 kHz arbeitende Schiffsecholot eingesetzt. Eine erhöhte Biomasse und eine leicht abweichende Zusammensetzung des Zooplanktons wurde an der angeströmten Seite des Berges festgestellt. Die Abundanz von Exuvien über dem Plateau war gegenüber tieferem Wasser erhöht. Vertikal wandernde Organismen wie Copepoden der Gattung *Pleuromamma* sowie Euphausiaceen wurden am Tage über dem Plateauboden in hohen Abundanzen gefunden. Letztere bildeten wahrscheinlich die an dieser Station aufgezeichneten Echostreuschichten. Es kann angenommen werden, dass die Verteilung des Zooplanktons im Bereich der Grossen Meteorbank sowohl von physikalischen wie biologischen Prozessen, wie Wegfrass, beeinflusst wird.

Introduction

Isolated oceanic seamounts are hydrographically and biologically exceptional within the ocean surrounding them. Their importance as habitats for an endemic flora and fauna as well as their influence on pelagic oceanic animals is still poorly understood and differs de-

Arch. Fish. Mar. Res. 51(1-3), 2004, 89–100

pending on geographical position, summit height and hydrographical conditions (Roden 1987; Rogers 1994).

In September 1998 an interdisciplinary expedition was carried out (on board the RV Meteor) to the Great Meteor Seamount in the subtropical northeast Atlantic. This steep mount rises from the deep sea floor at 4400 m depth up to 287 m below the surface. The plateau of the seamount measures about 1500 km^2 and its largest part is situated about 300 to 400 m below the surface.

This investigation examines whether and to what extent the isolated position of this large and levelled mount affects the composition and stock of the zooplankton community. The composition of the fauna in the water column above the plateau as well as above the slopes was analysed in order to detect possible fine-scale differences. The study took into consideration the hydrographical data gathered by the oceanographers during the expedition.

In particular, this research was designed to address the following questions:

- Is there a difference in biomass between plateau and slope?
- Does the topography influence possible vertical and horizontal migrations of the zooplankton, *i. e.*, is there a retention of organisms in the Taylor column and a trapping effect for animals that perform diurnal migrations into depths below the plateau level?
- Do the Longhurst-Hardy plankton recorder (LHPR) data confirm the echo sounder observations of movements of the sound-scattering layer?
- Do the results correspond to those of the oceanographic models of passively and vertically migrating particles or organisms?

Material and methods

The samples were gathered with a Longhurst-Hardy plankton recorder (LHPR) (Longhurst *et al.* 1966), mesh size 200 µm, at different times of day at 11 stations above both the plateau and the slopes of the mount.

The catches were preserved in 4 % buffered formaldehyde in seawater. The organisms were identified according to taxonomical classes, crustaceans to order, some taxa to species level, and subsequently enumerated. Copepod exoskeletons were counted separately. Abundances were standardised to individuals per 100 m^3. Biomass was measured as wet weight standardised to grams per 100 m^3. Statistical methods could not be used because of the inhomogeneity of the samples – in terms of depth, time of day, and location. Observations of acoustic scattering were made with the ship's echo sounder (ATLAS DESO 25/RS) at a frequency of 33 kHz.

Physical data showed the existence of a stable Taylor column above the Great Meteor Seamount during the time of the expedition (Mohn and Beckmann 2002). Because of a steady main current from the northeast and the periodical effect of the tides, an anticyclonic ring-shaped flow was formed around the seamount enclosing a body of water above the plateau. This trapped water body extended across the plateau, ending at the 500 m depth contour. It hardly mixed with the surrounding water masses and, if at all, only in a vertical direction. The speed of the anticyclonic circulation was highest in the vicinity of the 1000 m depth contour and decreased on a transect away from the mount to the 1500 m depth contour (Mohn, pers. comm.).

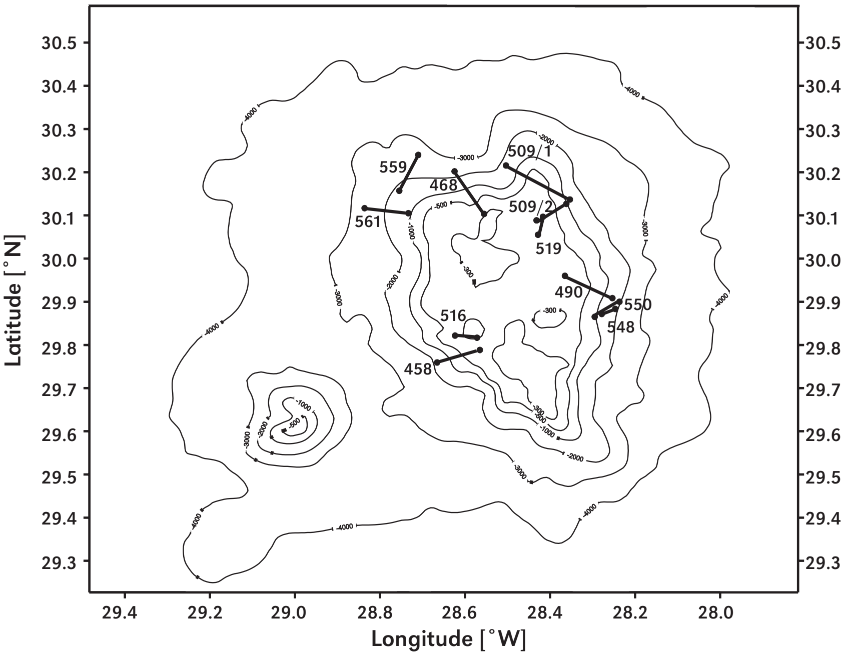

Figure 1: LHPR–stations.

On the basis of the oceanographic results, the samples were differentiated into the categories: "plateau" and "depth".

- Plateau: Samples from areas with bottom depth < 500 m (from the inside of the circulation cell of the Taylor column);
- Depth: samples from areas with bottom depths > 1500 m (probably beyond the influence of the Taylor column).

No samples were collected in the upper 100 m of the water column above areas with bottom depths between 500 and 1500 m. Therefore, only samples from the plateau and the depth can be compared in this study.

As the transects of the plankton recorder hauls in most cases extended across plateau and slope or slope and depth (Figure 1), the location of each discrete sample was calculated separately.

The LHPR data were overlaid on the echo sounder recordings taken at a frequency of 33 kHz during the hauls.

Results

Distribution of the zooplankton biomass

In the 222 discrete samples that were analysed for biomass no marked differences between "plateau" and "depth" stations could be detected (Figure 2a and b). In general, the highest biomass concentrations at each station were observed in the upper 150 m of the water

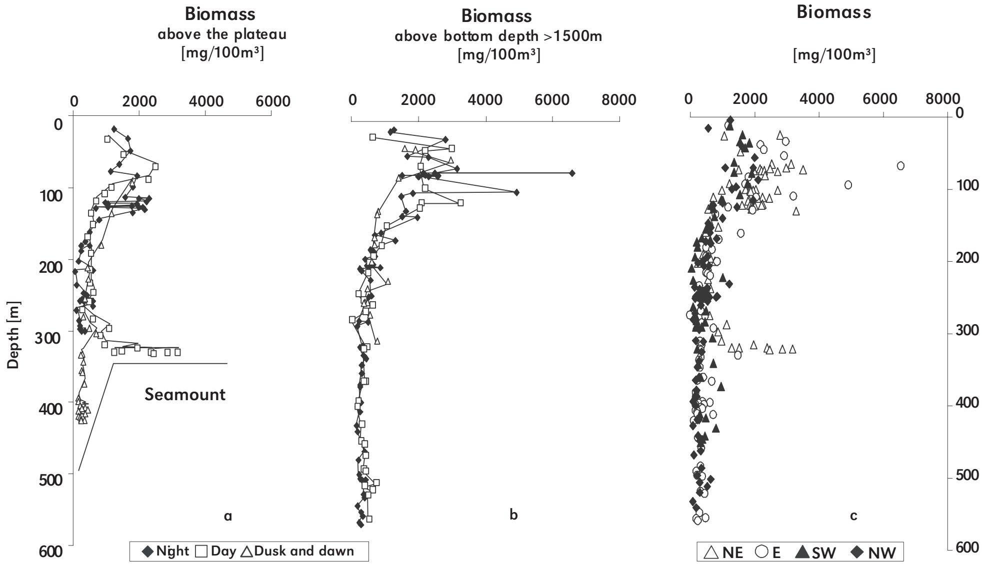

Figure 2: Distribution of biomass: a above the plateau, b above bottom depth > 1500m and c in different regions of the seamount, independent of bottom depth (NE: Station 509/1, 509/2, 519, E: St. 490, 548, 550, SW: St. 458, 516, NW: St. 468, 559, 561).

column by day and night, and decreased with depth. However, a higher biomass was found at 300 to 400 m during the daytime (No. 519) near the floor of the plateau (Figure 2a). This increase of biomass indicates a concentration of downward-migrating organisms that are trapped above the flat surface of the plateau.

To find possible regional differences at the seamount a total of 280 discrete samples of the northeastern, eastern, southwestern and northwestern stations were compared. A distinctly higher biomass was found at the northeastern and eastern stations, *i. e.*, on the upstream side of the seamount (Figure 2c).

Taxonomic composition of zooplankton

Figure 3 illustrates the taxonomic composition of the zooplankton caught at 4 stations in oblique hauls. The samples were taken from 0 to 530 m at two night-time stations in deeper water to the northeast and east of the mount. Over the plateau, hauls were carried out during the daytime in the northeast, and at night in the southwest, from the surface down to 20 m above the bottom.

The copepods were the dominant group at all stations (74 to 79 %). Other important groups were ostracods, with shares of 2 to 7 %, and chaetognaths, which comprised 3 to 4 % of the zooplankton composition.

The easterly station differed from the other stations with a clearly higher proportion of gelatinous organisms (cnidarians, siphonopheres, salps, appendicularians) and high percentages of cladocerans and euphausiids, but lower relative abundance of ostracods (Figure 3b).

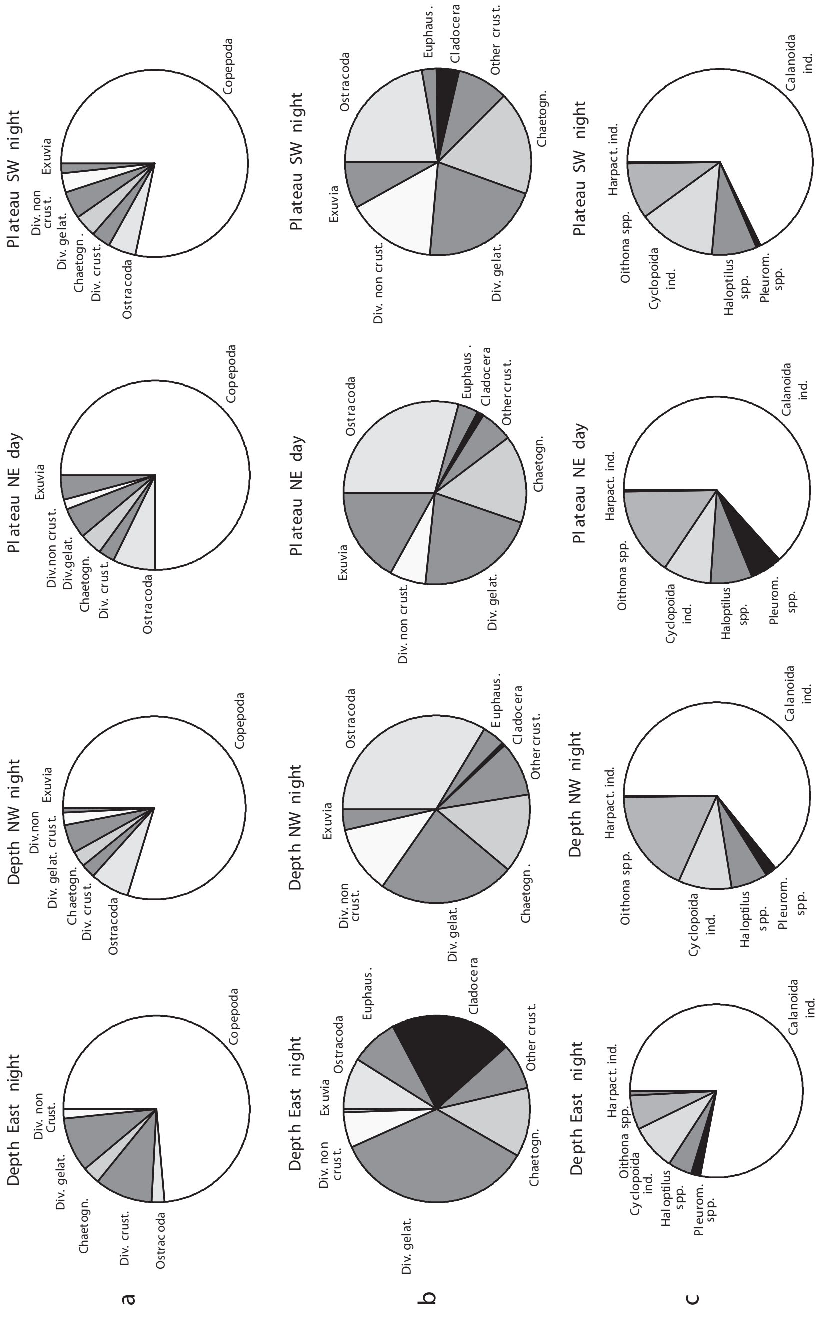

Figure 3: Composition of zooplankton at two stations above deeper water (caught in oblique hauls from 0-530m) and two stations above the plateau (0-20m above bottom). a zooplankton groups, b zooplankton groups without copepods, diverse crustaceans in more detail, c copepods.
Div. crustaceans include decapods, euphausids, mysiids, amphipods, isopods, cladocerans and crustecean larvae, div. gelatinous organisms include cnidarians, siphonophores (parts), salps and appendicularians, div. non crustaceans include fish larvae, polychaets, molluscs, echinoderm larvae and unidentified organisms.

Within the copepods (Figure 3c) there are noticeable differences in the relative proportion of *Oithona* spp. and *Pleuromamma* at the different stations. In deep water in the northwestern area, the proportion of *Oithona* is three times as high as in the easterly region. Above the plateau, the genus *Oithona* constitutes 16 % of the copepod population in the northeast and 10 % in the southwest. At night, *Pleuromamma* above deeper areas represents 2 % and above the plateau 1 %, whereas during the daytime in the northeast above the plateau it is 4 %.

Above the plateau, the relative abundance of cyclopoid copepods is much higher in the northeast (14 %) than at other stations (9 %, 9 % and 8 %).

In summary, the results suggest regional variations rather than cardinal differences between the plateau and slope. The easterly station shows the greatest variation in the composition of zooplankton.

Copepod exoskeletons were found in higher abundances above the plateau than above areas with a bottom depth of > 1500 m (see Figure 3a and b).

Vertical distribution, day-night variations, and possible retention of zooplankton

In order to examine the vertical distribution of organisms above the plateau and in deeper water during different times of day, samples from different hauls were clustered according to depths and time of day.

In most of the groups neither a diurnal vertical movement nor an obvious difference between the samples from above the plateau vs. deeper water could be discerned.

Exceptions to this tendency are as follows: Euphausiids (Figure 4) and calanoid copepods of the genus *Pleurommama* (Figure 5) as well as molluscs accumulate in the near-bottom layer above the plateau during the daytime. For ostracods and polychaets, a day/night distribution shift both above the plateau and in deeper water has been detected (Figure 6 and 7). Copepod exoskeletons are more abundant above the plateau than in deeper water (Figure 8).

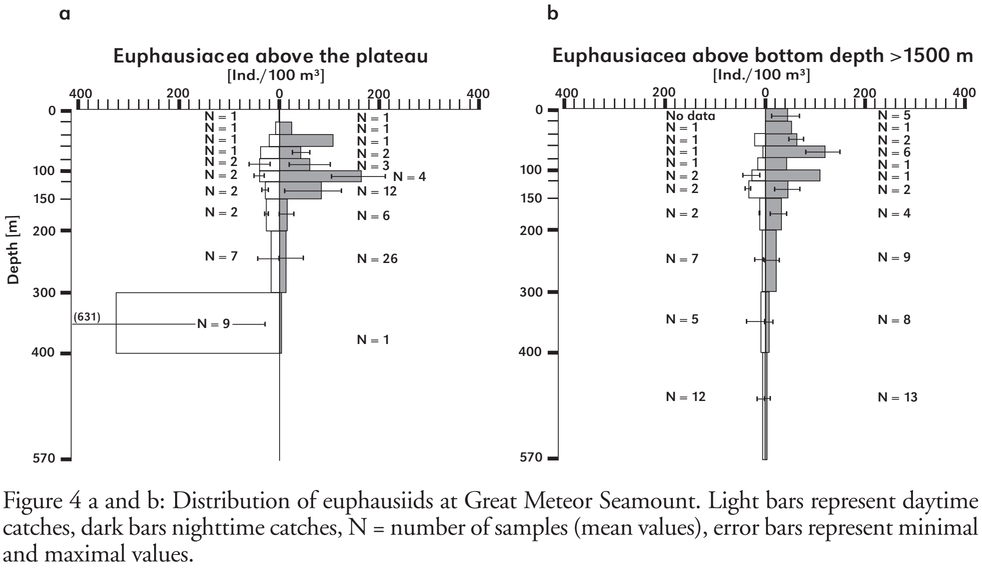

Figure 4 a and b: Distribution of euphausiids at Great Meteor Seamount. Light bars represent daytime catches, dark bars nighttime catches, N = number of samples (mean values), error bars represent minimal and maximal values.

Observation of sound scattering layers

Echo sounder recordings were evaluated at four stations: One station each for the plateau and deep water, with day and night recordings at each. The acoustic data were then compared to the biomass data from the LHPR hauls.

Above deep bottoms, three sound-scattering layers could clearly be discerned: a wide layer at 400 to 600m, a thinner layer at 200 m both in the daytime and at night, and a third layer that was thin in the daytime at 100m and wider at night at 0 to 130 m (Figure 9a and b).

The biomass data from the individual hauls of the deep-water station at night correspond to the acoustic data in the upper 150 m of the water column, whereby high biomass

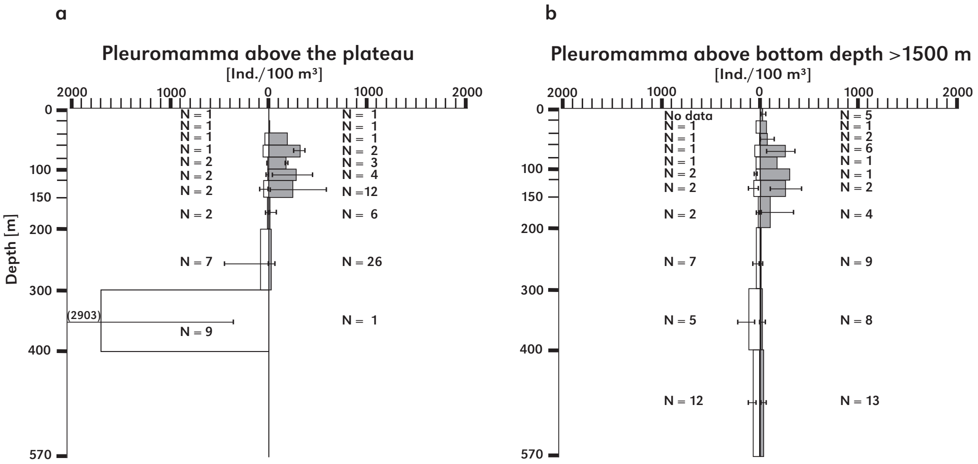

Figure 5 a and b: Distribution of *Pleuromamma* at Great Meteor Seamount. Light bars, dark bars, N see above.

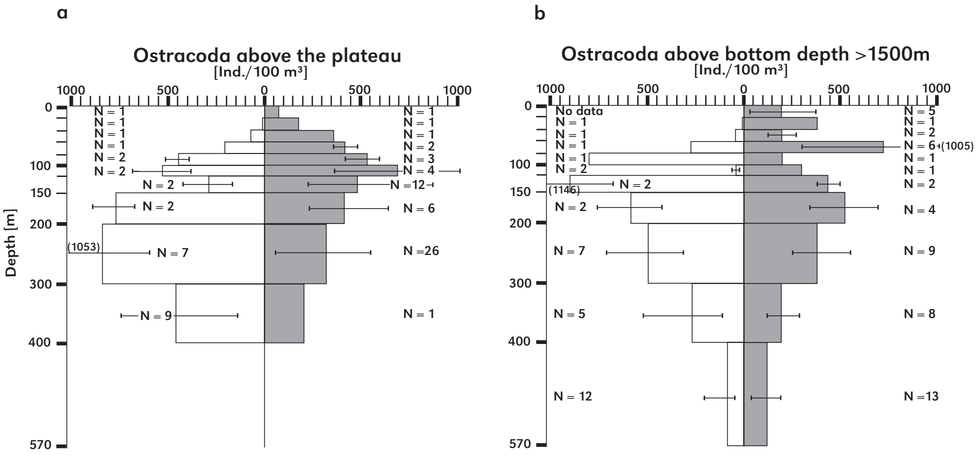

Figure 6 a and b: Distribution of ostracods at Great Meteor Seamount. Light bars, dark bars, N see above.

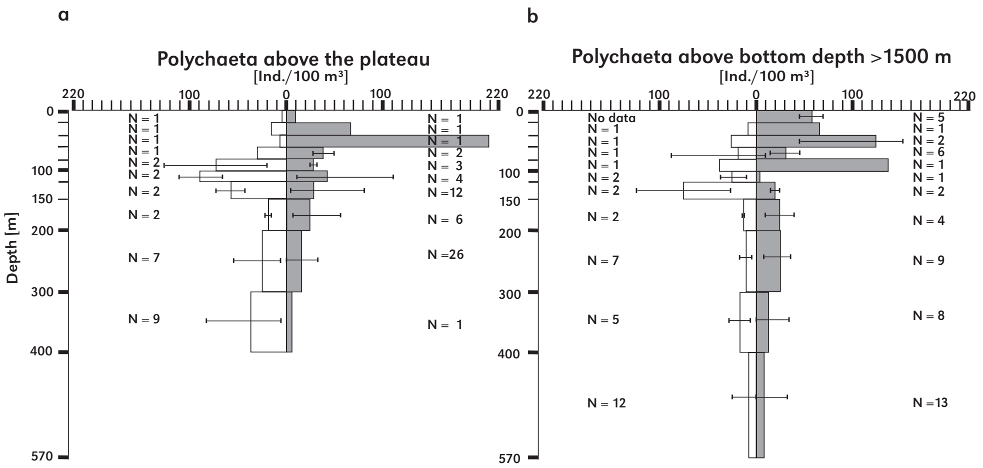

Figure 7 a and b: Distribution of polychaets at Great Meteor Seamount. Light bars, dark bars, N see above.

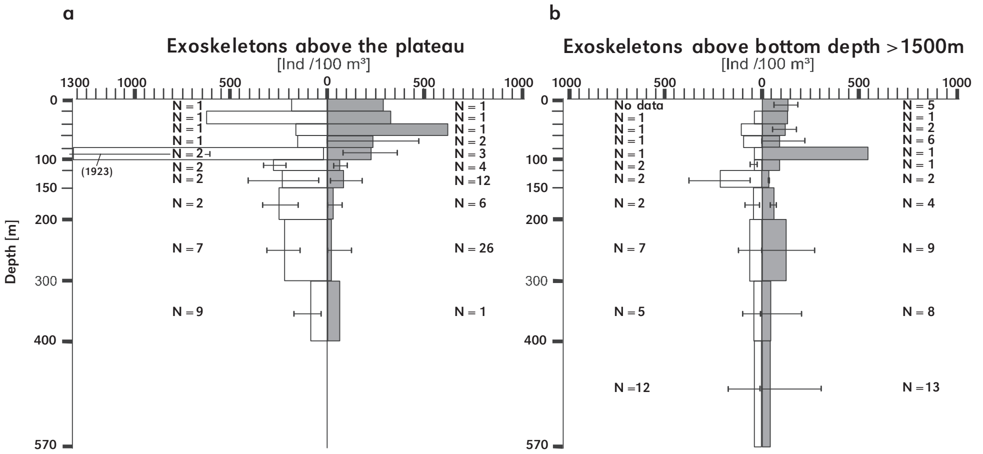

Figure 8 a and b: Distribution of exosceletons at Great Meteor Seamount. Light bars, dark bars, N see above.

was found during the daytime not only at 100 m depth, but also through the upper 130 m of the water column. Neither at 200 m nor at 400 to 600 m could an increase of biomass be detected in the LHPR samples.

Above the plateau an upper scattering layer at 100 m and another layer close to the bottom during the daytime could be discerned. At night one scattering layer extended from the surface down to 130 m depth. All of these layers seem to correspond to the biomass found in the zooplankton samples (Figure 10a and b).

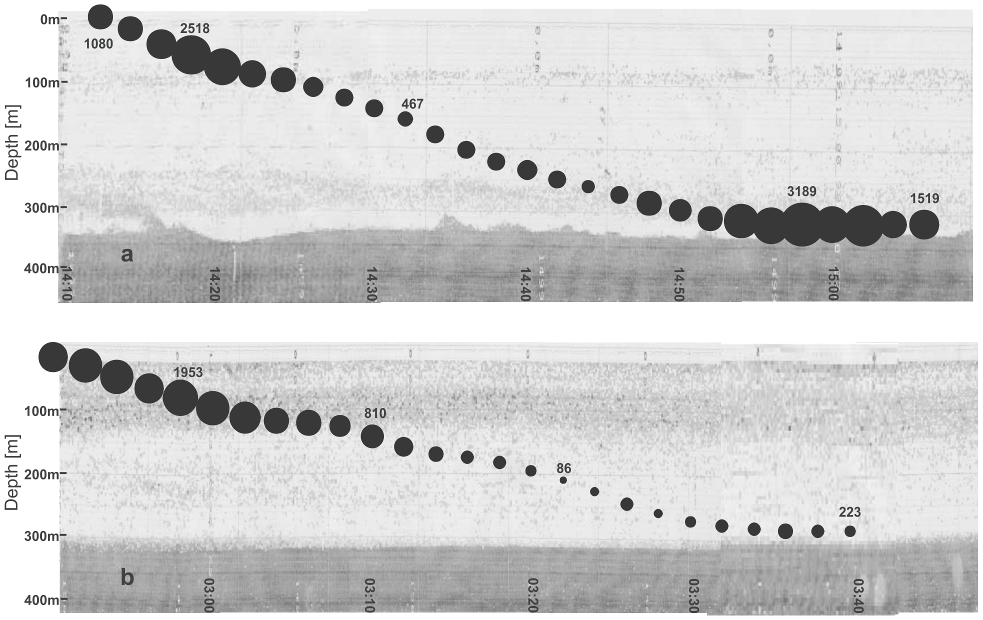

Figure 9: Biomass [mg/100m³] vs. echo sounder recordings (33 kHz). Bubble size corresponds to the biomass of the discrete samples. Some values are shown in the graph a: East, day, above deeper water (St. 548), b: Southwest, night, above deeper water (St. 559).

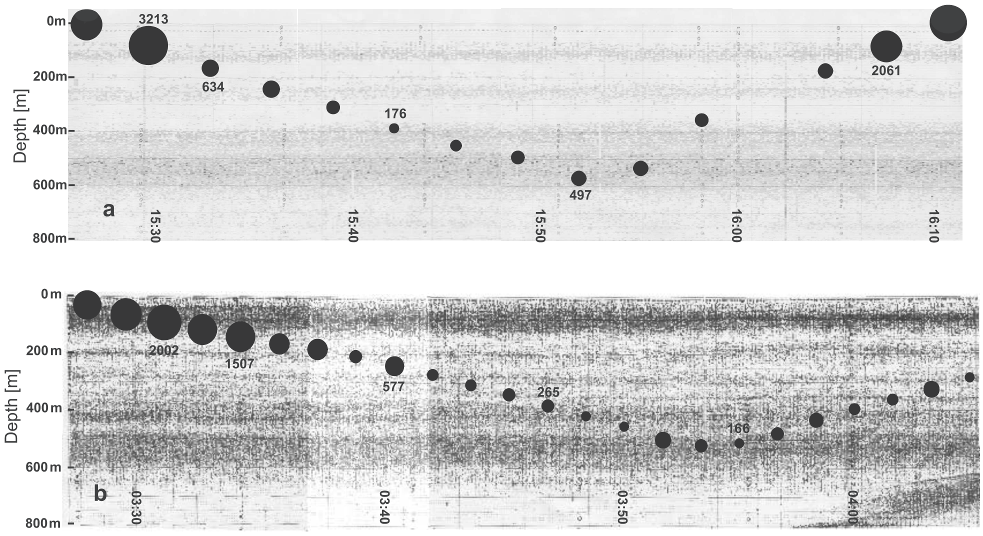

Figure 10: Biomass [mg/100m³] vs. echo sounder recordings (33 kHz). Bubble size corresponds to the biomass of the discrete samples. Some values are shown in the graph a: Northeast, day, above the plateau (St. 519), b: Southwest, night, above the plateau (St. 516).

Discussion

The general comparison between the plateau area of the seamount and the surrounding slopes suggests that there is no clear difference between the zooplankton communities inside and outside the Taylor column – a result that applies to both biomass and taxonomical composition. This corresponds to the data taken by Dower and Mackas (1996) above a seamount in the NE Pacific, but not to those obtained by Nellen (1973), who found a significantly lower biomass above the summit plateau of the Meteor Seamount as compared to the slopes.

The results of the present study suggest highest zooplankton biomasses on the upstream side of the mount as well as near the bottom during daytime.

In addition, the fact that the taxonomic composition of the zooplankton found at an easterly station differs in comparison to the other stations suggests faunal variations between the upstream region of the mount and the other areas under examination (Figure 3).

The relatively high biomass above the floor of the plateau at daytime (Station 519) can be explained in terms of the vertically migrating euphausiids and the copepods of the genus *Pleuromamma*. In general, euphausiids and *Pleuromamma* undertake considerable diurnal migration (Andersen and Sardou 1997; Schirmer 1975).

Here euphausiids constitute about one third of the total wet weight and *Pleuromamma* more than half of the copepod stock. The four *Pleuromamma* species (*P. abdominalis, P. gracilis, P. xiphias, P. piseki*) found here are known from the subtropical northeast Atlantic (Schirmer 1975; Hays *et al.* 2001). Weigmann (1974) found that all euphausiids caught above the Great Meteor Seamount were subtropical oceanic species. We assume that these organisms have been trapped on the plateau of the seamount.

Several authors (Kinzer and Hempel 1970; Nellen 1973; Genin *et al.* 1994) have raised the hypothesis that those organisms which migrate upwards into shallower waters upstream of seamounts at nighttime are drifted across the summit by near-surface currents. When they migrate downwards at dawn, they are blocked by the shallow bottom and are preyed upon by predators, which are typically found in greater numbers on the summit than in the surrounding ocean.

Fock *et al.* studied the species-environment relationships (Fock *et al.* 2002a) as well as diel- and habitat-dependent resource utilisation of fishes at the Great Meteor Seamount (Fock *et al.* 2002b). The authors analysed 4 dominant fish species whose diets consisted primarily of pelagic food. This result supports the assumption that the predators are following their prey during diurnal migration.

Ehrich (1974), also studying fish species caught on the Great Meteor Seamount, found their stomachs to contain euphausiids as well as *Pleuromamma*. Genin *et al.* (1988) describe euphausiids to be the dominant prey of fish caught above a flat bank in the California Bight. This study proposes that migrating organisms like euphausiids as well as *Pleuromamma* could play a significant role in maintaining the fish stock on the Great Meteor Seamount.

Haury *et al.* (2000) examined four different seamounts in the NE Pacific. They found an increase of fine-scale patchiness of zooplankton over and downstream of seamounts at night. The reasons for this could be both biological and physical: most zooplankton that descend above the mount at dawn are either preyed upon or advected off the summit during the daytime, which causes gaps in the upward-moving sound-scattering layer at the following dusk. However, Haury *et al.* (2000) suggested that physical processes related to seamount size and summit depth might be of greater importance than predation. To detect the influence of physical processes on the zooplankton at Great Meteor Seamount, the oceanographers developed models to simulate the behaviour of both passive and vertically migrating particles/organisms (Beckmann and Mohn 2002). The models suggest that passive particles are held back in the Taylor column over the plateau with a retention time up to ten times higher than in the surrounding waters. This retention time decreases during stormy weather. However, actively vertically migrating zooplankton is not retained, as it is advected by the currents into deeper layers. In the model these organisms move west to southwest at the same order of magnitude as the far field currents (Beckmann and Mohn 2002).

The model for passive particles could explain the higher abundances of exuvia above the plateau.

However, the extent to which the model of active organisms can explain the movements of living zooplankton remains to be examined in more detail. The calculation has to take into consideration both velocity and direction, as well as the distance covered by the organisms, because the movement patterns vary according to species.

The present study suggests that the combined effect of physical and biological factors explains both the even distribution of biomass and zooplankton composition above the summit and deeper waters, as well as fine-scale differences between the individual stations.

Concerning the echo-sounder observations of the stations in deeper water, it is apparent that, in depths greater than 200 m, the biomass data do not correspond with the acoustic data. However, close to the floor of the plateau during the daytime the results of the catches match those of the acoustic observations. It can be assumed that the acoustic signals are caused by euphausiids, because organisms smaller than 2 cm are hardly reflected by frequencies of 30 kHz and lower (Krause 1978).

This study proposes that in future investigations of the zooplankton community at seamounts, samples have to be taken in a wide radius up- and downstream of the summit, because the ‘seamount effect’ that has been detected by the oceanographers extends far beyond the area of the plateau.

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Acknowledgements

The authors would like to thank all persons that gave support to the progress of this work, especially Dr. Christian Mohn for providing and discussing the hydrographical data and Tink Diaz for improvement of the English language. This research was part of the Cruise No. 42 of RV Meteor, *Ostatlantic 1998,* and of the science project *Pelagische Seebergbiozönose,* DFG/Ne 99-25/1&2. Both were funded by the Deutsche Forschungsgemeinschaft, the financial help of which is highly appreciated.

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Received: 6 January 2003, accepted: 23 September 2003, print proof received from author: 29 July 2004.

Manuskript 2

Deep-Sea Research II (accepted by guest editors)

Distribution of zooplankton biomass at three seamounts in the NE Atlantic

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Abstract

During different seasons of the years 2003-2005 in the NE Atlantic, zooplankton were sampled with a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System, mesh size 333 µm) above the slopes and summits of Seine, Sedlo and Ampère Seamounts and at remote reference sites outside the influence of the seamounts (far field). Wet weights of different zooplankton size classes (<0.5 cm, 0.5-2 cm, >2 cm) were measured. Night and day hauls were analysed in order to detect diel vertical migrations of the zooplankton, as well as a possible trapping effect due to the shallow topography.

Biomass concentrations, independent of daytime, season and summit height, were reduced above the summits at all three seamounts compared to the slope and far field sites. No trapping effect or retention of biomass was apparent above the seamounts. The vertical distribution patterns of the size class <0.5 cm did not differ between night and day hauls at most sites, but indications of diel vertical migrations were found in the larger size fractions. With the exception of gelatinous organisms, zooplankton >0.5 cm were nearly absent above the summits of Seine and Ampère Seamounts, but considerable numbers were found above the slopes and at the far field sites.

Possible explanations for the observed distribution patterns of zooplankton biomass and size classes are discussed, including retention and lateral advection due to the hydrography at the seamounts, as well as predation by resident seamount fish.

Keywords: Seamounts; zooplankton; distribution; biomass; NE Atlantic

1. Introduction

In recent years, oceanic seamounts have attracted increasing scientific and public interest due to reports of enriched biodiversity, higher biological productivity, and an increase of commercially valuable fish stocks as compared to the open ocean (e.g. Isaacs and Schwartzlose, 1965; Dower *et al.*, 1992; Parin *et al.*, 1997; Rogers, 1994). However, the origin of available food to sustain the seamount-associated communities in surroundings of variable nutrient loading remains under discussion (e.g. Nellen, 1973; Parin *et al.*, 1997; Genin, 2004).

In general, ocean currents impinging on a seamount cause isopycnal doming, i.e. upwelling on the upstream side of the topography. If these currents are steady and strong enough they will lead to the formation of a Taylor cap or Taylor column, maintaining a region of weak or vanishing currents in the center (e.g. Chapman and Haidvogel, 1992; Beckmann and Mohn, 2002 and citations therein). These flow patterns can have an impact on the biological regime of the seamounts. For example, the occurrence of Taylor columns have been linked to enhanced levels of chlorophyll *a* (Chl a) above shallow topography (Genin and Boehlert, 1985; Dower *et al.*, 1992).

Whether and to what extent changes in current patterns generated by a seamount occur depends on a variety of factors including the strength of the mean flow, tides and size of the topography.

In the recent literature, three explanations for increased biomass and diversity at seamounts have been proposed, which are based on the modification of the current regime through the seamount:

1.) Enhanced primary and secondary production due to upwelling. However, direct evidence of this causal connection is weak (Uda and Ishino, 1958; Dower *et al.*, 1992; Dower and Mackas, 1996; Mourino *et al.*, 2001).

2.) Advection due to isopycnal doming, retention of organisms from the surrounding open ocean due to an altered flow field (such as a Taylor cap) in the vicinity of elevated bottom topography, and the interception of the topography with the diurnal vertically migrating organisms forming the sound-scattering layer (SSL) (Isaacs and Schwartzlose, 1965; Hesthagen, 1970; Rogers, 1994; Genin, 2004; Wilson and Boehlert, 2004).

3.) The feed-rest benefit hypothesis, which suggests that planktivorous fish benefit from amplified currents over topography. Amplified currents transport food to fish feeding sites, and topography provides shelter for resting fish during non-feeding intervals (Genin, 2004).

One can speculate that direct or indirect impacts of seamounts on the benthic and pelagic communities changes with form and height of the elevation, and also depends on the hydrographic conditions in the region that is influenced by the obstacle. Thus, seamounts reaching into the photic zone (classified as ‘shallow’ after Genin, 2004) could alter surface currents, the SSL, and the distribution of the near-surface planktonic organisms (Genin *et al.*, 1994), and ‘intermediate’ elevations (below the photic layer but shallower than ~400 m) could influence the distribution of the SSL. Furthermore, ‘deep’ seamounts extending to a depth of ~1500 m could still affect animals by acting as an obstacle to their vertical migration.

This study focuses on the influence of seamounts on oceanic zooplankton and the role of the zooplankton within the ecosystems of three seamounts of different sizes, fitting in the scheme above. For this purpose, the following main questions/objectives were investigated:

a. Is there a local increase of zooplankton biomass ‘on versus off’ the studied seamounts?
b. Are there differences in zooplankton distribution and biomass at the three studied seamounts?
c. To what extent may the zooplankton distribution be shaped by external forcings such as advection/retention and/or by non-hydrodynamic-related mechanisms like predation?

2. Material and Methods

The Seine, Sedlo and Ampère Seamounts are situated in the sub-tropical NE Atlantic basin between Portugal and the Azores (Fig. 1) and were studied during the years 2003-2005 in the context of the EU funded project OASIS: Oceanic Seamounts - an Integrated Study.

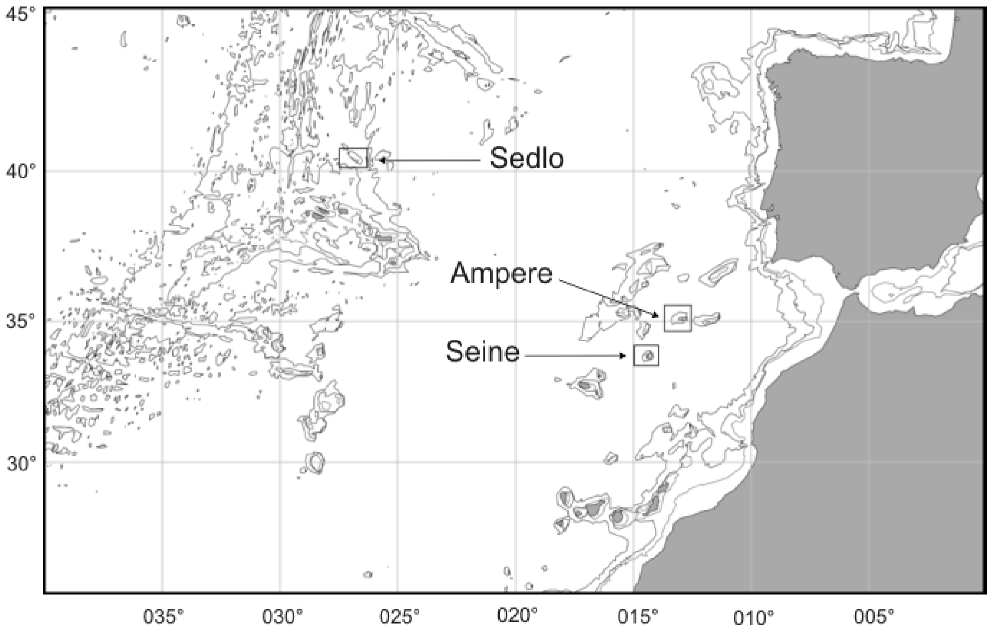

Fig. 1: Area of investigation.

Seine Seamount is an isolated seamount located north of Madeira at 33°50’N and 14°20’W (Fig. 2), rising from ~4000 m to 170 m summit height. The summit plateau is rather flat, spanning an area of ~50 km². The general flow, calculated from three months of mooring data in March-July 2004, was weak and directed southeastward. In spring 2003, a weeklong ADCP measurement showed northward currents above the summit, which could be an influence of the seamount. Anti-cyclonic circulation due to tidal amplification was observed above the seamount, which leads to the lowering of the thermocline over the summit and upwelling at the slopes (Mohn, pers. comm.). Variability of this pattern was mainly caused by Mediteranean Water vortices, which were observed in the seamount region (Bashmachnikov *et al.*, this issue.).

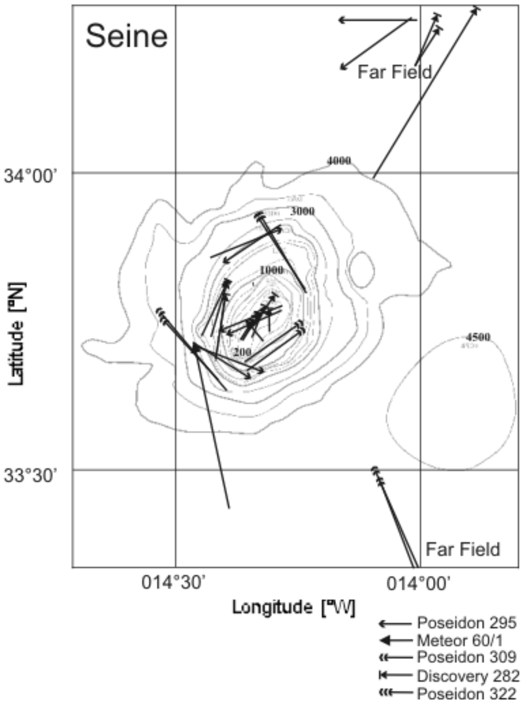

Fig. 2: Seine Seamount. Arrows represent station tracks.

Sedlo Seamount is located in the more temperate Azores region (40°20’N, 27°50’W) (Fig. 3). This study concentrated on the southeasterly of three peaks, which rises from ~2800 m to 750 m below sea level. The general flow changed from SW in summer to NW in winter with an average velocity of 5 cm s^{-1}. Hydrographic data collected from CTD, moorings and ADCP between March and December 2003 revealed a Taylor cap above the investigated peak, reaching up to 350 m above the summit, where a complete reversal of the flow was evident. The upper 100 m of the water column were, more or less, decoupled from the cap; for detailed description of the hydrography of Sedlo Seamount see White *et al.* and Bashmachnikov *et al.*, this issue.

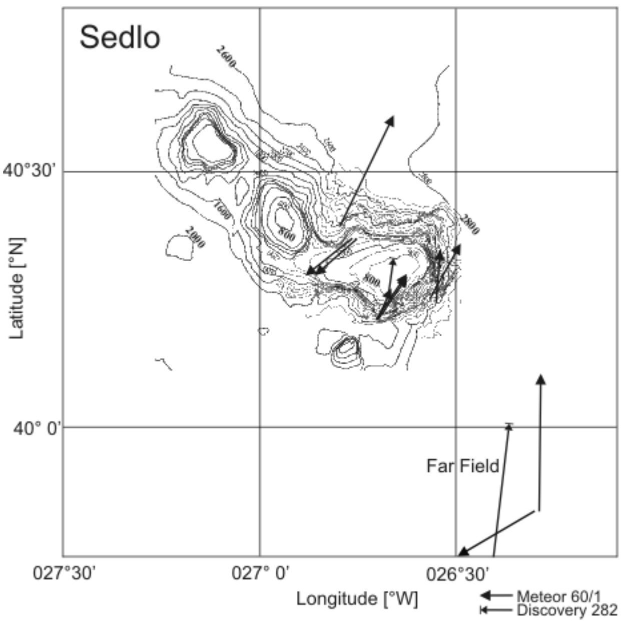

Fig. 3: Sedlo Seamount. Arrows represent station tracks

Ampère Seamount is located at 35°02'N and 12°54'W and is the shallowest of the studied seamounts, reaching well into the euphotic zone with a summit depth of 55 m (Fig. 4). Due to time constraints during the project, hydrographical data were not collected.

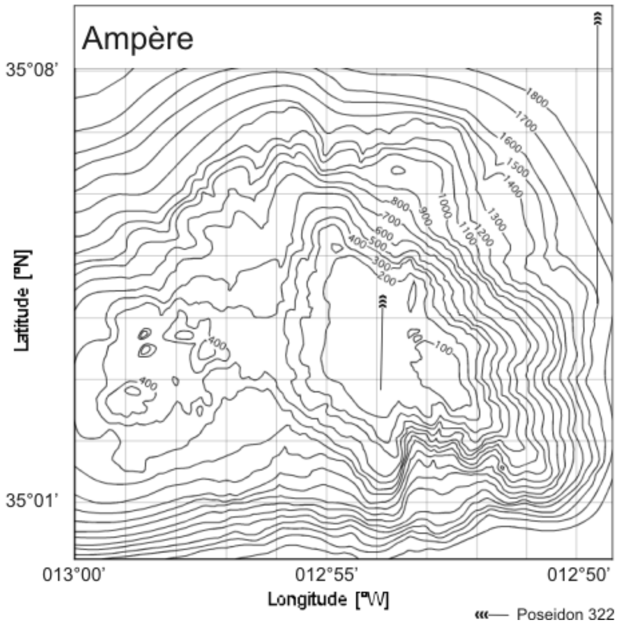

Fig. 4: Ampère Seamount. Arrows represent station tracks.

At Seine and Sedlo Seamounts, the sampling was designed to cover sites above the summits and slopes of the seamounts, as well as oceanic sites outside the influence of the seamounts (far field) (Fig. 2 and 3). The amplification of tidal currents caused by seamounts leads to a sub-mesoscale variability of 20-40 km (Mohn and Beckmann, 2002). Therefore, the far field sampling sites at Seine Seamount were choosen at a distance of 40 km from the seamount, while at Sedlo a distance of 65 km was chosen.

Driven by predator-prey interactions, the residence depth and diurnal movements of the zooplankton, micronekton and nekton are reflected as a SSL in echo-sound recordings. The diurnal vertical movement of the SSL is assumed to be different between the study areas because of the different summit heights of the seamounts. In autumn 2003 and summer 2004, recordings from the vessel-mounted ADCP (Acoustic Doppler Current Profiler, 38 kHz and 75 kHz respectively) were used prior to sampling to determine the depth of the SSL.

In order to detect vertical migration and trapping effects, diurnal and nocturnal samples were taken. Site-sampling details are shown in Table 1.The sampling gear was either a 1m^2-MOCNESS (Multiple opening/closing net and environmental sensing system; Wiebe *et al.*, 1985), equipped with nine nets, or a 1m^2-Double- MOCNESS with 20 nets. Mesh size for both was 333 µm. Environmental data (temperature, conductivity, pressure) were recorded concomitantly during sampling. The water column was traversed at 2 knots by 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.

Table 1: List of MOCNESS stations sampled during 5 cruises (2003-2005) in the NE Atlantic. FF = far field.

Seamount	Season	Region	Hauls	Daytime	Volume Filtered/Net (m^3)	Max. Catch Depth (m)
Seine	spring 2003	summit	2	night+day	364-1328	150
Seine	spring 2003	slope SW	2	night+day	327-2432	1000
Seine	spring 2003	FF	2	night+day	416-1172	1000
Seine	spring 2003	slope NNW	2	night+day	243-1420	1000
Seine	autumn 2003	summit	1	day	140-457	170
Seine	autumn 2003	FF	1	night	724-1478	3990
Seine	spring 2004	FF	2	night+day	144-3191	1000
Seine	spring 2004	summit	2	night+day	295-820	200
Seine	spring 2004	slope SW	2	night+day	203-1420	1000
Seine	spring 2004	slope NE	2	night+day	265-1765	1000
Seine	spring 2004	slope SE	2	night+day	153-1057	1000
Seine	summer2004	summit	3	dusk+night+day	128-627	140
Seine	summer 2004	FF	2	night+day	203-1166	1000
Seine	summer 2004	slope SW	2	night+day	289-1402	1000
Seine	spring 2005	summit	3	day	293-590	160
Sedlo	autumn 2003	slope E	2	night+day	185-1094	1000
Sedlo	autumn 2003	summit	3	night+day	245-920	800
Sedlo	autumn 2003	slope W	3	night+day	170-1250	2700
Sedlo	autumn 2003	FF	2	night+day	239-1095	3000
Sedlo	summer 2004	summit	1	day	307-1165	700
Sedlo	summer 2004	FF	1	night	279-1291	1000
Ampère	spring 2005	summit	1	day	267-557	0-123
Ampère	spring 2005	slope E	1	day	232-2423	0-1000

The catches were preserved in 4% formaldehyde-seawater solution buffered with borax. In the lab, the samples from Sedlo, Seine and Ampère Seamounts were fractionated by sieving into the size classes <0.5 cm, 0.5 cm-2 cm, >2 cm, and gelatinous organisms were sorted out from the size class >2 cm. Gelatinous organisms consisted of medusae, salps, parts of siphonophores and thaliaceans. The wet weight of each size fraction was measured after removal of the interstitial water with 50% alcohol according to the method of Tranter (1962). Wet weights were used to allow subsequent taxonomical identification of the sampled organisms.

The biomass distribution of animals <2 cm was displayed as contourplot maps using the software 'Ocean Data View', version 3.0 (Schlitzer, 2005). The results were presented in common logarithms.

Box-plots were constructed for the sampling sites at Seine and Sedlo to illustrate the possible difference of the biomass distribution of the different zooplankton size classes by day and night, excluding gelatinous organisms.

The difference in the percentage of biomass in the upper 100m between day- and nighttime was calculated as an estimate of the average proportion of zooplankton that conduct diel vertical migrations (DVM) at Seine and Sedlo Seamounts.

To give a coarse overview on the taxonomical composition of the zooplankton in the studied region, samples from two sites of one seamount were sorted and individuals were counted. The percentage of the main groups of animals is presented.

3. Results

3.1 Biomass distribution of zooplankton

In the following, only organisms <2 cm were taken into account because single or a few animals >2 cm, which we regard as not being sampled representatively, could skew the measurements of the biomass distributions of the smaller zooplankton size fractions.

3.1.1 Seine Seamount

In spring 2003, zooplankton biomass was ~100 mg m^{-3} in the upper 100 m of the water column at the far field site, decreasing to 10 mg m^{-3} at 700 m depth during the daytime (Fig. 5a). At night, part of the biomass moved up in the water column resulting in higher biomass concentrations in the upper 100 m (~130 mg m^{-3}) with a strong decrease below 200 m depth (Fig. 5b).

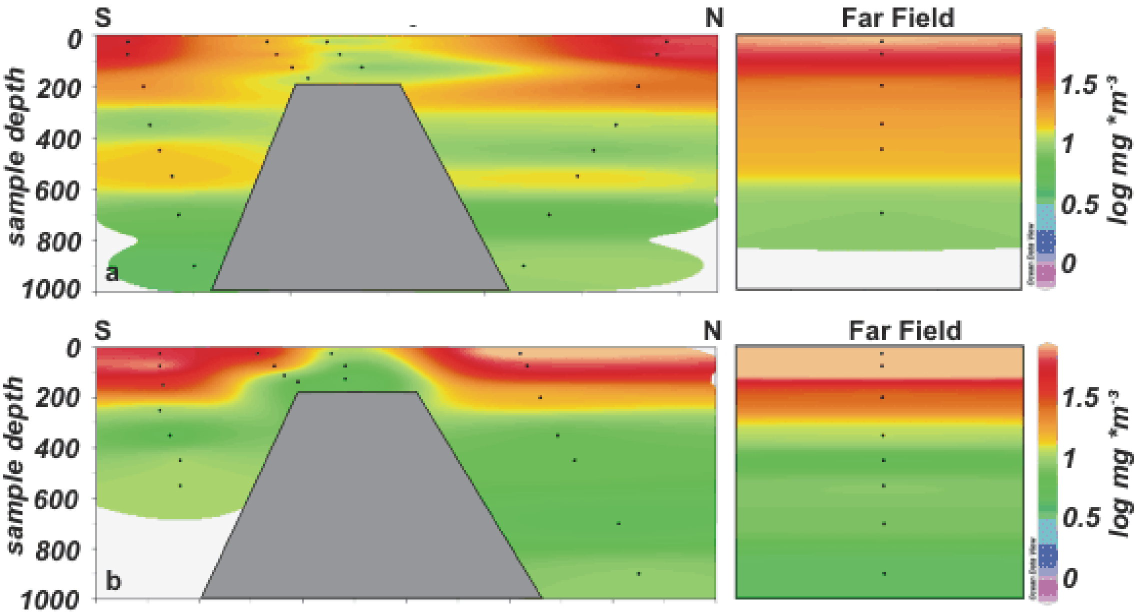

Fig. 5: Zooplankton biomass of the size class smaller 2 cm at Seine Seamount in spring 2003 at daytime (**a)** and nighttime (**b)**.
The black dots represent the averaged sample depth of a net.

Daytime concentrations above the N slope were similar to those at the far field site in the upper 100 m and approx. 1/3 higher than above the S slope (Fig. 5a). Below 100 m, biomass decreased but then slightly increased again between 400 and 600 m above the S slope and between 500 and 600 m above the N slope (Fig. 5a). At night, biomass was continuously low below 300 m depth (Fig. 5b). Above the summit, concentrations were about one order of magnitude lower than above the slopes and at the far field sites both during day and night (Fig. 5).

In autumn 2003, due to time constraints only daytime sampling over the summit of Seine Seamount was carried out. The situation differed to that in spring 2003, with higher biomass concentrations in the surface waters and very low concentrations at 10 m above bottom.

The situation in spring 2004 was similar to that of spring 2003 (Fig. 6 and 5, respectively). Above the summit, again, biomass concentrations were one order of magnitude lower than those above the slopes and at far field. The highest concentration of zooplankton biomass of all sampling sites in the upper 100 m was found at the far field site during night (Fig. 6b).

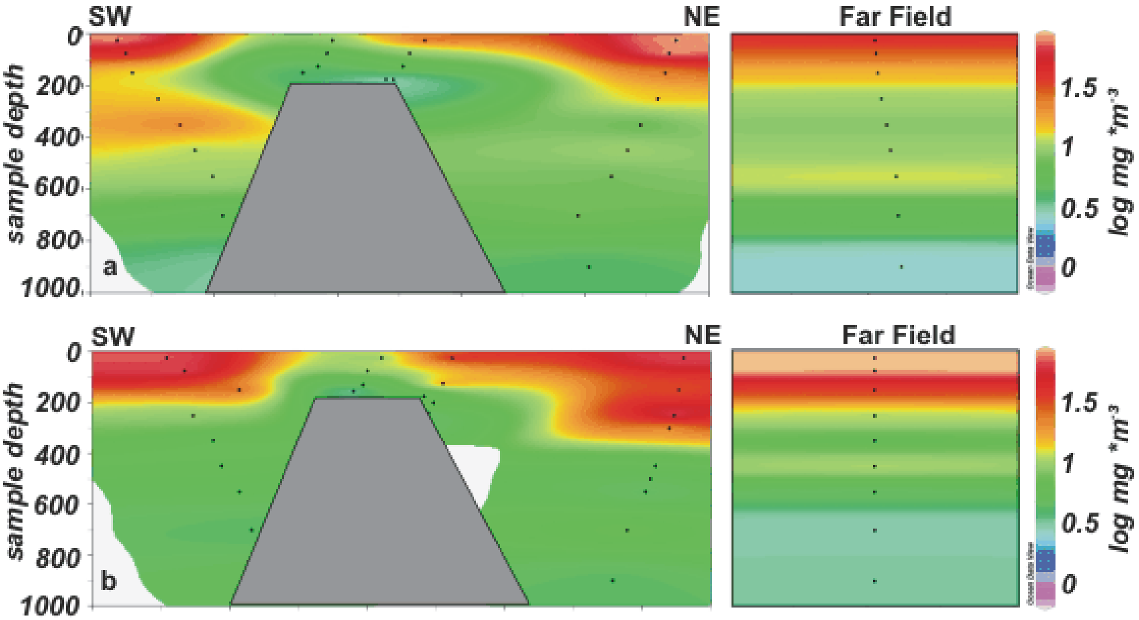

Fig. 6: Zooplankton biomass of the size class smaller 2 cm at Seine Seamount in spring 2004 at daytime (**a)** and nighttime (**b**).
The black dots represent the averaged sample depth of a net.

In summer 2004, the biomass was lower than in spring of the same year, with lowest concentrations again above the summit during day and night.

In order to determine whether vertical migrators stayed close to the summit bottom during daytime, repeated hauls were performed in spring 2005. During these hauls, several samples were collected at ~10 m above the bottom. Biomass concentrations near the surface above the summit were higher than the concentrations observed during the previous sampling periods but were still very low compared to those of the slope and far field sites in former years. In the layer 10 m above bottom, the average biomass of 9 mg m^{-3} was measured for the organisms <0.5 cm.

3.1.2 Sedlo Seamount

The pattern of biomass distribution at Sedlo in autumn 2003 differed from that of Seine Seamount (Fig. 7). The biomass of animals <2 cm in the upper 50 m above the summit at daytime was not reduced as compared to the slopes and far field (Fig. 7a). Biomass concentrations below 200 m were generally low (<10 mg m^{-3}); only above the seamount summit did biomass increase slightly again.

During the night, the biomass in the surface waters above the summit was reduced with only half of the biomass, as compared to the slopes and the far field site (Fig. 7b). At 200 to 400 m depth, the biomass concentrations were decreasing strongly with depth above the summit and at the far field site, but above the slopes this decrease was less pronounced. From 500 m down to 1000 m the concentrations rose again slightly.

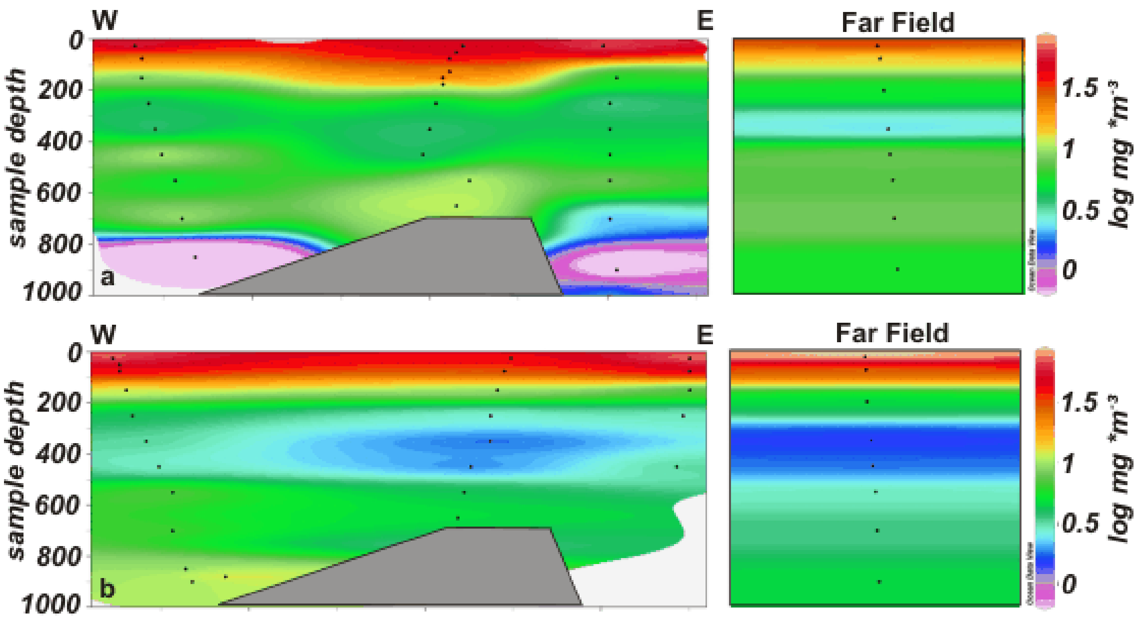

Fig. 7: Zooplankton biomass of the size class smaller 2 cm at Sedlo Seamount in autumn 2003 at daytime (**a)** and nighttime (**b**).
The black dots represent the averaged sample depth of a net.

In summer 2004, the summit was sampled only during the day, while the far field site was sampled during the night. In comparison, the far field site showed a 5 fold higher biomass concentration, which suggests similar reduction in the surface waters above the summit.

3.1.3 Ampère Seamount

The summit and the E slope were sampled in spring 2005. The biomass concentrations above the summit were similar to those of Seine Seamount of that year but much lower than those above the E slope. The biomass of the organisms <2 cm in the upper 100 m above the summit measured 50 mg m^{-3}, whereas above the slope measured 80 mg m^{-3}.

3.2 Size classes of zooplankton, their distribution and vertical migration

3.2.1 Seine Seamount

The size distribution of zooplankton above Seine summit differed from that of the slopes and the far field sites during all sampling periods: organisms >0.5 cm were rarely found above the summit, with the exception of larger gelatinous organisms including medusae and siphonophores (Fig. 8). The latter occurred in spring 2003 and 2005 at different depths. No clear differences in the day/night distribution due to vertical migrations were detectable above the summit in spring 2003.

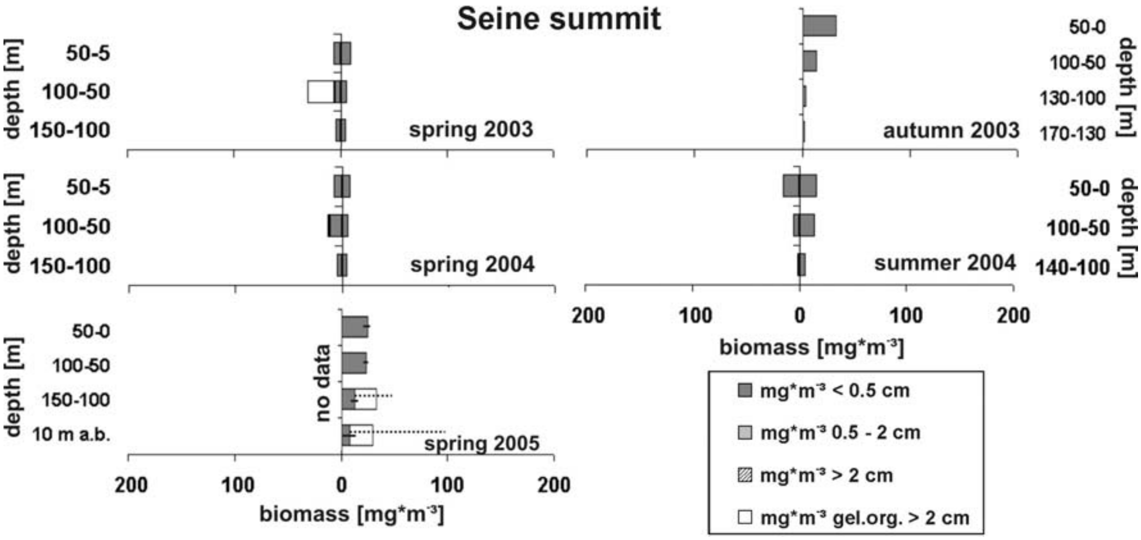

Fig. 8: Biomass of different size classes above Seine summit.
Left night hauls, right daytime hauls. The solid lines denote the range of the biomass of organisms > 0.5 cm of parallel hauls, the bar represents the mean.
The dotted lines denote the range of the biomass of gelatinous organisms of parallel hauls, the bar represents the mean.

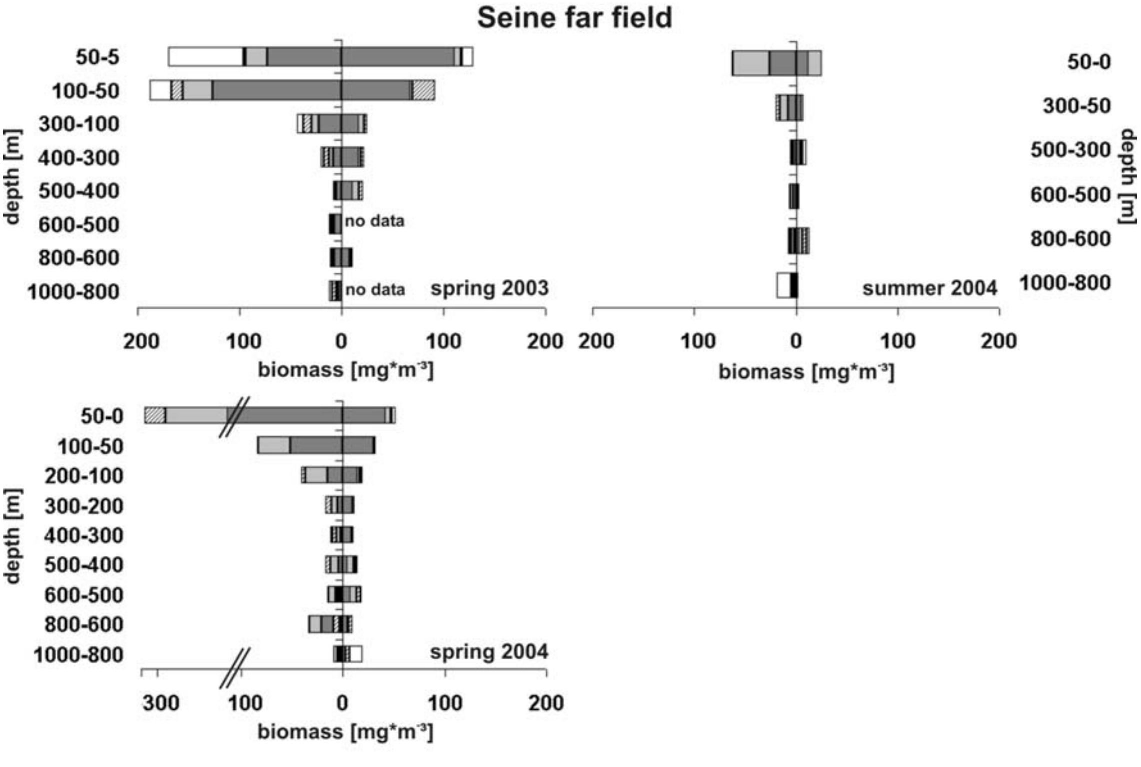

Fig. 9: Biomass of different size classes above Seine far field. Left night hauls, right daytime hauls. Legend see Fig. 8.

At the far field site, all size classes were present, but generally the smallest size class (<0.5 cm) dominated the total biomass (Fig. 9). The biomass concentrations of the size classes 0.5-2 cm and >2 cm in the upper 300 m of the water column were higher at night than at daytime. The picture was different above the SW slope in spring 2003 and summer 2004, with relatively high concentrations of animals >2 cm in the upper 100 m at night, but not in spring 2004 when higher biomass concentrations were measured in the upper water column at day, comprising mainly organisms in the size class 0.5-2 cm (Fig. 10).

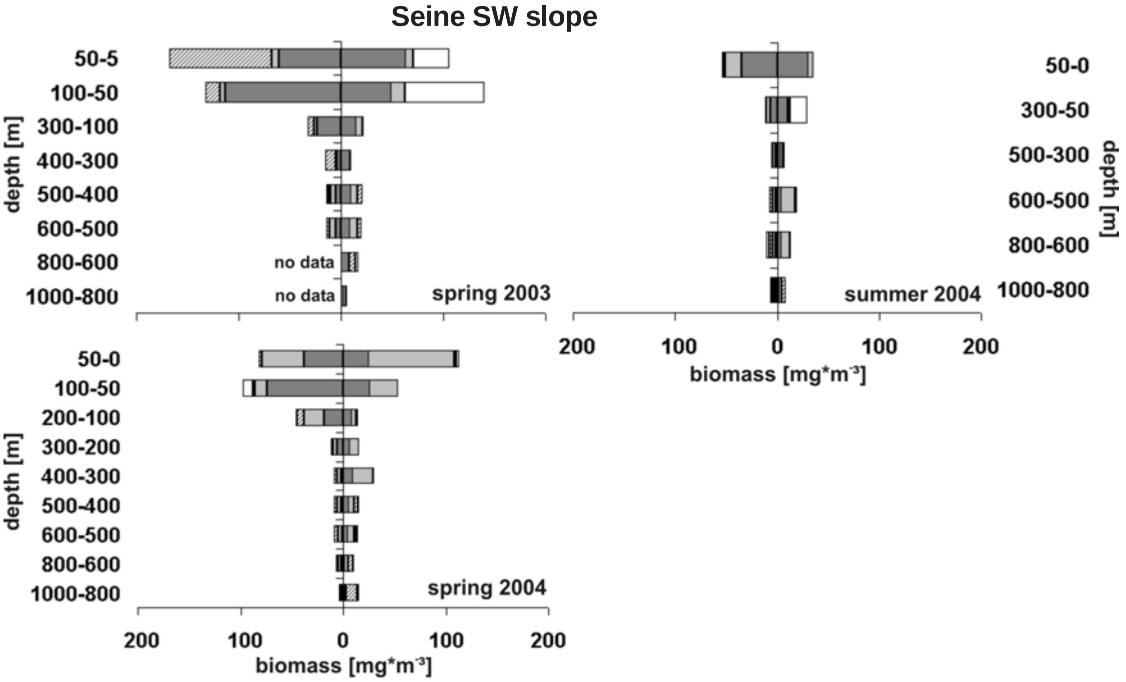

Fig. 10: Biomass of different size classes above Seine SW slope. Left night hauls, right daytime hauls. Legend see Fig. 8.

Distribution patterns, consisting of a shift in the population center toward greater depths during the day, indicate diel vertical migrations and such patterns were found for the size class >2 cm above the NW slope in spring 2003, above the SE and NE slopes in spring 2004, and in spring and summer 2004 for the far field site (Fig. 11). A similar but less pronounced pattern was observed for the medium size class (0.5-2 cm). The SW slope showed a reverse pattern in size class >2 cm at two of the three sampling dates, with an upward shift of the population center during daytime. No clear pattern was found for the smallest size class. Seine summit was not considered in the boxplots due to the lack of organisms larger than 0.5 cm.

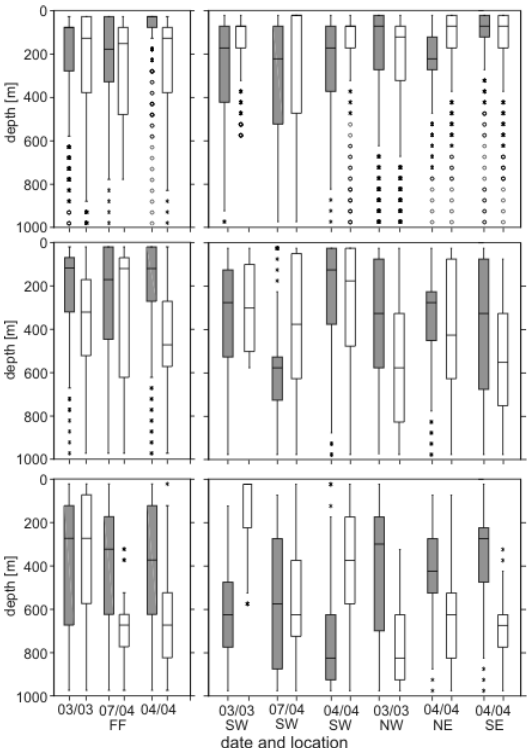

Fig. 11: Boxplots of vertical biomass distribution at Seine Seamount.
SW: southwestern slope, NW: northwestern slope, NE: northeastern slope, SE: southeastern slope. Top: size class <0.5 cm, centre: 0.5-2 m, bottom: >2 cm. Dark boxes: night, light boxes: day. The horizontal line denotes the median of the biomass distribution, the box delimits the interquartile range, the vertical line indicates the range, and outliers are marked with asterisks and circles.

Recordings from the ADCP (75 kHz) in the vicinity of Seine Seamount in summer 2004 showed echoes of downward migrating animals around 06:00 h with an adjacent increase of scatterers at 400–500 m depth (Fig. 12).

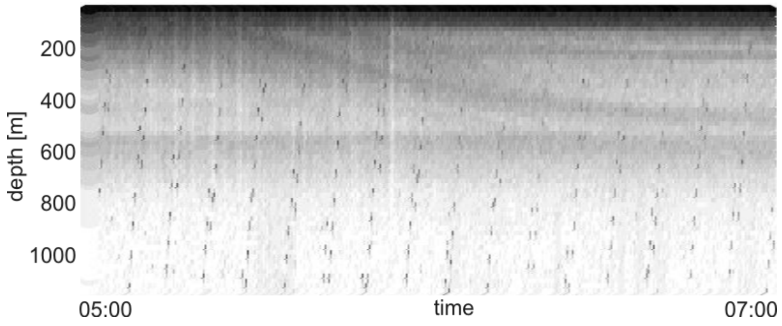

Fig. 12: Migration of scatterers in summer 2004, recorded with with 75 kHz ADCP in the vicinity of Seine Seamount at dawn.

3.2.. Sedlo Seamount

Above Sedlo summit, animals <0.5 cm dominated the total biomass in the surface waters during night and day. In contrast to Seine Seamount, larger animals were also present (Fig. 13), which contributed considerably to the total biomass at times. In autumn 2003, most of the animals larger than 0.5 cm (0.5-2 cm and >2 cm) located above Sedlo summit, far field, and slopes were found in the upper 200 m during night. During the day, these size classes were observed at depths below 400 m, although in smaller numbers. In summer 2004, data could only be compared between the summit at day and the far field site at night, but again the biomass of organisms larger than 0.5 cm was highest close to the bottom during day (summit), and in the upper water column during night (far field).

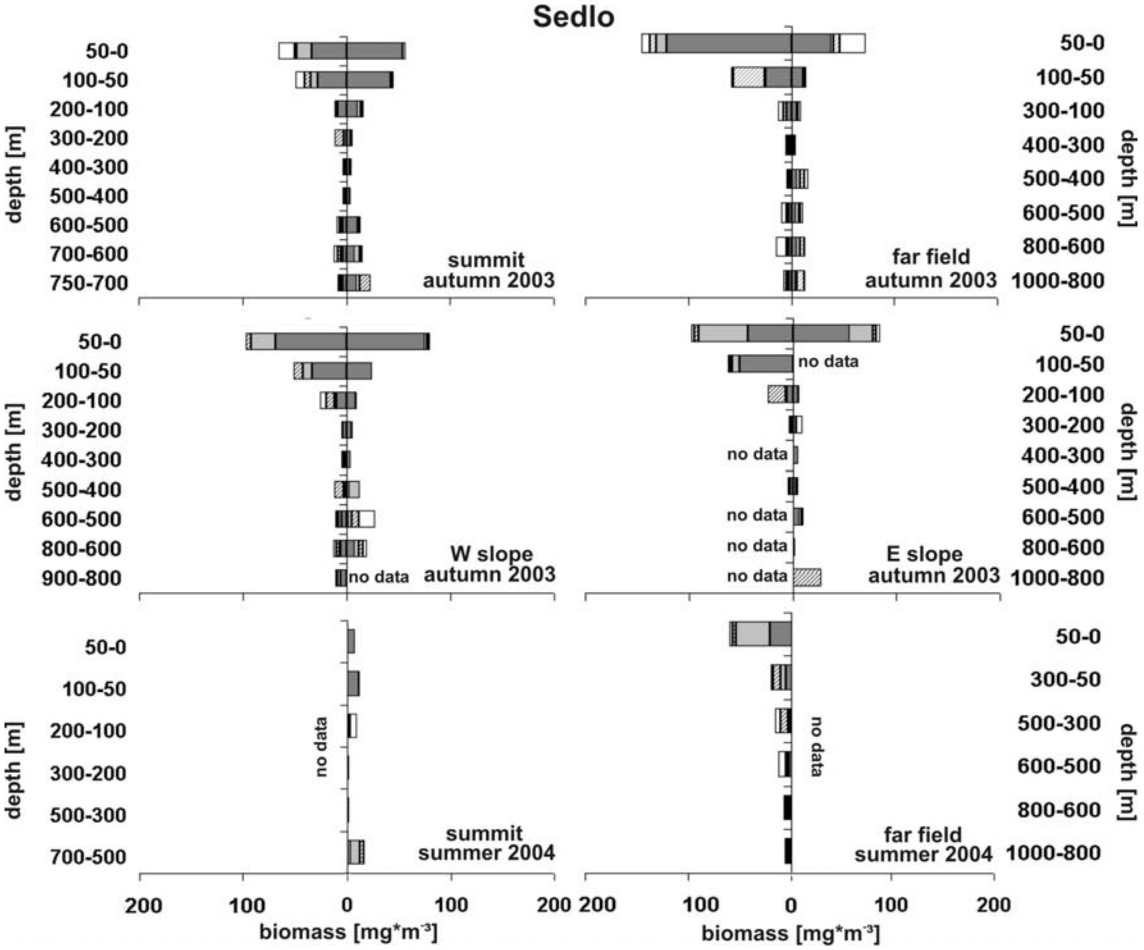

Fig. 13: Biomass of different size classes above Sedlo Seamount. Left night hauls, right daytime hauls. Legend see Fig. 8.

The boxplots (Fig. 14) show distinct day/night differences in the vertical distribution at Sedlo Seamount for the two larger size classes, which usually had population medians above 300 m during the night, but, with one exception, below 500 m during the day, indicating that a large part of these size groups perform daily vertical migrations.

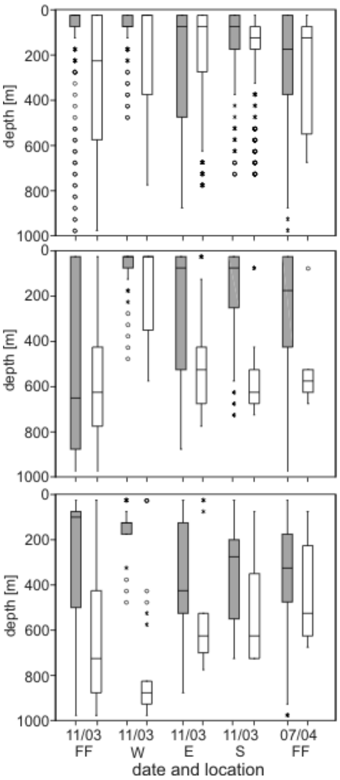

Fig. 14: Boxplots of vertical biomass distribution at Sedlo Seamount.
FF: farfield, W: western slope, E: eastern slope, S: summit. Top: size class <0.5 cm, centre: 0.5-2 m, bottom: >2 cm. Dark boxes: night, light boxes: day. The horizontal line denotes the median of the biomass distribution, the box delimits the interquartile range, the vertical line indicates the range, and outliers are marked with asterisks and circles.

From ADCP recordings (38kHz) from the Sedlo Seamount area in autumn 2003, daily migration of scatterers was visible around 08:00 h and around 19:00 h. At the far field site during daytime the recordings showed, apart from the echoes of the subsurface layers in the,upper 180 m, scatterers between 300 and 700 m depth, being most intensive at 300 and 550 m (Fig. 15, left). In the record of the summit during daytime (Fig. 15, right), deep scatterers were located from 350 m down to 600 m, most intensive at 350 and 550 m. A further thin band was visible at about 50 m above the bottom (Fig. 15, right).

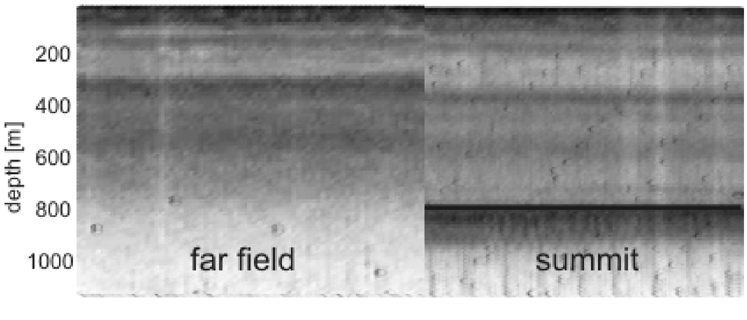

Fig. 15: Scatterers in autumn 2003, recorded with with 38 kHz ADCP at the far field site (left) and above the summit of Sedlo Seamount at noon (right).

In summer 2004, two bands of scatterers were visible at the far field site during daytime, one in the upper 200 m and the other at 300-400 m depth. Above the summit, the upper band reached down to 200 m as well, whereas a second deeper band was hardly detectable. In both seasons (autumn 2003 and summer 2004), the echo intensity of the deeper scattering layers was diminished above the summit compared to the open ocean.

3.2.3 Ampère Seamount

Above the summit, animals larger than 0.5 cm were very rare except for gelatinous organisms. Above the slope in the upper 100 m, the gelatinous organisms constituted more than 50% of the biomass at this depth. Animals of the size range 0.5-2 cm occurred at all sample depths above the slope, whereas larger ones were only found below 500 m depth (Fig. 16).

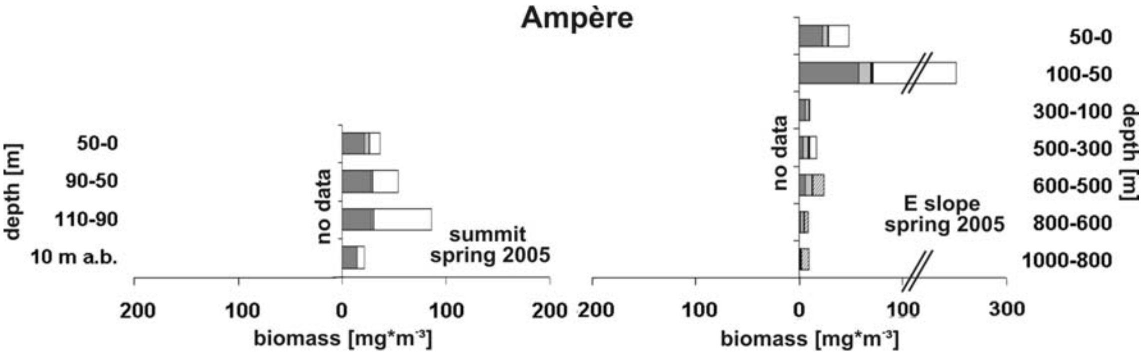

Fig. 16: Biomass of different size classes above Ampère Seamount. Left night hauls, right daytime hauls. Legend see Fig. 8.

3.3 Proportion of animals conducting diel vertical migration

At Seine Seamount, an average of 20% of the zooplankton larger than 0.5 cm migrated from the upper 100 m to greater depths during daytime. At Sedlo Seamount, the migrating proportion of the population showed an average of 56% for the size class 0.5-2 cm and an average of 32% for animals >2 cm. At Ampere Seamount, diel vertical migrations could not be determined because nighttime hauls were not conducted.

3.4 Taxonomic composition of zooplankton

Since this study focused on biomass, only a short overview of the taxonomic composition of zooplankton at Seine Seamount is presented here. At both the summit and the far field sampling sites the most abundant were copepods, which formed at least two-thirds of the community composition (Fig. 17). The most obvious differences between the summit and the far field site were the much higher abundance of exoskeletons and the absence of molluscs above the seamount summit. Animals like chaetognaths, polychaetes and non-crustacean larvae belonging to the group of ‘diverse non-crustaceans’ were less abundant above the summit as were larger crustaceans like decapods, mysids and euphausiids from within the group ‘diverse crustaceans’.

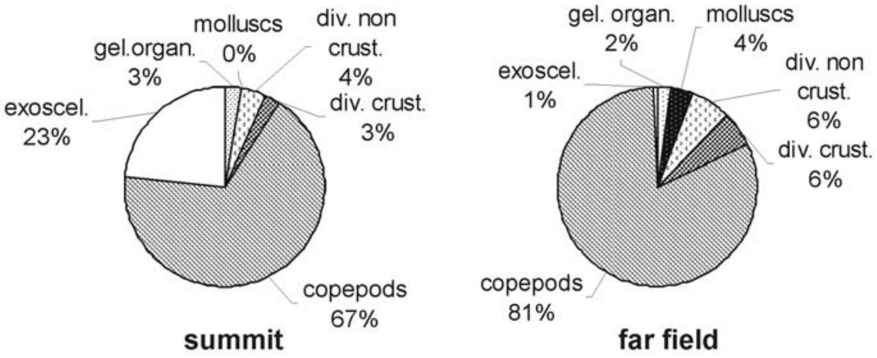

Fig. 17: Composition of zooplankton taxonomic groups at Seine Seamount in spring 2004 in the upper 100 m at night.
Exoscel. = exosceletons
Gel. organ. = gelatinous organisms, include cnidarians, ctenophores, siphonophores, salps
Div. non crust. = diverse non crustaceans, include chaetognaths, appendicularians, fish larvae, fish eggs, polychaets, non crustacean unidentified larvae
Div. crust. = diverse crustaceans, include ostracods, amphipods, isopods, decapods, euphausiids, mysids, crustacean larvae.

4. Discussion

In general, the standing crop of zooplankton at the reference far field sites of this study corresponds to other studies of the NE Atlantic (Roe, 1988; Angel, 1989). The biomass of the upper 1000 m in the vicinity of Seine Seamount in summer is in the same order of magnitude as that of Roe (1988) from 0-1050 m at the Madeira Abyssal Plain during the same season (Table 2). The standing crop above Sedlo summit and of the upper 1000 m at the far field site in autumn 2003 at daytime is consistent with the results of Angel (1989) from the vicinity of the Azores Front (Table 2).

Table 2: Biomass of zooplankton <0.5 cm in mg WW m^{-2} at different locations in the NE Atlantic.
(I) = this study, MOCNESS, 1 m^2, 333 µm, $*^1$ 0-50 m, $*^2$ 50-1000 m
(II) = Angel, 1989 , RMT, 0.8 m^2, 320 µm (wet weight was calculated from displacement volume after Cushing *et al.*, 1958)
(III) = Madeira Abyssal Plain, Roe, 1988, RMT, 0.8 m^2, 320 µm (wet weight was calculated from dry weight after Cushing *et al.*, 1958)

	season	night		day	
Seine summit (I)		**0–100 m**	**100-150 m**	**0–100 m**	**100-150 m**
	2003 spring	700	200	655	227
	2003 autumn			1961	
	2004 spring	920	221	648	202
	2004 summer	984	52	1478	208
	2005 spring			2296	773
	season	night		day	
Seine far field (I)		**0–100 m**	**100-1000 m**	**0–100 m**	**100-1000 m**
	2003 spring	9929	8393	8798	
	2004 spring	14223	3258	3504	
	2004 summer	$*^1$ 3281	$*^2$ 1238	1404	1798
	season	night		day	
Sedlo summit (I)		**0–100 m**	**100-750 m**	**0–100 m**	**100-750 m**
	2003 autumn	3029	2147	4782	4091
	2004 summer			$*^1$ 349	$*^2$ 1392
	season	night		day	
Sedlo far field (I)		**0–100 m**	**100-1000 m**	**0–100 m**	**100-1000 m**
	2003 autumn	7272	2180	2462	3493
	2004 summer	$*^1$ 2200	$*^2$ 1040		
	season	day			
Ampere summit (I)		**0–100 m**			
	2005 spring	2750			
	season	night		day	
Azores Front (II)		**0–100 m**	**100-1000 m**	**0–100 m**	**100-1000 m**
	1980 autumn 33°N 30°W	4000	11840	3600	12240
	1980 autumn 33°N 32°W	5200	7680	1760	7360
	1981 summer 30°N 34°W	3680	9920	3400	10040
	season	day			
MAP (III)		**0–100 m**	**100-1000 m**		
	1987 summer 31°N 25°W	710	4330		

The most conspicuous result of our investigations is the reduced biomass of zooplankton above the shallow summits of Seine and Ampère Seamounts relative to the other sampling sites at and around the seamounts during all periods of investigation. Above these two summits, the zooplankton biomass was not only low, but also generally the animals were of small size, except for gelatinous organisms. At Sedlo Seamount, the biomass above the summit was also reduced, but this was less pronounced than at Seine and Ampère and absent in autumn 2003 during daytime in the surface layers. The reduction of zooplankton biomass is particularly surprising because Aristegui *et al.* (this issue) and Kiriakoulakis *et al.* (this issue) found temporarily increased Chl a and particulate organic carbon (POC) as well as polyunsaturated lipids, above Seine and Sedlo Seamount.

Although above Seine summit, where a Taylor cap was detected temporarily, the zooplankton biomass was lower, the concentration of exoskeletons was much higher than at the far field site (Figure 17). This supports similar findings of Martin and Nellen (2004) investigating the Great Meteor Seamount, a seamount with a summit depth of ~300 m and a summit plateau of 1500 km². One explanation of these results can be found by applying two models of Beckmann and Mohn (2002), who simulated the behaviour of both passive and vertically migrating particles/organisms. The models were based on oceanographic data from the Great Meteor Seamount in 1998. They suggest that the retention time for passive particles in the Taylor column over the plateau is up to ten times higher than in the surrounding waters, whereas vertically migrating zooplankton are not retained but move at similar rates to those influenced by the far field currents.

The phenomenon of reduced zooplankton biomass above topographic structures such as seamounts and banks has been described in previous literature. Genin *et al.* (1988) reported that the dominant species *Euphausia pacifica*, which migrates several hundred meters diurnally, was absent or in very low numbers above the shallow Nidever Bank (100-140 m summit depth) as compared to high densities in the surrounding deep water. Rogers (1994) noted the possibility that strongly migrating taxa are reduced over seamounts due to displacement around the seamount during the day while they stayed at greater depth than that of the summit. This might explain why, unlike at Seine and Ampère Seamounts, larger zooplankton were found above the summit of Sedlo Seamount, near the surface at night and close to the bottom at daytime. Since most of the scatterers recorded by the ADCP around Sedlo migrated to a daytime depth of ~600 m, there was no interaction with the summit at 780 m depth.

Martin and Nellen (2004) found high concentrations of zooplankton very close to the bottom (<10 meters above the bottom) above the plateau of the Great Meteor Seamount during daytime.

By contrast, the day and night profiles of zooplankton biomass above Seine summit, including the near-bottom layer which was sampled several times in spring 2005, gave no indication that the absence of larger vertical migrators in the catches was caused by their ‘hiding’ close to the seafloor at daytime. However, the hauls, which were conducted as close as 10 m above the bottom, could still miss organisms that migrated even closer to the seabed.

At Seine Seamount, evidence for diel vertical migration was ambiguous. Although strong indications for a downward shift of zooplankton biomass during daytime was found for the size classes larger than 0.5 cm in spring 2004 at the far field site and at the NW and the E slopes, evidence for diel migration could neither be detected in spring 2003 at far field nor at the south-western slope during all sampling periods. Whether the reason for the different behaviour of the zooplankton between the years and sites is due to a change in hydrographical conditions or species composition cannot be answered here. A thorough taxonomical analysis (Martin and Christiansen, in prep) will provide insight into possible changes of the zooplankton community.

Genin *et al.* (1994) describes the formation of gaps in the biomass of vertically migrating zooplankton every evening above the summit of Sixtymile Bank, a shallow seamount south-west of San Diego, California (97 m summit depth). The authors proposed that predation by seamount-associated fauna on vertically migrating zooplankton located close to the bottom during daytime was responsible for the gaps, which were then transported downstream with the prevailing currents.

Hesthagen (1970) caught the near bottom fauna of Great Meteor and Josephine Seamounts using an epibenthic closing net of a mesh size of 0.5 cm. Calanoid copepods were the most abundant animals in the samples. The author recorded much lower numbers of calanoid copepods during daytime and no diurnal migration from Josephine Seamount compared to Great Meteor. The author also suggested that copepods impinging at the dome shaped narrow summit of Josephine Seamount at 170 m depth during their downward migration allows the copepods to avoid the contact with the sediment and be transported along the seabed by currents until the bottom permits further descent. If Hesthagen’s (1970) suggestions and the model of Beckmann and Mohn (2002) can be applied to the current regime in the Taylor cap above Seine summit, it can be assumed that the reduction of zooplankton and in particular of larger, actively moving animals is caused mainly by advection off the summit.

At Great Meteor Seamount, due to the expanse of the plateau, the bottom currents would not suffice to carry the bottom near water layers off the plateau during the daytime (Hesthagen, 1970). A seamount reaching into the range of the daytime depth of migrating zooplankton with a spatial extension and current velocities that cause traverse times of several days, such as the Great Meteor Seamount, should make plankton organisms strongly vulnerable to predation. Indeed, investigations of the zooplankton distribution at Great Meteor Seamount (Martin and Nellen 2004) showed high abundances of strongly vertically migrating zooplankton taxa like eupausiids and the calanoid copepod *Pleuromamma*, most of them larger than 0.5 cm, near the bottom of the summit plateau during daytime. These organisms were also found in the stomachs of fishes caught on the Great Meteor Seamount (Erich, 1974).

Predation by benthopelagic fish, most probably, is not the reason for the zooplankton gap above Seine Seamount, at least not for the absence of animals of the size classes larger than 0.5 cm. Christiansen *et al.* (this issue) studied the stomachs of planktivorous benthopelagic and pelagic fishes that were caught above Seine summit in 2005 and found almost exclusively small copepods (<0.5 cm) but no larger prey organisms in the gut contents. However in that study, pelagic fishes were not caught quantitatively by the gear used and therefore cannot be excluded as possible predators of zooplankton.

Gelatinous zooplankton could also be responsible for some of the predation but this was not investigated in our study.

Another, more speculative suggestion indicates that the absence of organisms larger than 0.5 cm above Seine summit, even in the surface layers, during day and night is caused by active avoidance of the summit region by these animals. However, which mechanism causes this behaviour is not yet known. Benoit-Bird (2006), whose study investigated the micronekton community around the Hawaiian Islands, observed a SSL comprised mainly of myctophid fish and shrimp that undergo vertical, as well as horizontal diel migrations. Onshore horizontal migration during night was limited to waters deeper than 23 m, which might be an indication for active avoidance of the seabed.

5. Conclusions

A seamount effect in the form of a general reduction in biomass was found above the summits at all three investigated seamounts, to a greater extent at the shallow Seine and Ampère Seamounts.

We hypothesize that the reduction of zooplankton biomass above seamounts may be caused by predation as well as by displacement of migrators and deep-water taxa during day, and more speculatively, by active avoidance of the seamount. We suggest that the size and height of the seamount determines the extent to which these mechanisms influence the distribution of the zooplankton. Displacement and the current regime probably have the dominant influence on the zooplankton distribution at seamounts with shallow summits and relatively narrow peaks, such as the Seine and Ampére. Furthermore, active avoidance may play a role. Displacement or avoidance concerns the larger, migrating taxa more than smaller, less mobile zooplankton. The reduction of the smaller animals may be caused by predation of seamount-associated fauna.

Predation might play a major role in reducing the biomass of all size classes of zooplankton at seamounts with a broad plateau reaching up into the daytime depth of migrators, like the Great Meteor Seamount, because it is within the reach of potential benthopelagic predators for longer periods of time.

Seamounts with a summit below the daytime depth of migrators, like Sedlo, are too deep to cause noticeable effects due to displacement. A decrease in biomass above the summit may be caused by predation, taking place in the upper water column at night as well as near the summit bottom during daytime.

6. Acknowledgements

This study is part of OASIS (OceAnic Seamounts: an Integrated Study), a research project supported by the European Commission under the Fifth Framework Programme and contributing to the implementation of the Key Action “Sustainable Marine Ecosystems” within the Energy, Environment and Sustainable Development; Contract n°: EVK3-CT-2002-00073-OASIS. Our thanks also go to the crew of R.V. Poseidon and R.V. Meteor for their skillful help and assistance. We are grateful for the comments of three anonymous reviewers which helped to improve the manuscript.

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Manuskript 3

Deep-Sea Research II (accepted by guest editors)

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 trophic 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 trophic blockage hypothesis suggests that benthopelagic fish benefit from vertically migrating zooplankton and micronekton 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.*, this volume). 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 (Fig. 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 centimetres above the sedimentary surface.

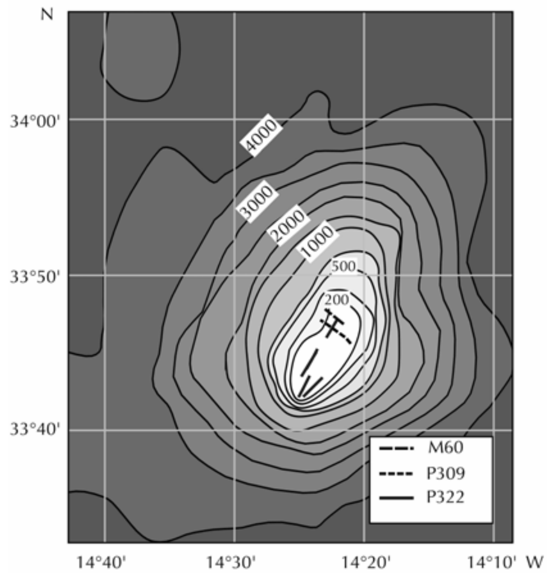

Fig. 1: Bathymetry of Seine Seamount with tracks of trawls.

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.

Tab. 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 (Tab. 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 (Fig. 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.

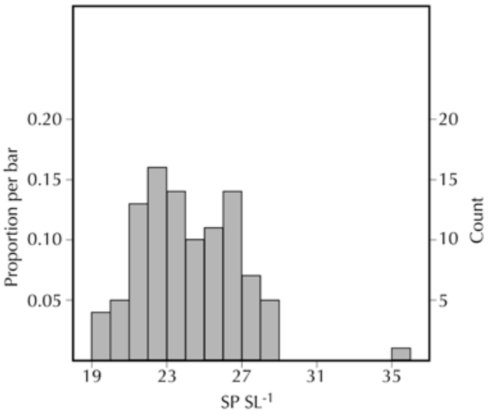

Fig. 2: *Macroramphosus* sp(p). Histogram of the ratio spike length/standard length.

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 (Tab. 2).

Tab. 2: Catch composition of benthopelagic fishes.

Order	Family	Species	Dec 03	Mar 04	May 05	May 05	May 05	May 05	Sum
			Meteor EBS 2m	Pos OT 45ft	Pos OT 80ft	Pos OT 80ft	Pos BT 2m	Pos BT 2m	
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*	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	

*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.

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.

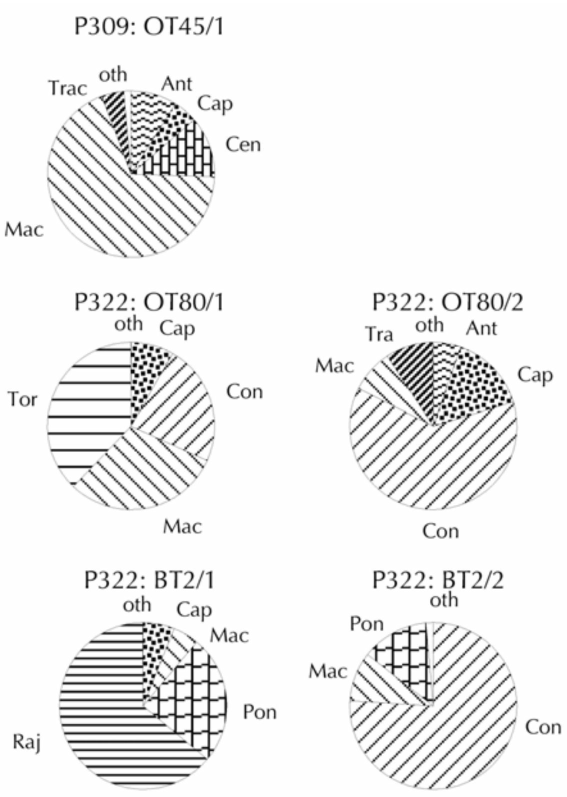

Fig. 3: Catch composition in terms of biomass (wet weight). Ant: *Anthias anthias and Callanthias ruber; Cap: Capros aper;* Cen: *Centracanthus cirrus*; Con: *Conger conger*; Mac: *Macroramphosus* sp(p).; Pon: *Pontinus kuhlii*; Raj: *Raja maderensis*; Tor: *Torpedo nobliliana*; Tra: *Trachurus picturatus.*

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 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).

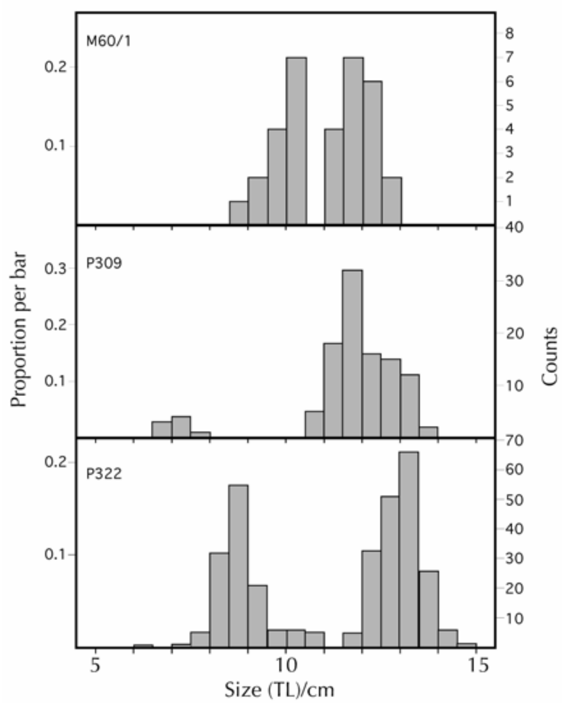

Fig. 4: Size spectra of *Macroramphosus* sp(p)., based on total length.

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 (Fig. 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 ($p<0.001$).

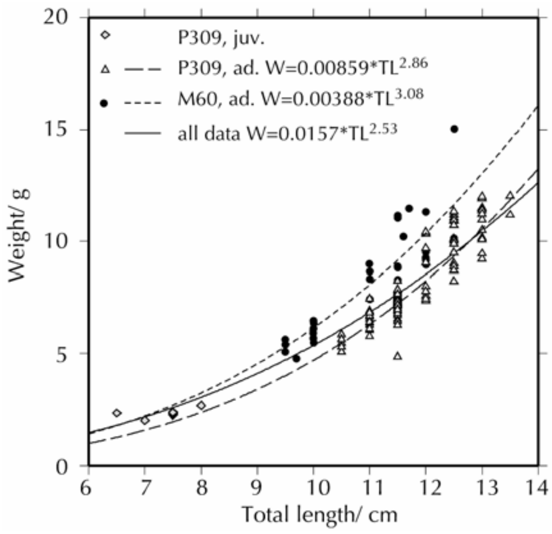

Fig. 5: Length/weight plot of *Macroramphosus* sp(p)., based on total length and wet weight.

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 (Fig. 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.

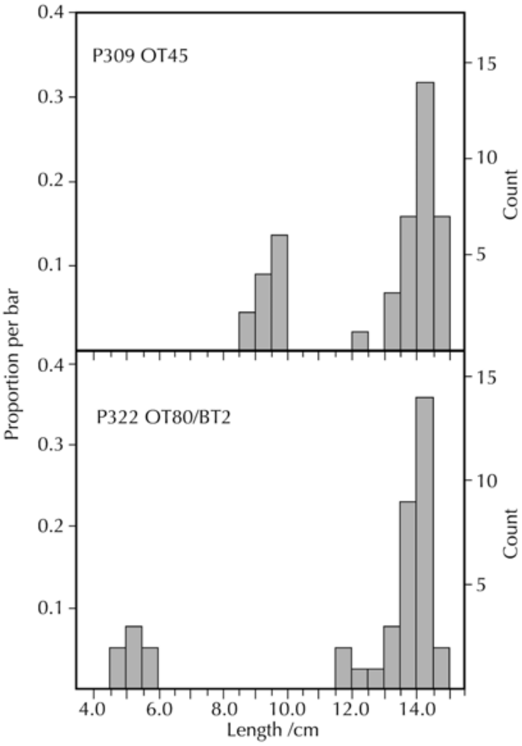

Fig. 6: Size spectra of *Capros aper*, based on total length.

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* (Fig. 7) indicates two or three size classes; however, the separation of the peaks is not very clear.

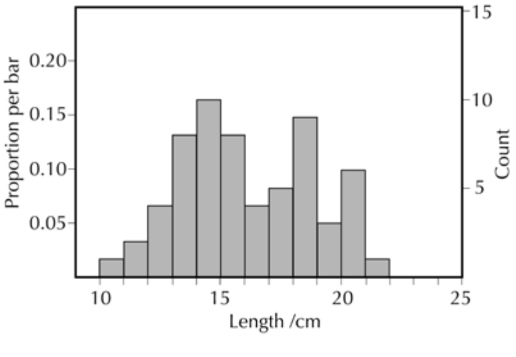

Fig. 7: Size spectra of *Anthias anthias*, based on total length.

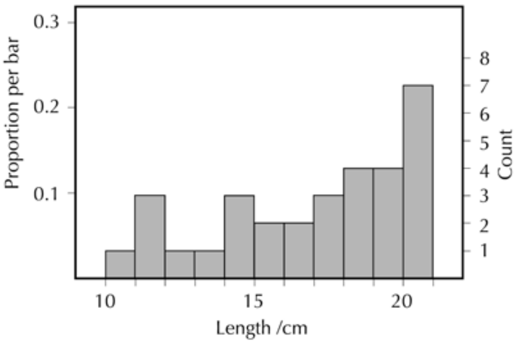

Fig. 8: Size spectra of *Callanthias ruber*, based on total length.

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 (Fig. 8).

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*.

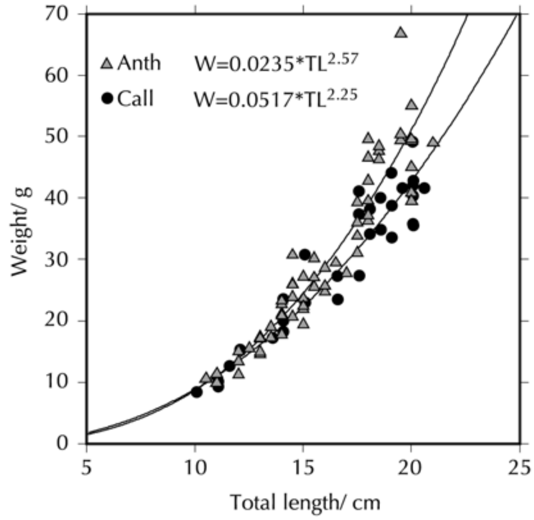

Fig. 9: Length/weight plot of *Anthias anthias* and *Callanthias ruber*, based on total length and wet weight.

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.

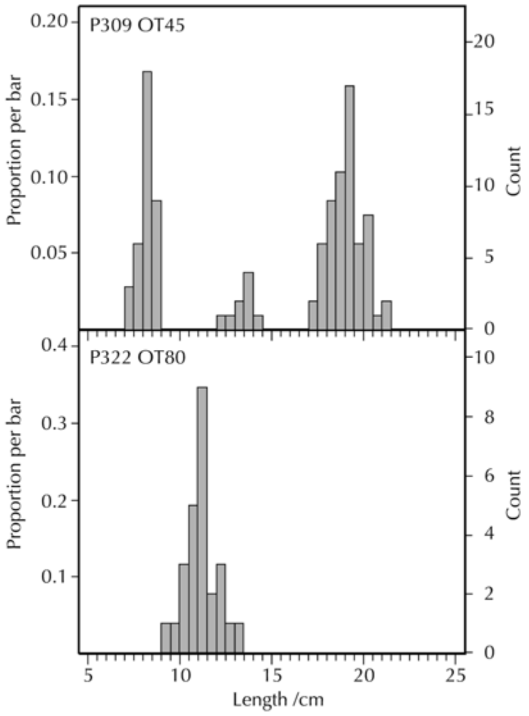

Fig. 10: Size spectra of *Centracanthus cirrus*, based on total length.

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 (Fig. 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.

The three size groups of the P309 samples also show up in the plot of weight versus total length (Fig. 11). The slope of the regression (3.13) indicates an isometric or slightly positive allometric growth.

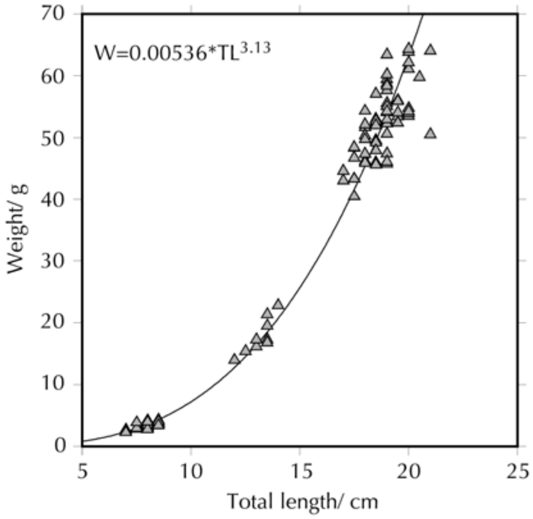

Fig. 11: Length/weight plot of *Centracanthus cirrus*, based on total length and wet weight.

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.

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.

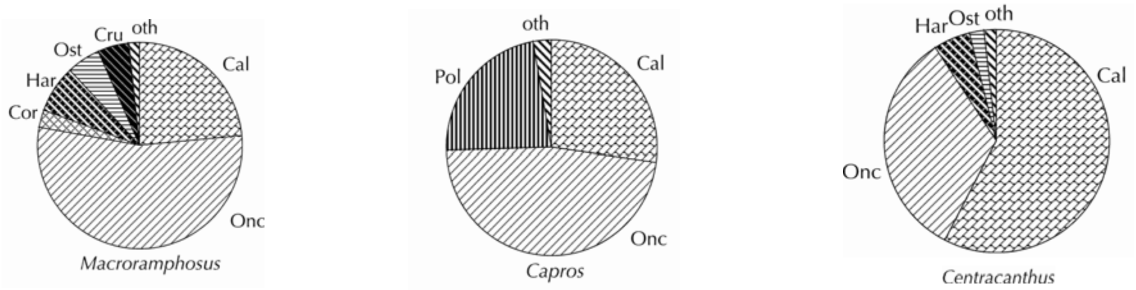

Fig. 12: Composition of fish stomach contents. Left: *Macroramphosus* sp(p).; middle: *Capros aper*; right: *Centracanthus cirrus*. Cal: calanoids; Cor: corycaeids; Har: harpacticoids; Onc: oncaeids; Ost: ostracods; Cru: other crustaceans.

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.*, in prep), 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 autumn.

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 conspicious 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 trawl, has three very distinct size groups with broad gaps in between 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 and 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 trophic 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.

Acknowledgements

These studies are part of OASIS (OceAnic Seamounts: an Integrated Study), a research project supported by the European Commission under the Fifth Framework Programme and contributing to the implementation of the Key Action “Sustainable Marine Ecosystems” within the Energy, Environment and Sustainable Development; Contract n°: EVK3-CT-2002-00073-OASIS.

Dr. R. Fricke confirmed part of the identifications. Three anonymous reviewers gave valuable comments. Our thanks go as well to the crew of R.V. *Poseidon* and R.V. *Meteor* for their skillful help and assistance.

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Manuskript 4

Deep-Sea Research II (accepted by guest editors)

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.

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?”

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, this volume). 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 three peaks, of which we investigated the shallowest that has a summit depth of ~750 m (Fig. 1).

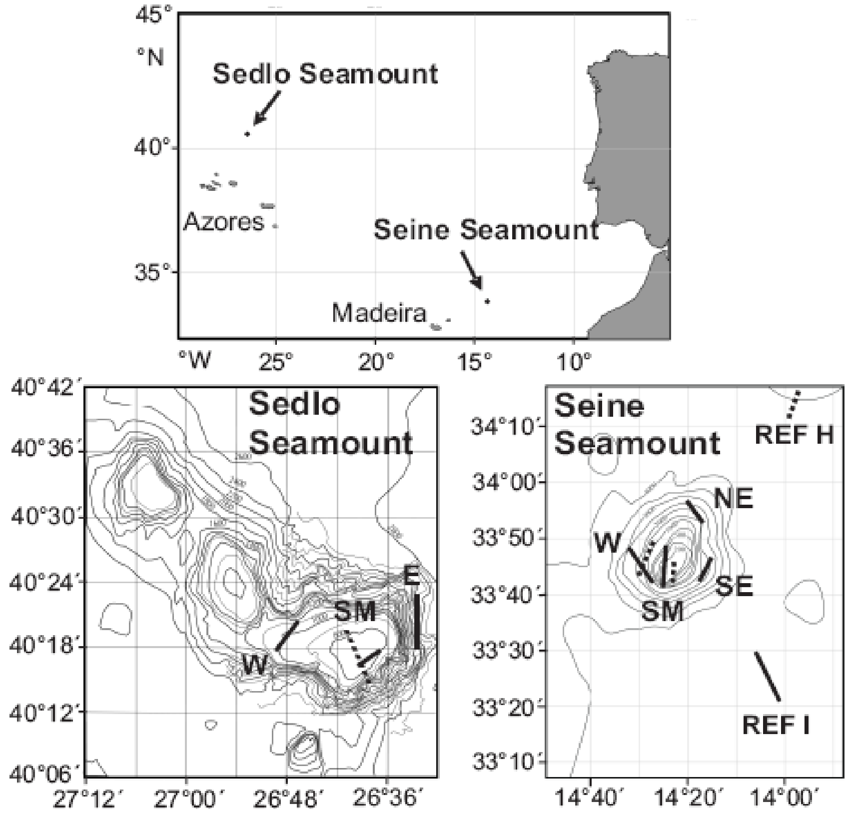

Fig. 1: Location and bathymetry of Sedlo Seamount and Seine Seamount. The locations of the MOCNESS zooplankton hauls (Table 1) are shown for Sedlo Seamount in November 2003 (solid line) and July 2004 (broken line) and for Seine Seamount in April 2004 (solid line) and July 2004 (broken line). Haul locations 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.

Zooplankton 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). 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.

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 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, this volume).

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, this volume). 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, this volume).

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).

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).

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**

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).

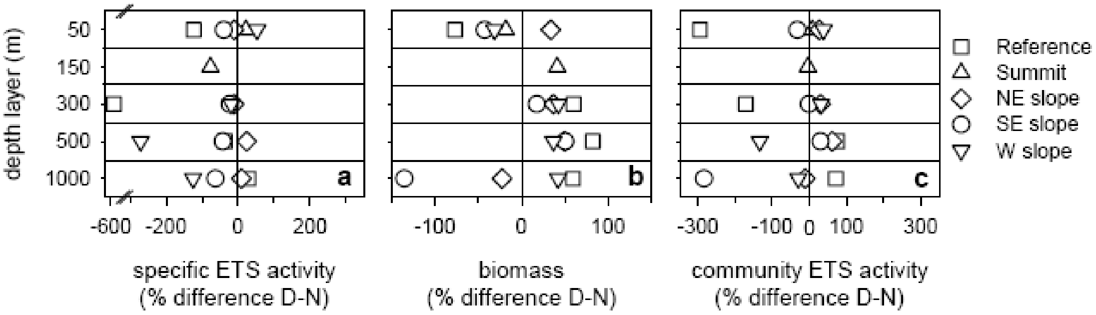

Fig. 2: Day minus night differences at Seine Seamount locations in April 2004. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

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).

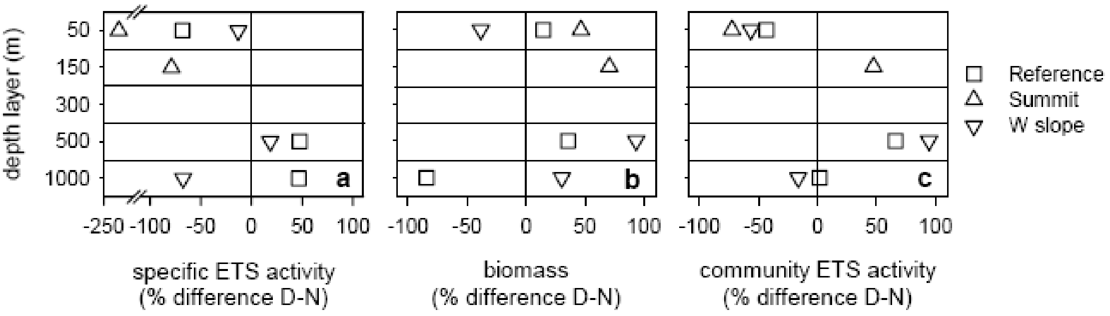

Fig. 3: Day minus night differences at Seine Seamount locations in July 2004. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

3.1.3 Sedlo Seamount

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.

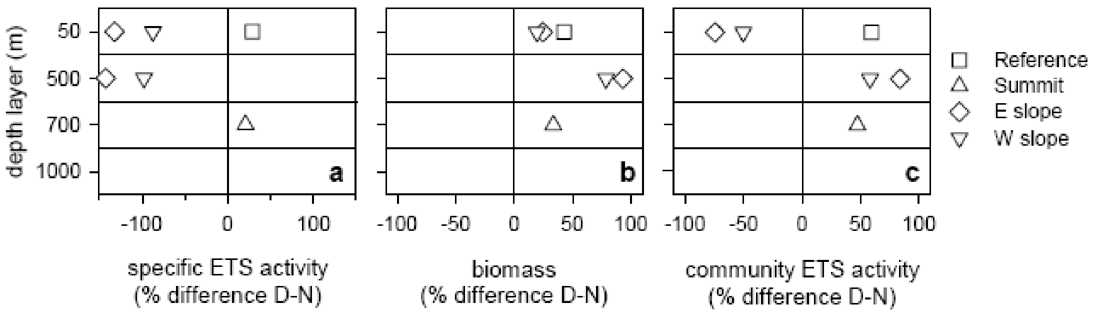

Fig. 4: Day minus night differences at Sedlo Seamount locations in November 2003. Day (D) minus night (N) values are given as % differences of (a) biomass-specific ETS activity, (b) biomass concentration, and (c) community ETS activity for the sampled depth layers.

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).

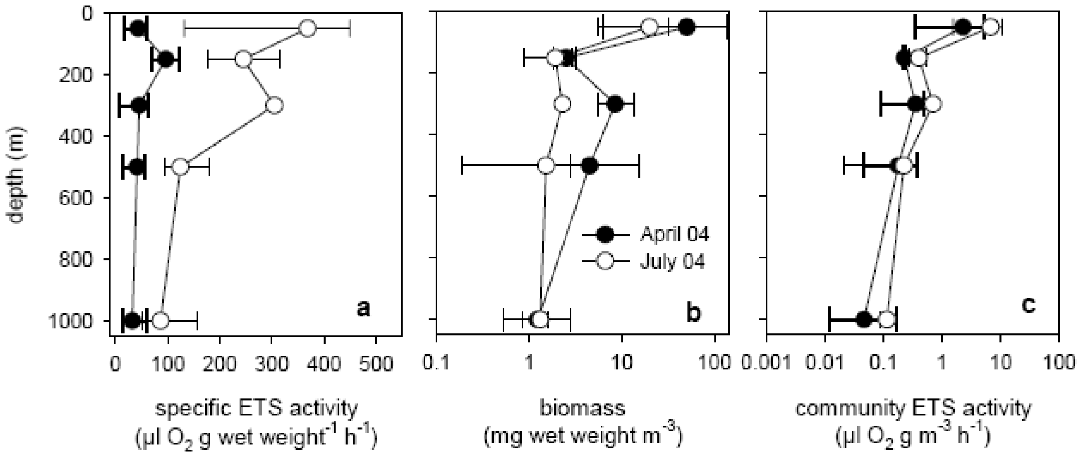

Fig. 5: Temporal variability at Seine Seamount between April 2004 and July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale are given as median ± range. Thin error bar lines represent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

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 ($p<0.05$).

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).

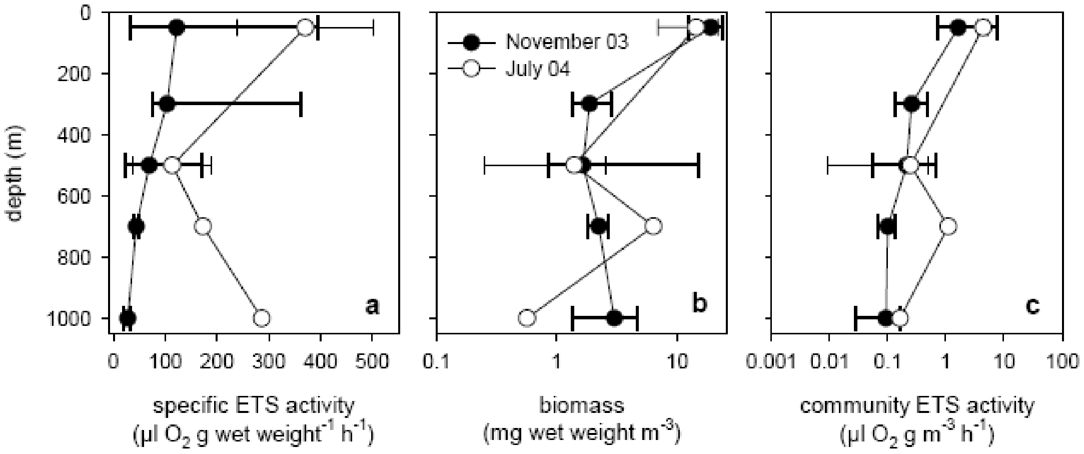

Fig. 6: Temporal variability at Sedlo Seamount between November 2003 and July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale are given as median ± range. Thin error bar lines represent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

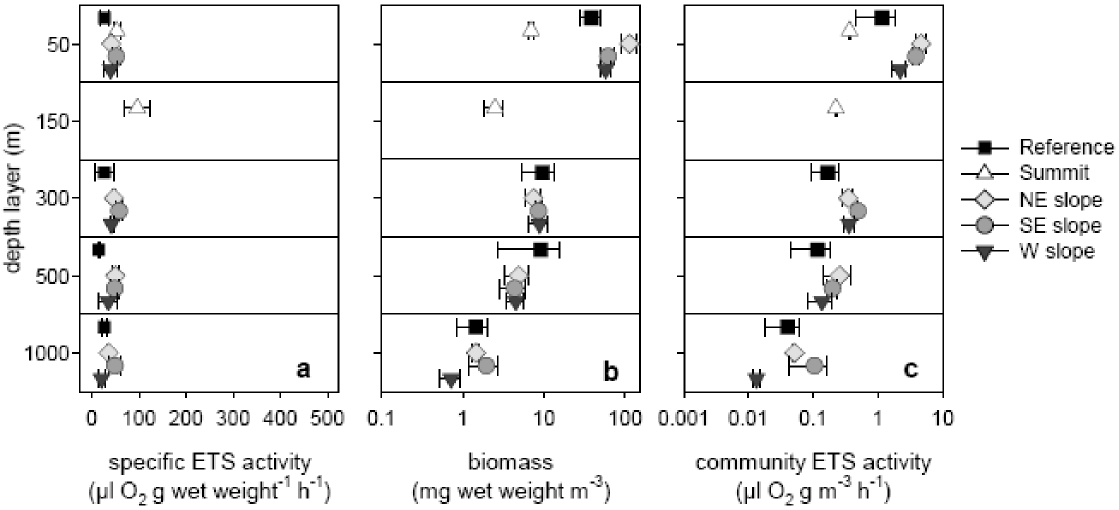

Fig. 7: Intra-seamount variability at Seine Seamount in April 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the slopes (northeast, southeast and west) and at the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

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).

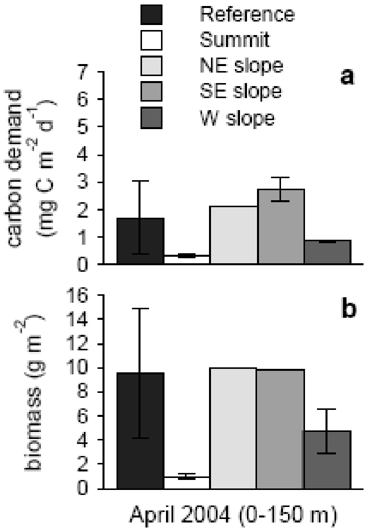

Fig. 8: Intra-seamount variability at Seine Seamount in April 2004. Comparison between water column-integrated (0-150 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the slopes (northeast, southeast and west) and at the reference location. Values are given as median ± range.

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.

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).

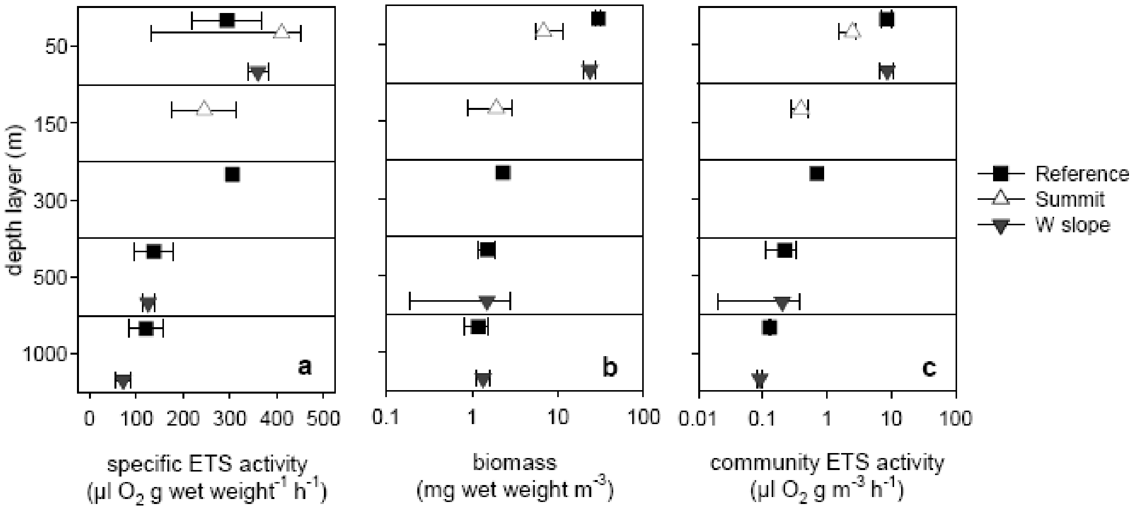

Fig. 9: Intra-seamount variability at Seine Seamount in July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the western slope and at the reference location are given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

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.

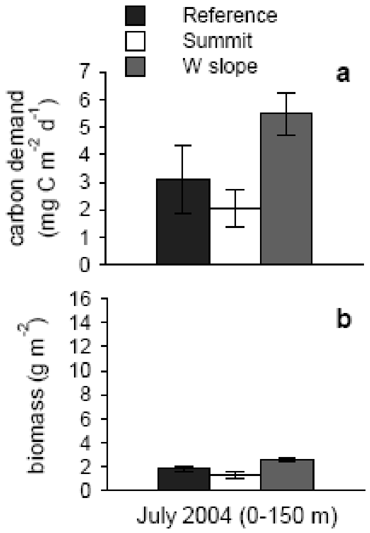

Fig. 10: Intra-seamount variability at Seine Seamount in July 2004. Comparison between water column-integrated (0-150 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the western slope and at the reference location. Values are given as median ± range.

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).

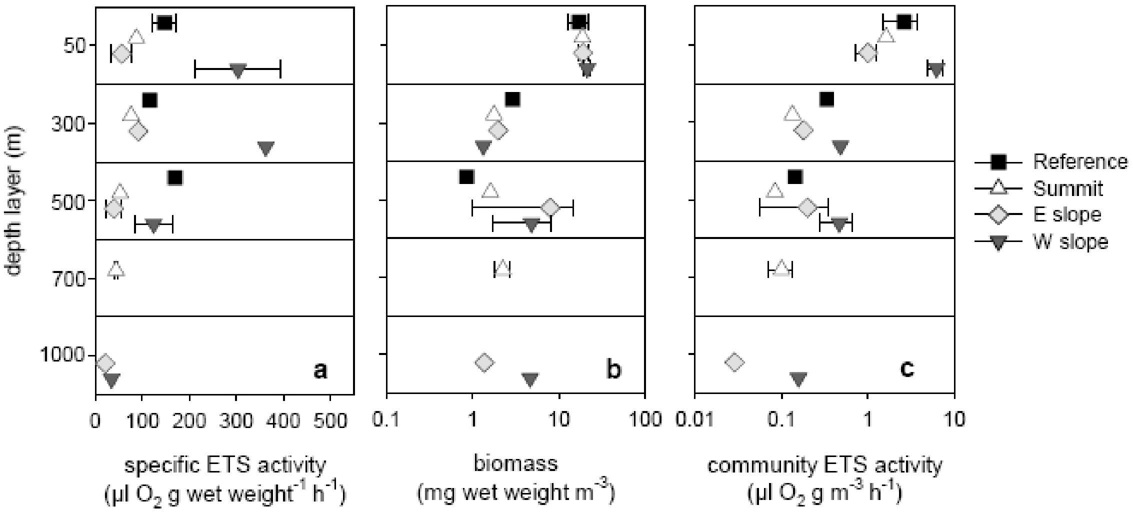

Fig. 11: Intra-seamount variability at Sedlo Seamount in November 2003. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and the slopes (east and west) and at the reference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

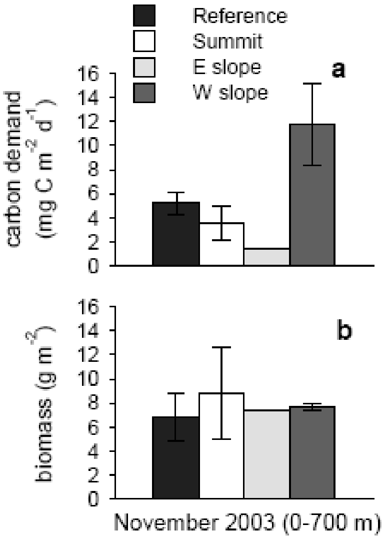

Fig. 12: Intra-seamount variability at Sedlo Seamount in November 2003. Comparison between water column-integrated (0-700 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and the slopes (east and west) and at the reference location. Values are given as median ± range.

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).

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).

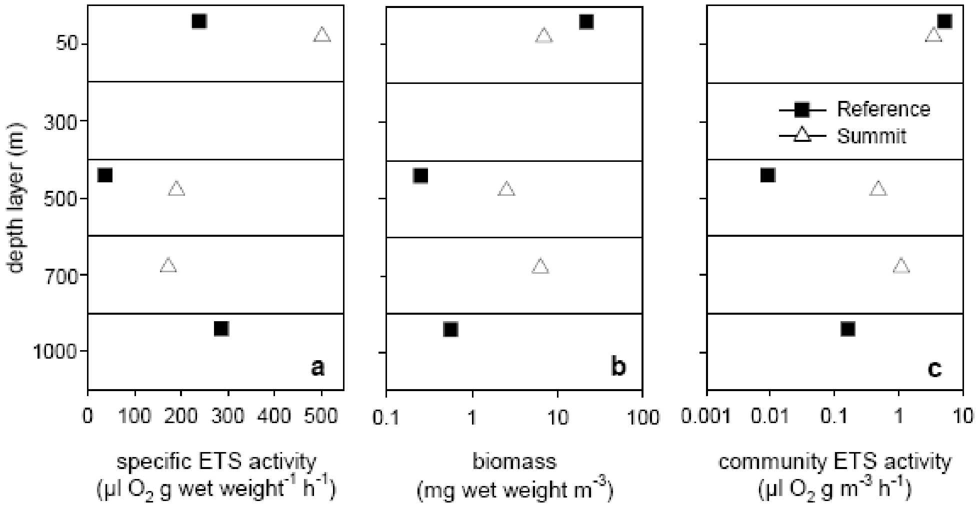

Fig. 13: Intra-seamount variability at Sedlo Seamount in July 2004. Vertical profiles of (a) biomass-specific ETS activity, (b) biomass concentration on a logarithmic scale, and (c) community ETS activity on a logarithmic scale above the summit and at the reference locations are given for the sampled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

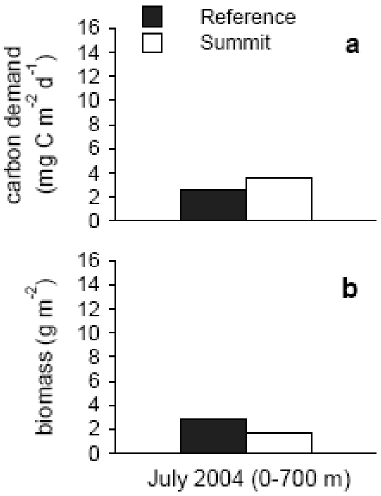

Fig. 14: Intra-seamount variability at Sedlo Seamount in July 2004. Comparison between water column-integrated (0-700 m) values of (a) respiratory carbon demand of the zooplankton standing stock and (b) zooplankton standing stock biomass above the summit and at the reference location.

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 (this volume) 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, this volume) 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.* (this volume) 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.

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.* (this volume) 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.* (this volume) 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 (Table 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.*, this volume) 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.

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	-

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.*, this volume), 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.

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.* (this volume), 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 (this volume) 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.* (this volume) 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.

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.

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

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.*, this volume). 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.*, this volume). 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.* (this volume) 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.* (this volume) 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.*, this volume). 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.* (this volume) 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.*, this volume) 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.

Acknowledgements

This research is part of the `OASIS´ project which is funded by the European Commission under the Fifth Framework Programme (contract EVK3-CT-2002-00073-OASIS). We thank the crews of the FS Meteor, FS Poseidon, and RRS Discovery for their professional support at sea. Two anonymous referees provided valuable comments on the original manuscript.

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Manuskript 5

Distribution and community composition of zooplankton at three seamounts in the NE Atlantic

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Abstract

Zooplankton were sampled with a MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System, mesh size 333 µm) at three seamounts in the NE Atlantic during cruises in 2003, 2004 and 2005. Sampling sites were choosen above the summits, at the slopes and at reference sites, which were not influenced by he topography.

The zooplankton composition and and the standing stocks differed between the seamounts. At Sedlo Seamount calanoid Copepoda clearly dominated the zooplankton (85% of the total zooplankton). At Seine and Ampère Seamounts Calanoida were also the most abundant group, but the proportion of cyclopoid Copepoda, other non-copepod Crustacea and gelatinous organisms was relatively higher than at Sedlo. The differences in the structure of the zooplankton communities are most probably caused by the influence of the Azores Current on Seine and Ampère Seamounts, which marks a change in the composition of the pelagic community between north and south. Differences in the standing stocks and abundances of zooplankton between the seamounts can be explained by the varying sampling seasons: The Sedlo sites were sampled in autumn and showed distinctivly lower standing stocks than Seine and Ampère Seamounts, wich were sampled in spring.

The comparison between the different sampling sites of the particular seamounts showed that the zooplankton standing stock of a comparable depth range (0-100 m) was distinctly lower above the shallow summits of Seine and Ampere Seamounts, compared to the slopes and far field sites. This difference was especially evident for the larger zooplankton (>0.5 cm). Not all taxa were equally affected by the reduction in abundance, leading to a different composition above the summits as compared to the other sites. At Sedlo Seamount no such differences between the deeper peak and the reference site could be found. Several possible explanations, like the influence of the current regime and possible predation by seamount associated fish, are discussed. Fisheggs and exosceletons were distributed to greater depths at the leeward slope of Seine Seamount compared to the other sampling sites, which might have been caused by an seamount originated eddy.

1. Introduction

Seamounts are large undersea elevations, characteristically of conical form, rising from the oceans abyssal plains, in some cases reaching into the euphotic zone. Menard (1964) defined ‘large’ as a height of more than 1000 m. In the last decades the strict 1000 m limitation has been relaxed, especially in geological literature, and the term ‘seamount’ has been applied more generally on undersea topographic elevations regardless of size (Epp & Smoot 1989). These ‘obstacles’ form diverse habitats distinctly different from the surrounding deep-sea. Seamounts do not only affect the flow field significantly, but geology, geochemistry, sedimentology and biology differ also distinctively from the surrounding deep-sea. Genin (2004) characterised seamounts reaching into the euphotic zone as ‘shallow’, those with summits below the euphotic zone but within the upper 400 m as ‘intermediate’, and those with peaks below 400 m as ‘deep’.

The interaction of the ocean current with the topography at seamounts may result in local upwelling, which could lead to an enhanced primary productivity at shallow seamounts, in the formation of closed circulation cells (Roden 1987; Chapman & Haidvogel 1992) which may retain particles and organisms at the seamount (Mullineaux & Mills 1997), and in enhanced flow velocities.

Research efforts concerning seamounts have increased in recent years because of reports of increased primary production (Genin & Boehlert 1985; Lophukin 1986; Dower *et al.* 1992; Mourino et al 2001), high abundances of fish (Hubbs 1959; Boehlert & Seki 1984; Boehlert 1988; Parin *et al.* 1997), enhanced biodiversity and a high degree of endemism of benthic fauna (Wilson & Kaufmann 1987; Richer de Forge *et al.* 2000; Rogers 1994; George & Schminke 2002). Furthermore, it is assumed that seamounts play a role as ‘stepping stones’ in the dispersion of shallower living organisms (Wilson & Kaufmann 1987). However, it is not clear whether attributes like enhanced diversity or high endemism apply to seamounts in general, and knowledge about the functioning of the seamount ecosystems and the mechanisms that form the structure of seamount food webs is still poor. Especially the assumption that standing stocks of marine biota and biological production are enhanced at seamounts has been discussed controversely (Boehlert 1988, Dower *et al.* 1992, Rogers 1994, Dower & Mackas 1996, Martin & Nellen 2004) and can not be adopted to seamounts in general (Martin & Christiansen, subm.).

The study presented here is part of the interdisciplinary EU- funded project OASIS (OASIS: Oceanic Seamounts - an Integrated Study) that has carried out biogeochemical, physical and biological research at three Atlantic seamounts. It focuses on the influence of the seamounts on the zooplankton community, a key player in oceanic food webs, by addressing the following main questions:

-Are there differences in the zooplankton composition and standing stock between different regions of a seamount, and between seamounts and open ocean reference stations?

-Do the seamounts affect the distribution of different taxonomic groups, especially concerning the residence depth?

-Which factors are responsible for a possible alteration of the zooplankton community by seamounts?

-Does a possible impact vary between the seamounts?

2. Material and Methods

The Seine, Sedlo and Ampère Seamounts are situated in the sub-tropical NE Atlantic between Portugal and the Azores (Figure 1). They were studied in the context of the project OASIS (OASIS Report 2006).

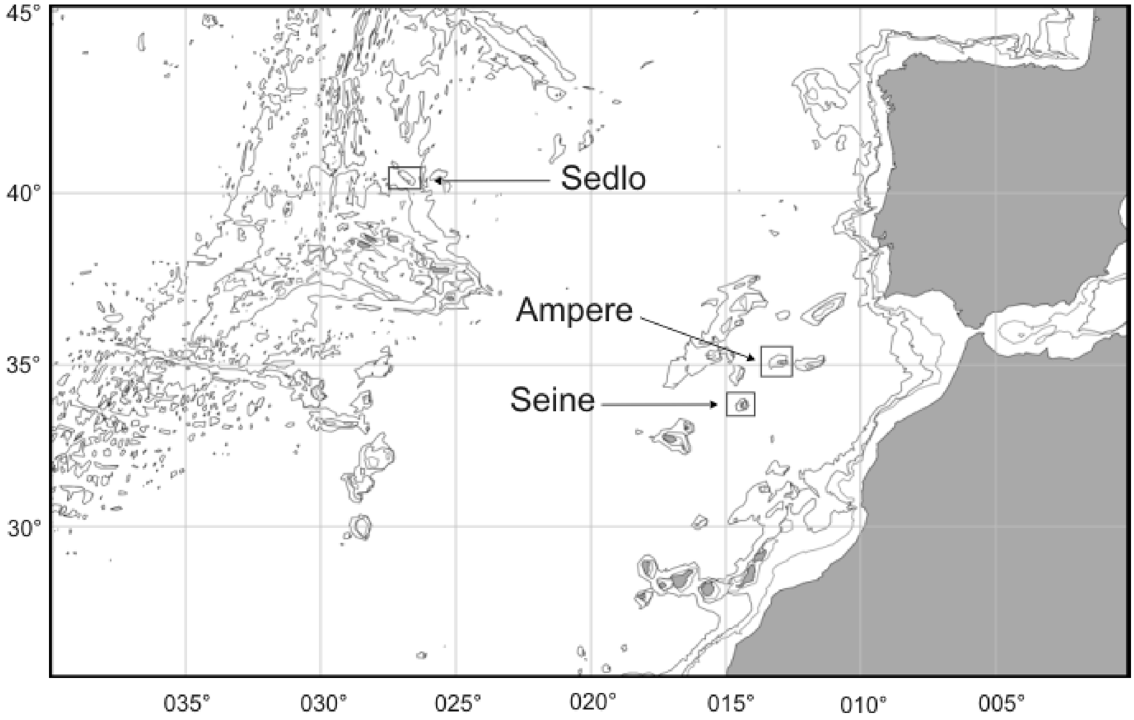

Figure 1: Location of the three studied seamounts in the NE Atlantic.

Sedlo Seamount is located in the temperate Azores region (40°20’N, 27°50’W), in the influence of the southern branches of the North Atlantic Current (NAC). It has an elongate shape with three peaks. (Figure 2). The investigations concentrated on the southeastern peak, which rises from 2800 m to 750 m below sea level. The general current changed from a southwestern direction in summer to a northwestern in winter with an average velocity of 5 cm s^{-1} (White *et al.* this issue). Hydrographic data collected from CTDs, moorings and shipbound ADCP between March and December 2003 revealed a Taylor cap above the investigated peak, reaching up to 350 m above the summit. Above this depth level, a counter- rotating vortex was measured with the shipbound ADCP during the cruise in November 2003 above the summit (White *et al.* subm.). The upper 100 m of the water column were, more or less, decoupled from the cap; furthermore, Mediterranean Water (MW) was detected in 800-1000 m. For a detailed description of the hydrography of Sedlo Seamount see White *et al.* and Bashmachnikov *et al.*, this issue).

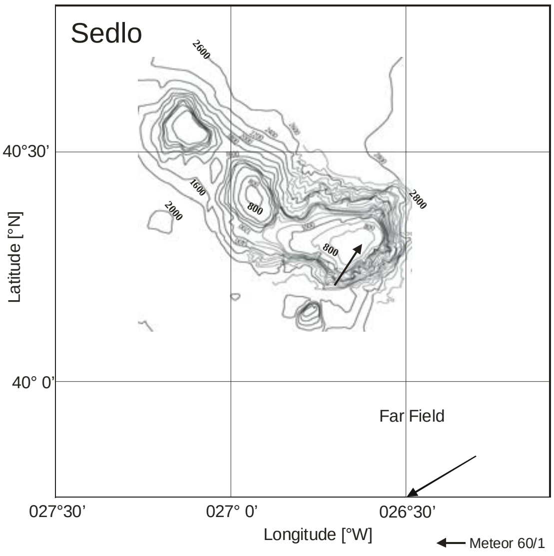

Figure 2: Sampling sites at Sedlo Seamount. Arrows represent sampling tracks.

Seine Seamount is an isolated seamount located in the subtropical NE Atlantic north of Madeira at 33°50'N and 14°20'W (Figure 3). It is in the area of direct influence of the Azores Current (AzC), being just south of its yearly mean position (Bashmachnikov *et al.*, this issue). It is rising from 4000 m to 170 m summit depth. The summit plateau is rather flat, spanning an area of ~50 km^2. The general flow, calculated from three months of mooring data in March-July 2004, was weak and directed southeastward. Anti-cyclonic circulation due to tidal amplification was observed above the seamount, which led to a lowering of the thermocline over the summit and upwelling at the slopes (Mohn, pers. comm.). Variability of this pattern was mainly caused by Mediteranean Water vortices (Bashmachnikov *et al.*, this issue).

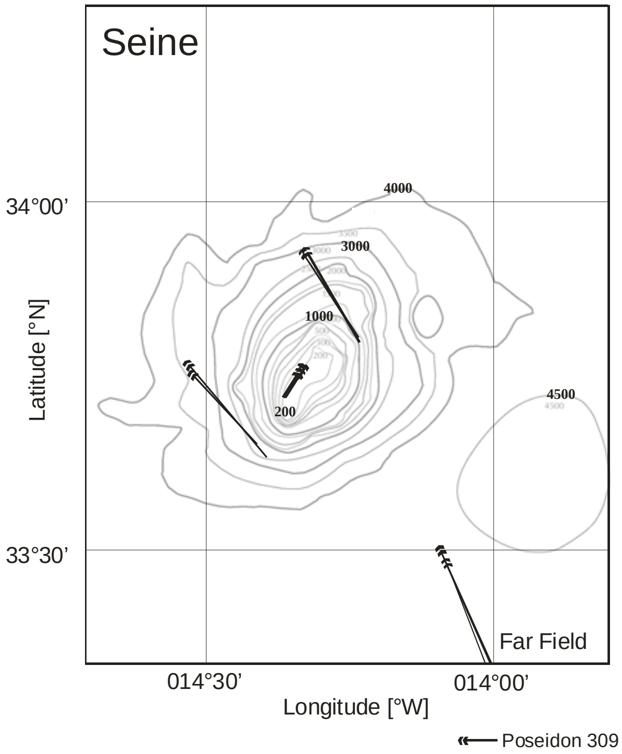

Figure 3: Sampling sites at Seine Seamount.   Arrows represent sampling tracks.

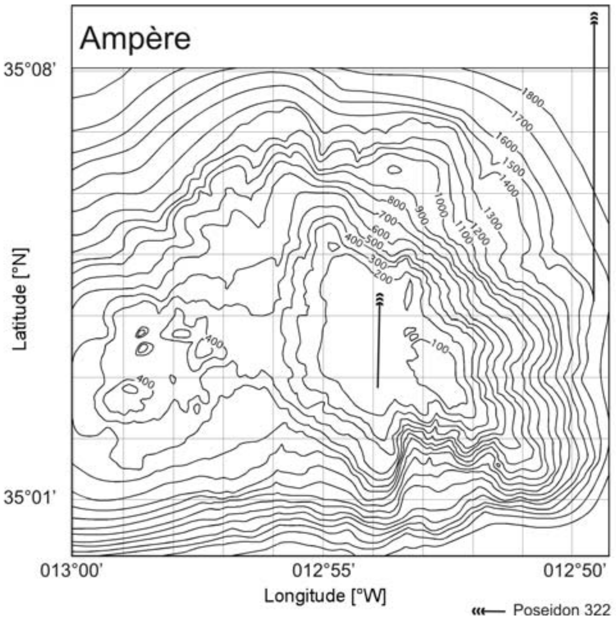

Figure 4: Sampling sites at Ampère Seamount.   Arrows represent sampling tracks.

Ampère Seamount is located northeast of Madeira at 35°02’N and 12°54’W and is the shallowest of the studied seamounts. It rises from ocean depths of about 4500 m well into the euphotic zone. The summit topograhy is rather disturbed with a summit plateau in about 120 m and a peak reaching up to 55 m (Figure 4). The seamount is situated in the region of the Azores

Front (Pingree 1999) and can be influenced at times by filaments of the northwest african upwelling (Aristegui *et al.* subm.). Below 800 m Mediterranean water has an impact on the seamount (Madelain 1967). Due to time constraints during the project, hydrographical data were not collected.

Zooplankton was sampled at Sedlo above the summit and at a reference station outside the influence of the seamount (far field) during a cruise on RV Meteor in autumn 2003 (Figure 2). The reference site for Sedlo was chosen upstream of the seamount at a distance >40 km because the amplification of tidal currents caused by seamounts leads to a sub-mesoscale variability of 20-40 km in the vicinity of the topography (Mohn and Beckmann, 2002). At Sedlo Seamount only nighttime sampling was carried out.

At Seine Seamount four sites were sampled during an expedition with RV Poseidon in spring 2004 : summit, SW slope, NE slope, and far field (Figure 3). Each site was sampled at night and day, but due to net damage the nighttime sampling at the NE slope could not be used. The far field site at Seine Seamount was chosen at a distance of 40 km from the seamount.

The zooplankton samples at Ampère Seamount were taken above the summit and at the E slope at daytime during a cruise on RV Poseidon in spring 2005.

Table 1: List of MOCNESS stations sampled during 3 cruises (2003-2005) in the NE Atlantic. FF = far field.

Seamount	Season	Region	Daytime	Hauls (No.)	Catch intervals	Max. Catch Depth (m)	Volume Filtered/Net (m^3)
Sedlo	autumn 2003	summit	night	1	9	750	245-920
Sedlo	autumn 2003	FF	night	1	8	1000	239-1095
Seine	spring 2004	summit	night+day	2	3	160/150	295-820
Seine	spring 2004	slope SW	night+day	2	9	1000	203-1420
Seine	spring 2004	slope NE	day	1	9	1000	265-1765
Seine	spring 2004	FF	night+day	2	9	1000	144-3191
Ampère	spring 2005	summit	day	1	2	90	267-557
Ampère	spring 2005	slope E	day	1	7	1000	232-2423

The sampling gear at Sedlo and Seine Seamounts was a 1m^2-Double-MOCNESS (Multiple opening/closing net and environmental sensing system; Wiebe *et al.*, 1985), equipped with 20 nets. At Ampère Seamount a 1m^2-MOCNESS, equipped with nine nets, was used. Mesh size of both devices was 333 µm. The water column was traversed at 2 knots by 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. Environmental data (temperature, conductivity, pressure) were recorded concomitantly during the MOCNESS tows. Table 1 gives an overview of the number of hauls, depth intervals and filtered volume of the MOCNESS catches at the different sampling sites.

Upon recovery of the gear the nets were rinsed with seawater and the catches were preserved immediately in a 4% formaldehyde-seawater solution buffered with borax. In the home laboratory the samples were fractionated by sieving into the size classes <0.5 cm, 0.5 cm-2 cm, >2 cm.

The organisms were transferred into a sorting solution (Steedman 1976), identified to taxonomical groups (crustaceans to orders, some taxa to species level) and subsequently enumerated. Crustacean exoskeletons were counted separately. Standing stocks were calculated as individuals per m^2 above 1000 m at the far field and slope sites, above 750 m at the Sedlo summit site, above 150 m at the Seine summit site, and above 90 m at the Ampère summit. For comparison, standing stocks were also computed for the water cloumn down to 100 m.

Box-plots were drawn using the Systat statistical package (SYSTAT version 8.0) to illustrate the residence depth of the different zooplankton groups at different sampling sites and times.

3. Results

3.1 Composition and standing stock of zooplankton

3.1.1 Standing stock general

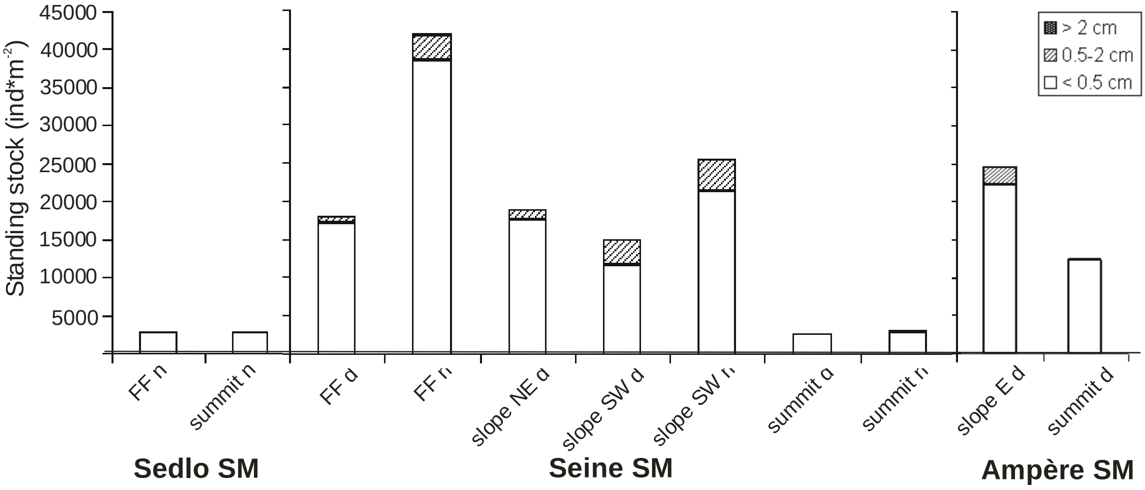

Figure 5: Standing stock of different size groups of zooplankton at the sampling sites. FF = far field.

The zooplankton standing stock at Sedlo Seamount was 2900 ind.* m^{-2} in autumn 2003 and did not differ between the summit and far field site, nor did the proportion of the different size classes (<0.5 cm 93 and 94%, 0.5 – 2 cm 6 and 5%, >2 cm both 1%, at far field and summit (Figure 5).

At Seine Seamount the largest standing stock of all sites was found at the far field site at night (41900 ind.* m^{-2}). The far field daytime catch (18000 ind.* m^{-2}) was similar to that at the NE slope (18900 ind.* m^{-2}) and at the SW slope (day 14900, night 25500 ind.* m^{-2}) (Figure 5). The standing stocks above the summit in spring 2004 (2700 at day and 3000 ind.* m^{-2} at night) was about one order of magnitude lower than the standing stocks at the slopes and at the far field site (Figure 5).

The fraction of the size group 0.5 – 2 cm above Seine summit (day <1%, night 3%) was smaller than that at the other Seine sites (far field: day 4%, night 8%; NE slope: 7%; SW slope: day 21%, night 16%). The size class >2 cm was missing completely above Seine summit and was < 1% at the other ampling sites at Seine Seamount.

The zooplankton standing stock at the E slope of Ampère Seamount in spring 2005 was in the range of the findings at the Seine slopes (24400 ind.* m^{-2}) (Figure 5). Above the summit, markedly lower with 12400 ind.* m^{-2}. Again, the proportion of the size class 0.5 – 2 cm was much smaller above the summit (1%) than above the slope (10%). Only a few animals > 2 cm were caught at the E slope (<1%) and were missing in the catches above the summit (Figure 5).

Except for the summits, the zooplankton standing stock at Seine and Ampère Seamounts was about one order of magnitude higher than at Sedlo Seamount.

3.1.2 Composition general

At Sedlo the composition of the major zooplankton groups and of exosceletons differed only slightly between the seamount and the reference sites. Calanoid Copepoda dominated at both sites with more than 80 % of the total zooplankton standing stock. Other Copepoda contributed 1% and 7%, respectively. The fraction of diverse non Crustacea was smaller above the summit (1%) as compared to the far field site (6%). Exosceletons made up 5% at far field and 4% above the summit (Figure 6).

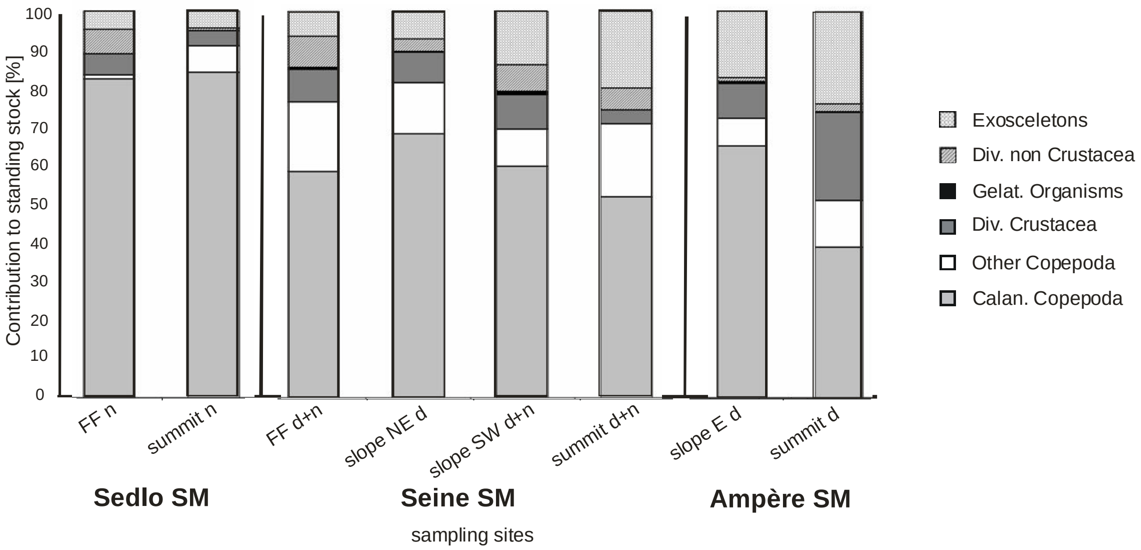

Figure 6: Proportion of major groups at the different sampling sites. FF = far field, n = night catch, d = day catch, d+n = day and night catches averaged.

At Seine Seamount day and night catches for each site were averaged. Calanoid Copepoda were again the dominant group with lowest percentages above the summit (51%) and highest at the NE slope (69%). Other Copepoda accounted for 10-18%. The proportion of exoskeletons was higher above the summit (20%) than at the other sites (7-14%) whereas the percentage of non-copepod Crustacea was lower above the summit(4% versus 8-9%).

The zooplankton composition at Ampère summit differed from that of the other seamounts by the much lower proportion of calanoid Copepoda (39%) whereas the percentages of exoskeletons (24%) and of diverse Crustacea (23%) were relatively high. The composition at the Ampère E slope site resembled that of the SW slope at Seine Seamount with 66% calanoid and 7% other Copepoda, 17% exoskeletons, and 9% diverse Crustacea (Figure 6).

3.3 Composition and standing stocks of the major taxonomical groups

The following comparative analysis presents the same taxonomical detail for all sampling sites. Several samples were identified to a lower taxonomical level; a detailed list of all identified organisms is given in Table A in the appendix.

3.3.1. Copepoda

Calanoid Copepoda

Unidentified calanoid Copepoda comprised the highest proportions of the standing stocks at all sampling sites (Table 2 and 3). Most of the animals in this group were juveniles which could not be assigned to any genus.

Within the identified taxa, *Clausocalanus* spp. were dominant at the Sedlo far field and summit sites, followed by *Pleuromamma* spp. and *Euchaeta* spp. (Table 2). All other taxa of calanoid

Copepoda comprised 3% or less of the catches (Table 2).

Table 2: Composition and standing stock of calanoid Copepoda at the three investigated seamounts. P = proportion (%), SS = standing stock (ind.*m^{-2}). FF = far field, d = day catch; d+n = day and night catches averaged. Bold numbers = taxa comprising more than 10% of the standing stock. - = not identified to taxa.

	Sedlo				Seine								Ampère			
sampling site	FF		summit		FF		NE		SW		summit		E		summit	
catch depth (m)	n		n		d+n		d		d+n		d+n		d		d	
	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
unid./juv. Cal.	**43**	1198	**43**	960	**62**	11038	**50**	6865	**69**	9500	**50**	881	**55**	12554	**100**	7702
Temora spp.	<1	8	0	0	2	366	5	685	1	178	7	116	<1	5	-	-
Pleurom. spp.	**10**	215	**10**	289	7	1278	7	928	6	811	2	28	6	794	**-**	**-**
Haloptilus spp.	<1	2	<1	1	1	245	<1	52	1	139	1	14	<1	21	-	-
Lucicutia spp.	3	61	2	56	6	1054	8	1120	2	312	**13**	237	1	93	-	-
Aetideidae	3	62	1	34	1	135	1	110	<1	44	1	16	2	294	-	-
Euchaeta spp.	7	164	4	119	3	544	4	605	5	631	**10**	175	**10**	1356	-	-
Calocal. spp.	0	0	<1	1	2	387	1	105	1	84	<1	7	0	0	-	-
Candacia spp.	<1	2	2	45	2	358	3	410	1	116	2	27	<1	60	-	-
Eucalanus spp.	<1	8	<1	6	4	681	1	175	1	74	2	31	<1	18	-	-
Calanoides car.	3	74	<1	11	1	202	1	189	1	127	<1	3	<1	45	-	-
Metridia spp.	<1	6	<1	1	<1	7	1	128	0	148	0	0	<1	94	-	-
Heterorh. spp.	1	18	1	19	<1	62	1	170	1	76	1	14	2	234	-	-
Clausocal. spp.	**28**	635	**35**	961	3	519	**14**	1874	**11**	1523	**10**	178	**21**	2959	-	-
Neocal. spp.	<1	2	0	0	2	406	<1	1	<1	10	<1	8	<1	55	-	-
Scoletricidae	<1	3	1	15	<1	86	1	178	<1	54	1	25	3	357	-	-
Rhincal. nas.	<1	2	<1	2	<1	30	1	91	<1	12	<1	2	<1	39	-	-
Calanus helgo.	1	16	<1	9	2	312	<1	1	<1	3	<1	2	0	0	-	-
Acartia spp.	<1	3	<1	2	1	130	0	0	<1	18	<1	4	<1	0	-	-

At the Seine far field site *Pleuromamm*a spp. and *Lucicutia* spp. were the most important identified calanoid Copepoda, followed by *Euchaeta* spp. and *Clausocalanus* spp. (Table 2). Other taxa comprised 2% or less to the standing stock. At the NE slope *Clausocalanus* spp. dominated the catches, *Lucicutia* spp.and *Pleuromamm*a spp. ranked second and third. At the SW slope *Clausocalanus* spp. was again dominating, followed by *Pleuromamm*a spp. and *Euchaeta* spp. The catches above the summit differed from those at the other sampling sites. *Lucicutia* spp. were the most important identified calanoid, followed by *Clausocalanus* spp., *Euchaeta* spp. and *Temora* spp.

Like at Sedlo and Seine Seamounts the identified Calanoida at Ampère E slope were dominated by *Clausocalanus* spp., followedby *Euchaeta* spp. and *Pleuromamma* spp. (Table 2). Scoletricidae accounted for 3%. Other taxa were found in small proportions of 2% or less. Unlike at Sedlo and Seine Seamounts, *Calocalanus* spp. and *Calanus helgolandicus* were not found at Ampère Seamount. The catches of calanoid Copepoda above Ampère summit were not identified in detail.

For all major calanoid groups, the standing stock at Sedlo Seamount in the upper 100 m did not differ between the summit and the farfield site (Table 3). At Seine Seamount, the standing stocks of the major groups was about one order of magnitude lower above the summit than at the other sites. Similarly, at Ampère the standing stock of calanoids was lower above the summit than above the slope, but the difference was less pronounced than at Seine.

Table 3: Composition and standing stock of calanoid Copepoda comprising 10% or more in Table 2, in the upper 100 m, at Ampère summit in the upper 90 m. See Table 2 for explanation. n.i.: not identified.

	Sedlo				Seine								Ampère			
sampling site	FF		summit		FF		NE		SW		summit		E		summit	
catch depth (m)	n 1000		n 750		d+n 1000		d 1000		d+n 1000		d+n 150		d 1000		d 90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
unid./juv. Cal.	**43**	560	**36**	421	**69**	9498	**69**	2849	**72**	7242	**49**	499	**68**	10157	**100**	7702
Pleurom. spp.	**11**	141	**17**	203	3	435	3	1036	2	221	1	8	1	190	-	-
Lucicutia spp.	0	2	0	0	4	562	4	1686	1	120	9	96	0	50	-	-
Euchaeta spp.	7	96	7	85	2	334	2	1001	5	471	6	64	7	1095	-	-
Clausocal. spp.	**36**	469	**35**	411	2	268	2	804	**15**	1490	**15**	149	**19**	2899	-	-

Non-calanoid Copepoda

Oncaeidae were the dominant group within the non-calanoid Copepoda at the Sedlo summit and far field site (Table 4). Corycaeidae ranked next, followed by Harpacticoida. From the other groups, only single specimens of *Copilia* were fond.

Table 4: Composition and standing stock of non-calanoid Copepoda at the three investigated seamounts. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS	P	SS
Oncaeidae	**72**	22	**92**	187	**35**	1917	**54**	1442	**55**	1090	**48**	313	**55**	1191	**24**	281
Corycaeidae	**16**	5	2	3	**45**	2529	**27**	712	**25**	502	**34**	223	**18**	378	**40**	464
Oithona spp.	0	0	0	0	**12**	676	**11**	288	**14**	280	**14**	89	**24**	500	**38**	418
Copilia spp.	0	0	<1	1	2	86	2	48	1	15	2	11	<1	8	<1	1
Saphirina spp.	0	0	0	0	4	196	2	52	2	44	2	11	<1	11	0	0
other Cyclopoida	0	0	0	0	<1	11	0	0	1	15	<1	1	<1	14	0	0
Harpacticoida	**12**	4	6	11	2	133	4	114	2	42	0	0	1	13	<1	3

At Seine Seamount Oncaeidae and Corycaeidae dominated the non-calanoid Copepoda at all sampling sites (Table 4). *Oithona* spp. was the next important group at all sites. Other non-calanoid Copepoda were found in low numbers.

Above the Ampère slope Oncaeidae were the dominant non-calanoid Copepoda, followed by *Oithona* spp. and Corycaeidae (Table 4). By contrast, above the summit Corycaeidae and *Oithona* spp. were more abundant than Oncaeidae. Other non-calanoid Copepoda like *Copilia* spp., *Saphirina* spp. and Harpacticoida were found in proportions of 1% or less (Table 4).

In the upper 100 m at Sedlo summit Oncaeidae were the only non-calanoid Copepoda, at the far field site Oncaeidae comprised half of the standing stock, the other half was made of Corycaeidae. Other non-calanoid Copepoda were not found (Table 5).

Oncaeidea and Corycaeidae dominated the standing stocks in the upper 100 m at all sites at Seine Seamount, *Oithona* spp. ranked next. Other non-calanoid Copepoda were found in low numbers.

At the E slope of Ampere Seamount Oncaeidae made up 2/3 of the catches in the upper 100 m, followed by Corycaeidae and *Oithona* spp., above the summit Corycaeidae and *Oithona* spp. were more important than Oncaeidae, the proportion of other non-calanoids was < 1%.

Table 5: Composition and standing stock of non-calanoid Copepoda in the upper 100 m, at Ampère summit in the upper 90 m. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Oncaeidae	**57**	6	**10**	150	**28**	369	**49**	778	**54**	632	**45**	194	**62**	860	**24**	281
Corycaeidae	**43**	5	0	0	**37**	482	**35**	547	**28**	336	**39**	170	**22**	312	**40**	464
Oithona spp.	0	0	0	0	**26**	335	5	83	**14**	164	**13**	59	**15**	215	**38**	418
Copilia spp.	0	0	0	0	3	32	2	38	1	16	2	11	<1	2	<1	1
Saphirina spp.	0	0	0	0	6	75	3	41	3	30	1	5	1	11	0	0
other Cyclopoida	0	0	0	0	<1	1	0	0	<1	2	<1	1	0	0	0	0
Harpacticoida	0	0	0	0	<1	2	6	93	<1	4	0	0	0	0	<1	3

3.3.2. Non-copepod Crustacea

Ostracoda were the most abundant non-copepod Crustacea at Sedlo far field, where they contributed more than half to this group; above the summit their percentage was less than 40 %, whereas Euphausiacea made up 50 % of the standing stock (Table 6). Crustacean larvae were more important at the far field site (28 %) than above the summit (9 %). Decapoda and Amphipoda were caught in small numbers at both sampling sites (Table 6), while Mysidacea were found only at far field. No Cladocera were found in the samples at Sedlo Seamount.

Table 6: Composition and standing stock of non-copepod Crustacea at the three investigated seamounts. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Ostracoda	**56**	96	**37**	44	**68**	1799	**40**	648	**50**	100	**54**	66	**27**	700	3	74
Amphipoda	2	3	4	4	8	197	3	42	6	123	2	3	**11**	275	5	118
Cladocera	0	0	0	0	<1	8	0	0	**12**	246	3	4	**46**	1224	**85**	188
Decapoda	2	4	1	1	<1	4	<1	1	<1	5	6	7	<1	1	0	0
Euphausiacea	**10**	16	**49**	58	7	171	**14**	220	**10**	197	5	6	6	157	<1	1
Mysidacea	2	3	0	0	1	13	<1	5	1	17	5	7	1	16	0	0
Crust. Larvae	**28**	47	9	11	**16**	402	**43**	683	**21**	433	**25**	30	9	238	7	151

At Seine Seamount Ostracoda were the dominant non-copepod crustacean group at all sampling sites except at the NE slope, where crustacean larvae dominated the catches (Table 6). At far field, SW slope and summit, crustacean larvae were second abundant. Euphausiacea were found in higher proportins at the NE and SW slope compared to the far field and summit sites. The proportion of Cladocerans was relatively high at the SW slope, where they reached 12%, but at far field and above the summit these organisms were found in small numbers, at the NE slope they were missing. Decapoda and Mysidacea were caught in low numbers at all sites, as were Amphipoda.

At Ampère Seamount, by contrast to Sedlo and Seine Seamounts, Cladocera dominated the catches at both sites, above the summit they made up more than 80% of all non-copepod Crustacea. Besides Cladocera, only Ostracoda and Amphipoda reached more than 10 % at the slope. Decapoda and Mysidacea were found only at the slope.

Table 7: Composition and standing stock of non-copepod Crustacea in the upper 100 m, at Ampère summit in the upper 90 m. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Ostracoda	0	0	0	0	**64**	826	9	77	**30**	331	**47**	41	5	86	3	74
Amphipoda	**1**	1	2	1	**10**	127	4	31	7	73	2	2	**12**	218	5	118
Cladocera	0	0	0	0	<1	6	0	0	**22**	245	4	3	**67**	1213	**85**	1880
Decapoda	4	1	0	0	<1	1	0	0	<1	1	8	7	<1	1	0	0
Euphausiacea	**70**	11	**97**	30	3	39	**18**	15	7	83	6	5	6	113	<1	1
Mysidacea	0	0	0	0	1	7	0	0	1	15	7	6	1	11	0	0
Crust. Larvae	**25**	4	1	1	**21**	274	**69**	577	**33**	362	**26**	22	9	159	7	151

At Sedlo Seamount the standing stock of non-copepod Crustacea in the upper 100 m was clearly dominated by Euphausiacea, above the summit they made up 97%; at far field they comprised 70%, followed by crustacean larvae with 25%. Furthermore, small numbers of Amphipoda and Decapoda were caught (Table 7).

At all sites at Seine Seamount Ostracoda and crustacean larvae were the most important groups, followed by Amphipoda at far field, whereas at the NE slope Euphausiacea were next important and at the SW slope Cladocera. All other groups comprised less than 10% at the Seine sampling sites.

At Ampere slope and summit Cladocera were most important in the upper 100 m, followed by

Amphipoda at the slope and crustacean larvae above the summit, the latter less than 10%.

3.3.3. Non-Crustacea (except gelatinous organisms)

Mollusca were virtually the only non-Crustacea group at the Sedlo far field site; however, above the summit they only represented 34% of the catch, whereas Fishlarvae made up about half of the non-Crustacea at this site (Table 8). Polychaeta comprised 18% of the catch above the summit. Chaetognatha were found only in low numbers, and at both sites neither Appendicularia, non-crustacean larvae nor fisheggs were found (Table 8).

Table 8: Composition and standing stock of non-Crustacea at the three investigated seamounts. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Appendicularia	0	0	0	0	<1	2	<1	1	**43**	666	1	2	0	0	1	3
Fishlarvae	4	7	**46**	10	2	49	8	54	3	39	1	1	6	22	<1	1
Fisheggs	0	0	0	0	**13**	316	**26**	175	**13**	208	**77**	150	0	0	0	0
Chaetognatha	<1	1	2	1	**45**	113	**44**	289	**25**	384	**13**	25	**60**	201	9	18
Polychaeta	1	1	**18**	4	5	129	2	12	2	31	0	0	9	31	0	0
Mollusca	**95**	178	**34**	8	**35**	875	**17**	114	**14**	222	2	4	**24**	81	**90**	183
Non Crust.Larvae	0	0	0	0	<1	2	3	17	<1	1	6	11	1	3	0	0

At Seine, Chaetognatha were the dominant group of non-Crustacea at far field and NE slope, whereas Appendicularia, which were rarely found at the other sites, predominated at the SW slope (Table 8). Above the summit fisheggs made up nearly 80 % of the non-Crustacea; their percentage was much lower at the other sites. Mollusca ranked second at far field and third at the slopes.

Above Ampère summit Mollusca made up 90% of all non-Crustacea; at the slope Chaetognatha predominated (Table 8). All other groups reached less than 10 % at both sites; Fisheggs were not found.

At Sedlo Seamount Mollusca dominated the catches in the upper 100 m with 100 and 88%, respectively (Table 9).

At the Seine far field and NE slope Chaetognatha were more important than the second ranking Mollusca. At the SW slope Appendicularia comprised nearly 50% of the standing stock, followed by Chaetognatha, fisheggs an non crustacean larvae. Above the summit fisheggs made up 88% of the catches, Chaetognatha 11%. All other taxa comprised less than 10%.

At Ampère E slope Chaetognatha dominated the standing stock of the upper 100 m with 64%, Mollusca made up 36%; above the summit the latter comprised 90% of the catches, Chaetognatha only 9%.

Table 9: Composition and standing stock of non-Crustacea in the upper 100 m, at Ampère summit in the upper 90 m. See Table 2 for explanation.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Appendicularia	0	0	0	0	**<1**	1	**0**	0	**44**	384	**1**	1	0	0	1	3
Fishlarvae	**<1**	1	7	1	**1**	20	**7**	20	**1**	5	**1**	1	<1	1	<1	1
Fisheggs	0	0	0	0	**14**	261	<1	1	**21**	177	**81**	149	**0**	0	0	0
Chaetognatha	0	0	0	0	**41**	768	**64**	186	**21**	175	**11**	20	**64**	128	9	18
Polychaeta	0	0	5	1	5	85	<1	1	1	**12**	0	0	<1	1	0	0
Mollusca	**10**	174	**88**	6	**39**	717	**23**	69	0	0	1	1	**36**	73	**90**	183
Non Crust.Larvae	0	0	0	0	<1	2	6	17	**10**	**100**	5	9	<1	1	0	0

3.3.4. Gelatinous organisms

Siphonophora were counted as parts due to damage caused during the catch. These parts were found in high numbers at all sampling sites. Like ‘unidentifiable gelatinous organisms/parts’ they were not included in the standing stock calculations, instead their relative presence at the different sites was noticed.

At Sedlo Seamount gelatinous organisms were rare except for Siphonophora; Cnidaria were the only identifiable gelatinous organism in the catches (Table 10).

Table 10: Composition and standing stock of gelatinous organisms at the three investigated seamounts. See Table 2 for explanation. Relative presence low - high: x – xxx.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Siphonophora	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	**xxx**
Cnidaria	**100**	1	**100**	1	**48**	72	2	1	**79**	16	0	0	6	8	2	1
Thaliacea	0	0	0	0	**52**	79	**98**	11	**21**	42	0	0	**94**	122	**98**	10
unid. gelat. Org.	x	x	x	x	**xxx**	xxx	**xxx**	xxx	**xx**	xx	**xx**	xx	**xxx**	xxx	**xx**	**xx**

At the Seine far field site the proportion of Thaliacea and Cnidaria was similar (48 and 52%, respectively) (Table 10). Thaliacea made up for 98% of the identifiable gelatinous organisms at the NE slope. At the SW slope Cnidaria were more abundant than Taliacea (Table 10). Both groups were not present above the summit.

At Ampère Seamount Thaliacea comprised more than 90% of the identifiable gelatinous organisms at both sampling sites (Table 10).

Table 11: Composition and standing stock of gelatinous organisms in the upper 100 m, at Ampère summit in the upper 90 m. See Table 2 for explanation. Relative presence low - high: x – xxx.

	Sedlo				Seine								Ampère			
sampling	FF		summit		FF		NE		SW		summit		E		summit	
site	n		n		d+n		d		d+n		d+n		d		d	
catch depth (m)	1000		750		1000		1000		1000		150		1000		90	
	P	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**	**P**	**SS**
Siphonophora	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx	**xxx**	xxx
Cnidaria	100	1	0	0	0	0	0	0	**86**	158	0	0	**54**	6	2	1
Thaliacea	0	0	0	0	**10**	36	0	0	**14**	26	0	0	**46**	5	**98**	10
unid. gelat. Org.	0	0	0	0	xxx	xxx	0	0	xx	xx	0	0	**xxx**	xxx	**xx**	xx

In the upper 100 m ar Sedlo Seamount, except parts of Siphonophara, only one Cnidaria was found (Table 11).

At Seine far field Thaliacea comprised 100% of the identified gelatinous organisms in these depths, at the SW slope Cnidaria made up 86% and Thaliacea 14%. At these sites Siphonophara and unidentified gelatinous organisms were found in higher numbers, at the NE slope and above the summit only parts of Siphonophora were caught.

At both Ampère sampling sites parts of Siphonophoras well as unidentified gelatinous organisms were found. The numbers of Cnidaria and Thaliacea were similar at the slope whereas above the summit the latter comprised nearly 100% of the identified gelatinous organisms in the upper 100 m.

3.4 Depth distribution

3.4.1. Copepoda

Calanoid Copepoda

Taxa with distribution focus in the epipelagial (Figure 7)

Most of *Euchaeta* spp. and *Clausocalanus* spp. were located in the upper 200 m, *Candacia* spp. and Scoletricidae in the upper 100 m at all sampling sites. *Temora* spp. was mainly located in the upper 100 m; however, at Seine far field a considerable portion of the stock reached deeper.

Acartia spp. and *Calocalanus* spp. (not shown) were not found at Ampère, at the two other seamounts mainly in the upper 100 m. These taxa resided in the epipelagial independent of daytime.

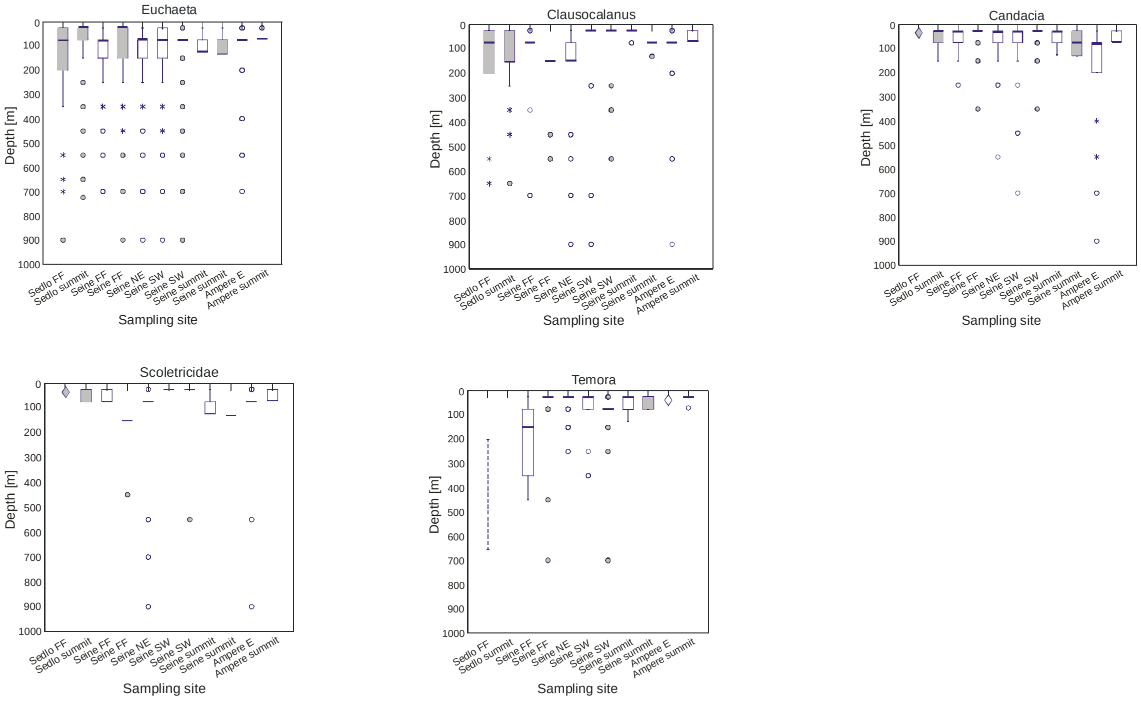

Figure 7: Box plots of vertical distribution of *Euchaeta* spp. (upper left), *Clausocalanus* spp. (upper middle), *Candacia* spp. (upper right), Scoletricidaedae (lower right) and *Temora* spp. (lower left) at the different sampling sites.
Dark boxes: night, light boxes: day. The horizontal (bold) line denotes the median of the distribution, the box delimits the interquartile range, the vertical line indicates the range, and outliers are marked with asterisks and circles. In case the number of caught individuals was < 50 the intermittent line represents the range, a diamond is used for findings in only one depth interval.

Taxa with heterogenous distribution and migrating taxa (Figure 8)

The median depth of *Lucicutia* spp. at the Seine Seamount sites was, with 150-250 m, deeper during the day than that at night, when half of the standing stock was found above 100 m. At Ampère (only daytime catches), this genus was restricted to the upper 200 m. However, at both Sedlo sites nearly all *Lucicutia* were found below 450 m.

The distribution of *Heterorhabdus* spp. did not show a clear pattern; most individuals were found between 100 and 700 m, except above the shallow summits of Seine and Ampère Seamounts. The deepest distribution was found at Seine NE slope where the median of the distribution was in 650 m.

Calanoides carinatus was caught mainly at depths greater 600 m at Sedlo Seamount. At Seine Seamount, most individuals were found between 100 and 700 m, at night deeper than at day. At Ampère *Calanoides carinatus* was found throughout the water column at the slope and above the summit close to the bottom.

The daytime depth of *Pleuromamma* spp. was 250 m or deeper at all sites except above the shallow summits of Seine and Ampère Seamounts, at night the main fraction of *Pleuromamma* spp. had migrated to shallower depths between 50 and 200 m.

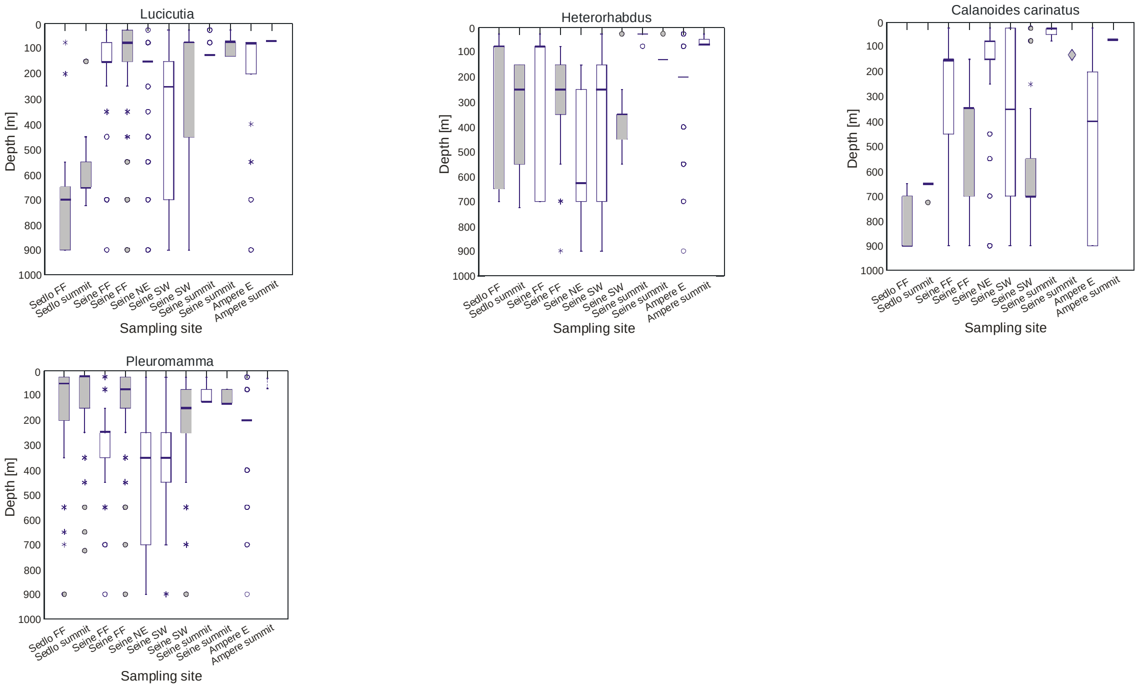

Figure 8: Box plots of vertical distribution of *Lucicutia* spp. (upper left), *Heterorhabdus* spp. (upper middle), *Calanoides carinatus* (upper right), *Pleuromamma* spp. (lower left) at different sampling sites at three seamounts. See Figure 7 for explanation.

The following taxa are not presented in figures due to the low numbers of caught animals. *Rhincalanus nasutus* occurred at Sedlo between 200 and 700 m. At Seine it was mainly caught in the upper 100 m at all sites but the SW slope, where 50% of the population was found between 200 and 700 m during daytime and above 450 m at night. At Ampère summit a few individuals were located in 50-90 m, at the slope *Rhincalanus* was caught at all depths. Most *Eucalanus* spp. were found in the upper 200 m, except at Sedlo summit and Ampère slope where the largest part of the population was caught between 400 and 700 m. The main part of the *Haloptilus* spp. stock at the Seine sampling sites and at Ampère Seamount was located in epipelagic waters except at Seine far field during nighttime, where the distribution reached down to mesopelagic depths (300-400 m). At Sedlo, *Haloptilus* spp. was caught at greater depths, around 500 m above the summit and at 900 m at the far field site.

Taxa with distribution focus in the mesopelagial (Figure 9)

Most of the Aetideidae resided between 150 and 350 m at all sites and daytimes except above Seine summit where they were caught between 100 and 150m. At this site catches only reached down to 150 m, corresponding to a bottom distance of 30 m. Above the even shallower Ampère summit Aetideidae were not found.

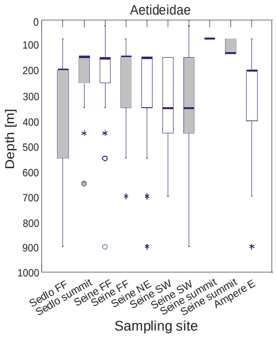

Figure 9: Box plot of vertical distribution of Aetideidae at different sampling sites at three seamounts. See Figure 7 for explanation.

Metridia spp., not presented by Figure, showing generally low abundances, occurred mostly between 300 and 600 m and were not caught above any of the summits.

Non-calanoid Copepoda (Figure 10)

Most cyclopoid Copepoda (Oncaeidae and Corycaeidae) were caught in the upper 200 m of the water column, both day and night. Only at Sedlo far field half of the stock of Oncaeidae was located below 200 m.

Harpacticoid Copepoda had no clear distribution pattern. At Sedlo Seamount they were were caught at mesopelagic depths between 450 and 700 m. At Seine and Ampère Seamounts their distribution ranged from the surface to the deepest layer sampled.

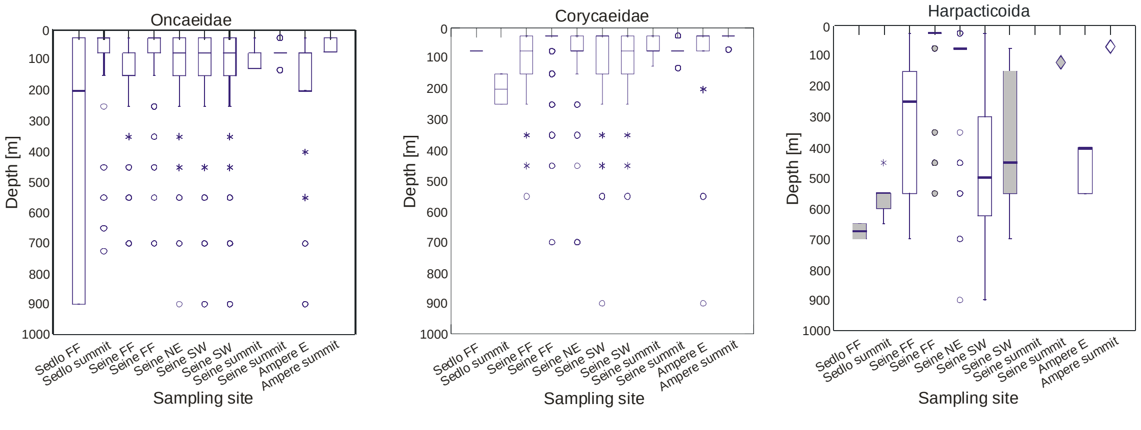

Figure 10: Box plots of vertical distribution of Oncaeidae (left), Corycaeidae (middle) and harpacticoid Copepoda (right) at different sampling sites at three seamounts. See Figure 7 for explanation

3.4.2. Non-copepod Crustacea (Figure 11)

The Ostracoda at the Sedlo sites were distributed from 150 m down to 900 m, with the median of 550 m at the far field site and 250 m above the summit. At Seine far field and SW slope and at Ampere slope the ranges of daytime catches were similar to those at Sedlo, but at nighttime most of the individuals were found at shallower depths (25-200 m).

Most of the Euphausiacea were caught in the upper 300 m at all sites. Crustacean larvae were caught mainly in the upper 200 m, with the exception of the Sedlo far field night sample, where their distribution reached down to 900 m.

Decapoda and Mysidacea (not shown) were found in small numbers throughout the depth range at most of the sampling sites. Decapoda were not caught above the summits of Seine and Ampère Seamounts, and Mysidacea not above Sedlo and Ampère summits. The distribution of Amphipoda and Cladocera (not shown) focused on the upper 200 m at all sampling locations, independent of daytime.

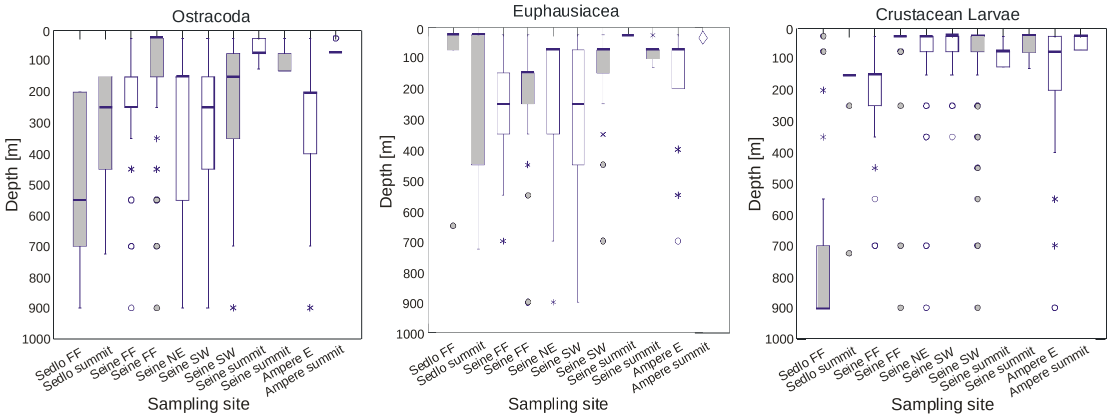

Figure 11: Box plots of vertical distribution of Ostracoda (left), Euphausiacea (middle) and crustacean larvae (right) at different sampling sites at three seamounts. See Figure 7 for explanation.

3.4.3. Non-Crustacea (except gelatinous organisms) (Figure 12)

Mollusca and Chaetognatha were caught at all sampling depths, but the largest part of their stocks was usually found above 250 m. No daytime trend was observed.

Most of the Polychaeta were caught in the layers between the surface and 350 m with medians between 50 and 150 m; only at the Seine NE slope and at the Ampère slope the population centre was located deeper, at 700 and 550 m, respectively. No Polychaeta were caught above the summits of Seine and Ampère Seamounts.

Fishlarvae were located in a wide depth range. At the Sedlo sites the median was between 600 and 700 m. At the Seine far field and slope sites the median was located at 450 m during daytime, at Ampère slope at 550 m. At night the median at Seine far field was located in 50 m, at the SW slope at 250 m. No fishlarvae were caught above Ampère and Seine summit at night, only few individuals at Seine summit during daytime.

Fisheggs were distributed in the upper 200 m with the exception of Seine NE slope where most of them were found between 350 and 700 m. At Ampère no fisheggs were caught. Appendicularians and non-crustacean larvae (not shown) were caught in small numbers at all Seamounts, mainly in the upper 200 m.

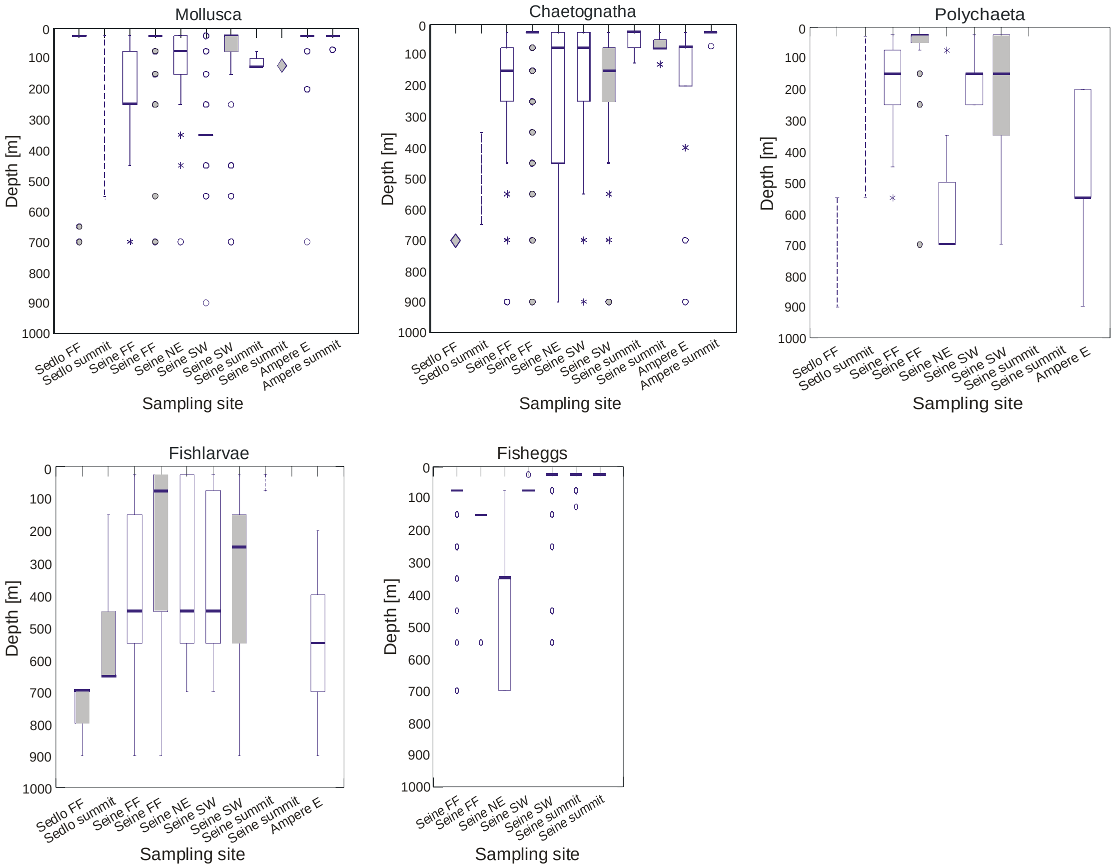

Figure 12: Box plots of vertical distribution of Mollusca (upper left), Chaetognatha (upper middle), Polychaeta (upper right), fishlarvae (lower left) and fisheggs (lower middle) at different sampling sites at three seamounts. See Figure 7 for explanation.

3.4.4 Gelatinous organisms (Figure 13)

Gelatinous organisms, including parts of Siphonophora, were found throughout the water column; the median of the depth distribution of this group was in the upper 200 m during day and night at all sampling sites.

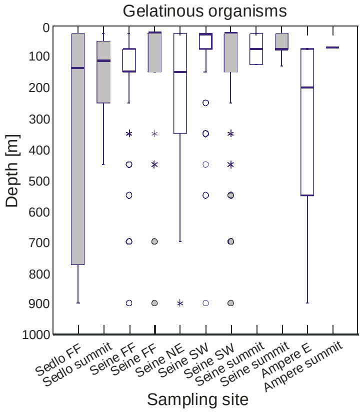

Figure 13: Box plots of vertical distribution of gelatinous organisms/parts at different sampling sites at three seamounts. See Figure 7 for explanation.

3.4.5. Exoskeletons (Figure 14)

Exoskeletons were found througout the water column at all sites; the median of the distribution was between 100 and 200 m. Only at the Seine NE slope the population centre was slightly deeper at 350 m.

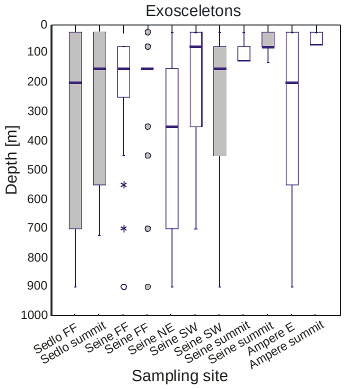

Figure 14: Box plots of vertical distribution of exoskeletons at different sampling sites at three seamounts. See Figure 7 for explanation.

4. Discussion

Differences between the seamounts

The results show that the three seamounts studied differ in composition and standing stocks of the zooplankton. The low standing stocks at Sedlo Seamount and at its reference site in autumn compared to those of Seine and Ampere Seamounts in spring can be explained by seasonal differences in the biological production. Comparing mesozooplankton sampled during transects of the Azores Tropical Front (22°W), Head et al. (2002) estimated twice the biomass in April as compared to August. Deevey & Brooks (1977) reported for the NW Atlantic a spring maximum of Copepoda and a minimum in late fall. Their long-term annual mean values of the standing stock of Copepoda account for half of the values of Seine far field in spring (Table 7). Standing stocks reported by Koppelmann & Weikert for spring at 47°N were lower than those at Seine

Seamount but still in the same order of magnitude (Table 7). The results of the catches from the Ampère summit and slope sites could not be quoted in this context, because for the detection of regional differences only ‘undisturbed’ reference sites are comparable with other studies in the NE Alantic.

Table 7: Standing stock (ind. m^{-2}) of zooplankton in the upper 400 or 500 m of different oceanic areas. TZ: total zooplankton; C: Copepoda.

Depth (m)	33°N 14°W (Seine FF) This study		40°N 26°W (Sedlo FF) This study		47°N 20°W Koppelmann & Weikert 1992		32°N 64°W Deevey & Brooks 1977	
	TZ	C	TZ	C	TZ	C		C
0-400					17000	14000		
0-500	29000	23000	2600	2300				13000
Mesh size	333		333		333		363	
Remarks	spring		autumn		spring		annual mean	

One obvious difference between the seamounts regards the relative abundance of Copepoda, especially Calanoida. The contribution of Calanoida to the total standing stock was highest at Sedlo and markedly lower both at Seine and Ampère Seamounts. Pelagic Copepoda are dominant in terms of abundance in plankton samples from most sea areas (Longhurst 1985). However, the importance of Copepoda generally decreases from boreal to tropical waters while that of Euphausiacea, Amphipoda, Ostracoda and gelatinous organisms increases, and, within the Copepoda, the proportion of Calanoida decreases in favour of Cyclopoida (Longhurst 1985). Concurrently, the feeding types within the zooplankton community change from a higher proportion of coarse-filter feeders (feeding on large phytoplankton such as diatoms) in polar regions to a predominance of omnivoruos zooplankton in temperate waters, and an increasing proportion of predators and fine-filter feeders (feeding on small plankton such as dinoflagellates) in tropical regions (Schneider 2002).

The latitudinal distance between Sedlo and Seine is only 6°, between Sedlo and Ampère only 3°, and all three seamounts are located within the same biogeochemical province (Longhurst 1998). However, Seine Seamount is in the area directly influenced by the Azores Current (AzC), which is typically observed down to depths of 800-1000m (Bashmachnikov *et al.* subm.), while Sedlo Seamount is located north of it. The AzC, a branch of the Gulf Stream, forms meanders crossing the Atlantic (Klein & Siedler 1989; Siedler & Onken 1996). Related to the current is the Azores Front (AzF) (south of 40° N), separating colder and less saline waters to the north from warmer and saltier waters of the subtropical Atlantic (Head et al. 2002). Ampère is located in the area of the AzF (Pingree *et al.* 1999). The front changes the composition of zooplankton drastically; the percentage of calanoid Copepoda is markedly higher to the south, while that of cyclopoid Copepoda is lower (Schneider 2002). Furthermore, the fraction of gelatinous plankton like

Siphonophora and Tunicata increases southwards. Consequently, a more diverse species composition (see Figure 6) and a higher proportion of cyclopoid Copepoda and gelatinous organisms were observed in the Seine and Ampère region, which implicits a higher proportion of omnivorous (f.e. Cyclpoida) and carnivorous zooplankton (f.e. Cnidaria), as compared to Sedlo.

Several taxa showed different depth distributions at the seamounts. The copepod *Calanoides carinatus* was caught throughout the water column at Seine and Ampère Seamounts, but at Sedlo only below 600 m. *C. carinatus* is known as a key species in the African upwelling regions (Smith 1982). It carries out vertical migrations depending on the upwelling conditions: when surface temperatures rise due to decreasing upwelling intensity, it sinks to depths of 600-1000 m, while in times of food-rich conditions during upwelling it moves to shallower waters (Smith 1982 and 1984). This organism could have been transported to the seamounts by filaments from the NW African or Portuguese upwelling regions, which have been observed on satellite images (Aristegui *et al.* subm.), and descend to mesopelagic depths due to the nutrient-poor situation at Sedlo Seamount in autumn. Similarly, *Lucicutia* spp., Cyclopoida, Ostracoda, crustacean larvae and fishlarvae were found at greater depths at Sedlo compared to the two other seamounts. Because these taxonomical groups were not identified to species level we do not know wether the different distributions reflected differences in species composition, seasonal influences or physical dynamics.

Differences between sampling sites at the seamounts

Both Seine and Ampère Seamounts had standing stocks of total zooplankton in the upper 100 m distinctly lower above the summits compared to the slopes and the reference site, whereas at the deeper Sedlo Seamount, no such difference between summit and far field was observed. A reduced abundance and biomass above shallow topography was described by Dower and Genin (2007) and Martin and Nellen (2004), and was also reported for the biomass at Seine and Ampère by Martin and Christiansen (subm.). Besides an overall reduction of zooplankton, the biomass of organisms > 0.5 cm was extremely low above the summits of the shallow seamounts, which is supported by our findings of low abundances or absence of larger zooplankton like Euphausiacea, Polychaeta and fishlarvae above the summits of Seine and Ampere Seamounts, compared to the slopes of both seamounts and the far field site of Seine. Genin et al. (1988) reported that *Euphausia pacifica*, which migrate several hundred meters diurnally, were absent or very low in numbers above the summit of the shallow Nidever Bank (100-140 m summit depth), but showed high densities in the surrounding deep water. Hesthagen (1970) proposed displacement as the possible reason for a reduction of zooplankton above certain seamount summits. He studied the near bottom fauna of Great Meteor and Josephine Seamounts (summit depth ~ 300 m and 170 m, respectively) using a Beyer epibenthic sledge with a mesh size of 0.5 cm. Calanoid Copepoda were the most abundant animals in the samples. The author recorded higher numbers of calanoid Copepoda during daytime compared to nighttime near the bottom of the summit at Great Meteor concluding that the caught taxa had been stranded during their diurnal migration. No such day/night differences were detected at Josephine Seamount. The author suggested that downward migrating organisms impinging on a seamount summit avoid the contact with the sediment and are transported along the seabed by currents until the bottom permits further descent. At the dome-shaped narrow summit of Josephine Seamount this might not take long, , whereas above the large summit plateau of Great Meteor the near bottom currents would not suffice to carry the deep-seeking animals off the plateau in the course of the day. Rogers (1994) noted the possibility that vertically migrating taxa are reduced over seamounts due to displacement around the seamount during the day while they stay in layers deeper than the summit depth. These mechanisms of avoiding bottom contact together with transport down the slopes and displacement during daytime could be the reason for the low numbers of Euphausiacea, Polychaeta and fishlarvae in our samples. Euphausiacea are known to conduct extensive vertical migrations (Weigmann 1974; Hargreaves 1985), but in our study their depth distribution does not show such a behaviour. However, Polychaeta and fishlarvae at the Seine sites were found at greater depths during the day compared to the night. The relative abundance of another vertical migrator, the calanoid Copepoda *Pleuromamma*, which showed a conspicous different residence depth between night- and daytime in our study, was also distinctly lower over the Seine and Ampère summits as compared to the other sites.

Predation by the seamount-associated fish fauna may be another reason for the reduced standing stock of zooplankton above the summits. Investigations of the zooplankton distribution at Great Meteor Seamount (Martin & Nellen 2004), a seamount with a summit plateau of 1500 km² at a depth of about 300 m, showed high abundances of vertically migrating zooplankton taxa like *Pleuromamma* and Euphausiacea close to the bottom of the plateau during daytime. These organisms were also found in the stomachs of fishes caught on the Great Meteor Seamount (Erich, 1974). Genin *et al.* (1994) found gaps in the biomass of vertically migrating zooplankton every evening above the summit of Sixtymile Bank (97 m summit depth). The authors proposed that predation on vertically migrating zooplankton by seamount-associated fauna located close to the bottom during daytime was responsible for the gaps, which were then transported downstream with the prevailing currents. Studies of stomach contents of benthopelagic fishes at Seine Seamount (Christiansen *et al.* subm.) could not confirm the hypothesis of predation of migrators by this group of fishes. Their diet consisted mainly small cyclopoid and calanoid Copepoda. However, we cannot exclude that pelagic predators might have fed on zooplankton during their downward migration.

Distinctly lower standing stocks in the upper 100 m above the summits as compared to the slopes of the two shallow seamounts were common for most of the zooplankton taxa, but a few groups showed a different distribution. At Ampère, only small differences between summit and slope were found for Corycaeidae, *Oithona spp.*, Ostracoda and Mollusca; Cladocera were even more abundant above the summit. At Seine, fisheggs were nearly evenly distributed across all sites, the proportion of exosceletons was slightly higher above both shallow summits compared to the other sampling sites. The reason for the differences in distribution pattern is unclear. However, most of the species of Cladocera are inhabiting coastal and shelf regions (Vinas *et al.* 2007). Their occurrence in high number above Ampère Seamount suggests that they are shallow water forms that may have dispersed from the Portugese shelf via the Horseshoe Seamount Chain and found a suitable habitat above the shallow Ampère Seamount. However it needs a more detailed taxonomical analysis to evaluate if there are close relationships between the seamount and shelf Cladocera. Beckmann and Mohn (2002) designed models that simulated the behaviour of both passive and vertically migrating particles/organisms at seamounts if a Taylor column is present. The models were based on oceanographic data from Great Meteor Seamount in 1998. They suggest that the retention time for passive particles in the Taylor column over the plateau was up to ten times higher than in the surrounding waters, whereas vertically migrating zooplankton was not retained but moved at rates similar to those influenced by the general currents. At Seine Seamount, a Taylor cap was observed during the time of our investigations, which might explain that the immobile fisheggs and exosceletons were not as reduced above the shallow summits as were most of the taxa. Due to the lack of hydrographical data we can only speculate that this was the case at Ampère Seamount as well.

The standing stocks in the upper 1000 m at the Seine far field and slope sites were generally very similar. However, Chaetognatha and some Copepoda were found in higher abundance at the far field site than at the slopes of the seamount. By contrast, indications for higher standing stocks at the seamount were observed for the Copepoda *Metridia* spp. and *Clausocalanus* spp. Other taxa were found in markedly higher number at only one slope , like the copepod *Lucicutia* spp. above the NE slope and Appendicularia and Cladocera above the SW slope. The distributional patterns show that for most taxa no indications for increased productivity can be detected. However, the interaction between seamount and plankton seems to be different for the studied taxa. Different exposure to seamount induced currents, for example taxa like *Clausocalanus* spp. residing in epipelagial depth above Seine Seamount might have been less influenced by Taylor cap induced currents than vertical migrators (see above) , as well as possible prey selection by the local fish fauna may cause the variations.

At Seine Seamount exoskeletons as well as fisheggs were apparently distributed to greater depth at the NE slope (leeward side) compared to the other sampling sites. Dower & Perry (2001) reported of Cobb Seamount, that the ichthyoplankton community within 30 km from the Seamount was dominated by larvae of various rockfish (*Sebastes*) species. The authors suggest that a persistent clockwise (i.e. downwelling) eddy, consistent with a stratified Taylor cap, plays a role in retaining larval rockfish over the seamount, contributing to the process of self recruitment. Excessive current speeds at Taylor columns can result in eddies beeing shed downstream (Hogg 1980). Boehlert und Mundy (1993) propose that such eddies cause biological variability in downstream waters, including the retention of ichthyoplankton for periods up to several weeks. Observations from satellite-tracked drifters show that cold core rings may remain in the vicinity of seamounts for nearly a month (Cheney et al. 1980). A likewise emerged eddy could also be the reason for the displacement of fisheggs and exoskeletons to greater depth leeward of Seine Seamount. Because the fisheggs were not identified to species we can only speculate that the sampled fish eggs were derived from seamount associated fish and retained in the vicinity of their spawning grounds by the mechanisms described above.

5. Conclusions

At none of the studied seasons indications of enhanced productivity could be detected. The differences between the seamounts in taxonomical composition and standing stocks of the zooplankton can be attributed to regional and seasonal influences. The comparison between the different sampling sites showed a ‘seamount effect’ in form of a reduction of the standing stocks for most of the studied taxa for the shallow Seine and Ampère Seamounts. However, zooplankton taxa were differently affected. We assume that the reduction of zooplankton, especially of the larger size groups, is caused mainly by displacment of diurnally migrating animals by the topography and the topographically induced currents. Predation by the seamount associated pelagic fish fauna as well as active avoidance can only be a speculation. The divergent pattern in depths distribution of fisheggs and exosceletons leeward of Seine Seamount could be caused by seamount induced variations in the current regime downward of the seamount.

6. Acknowledgements

This study is part of OASIS (OceAnic Seamounts: an Integrated Study), a research project supported by the European Commission under the Fifth Framework Programme and contributing to the implementation of the Key Action “Sustainable Marine Ecosystems” within the Energy, Environment and Sustainable Development; Contract n°: EVK3-CT-2002-00073-

OASIS. Our thanks also go to the crew of R.V. Poseidon and R.V. Meteor for their skillful help and assistance.

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Appendix 1: List of identified taxa at the three seamounts. Groups or taxa marked with ‘+’ or ‘0’ were present or not present at the sampling site. At particular sampling sites some taxa were identified to a lower level and marked with ‘x’, while at sites marked with ‘-‘ a more detailed identification did not take place.

								Seine			Sedlo		Ampère	
Phylum	Subphylum	class	subclass	order	superfamily	family	species	FF	slopes	summit	FF	summit	slope	summit
Cnidaria		Hydrozoa		Siphonophora			Siphonophora ind.	+	+	+	+	+	+	+
		Scyphozoa					Medusae ind.	+	+	0	+	+	+	+
Ctenophora							Ctenophora ind.	0	+	0	+	0	+	0
Mollusca		Cephalopoda					Cephalopoda ind.	+	+	0	+	0	+	0
							Mollusca ind.	+	+	+	+	+	+	+
		Gastropoda					Gastropoda ind.	-	x	+	-	-	-	-
				Pteropoda			Pteropoda ind.	+	+	+	+	+	+	+
				Heteropoda			Heteropoda ind.	-	x	x	-	-	-	-
		Scaphopoda					Scaphopoda ind.	+	+	+	+	+	+	+
		Bivalvia					Bivalvia ind.	-	x	x	-	-	-	-
Annelida		Polychaeta					Polychaeta ind.	+	+	0	+	+	+	+
?							div. non crust. Larvae	+	+	+	0	0	+	0
Arthropoda	Crustacea	Branchiopoda	Diplostraca	Cladocera			Cladocera ind.	+	+	+	+	+	+	+
							Evadne spinifera	-	x	x	-	-	-	-
		Maxillopoda					Crustacea larvae	+	+	+	+	+	+	+
			Copepoda	Calanoida			Calanoida ind./juv.	+	+	+	+	+	+	+
					Augapti-loidea	Augaptilidae	*Augaptilus spp.*	-	x	-	-	-	-	-
							Euaugaptilus hecticus	-	+	-	-	-	-	-
							Haloptilus spp.	+	+	+	+	+	+	+
							Haloptilus longicornis	-	x	x	-	-	-	-
						Heterorhabdidae	*Heterorhabdus spp.*	+	+	+	+	+	+	+
						Lucicutiidae	*Lucicutia spp.*	+	+	+	+	+	+	+
							Lucicutia flavicornis	-	x	-	-	-	-	-
							Lucicutia grandis	-	x	-	-	-	-	-
							Lucicutia longiserrata	-	x	-	-	-	-	-
							Lucicutia gemina	-	x	+	-	-	-	-
						Metridinidae	*Metridia spp.*	+	+	0	+	+	+	+
							Pleuromamma spp.	+	+	+	+	+	+	+
					Centropa-goidea	Acartiidae	*Acartia spp.*	+	+	+	0	+	0	0
						Candaciidae	*Candacia spp.*	+	+	+	+	+	0	+
						Centropagidae	*Centropages spp.*	+	+	+	+	+	+	+
						Temoridae	*Temora spp.*	+	+	+	+	+	+	+

Appendix 1 (cont.)

							Gaetanus spp.	+	+	+	+	+	0	0
						Clausocalanidae	*Clausocalanus spp.*	+	+	+	+	+	+	0
						Euchaetidae	*Euchaeta spp.*	+	+	+	+	+	+	+
						Scolecitrichidae	Scolecitrichidae ind.	+	+	+	+	+	+	0
							Scaphocalanus spp.	-	x	x	-	-	-	-
						Spinocalanidae	*Spinocalanus spp.*	-	x	-	-	-	-	-
							Spinocalanus abyssalis	-	x	0	-	-	-	-
							Monacilla spp.	-	x	x	-	-	-	-
					Eucalanoidea	Eucalanidae	*Eucalanus spp.*	+	+	+	+	+	+	+
							Eucalanus attenuatus	-	x	x	-	-	-	-
							Eucalanus elongatus	-	x	0	-	-	-	-
							Eucalanus monachus	-	x	x	-	-	-	-
							Rhincalanus nasutus	+	+	+	+	+	+	+
					Megacalanoidea	Calanidae	Calanidae ind.	+	+	+	+	+	+	+
							Calanus helgolandicus	+	+	+	+	+	+	0
							Calanoides carinatus	+	+	+	+	+	+	+
							Nannocalanus spp.	-	-	+	-	-	-	-
							Neocalanus spp.	+	+	+	+	+	+	0
						Calocalanidae	*Calocalanus spp.*	+	+	+	0	+	+	0
						Mecynoceridae	*Mecynocera spp.*	+	0	+	0	0	0	0
				Harpacticoida			Harpacticoida ind.	+	+	+	+	0	0	+
						Clytemnestridae	*Clytemnestra spp.*	-	-	-	-	-	-	+
					Cervinioidea	Aegisthidae	*Macrosetella spp.*	+	+	0	+	+	+	+
							Aegisthes spp.	+	+	0	0	0	+	0
				Cyclopoida			Cyclopoida ind.	+	+	+	0	0	+	0
						Oithonidae	*Oithona spp.*	+	+	+	0	+	+	+
				Poecilostomatoida		Corycaeidae	*Corycaeus spp.*	+	+	+	+	+	+	+
						Oncaeidae	*Oncea spp.*	+	+	+	+	+	+	+
							Pachos spp.	-	x	x	-	-	-	-
						Lubockiidae	*Lubockia spp.*	-	x	x	-	-	-	-
						Sapphirinidae	*Sapphirina spp.*	+	+	+	0	0	+	0
							Copilia spp.	+	+	+	0	+	+	+
				Mormonilloida		Mormonilloidae	*Mormonilla spp.*	-	x	-	-	-	-	-

Appendix 1 (cont.)

		Ostracoda					Ostracoda ind.	+	+	+	+	+	+	+
		Malacostraca					Malacos. larvae ind.	+	+	+	+	+	+	+
			Eumalaco-straca	Mysidacea			Mysidacea ind	+	+	+	+	+	+	0
				Amphipoda			Amphipoda ind.	+	+	+	+	+	+	+
						Hyperiidae	Hyperiidae ind.	+	+	+	+	+	+	+
				Isopoda			Isopoda ind.	+	0	+	0	+	+	0
				Euphausiacea			Euphausiacea ind.	+	+	+	+	+	+	+
						Euphausiidae	*Euphausia spp.*	x	-	0	-	-	-	-
							Thysanopoda spp.	x	-	x	-	-	-	-
							Nematobrachion spp.	x	-	x	-	-	-	-
							Stylocheiron spp.	x	-	x	-	-	-	-
				Decapoda			Decapoda ind.	+	+	+	+	+	+	0
Chaetognatha							Chaetognatha ind.	+	+	+	+	+	0	+
Tunicata		Appendicularia					Appendicularia ind.	+	+	+	0	0	+	+
		Thaliacea					Thaliacea ind.	0	+	+	0	+	0	+
Vertebrata		Osteichthyes	Actinopterygii				Fish eggs ind.	+	+	+	0	0	+	+
							Fish larvae ind.	+	+	+	+	+	0	+
				Perciformes	Percoidei	Sciaenidae	Sciaenidae ind.	-	-	x	-	-	-	-
					Blennoidei	Parabrotulidae	*Parabrotula plagiophthalmus*	-	-	+	-	-	-	-
				Clupeiformes	Stomiatoidei	Photichthyidae	*Vincinguerria spp.*	-	-	x	-	-	-	-
						Gonostomatidae	*Cyclothonespp.*		x	x	-	-	-	-
				Scopeliformes	Myctophoidei	Myctophidae	Myctophidae ind.	-	-	x	-	-	-	-
							Hygophum reinhardtii	-	-	x	-	-	-	-
							Lampanyctus alatus	-	-	x	-	-	-	-
							Lepidophanes gaussi	-	-	+	-	-	-	-
					Alepisauroidei	Paralepididae	*Paralepis spp.*	-	-	+	-	-	-	-
							Paralepis atlantica	-	-	+	-	-	-	-
						Parabrotulidae	*Parabrotula plagiophthalmus*	-	-	+	-	-	-	-

Schlussfolgerungen

Die durchgeführten Untersuchungen ergaben weder erhöhte Biomasse- noch erhöhte Abundanzbestände von Zooplankton an den Seebergen (Manuskript Nr. 1, 2, 5) im Vergleich zum umgebenden Ozean. Im Gegenteil waren Zooplankton-Biomassen und -Bestände über den Gipfeln der beiden flachen Seeberge Seine und Ampère sehr niedrig, verglichen mit den Hängen und den ozeanischen Referenzstationen (Manuskript Nr. 2). Besonders deutlich war die Verminderung der Bestände bei den größeren Planktern. Am Sedlo Seamount dagegen, dem tiefsten der 4 untersuchten Berge, wurden nur geringe Bestandsunterschiede zwischen Gipfel und ozeanischer Referenzstation gefunden, und auch die Untersuchungen an der Großen Meteor Bank ergaben keine deutlichen Unterschiede zwischen den Hängen und dem Plateau. Eine Ausnahme bildeten hier die relativ hohen Biomassen der Tagesfänge direkt über dem Boden des Gipfelplateaus. Die taxonomische Untersuchung ergab, dass es sich bei den gefangenen Tieren zu einem großen Teil um vertikal wandernde Arten des Zooplankton handelte. Die Fänge stützen die Theorie des ‚trapping effect' und man kann vermuten, dass der Umfang des Plateaus (1500 km²) sowohl ein mögliches Ausweichen der mobileren Tiere als auch eine durch topographisch bedingte Strömungen verursachte Verdriftung vom Gipfel fort unmöglich gemacht hat. Ein anderer möglicher Grund für diesen Unterschied im Verteilungsmuster könnte methodisch bedingt sein: über der Großen Meteor Bank war der geringste befischte Bodenabstand ca. 1 m, während er über den Gipfeln der übrigen Seeberge mindestens 10 m betrug und somit eine mögliche Akkumulation direkt über dem Boden nicht erkannt worden sein könnte. Die Ergebnisse von der Großen Meteor Bank zeigen, dass es auf dem ausgedehnten Plateau dieses Bergs einen ‚trapping-effect' von Vertikalwanderern gibt (Manuskript Nr. 1); die hier, wie in anderen Arbeiten beschrieben, eine wichtige Nahrungsquelle der ansässigen Fischfauna sind. Auch die Bestände der benthopelagischen Fische, die über dem Gipfel des Seine Seamount gefangen wurden, deuteten nicht auf eine seebergbedingte Akkumulation hin (Manuskript Nr. 3).

Bei der Untersuchung der Stoffwechselraten des Zooplanktons wurde zwar z.T. eine erhöhte ETS-Aktivität über den Bergen gemessen, diese lag jedoch nicht klar über der hohen zeitlichen und räumlichen Variabilität zwischen den Untersuchungsstationen. Die biochemischen Untersuchungen konnten daher die Theorie von lokal erhöhter Produktion ebenfalls nicht stützen (Manuskript Nr. 3).

Unterschiede in der Tiefenverteilung einiger Gruppen in verschiedenen Bereichen des Seebergs bzw. an den ozeanischen Referenzstationen deuten auf einen Einfluss der topographisch bedingten Strömung hin. So fanden sich relativ höhere Anteile von Organismen bzw.

Organismenteilen ohne Eigenbewegung wie Fischeier und Exoskeletten von Crustaceen im Bereich über den Gipfeln und leewärts der Seeberge (Manuskript Nr.1, 5).

Die taxonomische Zusammensetzung des Zooplanktons konnte die Hypothese von autochthonen Beständen, im engeren Sinne seeberg-spezifischen Arten, nicht generell bestätigen; allerdings wurde am Seine und Ampère Seamount festgestellt, dass im Gegensatz zum allgemeinen Trend einige taxonomische Gruppen eine Affinität zu den Bergen zeigten. Insbesondere wurden am Ampère Seamount hohe Bestände von Cladoceren festgestellt, die typische Schelfmeerbewohner sind und vom europäischen Schelf her über die Horseshoe-Seamountkette den Ampère Seamount besiedelt haben könnten (Manuskript Nr. 5).

Abschließend ist zu sagen, daß entgegen der verbreiteten Auffassung einer erhöhten Produktivität und damit verbundenen erhöhten Organismenbeständen an Seebergen keiner der untersuchten atlantischen Seeberge eine Akkumulation von Zooplankton zeigte, obwohl die theoretischen Voraussetzungen wie Ausbildung einer Taylorkappe oder Tidenverstärkung vorlagen. Die Gründe hierfür sind unklar. Berichte über erhöhte Organismendichten an pazifischen Seebergen könnten Einzelbeobachtungen sein. Eine erhöhte Produktivität an den Bergen kann aber nicht ausgeschlossen werden, da die Möglichkeit besteht, dass pelagische Räuber, die hier nicht untersucht wurden, das Zooplankton dezimiert haben oder es durch topographisch bedingte Strömungen abtransportiert worden ist. Die deutlichen Seebergeffekte an den drei flachen Seebergen in Bezug auf die Verteilung und Zusammensetzung des Zooplanktons, insbesondere die verringerten Bestände über den Gipfeln, legen als Ursache einen Einfluss der lokalen, seeberginduzierten Strömungsmuster auf allochthone Bestände nahe, der durch Wegfraß durch Räuber oder ein aktives Vermeiden der flachen Gipfelbereiche noch verstärkt worden sein könnte.

Bei zukünftigen Untersuchungen der Zooplanktongemeinschaften an Seebergen sollte eine höhere zeitliche und räumliche Auflösung der Probennahmen und der physikalischen Messungen angestrebt werden. Nur so kann das Zusammenwirken der physikalischen Dynamik am Berg mit den Verhaltens- und Verteilungsmustern der Organismen und ihre Stellung im Seebergökosystems besser verstanden werden.

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Darlegung des Eigenanteils an den wissenschaftlichen Manuskripten

Manuskript Nr. 1 ‘Composition and distribution of zooplankton at the Great Meteor Seamount, subtropical Northeast Atlantic’
Die taxonomischen Arbeiten, die Aufnahme der Daten und deren Analyse sowie das Verfassen des Textes und die Anfertigung der Graphiken wurden von Bettina Martin mit Betreuung von Prof. Dr. Walter Nellen durchgeführt.

Manuskript Nr. 2 ‘Distribution of zooplankton biomass at three seamounts in the NE Atlantic’
Die taxonomischen Arbeiten, die Aufnahme der Daten und deren Analyse sowie das Verfassen des Textes und die Anfertigung der Graphiken wurden von Bettina Martin mit Betreuung von Dr. Bernd Christiansen durchgeführt.

Manuskript Nr. 3 ‘The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: Composition, population structure and diets’
Der Eigenanteil an diesem Manuskript bestand, neben der Diskussion der Ergebnisse mit den Co-Autoren, in der Hauptsache aus der taxonomischen Bearbeitung der Fische und der Feststellung der Alterstruktur der einzelnen Arten.

Manuskript Nr. 4 ‘Zooplankton metabolism and carbon demand at two seamounts in the NE Atlantic’. Der Eigenanteil an der Arbeit bestand in der Bearbeitung des Zooplanktons, insbesondere der Feststellung der Grössenklassen und der Biomassen an den einzelnen untersuchten Stationen.

Manuskript Nr. 5 ‘Distribution and community composition of zooplankton at three seamounts in the NE Atlantic’
Die taxonomischen Arbeiten, die Aufnahme der Daten und deren Analyse sowie das Verfassen des Textes und die Anfertigung der Graphiken wurden von Bettina Martin mit Betreuung von Dr. Bernd Christiansen durchgeführt.

Danksagung

Abschließend möchte ich mich bei allen Menschen bedanken, die mich während meines Studiums und der folgenden Projektarbeit unterstützt haben.

In allererster Linie danke ich Dr. Bernd Christiansen, der diese Arbeit betreut und sie überhaupt erst möglich gemacht hat. Seit meiner ersten Seereise hat er meinen Berufsweg unterstützend begleitet und mir vermittelt, was wissenschaftliches Arbeiten bedeutet. Bernd, ohne dich wäre mein Lebensweg sicher anders verlaufen. Ich danke dir für deine Geduld und dafür, dass du mir gezeigt hast, was ein guter Seemann ist.

Dr. Rolf Koppelmann stand mir immer in schwierigen Situationen mit Rat und Tat zur Seite. Alles was ich über die Bedienung des MOCNESS weiß, hat er mir beigebracht, und auch, an den Tücken des Geräts nicht zu verzweifeln. Ich freue mich auf unser nächstes gemeinsames Projekt und die zukünftigen Seereisen vor der Küste Afrikas.

Prof. Mike St.John danke ich für die Betreuung und Begutachtung der Arbeit und für hilfreiche Anregungen.

Prof. Axel Temming danke ich für seine Unterstützung und sein großes, nicht ermüdendes Engagement für unsere Arbeit und unser Institut.

Prof. Christian Möllmann danke ich sehr dafür, dass er sofort bereit war, diese Arbeit zu begutachten.

Prof. Dr. Walter Nellen hat in mir die Beigeisterung für Seeberge geweckt, in dem er mir seine Proben von der Großen Meteor Bank anvertraut hat. Ich möchte mich bei ihm auch dafür bedanken, dass er nicht nur immer für Fragen und Diskussionen zur Verfügung stand, sondern auch den Spaß daran vermittelt hat.

Silke Janssen hat mir an Land und auf See bei meiner Arbeit und Freizeitgestaltung sehr geholfen. Silke, unser gemeinsamer MOCNESS Hol durch das Kaltwasser-Korallenriff wird mir immer unvergessen sein.

Liesel Neugebohrn verdanke ich einen Großteil meiner taxonomischen Kenntnisse des Zooplanktons. Oft genug hat sie mir geholfen, nicht an der Bestimmung der Copepoden-Taxa anhand des 5. Beinpaares zu verzweifeln.

Anneke Denda bin ich dafür dankbar, dass sie mit mir die Liebe zur Seefahrt und die Begeisterung für untermeerische Berge teilt. Anneke, es macht unheimlich viel Spass, mit dir MOCNESS zu fahren und ich hätte mir keine bessere Kollegin im Büro vorstellen können.

Ohne Sabine Eberle, die ohnehin die hilfreichste Person ist, die ich kenne, wären die letzten beiden Nächte vor der Fertigstellung der Arbeit finster geworden. Danke!

Jutta und Angela danke ich dafür, dass sie unabhängig von Erfolg und Misserfolg, an meiner Seite stehen.

Meinen Eltern und meiner Großmutter möchte ich hier gedenken. Sie haben mir mein Studium und das wissenschaftliche Arbeiten in projektlosen Zeiten ermöglicht.

Meinem Mann Nik danke ich für sein Verständnis, dass die Arbeit länger gedauert hat, als geplant und dass er mich in meiner Begeisterung für die Seefahrt bestärkt hat.

Ohne die Fortwährende Hilfe der Crews von F.S. *Poseidon* und F.S *Meteor* hätte es diese Arbeit nicht gegeben. Insbesondere danke ich dem hervorragenden Bootsmann Frank Schrage. Frank, ich hoffe, wir werden noch viele gemeinsame Seereisen unternehmen.