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Distribution and Feeding Ecology of Bathylagus euryops (Teleostei: Microstomatidae) along the Northern Mid-Atlantic Ridge from Iceland to the Azores

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DISTRIBUTION AND FEEDING ECOLOGY OF *BATHYLAGUS EURYOPS* (TELEOSTEI:

MICROSTOMATIDAE) ALONG THE NORTHERN MID-ATLANTIC RIDGE, FROM

ICELAND TO THE AZORES

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A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

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By

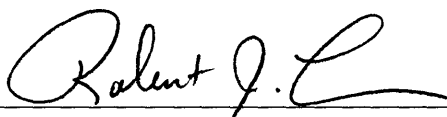Christopher J. Sweetman

2012

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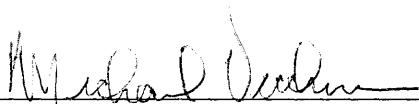
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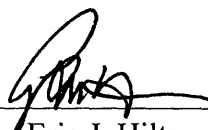
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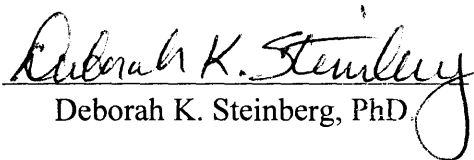
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DEDICATION

I dedicate this work to the memory of my grandfathers, Charles F. Sweetman (1918 - 2011) and Richard N. Langevin (1935 - 2008), whose strength and wisdom continue to be a source of inspiration. You are both missed every day and I'll do my best to try and "save the oceans" during my lifetime.

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PREFACE

Chapter 1 of this thesis will be submitted for publication in *Deep-Sea Research I* and Chapter 2

will be submitted for publication in *Marine Ecology Progress Series*, and each are formatted

under the guidelines of those specific journal

ACKNOWLEDGEMENTS

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DISTRIBUTION AND FEEDING ECOLOGY OF *BATHYLAGUS EURYOPS* (TELEOSTEI:

MICROSTOMATIDAE) ALONG THE NORTHERN MID-ATLANTIC RIDGE, FROM

ICELAND TO THE AZORES

ABSTRACT

The northern Mid-Atlantic Ridge, from Iceland to the Azores (MAR), ranges in depth

from 800 – 4500 m and extends over an area of 3.7 million km^2. Recent evidence from MAR-

ECO, a Census of Marine Life field project, reported increased abundance and biomass of deep-

pelagic fishes below 1000 m on the MAR. Among the fishes sampled, *Bathylagus euryops* was

found to be the biomass-dominant species and ranked third in total abundance. In this thesis, we

characterize the distribution and feeding ecology of *B. euryops* as a function of physical,

biological, and life history parameters along a mid-ocean ridge system. Multiple biologically

plausible general linear models were fitted to *B. euryops* catch-per-unit-effort (CPUE) data to

investigate the role of various combinations of explanatory variables on the distribution of this

species. Results indicated that a model containing categorical depth and geographic location

variables provided the most parsimonious description of *B. euryops* CPUE data. Vertical

migration analyses were also conducted to investigate the vertical distribution of *B. euryops*

along the MAR and results indicated that time of day had little influence, whereas ontogeny

likely influenced the vertical distribution of *B. euryops*. To describe the feeding ecology of *B.

euryops*, a general diet composition was determined. Multivariate analyses, including a cluster

analysis and a canonical correspondence analysis, were utilized to investigate factors that cause

variability within the diet of *B. euryops*. Results revealed that fish size and geographic location

significantly influenced the diet of *B. euryops*. Furthermore, daily rations were estimated to

better understand the role of *B. euryops* in the food webs of the North Atlantic and results were

consistently estimated to be less than 1% of the average wet weight along the MAR. The general

trend observed was a southward increase in daily ration estimates along the MAR.

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GENERAL INTRODUCTION

The Atlantic Ocean is the second largest of the world's oceans with an area of $87.0 \cdot 10^6$ km^2, or roughly half the size of the Pacific Ocean (Jennings et al., 2001). Depths average 3600 m and are deepest in the Puerto Rico Trench (9560 m). The Atlantic is the only ocean with a major connection to the Arctic Ocean, and hydrography is greatly affected by inflows of the Mediterranean Sea, the Caribbean Sea and the Indian Ocean. The inflows to the Atlantic are balanced by the formation and subsequent outflow of North Atlantic Deep Water, which supplies deep water to all other major oceans via thermohaline circulation. The geological morphology of the oceanic basin in the Atlantic Ocean plays a key role in determining its ecological characteristics. For example, the Mid-Atlantic Ridge blocks the northward spread of Antarctic bottom water and essentially modifies the hydrography of the whole Atlantic (Angel, 1997). The scale of the Mid-Atlantic Ridge (MAR) is so large that, in order to describe, analyze, and predict relationships among the organisms within it, a sensible approach of dividing the whole ecosystem into ecological subsets must be taken (Herring, 2002).

The strongest and most predictable gradients in the open ocean are in the vertical dimension. Many fundamental ecological processes are strongly influenced by the vertical structure of the water column and the associated relationships with depth are typically complex. Vertical gradients are usually related to the density structure of the upper water column. The vertical variability of the open ocean has led to its division into three main oceanic zones, defined here as: the epipelagic zone (generally surface to 200 m), the mesopelagic zone (200 to 1000 m), and the bathypelagic zone (1000 to near the bottom). Interfaces between zones tend to fluctuate with time and space, are neither abrupt nor solid, but ultimately reflect biological responses to varying environmental conditions. With the exception of chemoautotrophy in deep hydrothermal vent or cold seep systems (Ramirez-Llodra et al., 2010), all primary production

occurs in the epipelagic zone, where seasonal variations are evident (Haedrich, 1997). Light from the surface penetrates to about 1000 m, but there is too little for plant growth below 200 m. The mesopelagic zone encompasses most of the primary thermocline, where conditions become much more stable and invariant compared to the surface layers. Water temperature is relatively constant and very low in the mesopelagic zone and nutrient concentrations are typically high. The bathypelagic zone, however, is apparently too deep for sunlight to play a significant role in the behavior and distributions of organisms (Angel, 1997).

Primary production varies greatly in the Atlantic Ocean but in general is extremely high, around 13.7 Pg C per year (Behrenfeld and Falkowski, 1997), and is acutely seasonal. In winter, surface waters are cool through a lack of solar heating, and winter storms cause deep mixing down to 600 – 700 m. Light intensity during the day is low and day length is short, therefore the critical depth (the depth where phytoplankton growth is equivalent to losses) is much shallower than the mixing depth. During this season, respiration greatly exceeds photosynthetic input so the result is a net loss of energy to the system. At the onset of spring, light increases in both intensity and duration, thus driving the critical depth deeper. Storms begin to subside and the increase of light combined with high concentrations of nutrients from previous mixing causes a substantial photosynthetic gain. The spring bloom occurs when positive heat fluxes cause the mixed layer to become shallower in the water column, thus allowing phytoplankton to remain long enough above the critical depth to induce positive growth (Bagniewski et al., 2011). These blooms directly influence the food available to deep-sea fauna through enhanced particle flux (Herring, 2002). Organic particles are also consumed by microbes as they sink into the deep ocean and therefore the speed in which they sink will determine the depth at which the particles can be recycled (Bagniewski et al., 2011). In the summer, growth of the bloom is limited by the

rapid removal of nutrients. Losses due to grazing and sinking during this time are significant and a corresponding increase of organic flocculent can be observed on the seafloor (Lampitt et al., 2010, Martin et al., 2011). During autumn there is a decline in the number of zooplankton grazers, and increased mixing from storms forces the mixed layer deeper, bringing nutrients to the surface. The critical depth is relatively deep and light levels are still high, thus causing a minor secondary phytoplankton bloom.

The fixation of carbon by phytoplankton and its transfer in food webs is strongly related to the production of fished species (Nixon and Buckley, 2002). Previous estimates of capture fisheries production in the Northeast Atlantic Ocean was about 8.6 million tons, ranking it the most productive area in the Atlantic Ocean and fourth most productive when all areas of the world's oceans were considered (FAO, 2010). As coastal fisheries around the world become depleted, commercial fishing has spread to the high seas and deep water in search of the last economically attractive concentrations of fish biomass (Moore, 1999). Although the deep sea is by far the largest ecosystem in the ocean, it is also the least productive and understood (Webb et al., 2010). Topographic features such as seamounts and mid-ocean ridges can support commercially valuable species because these features modify the physical and biological dynamics in ways that enhance and retain food availability (Genin and Dower, 2007). Some species form dense breeding aggregations over seamounts and mid-ocean ridges, therefore increasing biomass concentrations and providing large catches. Most deep-sea fishes have life history characteristics, such as slow growth and late maturity, which make them less resilient than shallow-water fishes to heavy fishing pressure (Norse et al., 2012). It is therefore critical to improve our understanding of the ecosystem processes that govern deep-sea fish population dynamics in order to effectively manage vulnerable species.

Our knowledge of deep-sea ecosystems has increased dramatically since Forbes' 1864 Azoic zone hypothesis, which stated that conditions in the deep sea are so unfavorable that it should be devoid of life (Forbes, 1844). The first effort to examine the occurrence of deep-sea fishes in the world's oceans was the *Challenger* expedition in 1872, which ultimately disproved the Azoic zone hypothesis (Thomson, 1873). Numerous species were described and, with the aid of additional research expeditions, distribution patterns of biota were outlined. Since that time many samples have been taken throughout the world's oceans and we have accumulated enough information to begin to interpret general distribution patterns, particularly for frequently sampled organisms. These patterns can then be linked to hydrographic measurements to investigate environmental drivers of species distributions. While the description of a species' distribution is critical, another important goal is to evaluate how distributions are maintained trophodynamically. These gaps in knowledge were some of the major issues targeted by the Census of Marine Life field project "Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic," MAR-ECO.

The primary aim of MAR-ECO was to describe and understand the patterns of distribution, abundance, and trophic relationships of the organisms inhabiting the mid-oceanic North Atlantic, and to identify and model ecological processes that cause variability in these patterns (Bergstad, O.A., Godø, 2003). Several research expeditions to the Mid-Atlantic Ridge, from Iceland to the Azores, were conducted and results to date have demonstrated that ecosystem processes along the MAR appear to operate differently from 'typical' open ocean ecosystems (Sutton et al., 2008; Vecchione et al., 2010). One of the more surprising findings was a water-column maximum in fish biomass between 1500 and 2300 m (Sutton et al., 2008), which stands in contrast to the typical view that fish biomass declines exponentially with increasing depth

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from the surface in open-ocean ecosystems. Another ecologically significant finding was the apparent influence of the Sub-Polar Front (SPF) on the distribution of various taxa along the MAR. The SPF was the major hydrographic feature observed along the MAR and is characterized by a near-surface frontal zone between cold, nutrient rich waters from the north and warm, saline waters from the south. The ecological processes in this hydrographically interesting area are not well understood and may influence the biogeographic and feeding patterns of deep-sea fauna.

Reported catch numbers from MAR-ECO sampling indicated that *Bathylagus euryops* (Argentiniformes: Microstomatidae) was the biomass dominant species along the MAR and ranked third in total abundance (Sutton et al., 2008). Several studies have described the general distribution and diet of *B. euryops*, however factors that cause variability within their distribution and diet have not been investigated. In general, midwater fishes serve as an important link between zooplankton and higher trophic level predators such as squids, piscivorous fishes, seabirds, and marine mammals (Porteiro and Sutton, 2007). Although there are no current fisheries for *B. euryops*, it is an important prey item for higher trophic levels, including commercially important species such as orange roughy (*Hoplostethus atlanticus*), alfonsino (*Beryx splendens*), and Greenland halibut (*Reinharditus hippoglossoides*) (Mauchline and Gordon, 1984; Chambers and Dick, 2007; Horn et al., 2010). Given the high biomass and abundance observed along the MAR combined with its importance as a prey item, *B. euryops* appears to play an important role in the oceanic food web of the North Atlantic.

The lack of information available for most deep-sea fishes precludes the formulation of proper management plans, thereby exacerbating the long-term effects of exploitation at current levels of fishing (Cotton, 2010). In order to properly manage deep-sea fisheries, managers need

basic ecological information, including but not limited to relative species abundances, distribution patterns, trophic interactions, feeding rates, the influence of ontogeny on distribution and feeding, and the relationship of physical conditions to these biological patterns. In order to address this need, I have provided detailed ecological information for *B. euryops* populations along the MAR. In Chapter 1 of my thesis, I characterize the distribution of *Bathylagus euryops* along the MAR and determine factors that influence this distribution. In Chapter 2, I describe the feeding ecology of *Bathylagus euryops* along the MAR, including their diet, how physical conditions affect their feeding, and calculate a daily ration. All of this information will be useful in advancing our knowledge of the role of *B. euryops* in oceanic food webs. Ideally, this information will be important in the establishment of proper management guidelines for commercially important species that depend upon *B. euryops* as an abundant food source.

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CHAPTER 1

DISTRIBUTION OF *BATHYLAGUS EURYOPS* (TELEOSTEI: MICROSTOMATIDAE)

ALONG THE NORTHERN MID-ATLANTIC RIDGE

Abstract

The northern Mid-Atlantic Ridge (MAR), from Iceland to the Azores, ranges in depth from 800 – 4500 m and extends over an area of 3.7 million km^2. Despite its size, few studies have described the distribution of pelagic fishes along the MAR. Recent evidence from MAR-ECO, a Census of Marine Life field project, reported increased abundance and biomass of deep-pelagic fishes below 1000 m on the ridge, which stands in stark contrast to the traditional view that abundance and biomass decline exponentially with increasing depth in 'typical' open-ocean ecosystems. Among the midwater fishes sampled during the MAR-ECO campaign, *Bathylagus euryops* (Argentiniformes: Microstomatidae) was the biomass-dominant species and ranked third in total abundance. In this paper, we characterize the distribution of *B. euryops* as a function of physical and biological parameters along the MAR. General linear models were fitted to *B. euryops* catch-per-unit-effort (CPUE) data to investigate possible influences on the distribution of this species. Analyses of diel and ontogenetic vertical migrations were also conducted to investigate the occurrence of *B. euryops* frequently observed in the epipelagic zone along the MAR. Results indicated that a model containing categorical depth and geographic location variables provided the most parsimonious description of *B. euryops* CPUE data, and that the vertical distribution of this species is likely related to ontogeny. Due to the high abundance and biomass observed along the MAR, *B. euryops* appears to be an important species in the oceanic food web of the North Atlantic Ocean.

1. Introduction

The deep-pelagic realm, ranging from 200 m below the ocean's surface to just above the sea floor, is the largest habitat on Earth and holds 97% of the global ocean's volume (Tyus, 2012). Generally thought of as one huge, continuous ecosystem, there is significant habitat heterogeneity in the deep sea, as exemplified by mid-ocean ridges and seamounts, which can have important impacts on ecosystem structuring and overall productivity. The Atlantic Ocean contains one of the largest topographic features in the world, the Mid-Atlantic Ridge (MAR). Despite the enormous size of the MAR, few studies have focused on characterizing the distribution of pelagic fauna along it (Vecchione et al., 2010), which, in part, inspired the initiation of the Census of Marine Life field project "Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic," MAR-ECO (Bergstad and Godø, 2003; Bergstad et al., 2008).

Open ocean ecosystems are ultimately dependent upon near-surface productivity for energy transfer to the meso- and bathypelagic zones. Food is extremely scarce in the deep pelagial and must first pass through a suite of vertebrate, invertebrate and bacterial consumers in the mesopelagic zone before reaching the bathypelagic zone. Therefore, there is a decrease in production with increasing distance from the surface. Vertical distribution profiles in the North Atlantic have shown that deep-pelagic zooplankton and micronekton biomass decline exponentially with depth (Angel and Baker, 1982; Reinthaler et al., 2006; Arístegui et al., 2009; Robinson et al., 2010). However, recent evidence of increased abundance and biomass of deep-pelagic fishes below 1000 m on the MAR (Sutton et al., 2008) contradicts the traditional view of vertical structuring in the open ocean. These observations suggest that ecosystems over the MAR are structured differently than 'typical' open ocean ecosystems (Fock et al. 2004; Sutton et al., 2008; Fock, 2009).

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Among the fishes sampled during the 2004 MAR-ECO R/V *G.O. Sars* expedition, *Bathylagus euryops* Goode and Bean 1896 was the biomass-dominant species and ranked third in total abundance (Sutton et al., 2008). Historically, *B. euryops* is known to inhabit the North Atlantic meso- and bathypelagic zones as far north as Greenland, extending south to Bermuda (Mauchline and Gordon, 1983; Cohen, 1984; Møller et al., 2010) and is not known to migrate vertically. However, Scott and Scott (1988) noted that *B. euryops* may be present in other oceans, thus highlighting the uncertainty of even the most basic ecology of this species. The deep-pelagic realm, overall, has been poorly sampled due to the technological challenges and high cost of sampling (Webb et al., 2010). Therefore, knowledge of large-scale horizontal and vertical distributions is limited for most deep-sea taxa, especially fauna in the vicinity of the complex topographic features of the MAR (Vecchione et al., 2010).

A central theme in ocean ecology is the relationship between biological patterns and regional physical conditions (Haedrich, 1997). In the North Atlantic Ocean, physical conditions can vary greatly across a large-scale latitudinal gradient. The open ocean is also structured in the vertical dimension, creating ecologically distinct habitats, and can be delineated by differences in solar illumination, temperature, hydrostatic pressure, and current shear (Angel, 1986; Tyus, 2012). Within these vertically structured habitats, abrupt topographical features, such as seamounts and mid-ocean ridges, can impinge on the deep-pelagic realm (Porteiro and Sutton, 2007). Major topographical features, such as the MAR, are known to influence local and regional circulation patterns (Roden, 1987) and thus can have important implications on the distribution of deep-pelagic organisms and their interactions with benthic fauna.

Along the MAR, Sutton et al. (2008) summarized the occurrence of bathypelagic fishes in the epipelagic zone, including abundant species not known to migrate vertically such as

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Cyclothone microdon and *B. euryops*. Physical factors may contribute to these previously

unobserved occurrences; however, behavioral or biological factors such as vertical migration

(both diel and ontogenetic) must also be considered. In this paper, we describe the distribution

of *B. euryops* over the MAR relative to hydrography, prey availability, ontogeny, and diel

patterns to understand better the influence each factor has on the habitat utilization of this

biomass-dominant species.

2. Methods

Specimens were collected during two separate MAR-ECO expeditions. The first was

Leg 1 of the R/V *G.O. Sars* expedition (Bergstad et al., 2008), 5 June – 3 July, 2004 from

Iceland to the Azores. Sampling occurred at 18 predefined stations along the MAR with

coverage across four different ridge sections (Fig. 1): Reykjanes Ridge (RR), Charlie-Gibbs

Fracture Zone (CGFZ), Faraday Seamount Zone (FSZ), and Azorean Zone (AZ). Vertical

profiles from the surface to near-bottom were generated with a CTD at all stations to characterize

the physical and chemical environment at the time of biological sampling (Søiland et al., 2008).

The CTD had dual sets of temperature and conductivity sensors, an Aquatracker III fluorometer

and a SeaBird oxygen sensor (SBE43). All sensors were calibrated prior to the research cruise.

The second expedition to the MAR was conducted aboard the NOAA FSV *Henry B.*

Bigelow, 12 June – 17 July, 2009. The objective of this expedition was to sample the fauna of

the near the Sub-Polar Front (SPF) region as previous studies indicated that the SPF influences

the faunal distribution of assemblages along the MAR (Hosia et al., 2008; Sutton et al., 2008;

Vecchione et al., 2010). Comparative day/night sampling occurred at 11 stations in two

transects, one with five stations northwest of the CGFZ, and one with six stations southeast of

the CGFZ (Fig. 2). Target depths were selected based on bottom depth with the goal to standardize the depth zones sampled to match those on the *G.O. Sars* cruise.

2.1. Trawl Sampling

Samples for this study were collected using a double-warp midwater 'Krill' trawl (6×6 m mouth opening, 6-mm mesh, stretched) deployed with standard pelagic trawl doors. The total trawl length from mouth to cod end was 45 m and the net was equipped with a multi-sampler (remotely operated multiple cod ends) with five 30-m long cod ends that enabled five discrete-depth samples per tow. Each cod end was rigged with a 7-L hard collection receptacle, in order to reduce physical damage to the organisms sampled. Additionally, the trawl was equipped with SCANMAR sensors to provide data on net mouth configuration and depth.

Sampling was performed along an oblique trajectory, from 3000 m to the surface, and nets were remotely opened and closed based on command from the ship during the 2004 expedition and a programmed timer was used during the 2009 expedition. The trawl was towed at an average speed of 2.2 knots and the duration that each depth stratum was sampled ranged between 10-40 minutes. The volume of water filtered was subsequently calculated for each cod end based on the door spread distance, speed of the ship during each sampling event, and duration of each sampling event. Further methodological details can be found in Wenneck et al. (2008).

In total, 113 discrete-depth samples were collected during the two research expeditions and used to characterize the distribution of *B. euryops* along the MAR. Samples were typically collected within one of five depth zones: (1) 0-200 m, (2) 200-750 m, (3) 750-1500 m, (4) 1500-2300 m and (5) >2300 m. Time of day was classified as day (D) or night (N) for each sample

based sunrise and sunset times for each sampling location. Samples that were collected during 'twilight' hours (one hour before and after sunrise/sunset), were not included in analyses where time of day was concerned. Following trawl retrieval, the catch was sorted by individual cod ends, corresponding to the depth stratum sampled, into major taxonomic groups which were further identified to species level.

2.2. Sample handling

During the 2004 *G.O. Sars* expedition, species abundance and total biomass (± 0.1 g) were recorded for each cod end and specimens were frozen at -20 °C at sea. When taxonomic identity was uncertain, specimens were preserved in 10% formalin and later identified at the Bergen Museum of Zoology, http://collections.uib.no/vertebrate/, the permanent repository for all pelagic fishes sampled during the 2004 expedition. During the 2009 *Henry B. Bigelow* expedition, *B. euryops* specimens were enumerated, measured (standard length, ± 0.1 mm), weighed individually (wet weight, ± 0.1 g), and frozen at -80 °C at sea. All pelagic fishes collected during this expedition were then stored at the Virginia Institute of Marine Science.

2.3. Statistical analyses

Fish abundance data collected during the 2004 *G.O. Sars* cruise were standardized into catch-per-unit-effort (CPUE) (individuals $\cdot 10^{-3} \cdot m^{-3}$ water filtered) and analyzed using general linear models (GLM). A GLM is defined by the underlying statistical distribution for the response variable and how a set of linearly related explanatory variables correspond to the expected value of the response variable (Maunder and Punt, 2003). The linear relationship

between explanatory variables and some function of the expected value of the response variable is given by:

$$g(\mu_i) = \mathbf{x}_i^T \boldsymbol{\beta} \ , \tag{1}$$

where $\mu_i = E(Y_i)$ with Y_i defined as the ith value of the response variable, $\mathbf{x}_i$ is the vector of associated explanatory variables, $\boldsymbol{\beta}$ is a vector of estimated parameters, and g is the differentiable monotonic link function that governs the relationship (linear or nonlinear) between the random (μ_i) and systematic ($\mathbf{x}_i^T \boldsymbol{\alpha}$) components of the model (McCullagh and Nelder, 1989; Maunder and Punt, 2003).

Histograms of raw CPUE data by ridge section and depth zone were consistently positively skewed which provided some evidence that the CPUE data may be lognormally distributed. Visual examination of QQ plots of normality and residuals plots for preliminary model fits assuming normally and lognormally distributed CPUE data provided additional support for application of a lognormal GLM (Zuur et al., 2010). Given the need for log transformation, a constant of 10^{-5} was added to all CPUE values to adjust for zero catches while maintaining the relative scale and the distributional shape of the data (note that model results were generally insensitive to the value of the constant added).

In an effort to identify the most parsimonious description of the CPUE data, seven model parameterizations were fitted where each reflected a unique hypothesis about the effects of various combinations of explanatory variables: M_1 included depth zone, M_2 contained ridge section, M_3 included both depth zone and ridge section, M_4 contained depth zone, ridge section, and the depth*ridge interaction, M_5 included depth zone, ridge section, and prey abundance

(derived from Amphipoda, Decapoda, Euphausiacea, and Cnidaria data collected with 'Krill'

trawl during cruises that were potential prey types for *B. euryops*; Vecchione et al., unpublished

data), M_6 included depth zone, ridge section, prey abundance, and the depth*prey interaction,

and M_7 included depth zone, ridge section, prey abundance, depth*prey, and depth*ridge

interactions. Other explanatory variables, including temperature, salinity, and depth from

bottom, were also investigated during preliminary analyses of the data, but were ultimately not

included in the parameterization analysis due to lack of significance. Using model M_5 as an

example (full main effects model), the exact structure is given by:

$$\log_e(\text{CPUE} + 10^{-5})_{drtp} = \beta_0 + \beta_d x_d + \beta_r x_r + \beta_t x_t + \beta_p x_p + \varepsilon_{drtp}, \tag{2}$$

where d, r, t, p index the depth zone (five levels), ridge section (four levels), and prey abundance

variables, respectively, and ε_{drtp} are the error terms. The identity link function was applied for all

fitted models.

Model comparisons were made using Akaike's Information Criterion corrected for small-

sample size (AIC_c):

$$AIC_c = -2\log(\hat{L}) + 2k + \frac{2k(k+1)}{n-k-1}, \tag{3}$$

where $\hat{L}$ is the estimated maximum likelihood value, k is the number of model parameters, and n

is the total sample size. The most parsimonious model of a given set has the lowest AIC_c value,

and because AIC_c is on a relative scale, it is important to calculate AIC differences (ΔAIC):

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$$\Delta AIC_c = AIC_c - AIC_{c\,min},\tag{4}$$

where $AIC_{c\,min}$ is the smallest AIC_c value within the candidate set of models. Generally, ΔAIC values between 0 and 2 are indicative of substantial empirical support for the fitted model, values between 4 and 7 are associated with models that have considerably less empirical support, and values >10 suggest virtually no empirical support (Burnham and Anderson, 2002). Predicted mean CPUEs were generated from the best fitting model by back transforming and multiplying by the bias correction term of $\exp(0.5\hat{\sigma}^2)$, where $\hat{\sigma}^2$ is the estimated residual error. Standard errors of the predicted mean CPUEs were estimated using a standard jackknife routine (Efron, 1981).

The occurrence of *B. euryops* in the epipelagic zone along the MAR is atypical for the species. Utilizing CPUE data from the 2009 FSV *Henry B. Bigelow* expedition, the possibility of *B. euryops* undergoing a diel vertical migration was investigated. Again, a log transformation was required to meet the assumptions of analysis with linear models, so a constant of 10^{-5} was added to all CPUE values to adjust for zero values associated with the catch data. The influence of time of day on the vertical distribution of *B. euryops* was examined using a general linear model of the following structure:

$$\log_e(CPUE + 10^{-5})_{ds} = \beta_0 + \beta_d x_d + \beta_s x_s + \varepsilon_{ds}\tag{5}$$

where d and s index the depth zone (five levels) and time of day (two levels) variables, respectively, and ε_{ds} are the error terms. The identity link function was again applied.

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Changes in vertical distribution as a result of ontogenetic habitat shifts could also explain the occurrence of *B. euryops* in surface waters near the Charlie-Gibbs Fracture Zone. Another general linear model was utilized to investigate this possibility with data from the *Henry B. Bigelow* expedition, where fish size (standard length, mm) was modeled as a function of depth to further elucidate patterns in the vertical distribution of *B. euryops*. QQ plots of normality and residuals plots for preliminary model fit assuming normally distributed fish size data were visually examined and demonstrated a normal distribution of the response variable and a reasonable model fit. The exact structure of the linear model with the identity link function is as follows:

$$\text{Fish Size}_d = \beta_0 + \beta_d x_d + \varepsilon_d \tag{6}$$

where d indexes the depth zone (five levels) variable and ε_d are the error terms.

Analyses of variance (ANOVA) was applied to the best fitting general linear model to facilitate post-hoc comparisons (pairwise *t-tests*) of mean CPUEs or fish sizes within treatment levels (e.g. depth, ridge section). A Bonferroni adjustment was applied to the pairwise *t-tests* to control for Type I error ($\alpha = 0.05$).

3. Results

Bathylagus euryops represented ~8% (n=4,543) of the total fish catch and ~25% (190,027 g ww) of the total biomass sampled during the 2004 *G.O. Sars* expedition (Sutton et al., 2008). During the 2009 *Henry B. Bigelow* expedition, *B. euryops* were < 2% of the catch (n=243), but contributed ~20% of the total pelagic fish biomass (6,436 g ww). Individual fish length were not

recorded during the *G.O. Sars* expedition, but ranged from 24.0 – 229.1 mm during the *Henry B. Bigelow* expedition.

Composite remote-sensing images identified the position of the Sub-Polar Front (SPF), which was near 52 °N, although the southern boundary of the SPF was very indistinct (Søiland et al., 2008). Additionally, four different hydrographic regions were identified in the upper 500 m along the MAR. Modified North Atlantic Water dominated at all stations north of 57 °N on the Reykjanes Ridge. Stations south of 57 °N, but north of the SPF, were dominated by Sub Arctic Intermediate Water. South of the SPF, a mixture of North Atlantic Modified Water and Sub Arctic Intermediate Water was observed and formed a complex pattern of eddies to 50 °N. At all stations south of 50 °N, the predominant surface water mass was North Atlantic Central Water (Vecchione et al., 2010).

Based on AIC_c and thus ΔAIC_c, model M_3 received the most empirical support, followed closely by model M_5. There was considerably less support for models M_4 and M_6 and virtually no support for models M_1, M_2, and M_7 (Table 1). Model M_3 contained depth and ridge section as explanatory variables and all of the estimated β_i coefficients associated with the various levels of those categorical variables, except that for depth zone 5 (> 2300 m), were statistically significant (Table 2). The model intercept, β_0, is the reference level of the depth and ridge section variables and it was defined to be the epipelagic zone in the AZ. Relative to the intercept estimate, all other estimated coefficients were positive and fairly large in magnitude, which suggests that the estimated CPUE of *B. euryops* is higher at all other depths and ridge sections sampled. The highest estimated CPUEs occurred in depth zone 3 (750 – 1500 m) and at the CGFZ, with the next highest estimated CPUEs being within depth zone 4 (1500 – 2300 m) and at the RR (note that these were similar in magnitude to the highest). Prey availability indices, which included

various genera of amphipods, decapod shrimp, euphausiids and coronate jellyfish, were not useful in explaining the distribution of *B. euryops* along the MAR.

ANOVA results based on M_3 revealed that both ridge section (F-value: 14.07, $p < 0.05$) and depth (F-value: 9.35, $p < 0.05$) had a significant effect on the mean CPUE of *B. euryops*. Post-hoc multiple comparisons applied to the four sections highlighted significant differences in the mean CPUE of *B. euryops* between the AZ and the two northern ridge sections (RR, $p < 0.05$ and CGFZ, $p < 0.05$). Mean CPUE differed weakly between the AZ and the FSZ ($p = 0.106$) and all other ridge section multiple comparisons were not significant. Similar multiple comparisons applied to the five depth strata resulted in significant differences in the mean CPUE of *B. euryops* in the epipelagic zone when compared to the mean CPUE at depth zones 2, 3, and 4 ($p < 0.05$). No significant differences were detected between the epipelagic zone and depths zone 5 ($p = 1.00$) and all other depth strata multiple comparisons also demonstrated no significant differences.

The diel vertical migration model contained solar cycle and depth zone as explanatory variables, and of the estimated β_i coefficients associated with the levels of those variables, only depth zone 3, was statistically significant (Table 3). The intercept reference level, β_0, was defined to be the epipelagic zone during the day. Relative to the intercept estimate, the estimated coefficient for night was negative, which suggests that CPUEs observed during the night were lower than those observed during the day. Concurrent day/night sampling during the *Henry B. Bigelow* expedition revealed that solar cycle did not significantly influence the vertical distribution of *B. euryops* at the CGFZ (F-value: 0.15, $p = 0.71$).

The ontogenetic model, with fish size as the response variable, contained depth as the only explanatory variable. Of the estimated β_i coefficients associated with the various levels of

the categorical depth variable, depth zones 3 (750 – 1500 m), 4 (1500 – 2300 m), and 5 (> 2300 m) were statistically significant (Table 4). The model intercept, β_0, is the reference level of the depth variable and was defined to be the epipelagic zone. All estimated coefficients were positive relative to the intercept estimate, meaning that there was a consistent increase in fish size with increasing depth from the surface. As such, the lowest estimated mean standard length occurred in surface waters whereas the highest estimated mean standard length occurred in the deepest depth zone. ANOVA results of the ontogenetic model further illustrated a significant relationship between fish size and depth   (F = 6.93, p < 0.05) and predicted means relative to each depth zone were plotted in Figure 4. Multiple comparisons statistics revealed that the mean size of *B. euryops* were significantly smaller in the epipelagic zone than in depth zone 4 (1500 – 2300 m; p < 0.05) and depth zone 5 (> 2300 m; p < 0.05). Similarly, fish size was significantly larger in depth zone 4 (1500 – 2300 m) when compared to those in depth zone 2 (200 – 750 m; p < 0.05) and depth zone 3 (750 – 1500 m; p < 0.05).

4. Discussion

4.1. Along-ridge distribution patterns

The analyses performed on the discrete-depth trawl samples collected during the MAR-ECO campaign represent the largest-scale geographical and vertical examination of the distribution of *B. euryops* to date. Results from the linear model analyses of CPUE revealed that a linear model containing depth and ridge section as explanatory variables (M$_3$) provided the most empirical support and that depth and ridge section were significant factors in the distribution of *B. euryops* along the MAR. In general, the vertical distribution patterns of *B. euryops* observed on the MAR agree with reported occurrences elsewhere in the North Atlantic.

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Previous studies have reported *B. euryops* occurrences between 500 and 3000 m depth (Cohen, 1964; Mauchline and Gordon, 1983; Moore, 2003), indicating a degree of depth structuring for this species. The fact that a deep-sea species' distribution is structured, in part, by depth is not too surprising as vertical zonation of pelagic fishes has been observed in all parts of the world's oceans (Haedrich and Merrett, 1988). However, the view of fishes zoned by depth is far too simplistic considering depth is a multivariate factor. Instead, deep-sea fish distributions are more likely linked to interacting physical gradients that act in concert with increasing depth from the surface (Angel, 1986), with the effects of individual physical elements being hardly separable from one another (Backus, 1986).

A clear geographic pattern was observed in the distribution of *B. euryops*, with maximum total integrated abundances occurring at the SPF/Charlie-Gibbs Fracture Zone area and declining southward to the Azorean Zone. Sutton et al. (2008) observed that the strongest differences in overall fish abundance and biomass were between the Azorean Zone and the two northern ridge sections (RR and CGFZ), which agrees with findings from this study (Fig. 3). Overall abundance of *B. euryops* was lowest at the Azorean Zone, where nearly all fish were sampled below 1500 m. The presence of *B. euryops* throughout the entire water column in the higher latitudes combined with the exclusion of *B. euryops* from the mesopelagic zone in the lower latitudes exemplifies the principles of tropical submersion, which has also been observed in other deep-sea fishes such as ceratioid anglerfishes (Helfman et al., 2009). However, additional sampling south of the Azores would be necessary to corroborate the concept of tropical submersion and a subsequent extension of *B. euryops* distributions into the South Atlantic Ocean. Alternatively, the Azorean Zone may be approaching the faunal boundaries of *B. euryops*. Vecchione et al. (2010) noted that along-ridge abundance patterns appear associated

with water-mass distributions and circulation features, however depth and topography likely play additional major structuring roles. Although there appeared to be an association of *B. euryops* with the Sub-Polar Front region, our observations are inferred from a small snapshot in time. The SPF varies both spatially (48-53°N) and temporally, and hence more information is needed to understand how the distribution of *B. euryops* varies in time relative to hydrographic frontal zones.

Findings from MAR-ECO have identified the SPF/Charlie-Gibbs Fracture Zone area as a region of maximum chlorophyll *a* concentrations (Gaard et al., 2008), where along-ridge abundance maximums were observed for a variety of taxa, including *Calanus* (Gislason et al., 2008) and *Paraeuchaeta* copepods (Falkenhaug et al, 2007), chaetognaths (Pierrot-Bults, 2008), gelatinous zooplankton (Youngbluth et al., 2008), and based on results from this study, *B. euryops* as well. Food supply is a major factor that influences the distribution and abundance of deep-sea fishes (Tyus, 2012), and all of the taxa listed above are known prey types in the diet of *B. euryops* (Mauchline and Gordon, 1983). Given the overall scarcity of food in the deep-sea, Genin (2004) postulated a trophodynamic mechanism, termed the 'topographic blockage' hypothesis, which suggests that seamounts and mid-ocean ridges are able to support enhanced standing stocks of fishes. The mechanism is related to the daily 'gap formation' of zooplankton over abrupt topographic features (Genin et al., 1994). During the night, zooplankton are advected over the summits of seamounts by near-surface currents. At dawn, the descent of the vertically migrating zooplankton is blocked by the shallow bottom and these areas typically correlated with high abundance of predators. The predators then feed on the trapped zooplankton, significantly reducing their numbers, and setting the stage for a gap formation where few zooplankton remain to ascend to the seamount summit the following evening.

Although this mechanism would most benefit site-attached demersal fishes, it may also have key implications for pelagic zooplanktivorous fishes like *B. euryops*. Wilson (1992) demonstrated with a time series of acoustic transects that sound scattering micronekton and fishes were able to maintain their position above the SE Hancock seamount despite strong currents that should have displaced the organisms to the surrounding deep waters. The ability to maintain location on the seamount, coupled with the observed year-long increase in body size of an apparent cohort of *Maurolicus muelleri* (Boehlert et al, 1994), indicated that the aggregations of micronekton and fish over the SE Hancock seamount were resident (Genin, 2004). Pelagic fishes would most certainly need to expend more energy relative to demersal fishes to stay near structure. For the 'topographic blockage' mechanism to hold true for pelagic fishes, the energy lost in maintaining their position against strong currents would need to be compensated by the enhanced trophic subsidy to these fishes. However, the prey availability index used in this study was not useful in explaining the distribution of *B. euryops*, likely due to gear constraints which lead to an inadequate representation of the prey field as it relates to *B. euryops*. Specifically, the mesh size of the 'Krill' trawl (6 mm, stretched) likely under-sampled a majority of the smaller mesozooplankton (2-5 mm) that *B. euryops* primarily consumes. Furthermore, the physical act of net sampling often destroys delicate gelatinous zooplankton (Harbison, 1986), an important prey group of *B. euryops*, and thus more accurate abundance estimates are needed to fully explore the role of prey availability in structuring the distribution of *B. euryops*.

4.2. Diel vertical migration

One unusual finding in this study was the presence of *B. euryops* in the epipelagic zone along the MAR, occasionally in large numbers. This either represents a new vertical range

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extension for the species, or the multi-sampler attached to the 'Krill' trawl was prone to selective contamination. Sutton et al. (2008) argued that the occurrence of bathypelagic fish in the upper 200 m was not artifactual during the 2004 *G.O. Sars* expedition. During the 2009 *Henry B. Bigelow* expedition, the observation of a variety of bathypelagic fauna, including *B. euryops*, in the epipelagic zone, led to post-hoc sampling of surface waters in an effort to investigate the contamination question. Consequently, catch observations from the post-hoc sampling effort of the epipelagic zone revealed that the presence of numerous bathypelagic taxa in surface waters was a biological signal and not an artifact of selective contamination. The occurrence of deep-pelagic fishes in surface waters is yet another indication that the abundance patterns and distribution of deep-pelagic fishes over the MAR is different from a 'typical' open-ocean ecosystem. Analysis of catch data based on day/night sampling revealed that the presence of *B. euryops* in the epipelagic zone was probably not due to an active diel vertical migration. From a physiological perspective, fishes with lipid-filled swimbladders are capable of extensive vertical migrations, whereas those with gas-filled swimbladders typically undergo reduced vertical migrations due to difficulties in secreting gas at very high pressures (Herring, 2002). The lack of a swimbladder in its entirety in *B. euryops*, coupled with greatly reduced musculature, would make an active diel vertical migration energetically demanding. Thus, it is not likely that solar cycle played a significant role in the vertical distribution of *B. euryops*.

4.3. Ontogenetic migration

In most, if not all midwater oceanic fishes, early development occurs in near surface waters followed by a descent into deeper zones (Pietsch, 2009). However, like most deep-sea fishes, early life history information is generally lacking for *B. euryops* (Fahay, 2007) and this

represents a critical knowledge gap in our understanding of its distribution. Results from this study revealed a significant positive relationship between fish size and depth, with smaller fish occurring in surface waters and larger individuals occurring at greater depth. Eggs of *B. euryops* have multiple oil globules (Ahlstrom et al., 1984) and larvae are elongate, with large fin folds and stalked eyes (Kenaley and Hamilton, Jr., 2006). These physiological traits are characteristic of an early life history adapted to conditions in surface waters. Oil globules in eggs are less dense than the surrounding water, thus providing lift and causing the eggs to ascend (Balon, 1975). The larval form of *B. euryops* optimizes its surface to volume ratio with temporary characters (e.g. large fin folds, stalked eyes) that reduce the tendency to sink, since drag is directly proportional to the surface area of an object (Pelster, 1997). By reducing the tendency to sink, the ability of larval *B. euryops* to locate food and grow quickly is enhanced in the productive waters of the euphotic zone. Findings from this study support the few, documented early life history patterns of *B. euryops*, indicating that a gradual ontogenetic migration occurs from the surface down to the bathypelagic realm. Thus, the presence of *B. euryops* in the epipelagic zone along the MAR is likely a function of early life history, and the overall range of the vertical distribution of *B. euryops* should subsequently be extended into surface waters.

5. Conclusion

The analyses of the distribution of *B. euryops* presented in this study as a function of life history characteristics and environmental variables provides valuable insights into the structure of deep-sea ecosystems along the understudied MAR. However, the task of determining distribution patterns in an ecosystem as large and deep as the MAR requires an integrated sampling approach, including obtaining information on ontogenetic and spatial changes in

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distribution. The patterns described in the present study are merely snapshots from the summer, after the peak in primary production from the spring bloom had already occurred. The primary remaining gaps in the knowledge of distribution patterns of *B. euryops* along the MAR is the determination of temporal patterns (seasonal and interannual) and resolving the influence of hydrography and water masses.

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Table 1. Fit statistics associated with the seven models fitted to the *Bathylagus euryops* catch-per-unit-effort data (individuals / $10^3 \cdot m^3$ collected at the northern Mid-Atlantic Ridge during the 2004 RV G.O. Sars expedition: model number, explanatory variables included in the model, -2 log($\hat{L}$), number of parameters, Akaike's Information Criterion for small sample size (AICc), and ΔAICc. Depth corresponds to the five depth zones sampled including 0-200 m, 200-750 m, 750-1500 m, 1500-2300 m, and >2300 m. Ridge corresponds to the four ridge sections sampled including Reykjanes Ridge, Charlie-Gibbs Fracture Zone, Faraday Seamount Zone, and Azorean Zone. Prey abundance (was derived at each depth zone/ridge section combination utilizing 'Krill' trawl catch data for amphipods, decapod shrimp, euphausiids, and cnidarians.

Model no.	Explanatory variables	-2 log($\hat{L}$)	No. of Parameters	AICc	ΔAIC$_c$
1	Depth	308.2	6	321.2	28.5
2	Ridge	308.8	5	319.5	26.8
3	Depth, Ridge	272.1	9	292.7	0.0
4	Depth, Ridge, Depth*Ridge	249.0	19	301.5	8.8
5	Depth, Ridge, Prey	270.0	10	293.2	0.5
6	Depth, Ridge, Prey, Depth*Prey	265.6	14	300.6	7.9
7	Depth, Ridge, Prey, Depth*Prey, Depth*Ridge	238.1	24	312.4	19.7

Table 2. Parameter estimates, estimated standard errors (SE), t-values associated with the test of the null hypothesis that β_i is equal to zero, and corresponding p-values obtained from model M_3 fitted to *Bathylagus euryops* catch-per-unit-effort data (individuals $\cdot 10^{-3} \cdot m^{-3}$) collected at the northern Mid-Atlantic Ridge during the 2004 RV *G.O. Sars* expedition. The parameter β_0 is the reference level of the depth and ridge section variables and defined to be depth zone 1 (epipelagic) within the Azorean Zone, the parameters β_{d2} through β_{d5} are the estimated effects on CPUE for depth zones 2-5 (200-750 m, 750-1500 m, 1500-2300 m, and >2300 m, respectively) relative to the depth zone 1, and the parameters β_{CGFZ}, β_{FSZ}, and β_{RR} are the estimated effects on CPUE for ridge sections Charlie-Gibbs Fracture Zone, Faraday Seamount Zone, and Reykjanes Ridge relative to the Azorean Zone. The estimated residual error, $\hat{\sigma}^2$, was 4.12.

Parameter	Estimate	SE	t-stat	p-value
β_0	-11.03	0.67	-16.41	< 0.001
β_{d2}	2.91	0.72	4.05	< 0.001
β_{d3}	4.11	0.76	5.43	< 0.001
β_{d4}	4.07	0.76	5.38	< 0.001
β_{d5}	1.04	1.03	1.01	0.31
β_{CGFZ}	3.95	0.67	5.92	< 0.001
β_{FSZ}	3.19	0.85	3.74	< 0.001
β_{RR}	3.60	0.69	5.22	< 0.001

Table 3. Parameter estimates, estimated standard errors (SE), t-values associated with the test of the null hypothesis that β_i is equal to zero, and corresponding p-values obtained from diel vertical migration model fitted to *Bathylagus euryops* catch-per-unit-effort data (individuals$\cdot 10^{-3} \cdot m^{-3}$) collected at the Charlie-Gibbs Fracture Zone during the 2009 FSV *Henry B. Bigelow* expedition. The parameter β_0 is the reference level of the time of day and depth variables and defined to be depth zone 1 (epipelagic) during the daytime, the parameters β_{d2} through β_{d5} are the estimated effects on $\log_e(CPUE)$ for depth zones 2-5 (200-750 m, 750-1500 m, 1500-2300 m, and >2300 m, respectively) relative to the depth zone 1, and the parameter β_{night} is the estimated effect on $\log_e(CPUE)$ at night relative to the daytime.

Parameter	Estimate	SE	t-stat	p-value
β_0	-5.12	1.53	-3.35	< 0.05
β_{night}	-0.69	1.17	-0.59	0.56
β_{d2}	2.61	1.67	1.56	0.13
β_{d3}	3.73	1.74	2.14	< 0.05
β_{d4}	2.42	2.08	1.16	0.25
β_{d5}	-0.56	2.08	-0.27	0.79

Table 4. Parameter estimates, estimated standard errors (SE), t-values associated with the test of the null hypothesis that β_i is equal to zero, and corresponding p-values obtained from ontogenetic vertical migration model fitted to *Bathylagus euryops* standard lengths (mm) collected at the Charlie-Gibbs Fracture Zone during the 2009 FSV *Henry B. Bigelow* expedition. The parameter β_0 is the reference level of the depth variable and defined to be depth zone 1 (epipelagic), the parameters β_{d2} through β_{d5} are the estimated effects on standard lengths for depth zones 2-5 (200-750 m, 750-1500 m, 1500-2300 m, and >2300 m, respectively) relative to the depth zone 1.

Parameter	Estimate	SE	t-stat	p-value
β_0	58.87	25.21	2.34	< 0.05
β_{d2}	35.90	26.09	1.38	0.17
β_{d3}	52.93	25.56	2.07	< 0.05
β_{d4}	96.48	27.96	3.45	< 0.05
β_{d5}	96.86	33.34	2.91	< 0.05
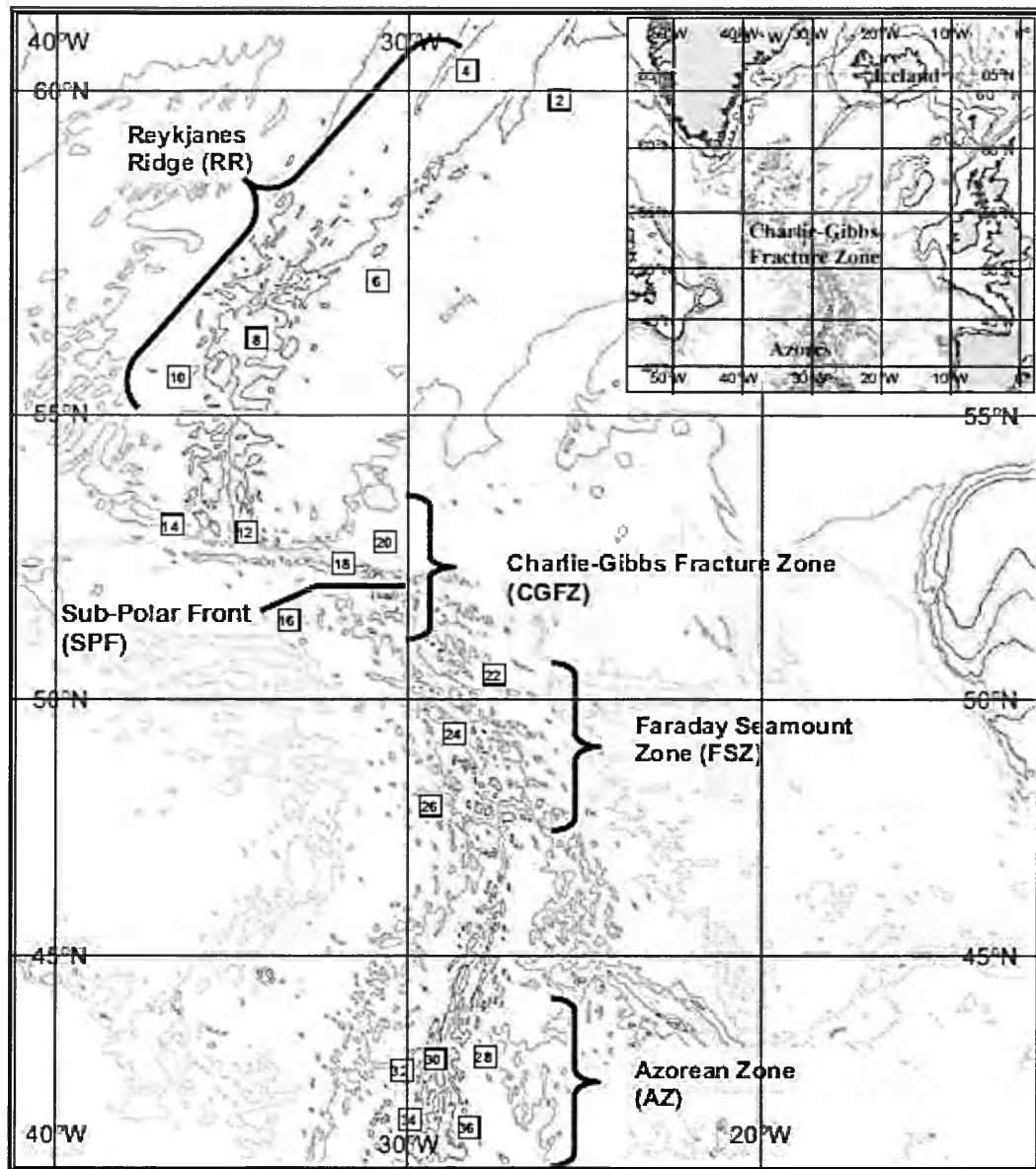
Figure 1. Trawl sampling stations for Leg 1 of 2004 R/V *G.O. Sars* MAR-ECO expedition to the Mid-Atlantic Ridge, from Iceland to the Azores (adapted from Sutton et al., 2008).
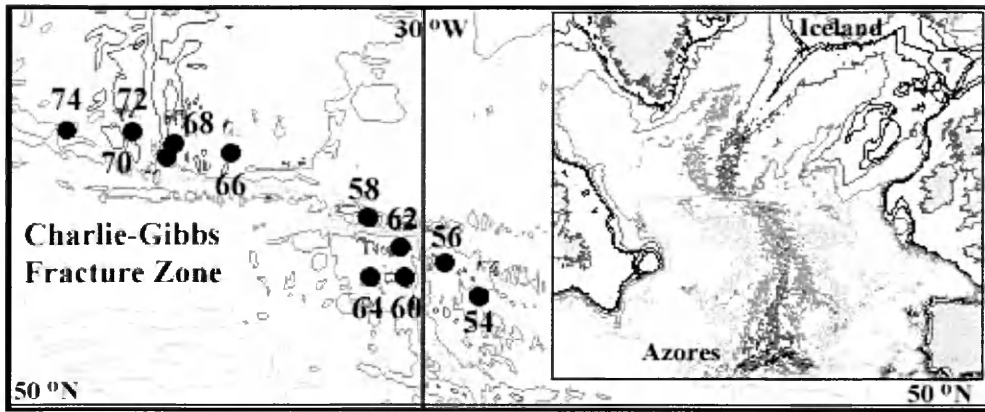
Figure 2. Cruise path and trawl sampling locations during the 2009 FSV *Henry B. Bigelow* MAR-ECO expedition to the Charlie-Gibbs Fracture Zone. Box at right shows the northern Mid-Atlantic Ridge, from Iceland to the Azores, with Charlie-Gibbs Fracture Zone offset at the center.

Reykjanes Ridge

Charlie–Gibbs Fracture Zone

Faraday Seamount Zone

Azorean Zone
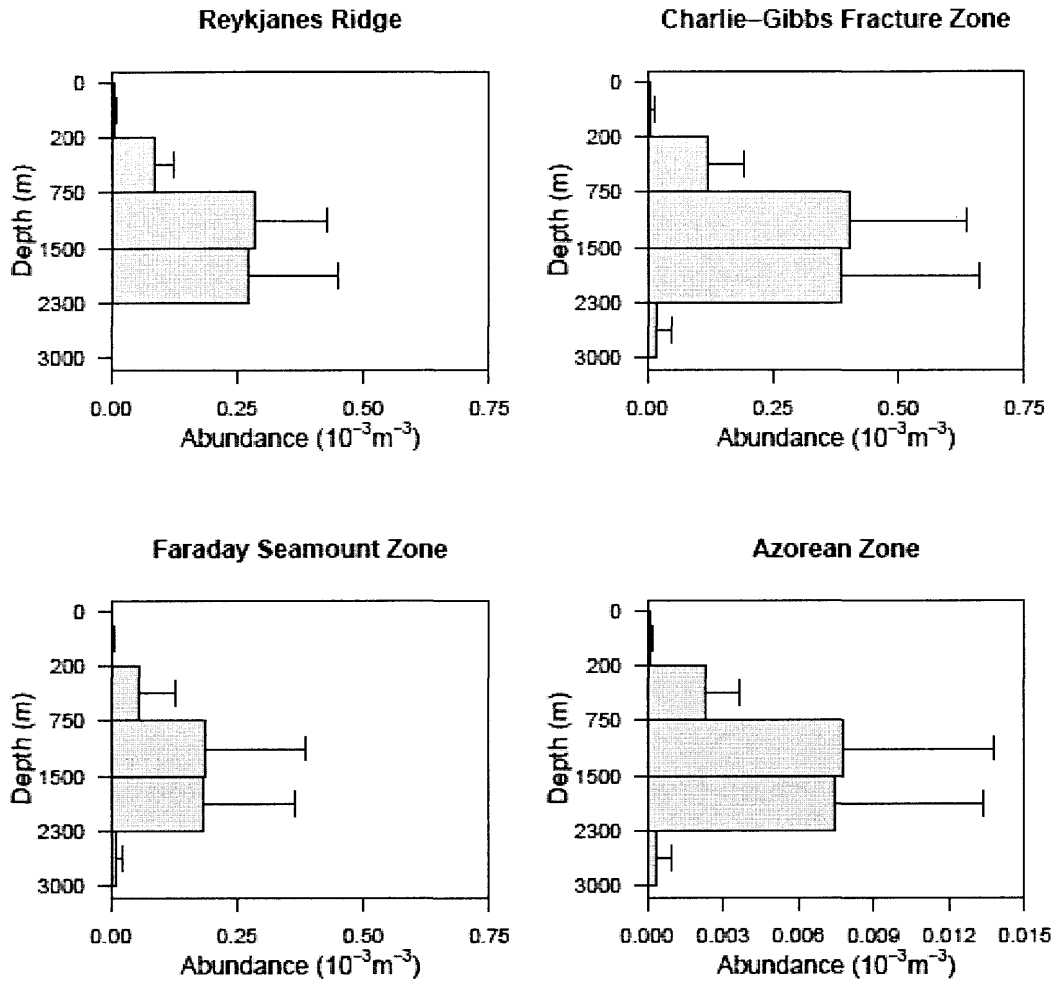
Figure 3. Predicted catch (individuals / $10^3 \cdot m^3$) of *Bathylagus euryops* per depth zone at each ridge section sampled along the MAR during the 2004 RV *G.O. Sars* expedition. Predicted catch based on GLM regression containing depth zone and ridge section as explanatory variables. Error bars represent standard error of the predicted CPUE values at each depth zone relative to the four ridge sections. Note: scale of the x axis at the Azorean Zone is an order of magnitude smaller than the other ridge sections.
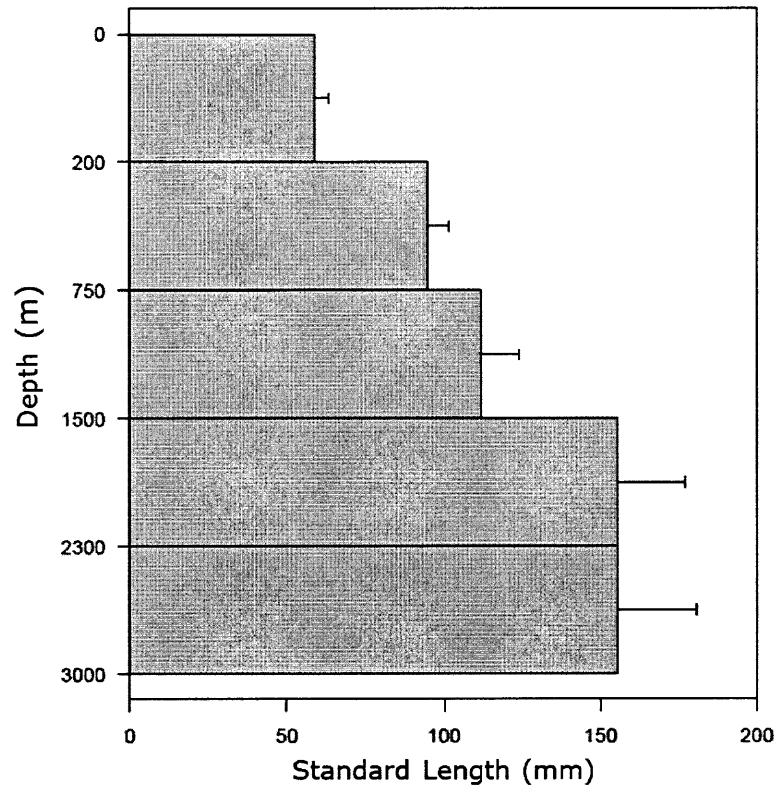
Figure 4. Predicted mean standard length of *Bathylagus euryops* relative to the depth zones sampled at the Charlie-Gibbs Fracture Zone. Error bars represent standard error of the predicted mean standard length values relative to depth zone. Results based on 46 discrete-depth 'macrozooplankton' trawl samples from 2009 FSV *Henry B. Bigelow* expedition.

CHAPTER 2

FEEDING ECOLOGY OF *BATHYLAGUS EURYOPS* (TELEOSTEI: MICROSTOMATIDAE)

ALONG THE NORTHERN MID-ATLANTIC RIDGE

ABSTRACT

The northern Mid-Atlantic Ridge, from Iceland to the Azores (MAR), is a massive ecosystem, yet despite its size few studies have described the feeding ecology of pelagic fishes along the ridge. Recent efforts from MAR-ECO, a Census of Marine Life field project, aimed to address this lack of knowledge. Among the midwater fishes sampled during the MAR-ECO campaign, *Bathylagus euryops* (Argentiniformes: Microstomatidae) was the biomass-dominant species and ranked third in total abundance. In this paper, we describe the feeding ecology of *B. euryops* as a function of life history and spatial parameters. Furthermore, daily ration estimates were generated based on different temperature and geographic location combinations. Multivariate analyses, including a cluster analysis and a canonical correspondence analysis, revealed that fish size and geographic location significantly influenced the diet of *B. euryops*. Furthermore, daily rations were consistently estimated to be less than 1% of the average wet weight of *B. euryops* along the MAR. The general trend observed was a southward increase in daily ration estimates along the MAR. Due to its high abundance and biomass observed along the MAR, *B. euryops* appears to be an important species in the oceanic food web of the North Atlantic Ocean.

I. Introduction

In the deep pelagic realm, little is known about how organisms acquire food necessary to sustain their metabolic needs. Knowledge about trophic interactions is the key to understanding how energy is transferred from the productive epipelagic zone to the meso- and bathypelagic zones. Because primary production is concentrated in the epipelagic zone, except in chemosynthetic systems, all life in the ocean is supported by the downward transfer of organic matter from the euphotic zone (Angel 1997). Because most productivity occurs in surface waters, sinking particle flux and biomass is thought to decrease exponentially with increasing depth from the surface; (Angel & Baker 1982; Reinthaler et al. 2006; Arístegui et al. 2009; Robinson et al. 2010). Thus, deep-sea ecosystems are generally perceived as food-limited environments.

Seamount and mid-ocean ridge ecosystems represent a deviation from the classic paradigm of deep-sea habitats. These physical structures act as obstacles to water circulation and can induce local currents. Abrupt topographic features can also enhance upwelling and may bring nutrients up from the deeper ocean, potentially increasing primary production and supporting a diversity of life (Rogers 1994). To support higher trophic levels, the injection of nutrients from upwelling must penetrate the photic later and remain long enough to affect zooplankton production (weeks to months), but evidence of this is limited (Genin & Dower 2007). Regardless, the importance of seamounts and mid-ocean ridges in supporting high fish biomass is being increasingly recognized. The apparent ecological importance of seamounts and mid-ocean ridges to fishes and other taxa, in part, inspired the initiation of the 'Patterns and Processes of the Ecosystem of the Northern mid-Atlantic' (MAR-ECO). MAR-ECO is a Census of Marine Life field project designed to describe and understand patterns of distribution,

abundance, and trophic relationships of organisms inhabiting the northern Mid-Atlantic Ridge, from Iceland to the Azores (MAR hereafter). Recent observations from MAR-ECO suggested a water column maximum in fish biomass between 1500 – 2300 m (Sutton et al. 2008). This finding stands in contrast to the traditional view that biomass declines exponentially with increasing depth from the surface.

Among the fishes sampled along the MAR, *Bathylagus euryops* (Argentiniformes: Microstomatidae) was the biomass dominant midwater species and ranked third in total abundance (Sutton et al. 2008). The trophic dynamics of *B. euryops*, like most deep-sea fishes, are poorly understood. Several dietary analyses have been conducted on this species (Mauchline & Gordon 1983; Klimpel et al. 2006; Busch et al. 2008), however, a majority of the prey items were deemed unidentifiable in each study. A clearer resolution of the diet of this abundant species is desired to facilitate an understanding of food web interactions in the MAR. *Bathylagus euryops* is distributed throughout the North Atlantic Ocean, from Greenland to Bermuda, predominantly in the meso- to bathypelagic depths. However, recent observations have demonstrated that *B. euryops* may exhibit an ontogenetic vertical migration which likely explains why smaller fish have been found in the surface waters (Sweetman et al., in prep.). Although there are no current fisheries for *B. euryops*, it is an important prey type for higher trophic levels, including commercially important species such as orange roughy (*Hoplostethus atlanticus*), alfonsino (*Beryx splendens*), and Greenland halibut (*Reinharditus hippoglossoides*) (Mauchline & Gordon 1984; Chambers & Dick 2007; Horn et al. 2010).

In general, midwater fishes serve as an important link between zooplankton and higher trophic level predators such as squids, piscivorous fishes, seabirds, and marine mammals (Porteiro & Sutton 2007). However, the ecosystem processes that govern the trophic dynamics

of fishes along seamounts and mid-ocean ridges are not fully understood. Several mechanistic

hypotheses have been postulated to explain how large aggregations of midwater fishes can be

supported in what is typically considered a food-limited environment. Initially proposed by

Isaacs & Schwartzlose (1965) and later corroborated by a series of studies over several shallow

and intermediate seamounts (Genin et al. 1988, 1994; Fock et al. 2002), the 'topographic

blockage hypothesis' describes how the trapping of vertically migrating zooplankton can provide

up to 40 times more food to seamount communities than export (via sinking particles) of

overlying primary production. Numerous species of oceanic zooplankton migrate daily between

the mesopelagic and epipelagic zones. Some vertically migrating zooplankton can reach 800 m

depth (Wiebe et al. 1979), but in the open ocean most reside in the upper 300-600 meters during

the day and migrate to surface waters at night (Steinberg et al. 2008). The summits of many

seamounts and mid-ocean ridges are well within the daily vertical migration range of

zooplankton. If the summit is shallower than preferred daytime depths of zooplankton, vertical

migration would become inhibited, resulting in trapping and increased vulnerability to predators

(Genin & Dower 2007). The topographic trapping of zooplankton would be most effective at

summits in the shallow to intermediate depth range and can greatly improve food availability to

zooplanktivorous fishes (Nonacs et al. 1994; Kiflawi & Genin 1997). Although this mechanism

would most benefit site-attached demersal fishes, it may also have key implications for pelagic

zooplanktivorous fishes like *Bathylagus euryops*. Wilson (1992) demonstrated that *Maurolocus*

muelleri and other micronekton, despite strong currents, were able to maintain their position

above the Southeast Hancock Seamount. These strong currents, in theory, should have displaced

the organisms to the surrounding deep waters. The ability for the fish and micronekton

aggregrations to maintain position above the Southeast Hancock Seamount, combined with the

observed year-long increase in body size of an apparent cohort of *M. muelleri* (Boehlert et al. 1992), indicated that these aggregations were resident (Genin 2004). Considering the itinerant behavior characteristic of pelagic fishes, an increase in energy expenditure relative to demersal fishes would likely be required for pelagic species to maintain proximity to structures such as seamounts. For the topographic blockage mechanism to hold true for pelagic fishes, energy lost in maintaining position against strong currents would need to be more than compensated by an enhanced trophic subsidy.

Determining biological and environmental patterns in the feeding ecology of deep-sea fishes remains problematic due to technological challenges of sampling the environment, and these challenges are further exacerbated when sampling over abrupt topography. Most studies to date have focused on descriptions of diet, feeding periodicity patterns, and prey selectivity of deep-pelagic fishes. Fishes that reside in the mesopelagic and bathypelagic zones are typically classified into three trophic guilds: zooplanktivores, micronektivores, and generalists (Gartner 1997). However, changes in diet and food web interactions occur as fishes continue to grow (Wootton 1998), and these ontogenetic changes are critical to understanding the ecology of fishes (Werner and Gilliam 1984) and when possible should be considered in dietary analyses.

Quantitative studies on food consumption by fishes represent a critical step towards understanding trophic dynamics of pelagic marine communities. Although extensive literature on the diet composition of midwater fishes is available (Collard 1970; Mauchline and Gordon 1985, 1986), the majority of analyses are non-quantitative in terms of trophic exchanges. Gastric evacuation and daily ration models have been widely applied to coastal fish communities to estimate consumption (Elliott and Persson 1978; Durbin et al. 1983), and the application of these

models to deep-sea species are needed to advance from a qualitative to a quantitative assessment of trophic relationships in the deep sea.

The high biomass and abundance of *Bathylagus euryops* observed over the MAR suggests their significant ecological importance in this ecosystem. In this paper, we describe the diet composition of *B. euryops* over the MAR as the percent composition by weight (mg) (% W) and the percent frequency of occurrence (% F) of each prey group. Variation in the diet of *B. euryops* is also investigated relative to ontogeny and environmental parameters, such as geographic location and depth. Additionally, we provide estimates of the daily ration of *B. euryops* to further elucidate its role in the food web as the biomass dominant species along the MAR.

II. Materials and methods

2.1. Field collections

Specimens were collected during Leg 1 of the R/V *G.O. Sars* expedition, 5 June – 3 July, 2004. Sampling occurred at 18 predefined stations along the MAR with coverage over four different ridge sections (Fig. 1): Reykjanes Ridge (RR), Charlie-Gibbs Fracture Zone (CGFZ), Faraday Seamount Zone (FSZ), and Azorean Zone (AZ). Vertical temperature profiles were generated from the surface to near-bottom with a CTD at all stations. Further methodological details for environmental data collection are provided in Søiland et al. (2008).

Samples were collected using a double-warp midwater 'Krill' trawl deployed with standard pelagic trawl doors. The 'Krill' trawl had a mouth area of 36 m^2 (6 × 6 m^2) and a net with a mesh size of 3 × 3 mm (6 mm stretched). Total trawl length was 45 m and the trawl body was equipped with a multi-sampler (remotely operated multiple cod ends) consisting of five 30

m long cod ends that allowed for five discrete-depth samples per tow. Additionally, the trawl was equipped with SCANMAR sensors to provide data on net mouth configuration and net depth. Oblique tows were performed, from 3000 m to the surface, and nets were remotely opened and closed at discrete-depth intervals. The trawl was towed at an average speed of 2.2 knots and retrieved at a rate of 25 m min^{-1}. Sampling duration at each depth stratum ranged between 10 – 40 minutes. The volume of water filtered was subsequently calculated for each cod end based on the door spread distance, speed of the ship during each sampling event, and duration of each sampling event to provide catch-per-unit-effort (CPUE) measurements.

Catches from each cod end were sorted separately to prevent mixing of specimens. The deepest net was usually sorted first, while subsequent catches were stored in a cold room to prevent sample degradation. *Bathylagus euryops* from each cod end were enumerated and weighed in bulk (± 0.1 g) on a motion-compensating scale. Specimens were then frozen in lots at -20 °C prior to storage at the Bergen Museum of Zoology, http://collections.uib.no/vertebrate/, the permanent repository for all pelagic fishes collected during the 2004 MAR-ECO expedition.

2.2. Identification of stomach contents

A total of 221 *Bathylagus euryops* specimens were selected for microscopic stomach content analysis. Bulk lots of *B. euryops* were selected based on ridge section, depth zone, and time of day. Specimens were randomly selected within the lots for use in this study. Standard length, from the most anterior portion of the premaxilla to the origin of the caudal fin, was recorded for each fish to the nearest 0.1 mm. An incision was made at the isthmus, continuing along the ventral midline, and ended at the anus to expose the internal organs. The most anterior portion of the stomach was cut, such that the liver was separated from the stomach. The

intestines were then cut as posteriorly as possible and the entire digestive tract was removed from each specimen. The contents of the stomach and intestine were removed separately. Small prey items were mixed in a glycerin and methylene blue solution, placed on a microscope slide, and sealed with Perimount for long term preservation. Larger prey items were placed in vials and stored in 70% ethanol.

Prey items that were highly masticated and/or digested prevented taxonomic resolution to species level. Consequently, prey types were classified into broad taxonomic levels in order to reduce potential biases in prey identification. Stomach and intestine contents were identified using a Nikon Eclipse 80i compound microscope for small prey items and a Nikon SMZ 1500 stereo microscope for large prey items. Prey encountered in the esophagus and buccal cavity were not included for identification to avoid possible bias due to post-capture ingestion (i.e., net feeding). To avoid the possibility of double-counting prey items within a stomach, organisms were considered separate only if a particular diagnostic feature was observed multiple times. For prey-biomass determination, length and width measurements were taken for each identified prey item using the Nikon Imaging Software Elements BR v.3.2. Body volume was estimated utilizing volumetric equations of shapes similar to that of the prey taxa (Table 1). Body volume was converted to wet weight under the assumption of specific gravity equivalence to one gram cm^{-3}.

2.3. General diet description

To summarize the diet composition of *Bathylagus euryops* along the MAR, dietary indices of percent composition by weight and percent frequency of occurrence were calculated for each prey type following Hyslop (1980). Dietary index % I_j, which can be the percent weight

or frequency of occurrence, was calculated using a cluster sampling (CS) estimator (Bogstad et al. 1995; Buckel et al. 1999; Latour et al. 2008) of the form:

$$\%I_j = \frac{\sum_{i=1}^{n} M_{ik} q_{ik}}{\sum_{i=1}^{n} M_{ik}} \times 100 \qquad (1)$$

such that,

$$\hat{q}_{ik} = \frac{\sum_{k=1}^{n_k} w_{ijk}}{\sum_{j=1}^{n_j} \sum_{k=1}^{n_k} w_{ijk}} \quad , \qquad (2)$$

where n is the number of tows containing $B.$ $euryops$, M_{ik} is the CPUE of $B.$ $euryops$ collected during each sampling event, n_j is the total number of prey types observed in the stomachs of all $B.$ $euryops$ examined, and n_k is the total number of positive stomachs examined. A sampling event was defined as a discrete-depth that was sampled at each station, whereas a positive stomach was defined as a gastro-intestinal tract that contained prey. In equation (2), $\hat{q}_{ik}$ represents the proportion of weight or occurrence of each prey type during each sampling event. To ensure that the data are scaled to represent population-level predatory impacts, the diet composition indices were calculated as a weighted average of $\hat{q}_{ik}$ with the abundance of $B.$ $euryops$ representing the scaling component. The variance estimate for $\%I_j$ was given by

$$\mathrm{var}(\%I_j) = \frac{1}{n\overline{M}^2} \frac{\sum_{i=1}^{n} M_{ik}(q_{ik} - I_j)^2}{n-1} \times 100^2 \qquad (3)$$

where $\overline{M}$ is the average number of $B.$ $euryops$ collected during a sampling event.

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2.4. Ontogenetic and spatial changes in diet

Body size has a major influence on an organism's metabolic requirements and its potential for resource exploitation. As a result, the ecological roles of different size conspecifics may be drastically dissimilar. To better understand the effect of fish size on diet, we calculated the weights of the diets of *Bathylagus euryops* (using Eq. 1) and grouped fishes into 30 mm size bins. An agglomerative hierarchical cluster analysis was conducted to identify dietary similarities among size categories, including empty stomachs, using a distance matrix of fish size bins and weights of different prey groups. Each size bin of *B. euryops* begins as a single object, and objects that are close together are merged into a cluster. "Close" was determined using the average linkage method, in which distance values between objects and clusters are computed as the average dissimilarity between clusters. Bray-Curtis dissimilarity distance coefficients were utilized to measure distances between objects. Ultimately, size groups were sequentially combined and a dietary interrelatedness of the different size-classes of *B. euryops* along the MAR was inferred from the resulting dendrogram. Ontogenetic changes in the diet determined from the cluster analysis were then used in subsequent analyses.

Canonical correspondence analysis (CCA; ter Braak 1986) was used to explore the relationship between the diet of *Bathylagus euryops* and three explanatory variables: ridge section (RR, CGFZ, FSZ, AZ), depth zone (0-200 m, 200-750 m, 750-1500 m, 1500-2300 m, >2300 m) and fish size (small, medium, large, as derived from the hierarchical cluster analysis). CCA ordination extracts the major gradients in a multivariate dataset (i.e., diet) and explains the gradients based on different combinations of explanatory variables (McGarigal et al. 2000). Each element of the response matrix was the mean percent weight of a given prey type within a

particular ridge section, depth zone, and fish size combination, so that the amount of variability in *B. euryops* diet was explained by the canonical axes. Significance of the explanatory variables was determined using permutation tests (ter Braak, 1986) and a prey group – explanatory factor biplot was generated to further explore dietary trends. Detailed diet descriptions were then developed for significant explanatory variables.

2.5. Gastric evacuation rate and daily ration

Gastric evacuation rates (*R*) and daily rations are typically obtained through laboratory starvation experiments. Due to the limitations of determining gastric evacuation rates in the lab for most deep-sea fishes, independent estimates of *R* were needed in order to calculate a daily ration. Numerous studies have concluded that the gastric evacuation rate in fishes is greatly affected by water temperature (Elliott and Persson 1978; Bromley 1994). Evacuation rates tend to increase with temperature and the relationship between the two usually follows an exponential curve (Elliott 1991) and can be estimated using the following equation:

$$R = ae^{bT} \tag{4}$$

where *R* is the gastric evacuation rate, *a* and *b* are constants, and *T* is temperature (^{o} C).

Temperature data from the *G.O. Sars* expedition, combined with a range of constants derived from the primary literature, were used to determine a range of potential gastric evacuation rates for *Bathylagus euryops* along the MAR. Constants *a* and *b* were selected from species that were either phylogenetically related to *B. euryops* (Superorder Protacanthopterygii, Order Salmoniformes) or species that inhabit similar environments (Order Stomiiformes). The species for which constants were used within the salmonids included *Salmo trutta, Salvelinus*

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alpinus, and *Onchorynchus nerka* (Elliot 1972; Doble and Eggers 1978; Amundsen and

Klemetsen 1988), which all predominantly live in shallow water ecosystems. The species for

which constants were used from the Order Stomiiformes included *Valenciennellus tripunctatus*,

Vinciguerria nimbaria, and *Danaphos oculatus* (Pakhomov et al. 1996). Gastric evacuation rates

were determined at each ridge section and incorporated temperatures in which *B. euryops* were

sampled utilizing Eq. 4, and a range of daily rations were subsequently estimated following

Elliott and Persson's (1978) model:

$$\text{Daily ration}_i = 24\,\bar{S}_i\,R \tag{5}$$

where $\bar{S}_i$ is the mean amount of food in the stomach of *B. euryops* at ridge section *i*, 24

represents the number of hours in a day, and R is the gastric evacuation rate (Tyrell et al. 2007;

Garrison et al. 2010). Due to the underlying assumptions of applying *a* and *b* constants derived

from different species, a sensitivity analysis was performed to understand the influence each had

on the overall magnitude of the daily ration of *B. euryops*. Ultimately, the highest and lowest R

values were used to estimate a high and low range of daily ration estimates at each of the ridge

section and temperature combinations. A percent difference between the high and low daily

ration estimates was then calculated to quantify the influence that the different R values used in

this study had on the daily rations.

III. RESULTS

3.1. General diet description

During the 2004 R/V *G.O. Sars* expedition, *Bathylagus euryops* were collected during 46

sampling events, and at least one *B. euryops* stomach from 35 sampling events contained prey.

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Prey were observed in 112 (50.7%) of the 221 stomachs collected. Twenty-nine prey types were observed in the diet of *B. euryops*, 20 of which were identifiable to family level and 19 identifiable to genus level.

The percent-wet weight dietary index indicated that copepods were the primary prey of *Bathylagus euryops* along the MAR, accounting for 37.8% of the diet (Fig. 2A). Decapod shrimp ranked second in dietary importance by weight and accounted for 20.5% of the diet. Gelatinous zooplankton (15.2%) and amphipods, mainly of the Suborder Hyperiidea (13.8%), were of tertiary importance. Ostracods were the only other prey group that contributed more than 5% of the diet by weight (8.7%). Remaining measurable and identifiable prey types, including chaetognaths and echinoderms, collectively represented less than 2% of the diet.

The percent-frequency-of-occurrence index also revealed that copepods were the major prey of *Bathylagus euryops*, occurring in 33.6% of positive stomachs (Fig. 2B). Ostracods were also important in the diet of *B. euryops*, occurring in 20.9% of positive stomachs. Amphipods (8.4%) and decapod shrimp (7.8%) ranked third and fourth in dietary importance based on the frequency of occurrence index. Chaetognaths and gelatinous zooplankton were nearly equally important at 5.9% and 5.8%, respectively. Other identifiable prey types including radiolarians, forams, gastropods, echinoderms, and cephalopods were found in 4.7% of positive stomachs combined. Unidentifiable prey items (i.e., crustacea fragments and unidentifiable material) were prevalent, occurring in 12.5% of fish containing prey.

3.2. Ontogenetic and spatial changes in diet

Specimens of *Bathylagus euryops* used in this study ranged in size from 40.2 to 215.0 mm SL (Fig. 3). Observations from the largest size bin (185 – 215 mm SL) were excluded from

the hierarchical cluster analysis due to low sample size in an effort to minimize the influence of outliers (McGarigal et al. 2000). A scree plot indicated three clusters (Fig. 4A) corresponding to three size-categories: < 95 mm (small), 95 – 155 mm (medium) and > 155 mm SL (large) (Fig. 4B). Canonical correspondence analysis indicated that dietary changes by fish size (F = 1.97, p = 0.05) and ridge section (F = 1.83, p = 0.10) were significant at α = 0.10, whereas depth zone (F = 0.64, p = 0.88) was not significant. Collectively, the explanatory variables accounted for 43.4% of the variability in the diet. The first and second canonical axes accounted for 63.1% and 31.8% of the explainable variation, respectively. Fish size more closely corresponded to the first canonical axis than the second, and represented the greatest component of diet variation. Conversely, ridge section and depth zone were more closely correlated to the second axis (Fig. 5).

Ostracods represented the dominant prey group in the small size class of *Bathylagus euryops* (< 95 mm SL), accounting for 49.1% of the diet by weight (Fig. 6A). Hyperiid amphipods ranked second in dietary importance at 28.6% of the diet by weight. Gelatinous zooplankton accounted for 17.5% of the diet, and copepods (4.8%) from the Order Calanoida were the only other prey group observed in the diet of small *B. euryops*. The diet composition of the medium size class of *B. euryops* (95 – 155 mm SL) was dominated by copepods, accounting for 32.6% of the diet by weight (Fig. 6B). Gelatinous zooplankton ranked second in dietary importance (24.5%), and decapod shrimp accounted for 14.7% of medium sized fish diet by weight, followed by amphipods (12.0%) and ostracods (7.3%). Diet of the large size class (>155 mm SL) was dominated by decapod shrimp and copepods, which represented more than 80% of diet by weight (47.5% and 35.5%, respectively, Fig 6C). Amphipods (13.1%), ostracods (2.2%), and gelatinous zooplankton (1.7%) contributed to the remaining diet weight profile.

Spatial changes in the diet of *Bathylagus euryops* was detected between the northern

ridge sections (RR and CGFZ) and the southern ridge sections (FSZ and AZ) (Fig. 9). In the

northern ridge sections, copepods (43.0%) and ostracods (15.6%) were more prevalent in the

diets when compared to the southern ridge sections (6.0% and 0.2%, respectively). Among the

copepods found in the diet of *B. euryops* along the northern ridge sections, *Calanus finmarchicus*

and *Microcalanus* spp. were the most prevalent taxa. The amount of amphipods and decapod

shrimps in the diets of *B. euryops* remained relatively consistent regardless of ridge section.

Gelatinous zooplankton were the only prey group more prevalent in the diet of *B. euryops* from

southern ridge sections (36.4%) relative to the northern ridge sections (5.8%). Chaetognaths and

echinoderms were observed in approximately 2% of the diet by weight in the northern ridge

sections, but were not present in the diets of fish sampled in the southern ridge sections.

3.3. Gastric evacuation and daily ration estimation

Bathylagus euryops were sampled in water temperatures ranging from $3 - 9$ ^{o} C along the

MAR, except in the Azorean Zone where fish were only collected in temperatures between $3 - 5$

^{o} C. Overall, daily rations were highest at 9 ^{o} C and lowest at 3 ^{o} C (Table 2). The average

weight of food in the stomach of *B. euryops* over a 24 hour period was highest at the

southernmost ridge section, the Azorean Zone (98.13 mg wet weight). To the north, the average

weight of prey in stomachs decreased to 83.64 mg wet weight at the Faraday Seamount Zone to

30.02 mg wet weight at the Charlie-Gibbs Fracture Zone. The average weight of prey in the

stomachs of *B. euryops* was lowest at the Reykjanes Ridge (12.54 mg wet weight). Regardless

of ridge section, daily ration estimates never exceeded 1% of the average wet weight of *B.*

euryops per day. When ridge section was considered, daily rations were highest at the

southernmost ridge section (Azorean Zone) and lowest at the northernmost ridge section

(Reykjanes Ridge). Results from a sensitivity analysis revealed that the different constants used

in Eq. 4 had minimal influence on the magnitude of the daily ration estimates. Overall, high and

low daily ration estimates differed at the most by only 0.63%.

IV. DISCUSSION

4.1. General diet description

      Bathylagus euryops feed on a diverse array of prey in the North Atlantic Ocean,

evidenced by the different taxa encountered in the diet in this study. Fishes from the Family

Microstomatidae are typically classified as zooplanktivores that specialize on gelatinous

zooplankton (Hopkins et al., 1996; Gartner Jr. et al., 1997; Arai, 2005). However, this study

found that gelatinous zooplankton represented 15.2% of the diet by (wet) weight and occurred in

only 5.9% of stomachs. While the rapid digestion of gelatinous zooplankton in fish stomachs

undoubtedly lead to an underestimation of their overall contribution to diet, methodical

discrepancies between study calculations also represent a plausible explanation for the observed

differences.

      In general, it is difficult to compare studies of diet composition of the same species due to

differences in survey design, dietary indices reported, and methods used to calculate these

indices. Overall, crustaceans dominated the diet of *Bathylagus euryops*, with copepods ranking

first in magnitude across the dietary indices generated in this study. Copepods are the

numerically dominant members of marine plankton at all depths in the ocean (Herring 2002) and

their importance in the diet of deep-sea fishes has been widely documented (Hopkins and Baird

1977). Mauchline and Gordon (1983) characterized the diet of *B. euryops* by generating a

frequency of occurrence dietary index and found that calanoid copepods were the main prey group observed in the stomach contents with identifiable food, and our results agree with the findings in this study. Klimpel et al. (2006) and Busch et al. (2008) also investigated the diet of *B. euryops* and reported percent-composition-by-weight dietary indices for unidentified crustaceans that ranged from 77.9 – 92.3%. While these studies were mainly focused on the occurrence of fish parasites in the deep-sea, and consequently provided low taxonomic resolution of diet, our results corroborate the importance of crustaceans in the diet of *B. euryops*. In the present study, unidentifiable prey items were observed in the stomachs where identifiable prey items were also found, and were likely the same prey types as the latter. However, these prey items were classified as unidentifiable to provide a conservative diet description.

4.2. SRS vs. CS estimation methods

In the present study we utilized a cluster sampling estimator in contrast to past use of the simple random sampling (SRS) estimator (e.g. Mauchline and Gordon 1983; Hopkins et al. 1996). By definition, SRS assumes each fish has an equal probability of being sampled out of a population of N fish (Cochran 1977). Accordingly, each fish sampled is assumed to be an independent sampling unit. However, fishes and their prey are known to distribute in spatially variable aggregations (Pitcher and Parrish 1993) as a result of biotic interactions and tolerances to physical conditions, including but not limited to, resource partitioning, food availability, reproduction, predation impacts, and temporal changes in the physical environment. Since fishes are typically not distributed evenly, the SRS assumption of equal probability of capture is frequently violated. Furthermore, zooplankton patch dynamics over abrupt topography may result in correlation among stomach content data within planktivorous fishes sampled at a single

location as it is metabolically cheaper to feed on patches of prey than on evenly distributed prey (Horwood and Cushing 1978). Thus, sampling using active gears may yield randomly collected clusters of fishes rather than a sample of randomly selected individuals. A cluster sampling (CS) estimator is appropriate if fishes are determined to be sampled in clusters, where the diets of those sampled within a gear deployment are more likely to be similar than those sampled between gear deployments.

Similarity among diets within and between sampling events can be formally considered by examining the intracluster correlation coefficient (ICC, ρ), which reflects the relationships of the variance within a cluster to the variance between clusters (Cochran 1977). ICC estimates can be produced for each prey type in the diet and values will range from 0 to 1. For circumstances where ρ is substantially greater than 0 for any prey types, variance between sampling events is greater than variance within sampling events and the collections of fish should be viewed as independent sampling units rather than the individuals within a collection (Bogstad et al., 1995). In this situation, a CS estimator is the most appropriate estimation method. Conversely, in circumstances where ρ is near 0, variance within a sampling event is substantially greater than variance between sampling events and a SRS estimator is most appropriate. The variability of *B. euryops* stomach contents was greater between samples than within samples as evidenced by ICC values of 0.49 for amphipods, 0.48 for copepods, 0.59 for gelatinous zooplankton, 0.51 for decapods, and 0.67 for ostracods. Ultimately, these ICC values indicated that the 'Krill' trawl yielded collections of *B. euryops* that were likely sampled in clusters and that the application of a CS estimator (Eq. 1) rather than a SRS estimator is the appropriate method to calculate diet composition. However, it should be noted that the ICC estimate is used to guide estimation methods and does not solely determine whether a SRS or CS estimator should be used to

generate dietary indices. In addition to the ICC estimate, sampling techniques, the ecology of the species of concern, and the dynamics that govern the distribution of prey must also be considered.

The manner in which fishes are sampled is an important consideration in dietary composition analyses as results may be drastically different with an SRS estimator versus a CS estimator. For example, if a SRS estimator were applied to this study, the results would conform to that of previous dietary descriptions for *Bathylagus euryops*, with gelatinous zooplankton accounting for about 50% of the diet by weight (as opposed to 15% of the diet by weight with a CS estimator). The application of the CS estimator essentially weights the stomach contents by the abundance of fish within a sampling event to ensure accurate population level predatory impacts. Despite its appropriateness for marine fish diet studies, the utilization of this approach is rarely reported in the literature, and may therefore entrain inaccurate dietary calculations, descriptions, and comparisons.

4.3. Ontogenetic and spatial changes in diet

Aside from general diet descriptions, ontogenetic and regional changes in feeding patterns have been used to explain the underlying variability in the diet of deep-sea fishes (Hopkins and Baird 1977). Cluster analysis revealed three size classes of fishes that grouped separately based on their diet composition, and a subsequent CCA determined that fish size significantly influenced the diet of *Bathylagus euryops* along the MAR. Small *B. euryops* fed predominantly on ostracods, while amphipods and gelatinous zooplankton were of secondary importance. An ontogenetic expansion in the diet occurred around 95 mm SL, as *B. euryops* began feeding on a wider variety of prey groups. Copepods represented the dominant

component of the diet in the medium size class, whereas ostracods were no longer a major component of the diet, and larger prey groups, such as decapod shrimp, began to appear in the diet. As fish increased in size to larger than 155 mm SL, decapod shrimp dominated the diet by weight, followed by copepods. Gape limitation, where the limits on food size are imposed by the size of the mouth opening, likely influenced some of the observed ontogenetic changes in diet. Some of the smallest prey items, such as ostracods, were most abundant in the diet of smaller fish. Conversely, decapod shrimp, which were among the largest prey groups, were observed primarily in the diets of larger *B. euryops*, which were presumably more capable of capture and ingestion of the larger prey. An increase in gape limitation would likely allow for a wider variety of prey groups to be consumed and this was observed between the small size class (35 – 95 mmSL) relative to the medium size class (95 – 155 mm SL). However, a decrease in the number of prey groups was observed between the medium size class and the large size class (> 155 mm SL) and this was likely an artifact of the small sample size analyzed in large size class (n = 35).

A central assumption in deep-ocean environments is that opportunistic generalist feeding strategies should be favored due to relatively sparse food availability, and that this pattern should be more apparent with increasing depth (Ebeling and Calliet 1974). Results from this study indicate that ontogenetic changes in the feeding of *Bathylagus euryops* may contribute to the observed dietary variation with size. An ontogenetic vertical migration was postulated by Mauchline and Gordon (1983) and recently observed in *B. euryops* along the MAR, where smaller fish were found in surface waters and larger fish at greater depths (Sweetman et al. in prep.). Dietary differences based on size may be a function of the vertical distribution of different size classes of *B. euryops* relative to the vertical distribution of the prey field. For

instance, *Calanus finmarchicus* is the most abundant copepod in the North Atlantic Ocean and may constitute ~80% of total copepod biomass in the North Atlantic Ocean (Gislason et al. 2008). During the summer months, *C. finmarchicus* resides in the mesopelagic zone as it matures in preparation for reproduction during the spring (Sameoto & Herman 1990). Copepods were a dominant prey group in both the medium and large size classes of *B. euryops*, and of the copepods observed in the diet of these size classes, *C. finmarchicus* was the most abundant. The depth distribution of *C. finmarchicus* during the summer likely explains the subsequent increase in copepod dietary importance with increasing fish size.

Another significant trend observed in the CCA was that most prey groups were more prevalent in the diet of *Bathylagus euryops* in the northern ridge sections when compared to the southern ridge sections, with gelatinous zooplankton representing the only major deviation from this pattern. The distributions of zooplankton in the open ocean are strongly regulated by, and spatially correlated with, physical oceanographic processes (Mackas et al. 1985) and the spatial changes observed in the diet of *B. euryops* relative to geographic location (e.g., ridge section) were likely reflective of the hydrographic patterns along the MAR at the time of sampling. Along the MAR, the Sub-Polar Front (SPF) is a major hydrographic feature and recent findings from MAR-ECO have shown it to be a biogeographic barrier for several zooplankton taxa (Falkenhaug et al. 2007). The SPF is a semi-permanent feature with a variable position south of the CGFZ. The SPF represents a boundary between the cool, lower salinity waters of the north and the southern warm and saline waters (Rossby 1999). Copepods dominated the diet of *B. euryops* in the northern ridge sections. Specifically, *Calanus finmarchicus* and *Microcalanus* spp. were the most frequently observed species in the stomachs of *B. euryops* from the northern ridge sections. These copepod taxa were also the most abundant calanoid copepods in waters

north of the SPF (Gaard et al. 2008). South of the SPF, abundances of *C. finmarchicus* and *Microcalanus* spp. markedly decline, and a corresponding decrease of copepod dietary importance was observed in *B. euryops*. Qualitatively, environmental availability of these copepod species appears to be proportionally reflected in *B. euryops* diet.

The other major spatial trend observed in the diet of *Bathylagus euryops* was the increase in importance of gelatinous zooplankton in the southern ridge sections. The importance of gelatinous zooplankton as both predators and prey in the open ocean is becoming increasingly recognized (Purcell and Arai 2001; Purcell 2005; Link and Ford 2006). However, due to the fragile tissue structure of these organisms, little information is available on large-scale spatial patterns of abundance, limiting quantitative inclusion of gelatinous zooplankton in dietary selectivity analyses. During the MAR-ECO campaign, several different sampling methodologies were used to elucidate distribution patterns of gelatinous zooplankton, including net sampling, underwater video profiling, stimulated bioluminescence, and remotely operated vehicles. Gelatinous zooplankton species richness was highest south of the SPF, where higher abundances of lobate ctenophores, siphonophores, thaliaceans, and *Aglantha* spp. were observed compared to regions north of the SPF (Hosia et al. 2008; Stemmann 2008; Youngbluth 2008). Conversely, medusae were more abundant along the northern ridge sections. Despite these observations, the importance of specific taxa of gelatinous zooplankton in the diet of *B. euryops* remains difficult to determine due to the highly digested state of the ingested material that prohibited further taxonomic resolution. The digestion of gelatinous zooplankton in fish stomachs may be nearly complete in one hour (Arai et al. 2003) and given that most midwater trawls take multiple hours from deployment to retrieval, additional methods, such as molecular identification, are needed to

further understand the importance of gelatinous zooplankton taxa in the diet of *B. euryops* and

other pelagic fishes along the MAR.

4.4. Gastric evacuation and daily ration estimates

Fish gastric evacuation rates and daily rations are often verified through laboratory

feeding experiments. This application, however, remains problematic in deep-sea research due

to difficulties in keeping deep-sea fishes alive in containment. When calculating R, it is critical

that the constants used reflect species with similar metabolic characteristics that are appropriate

for comparison when the data for the target species are unavailable. In an effort to provide

conservative daily ration estimates for *Bathylagus euryops*, a and b constants in Eq. 4 were

derived from the literature for phylogenetically-related species and those inhabiting similar

habitats (e.g. deep-sea fishes). Although the a and b constants used in this study were from

phylogenetically and ecologically different species, they did not have a major impact on the

overall daily ration estimates. We determined that daily ration of *B. euryops* increased

southward along the MAR and never exceeded 1% of the average wet weight per day. Only two

studies have estimated the daily ration for non-migrating fishes within the Family

Microstomatidae (Childress et al. 1980; Gorelova 1985). Although both studies applied different

methods to calculate a daily ration, each determined the daily ration to be very low, not

exceeding 1% of the body weight per day, and our results support these findings. The southward

increase in *B. euryops* daily ration may be explained by feeding responses correlated with water

temperature. Water temperatures were coldest at the RR and warmest at the AZ, and in the

absence of limiting factors, a temperature increase will increase the metabolic rate of fishes

(Hochachka and Somero 1984). While temperature likely explains much of the variability

observed in the daily ration estimates for *B. euryops*, other factors including social behavior, food availability, resource partitioning, predation impacts, and responses to environmental variables other than temperature likely play a role and should be examined further to better elucidate the feeding capacity of this species.

V. CONCLUSION

In conclusion, the combination of descriptive and quantitative analyses of food web interactions provides valuable insights into the structure of deep-sea ecosystems along the MAR. The incorporation of ontogenetic and spatial changes in the dietary analysis of *Bathylagus euryops* elucidated some of the ecosystem processes that govern the trophic dynamics of this species. These findings will ideally aid in the management of commercially important fishes that ultimately rely on *B. euryops* as prey. Furthermore, the estimation of a daily ration for *B. euryops* represents the first such estimate for the species and our results suggest that this species is an important consumer of oceanic zooplankton and macroplankton. Due to their high abundances and biomass observed along the MAR, *B. euryops* represents an important pathway in the transfer of carbon from the epipelagic zone to the deep ocean in the mid-oceanic North Atlantic. However, the patterns described in the present study are based on sampling that took place in the summer, after the peak in primary production from the spring bloom had already occurred. The primary remaining gap in the knowledge of the feeding ecology of *B. euryops* along the MAR is the influence of temporal patterns (diel, intra-annual, and interannual) and the influence of hydrography and water masses.

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Table 1. Zooplankton body type, corresponding geometric shapes, and body volume equations used for diet analysis of *Bathylagus euryops*
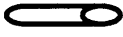
Body type	Shape	Taxa	Volume equation	Body volume equation
Prolate spheroid		Copepods, Ostracods, Ctenophores	$\dfrac{\pi\,(l)(d^2)}{6}$	$\dfrac{\pi\,(\text{prosome/body length }\mu m)(\text{prosome/body width }\mu m)^2}{6}$
Cylinder		Larvaceans, Chaetognaths	$\dfrac{\pi\,(d^2)(h)}{4}$	$\dfrac{\pi\,(\text{body width }\mu m)^2(\text{total length }\mu m)}{4}$
		Amphipods	$\dfrac{\pi\,(d^2)(h)}{4}$	$\dfrac{\pi\,(\text{prosome width }\mu m)^2(\text{total length }\mu m)}{4}$

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Table 2. Gastric-evacuation rates and daily-ration estimates of *Bathylagus euryops* at 3° C, 5° C, 7° C, and 9° C along the northern Mid-Atlantic Ridge in June 2004. Daily-ration estimates are mg wet weight of prey consumed per day and percent of the average body wet weight of *B. euryops* consumed per day. Daily rations were not generated for 7° C and 9° C in the Azorean Zone as specimens were not observed there.

Gastric Evacuation Rate		
Temp	Low	High
3° C	0.017	0.074
5° C	0.034	0.093
7° C	0.059	0.116
9° C	0.099	0.145

Reykjanes Ridge

	Daily Ration (mg per day)		Daily Ration (% weight per day)	
Temp	Low	High	Low	High
3° C	4.99	22.31	0.01	0.05
5° C	10.28	27.91	0.02	0.07
7° C	17.62	34.92	0.04	0.08
9° C	29.73	62.47	0.07	0.15

Charlie-Gibbs Fracture Zone

	Daily Ration (mg per day)		Daily Ration (% weight per day)	
Temp	Low	High	Low	High
3° C	11.95	53.43	0.03	0.13
5° C	24.63	66.85	0.06	0.16
7° C	42.21	83.63	0.10	0.20
9° C	71.2	104.7	0.17	0.25

Faraday Seamount Zone

	Daily Ration (mg per day)		Daily Ration (% weight per day)	
Temp	Low	High	Low	High
3° C	33.28	148.88	0.08	0.36
5° C	68.62	186.25	0.16	0.45
7° C	117.6	233.02	0.28	0.56
9° C	198.37	291.72	0.47	0.70

Azorean Zone

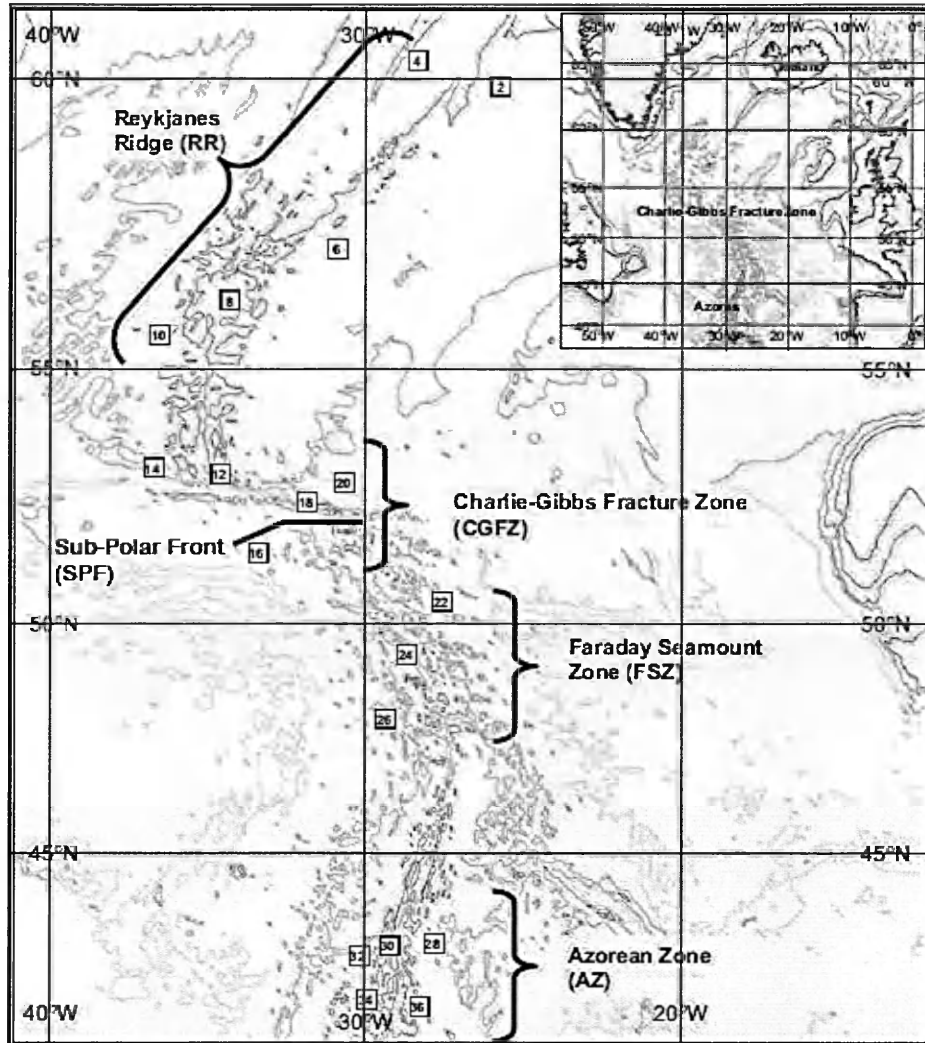|	Daily Ration (mg per day)		Daily Ration (% weight per day)	
Temp	Low	High	Low	High
3° C	39.05	174.67	0.09	0.42
5° C	80.51	218.52	0.19	0.52
7° C	-	-	-	-
9° C	-	-	-	-

Figure 1. Trawl sampling stations for Leg 1 of 2004 R/V *G.O. Sars* MAR-ECO expedition to the Mid-Atlantic Ridge, from Iceland to the Azores (adapted from Sutton et al., 2008).
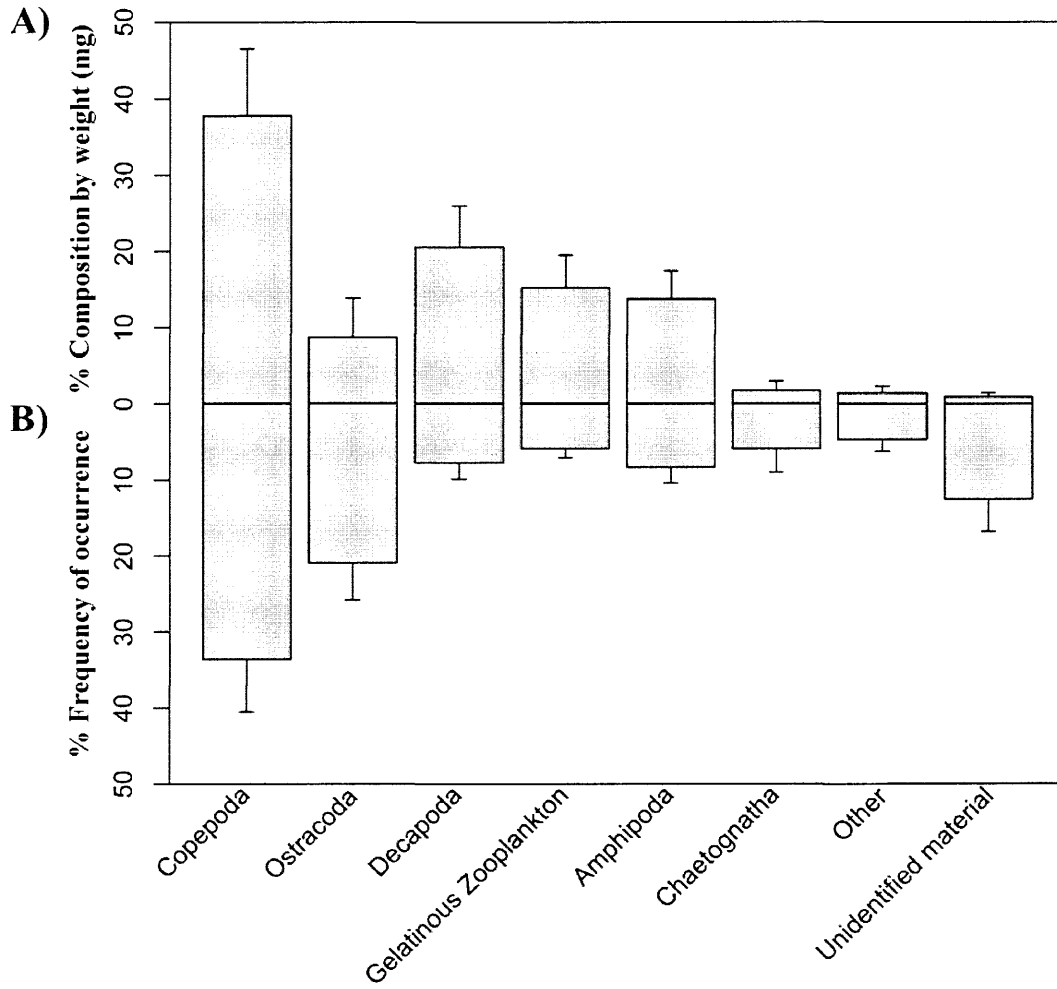
Figure 2. (A) Percent composition by wet weight in mg and (B) percent frequency of occurrence of prey groups in the diet of *Bathylagus euryops*. Dietary indices derived from samples (n = 221) collected during the 2004 R/V *G.O. Sars* MAR-ECO research expedition to the northern Mid-Atlantic Ridge. Standard error estimates, represented by error bars, were calculated from cluster sampling variance estimates.
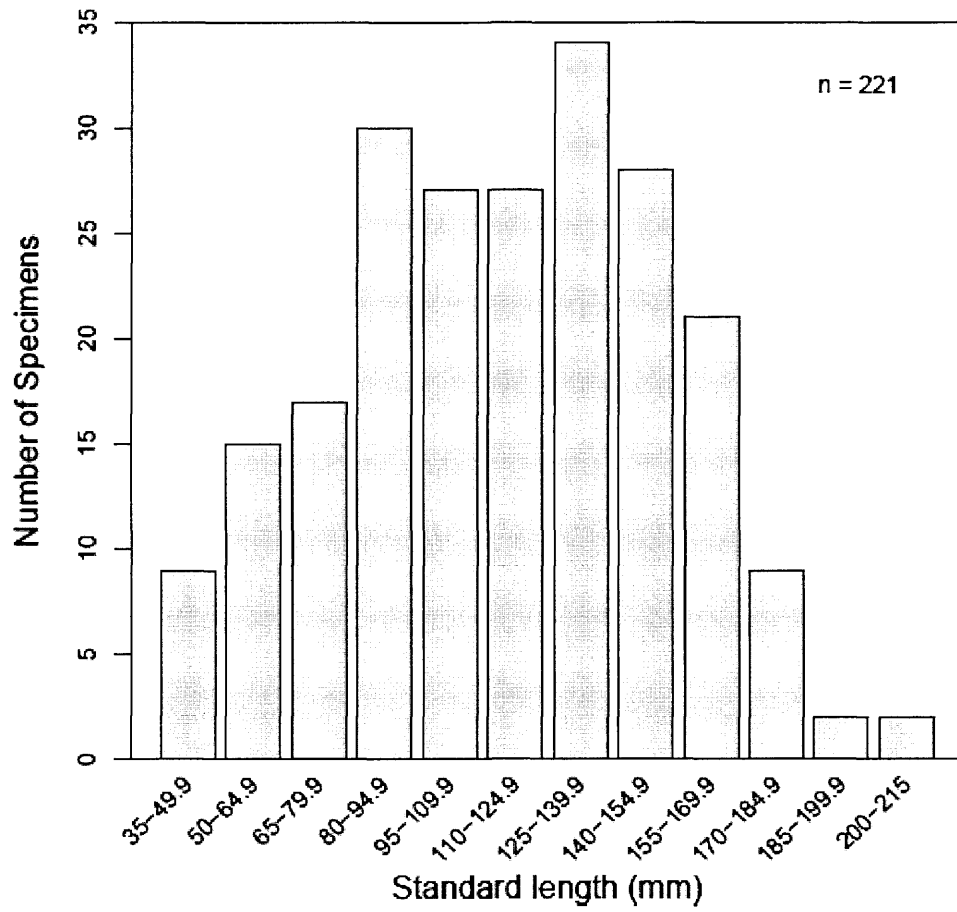
Figure 3. Size frequency of *Bathylagus euryops* sampled along the northern Mid-Atlantic Ridge in June, 2004 and used for dietary analysis.
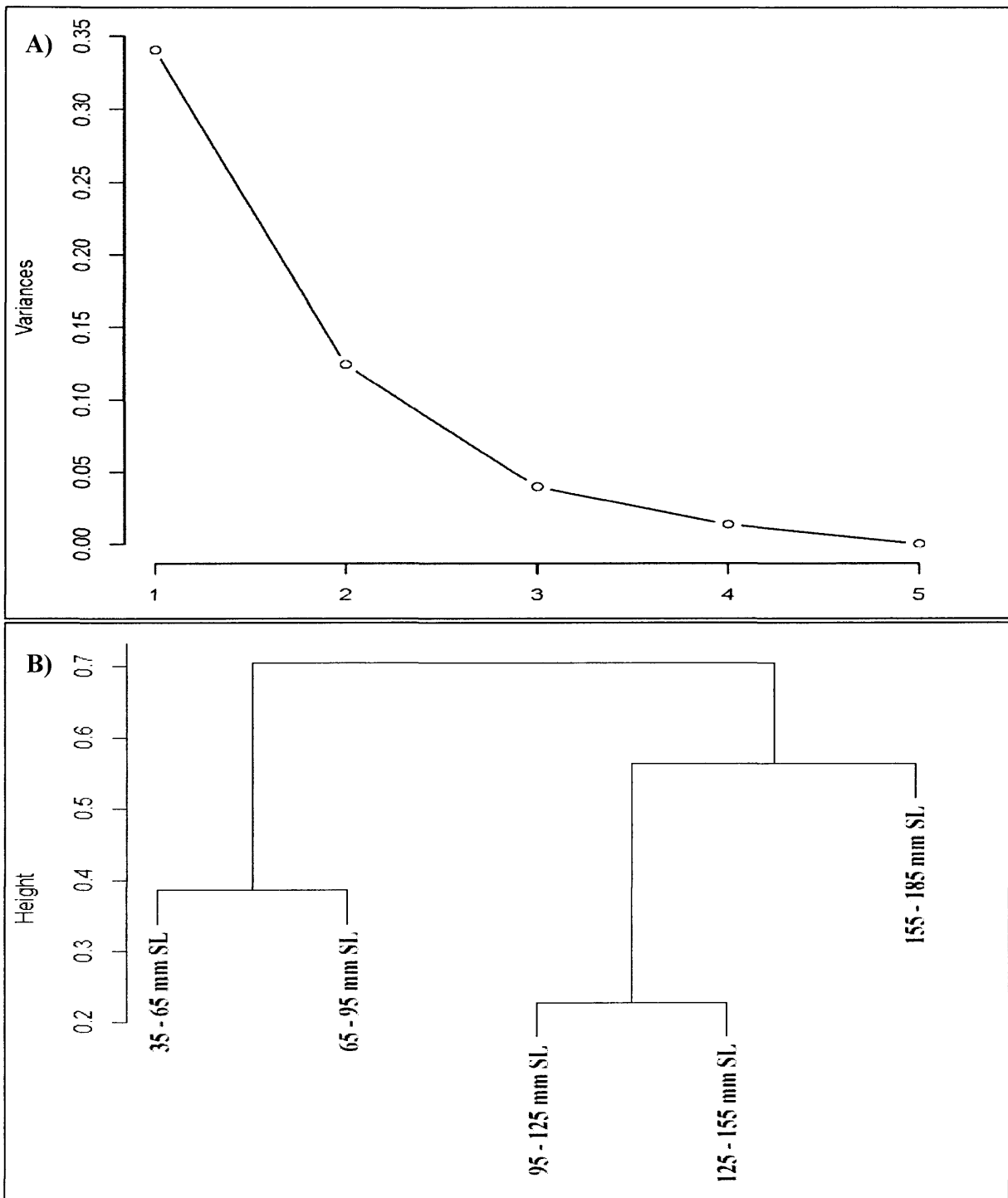
Figure 4. (A) Scree plot depicting average distance between clusters versus the number of clusters which was used to identify the number of clusters into which 30-mm (SL) size-classees of *Bathylagus euryops* should be grouped (three size groups were selected since the curve leveled out at four or more clusters), (B) dendrogram representing the relationships among the diet compositions of 30-mm (SL) size-classes of *Bathylagus euryops*. Height represents the coefficient used as a measure of dissimilarity among size-classes.

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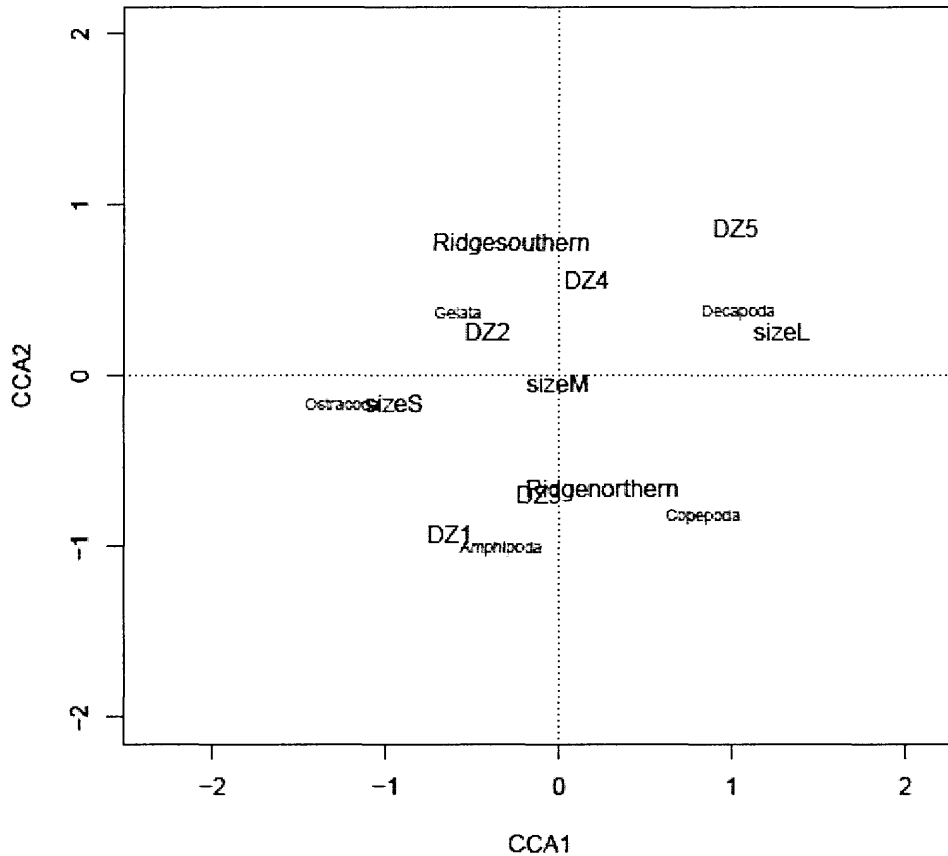**43.4% inertia, B. euryops diet ~ ridge + depth + size class**

Figure 5. Canonical correspondence analysis (CCA) biplot for *Bathylagus euryops* diet along the northern Mid-Atlantic Ridge, from Iceland to the Azores, in June of 2004. The canonical axes represent linear combinations of three explanatory variables (fish size, ridge section, and depth zone), of which fish size and ridge section were significant at $\alpha = 0.1$. Fish size was represented by a small size class (35-95 mm SL), a medium size class (95-155 mm SL), and a large size class (>155 mmSL). Ridge section was represented by a northern ridge section (Reykjanes Ridge and Charlie-Gibbs Fracture Zone) and a southern ridge section (Faraday Seamount Zone and Azorean Zone). Depth zone was represented by the five depth strata sampled, including DZ1 (0-200 m), DZ2 (200-750 m), DZ3 (750-1500 m), DZ4 (1500-2300 m), and DZ5 (>2300 m).
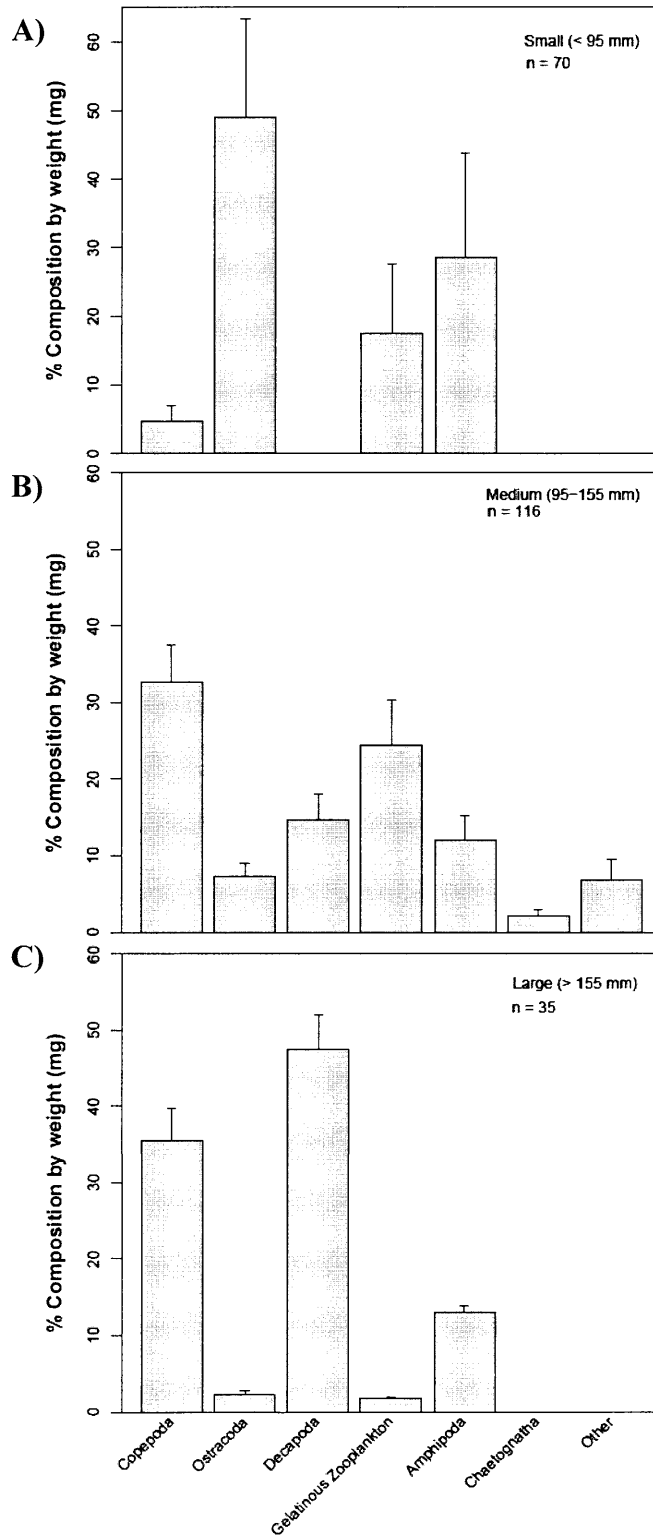
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Figure 6. Diet composition (percent weight) of *Bathylagus euryops* collected along the northern Mid-Atlantic Ridge presented by (A) small size class, (B) medium size class, and (C) large size class. n represents the total number of specimens. Error bars represent standard error of the percent weight values of each of the prey types in the small size class of *Bathylagus euryops*.
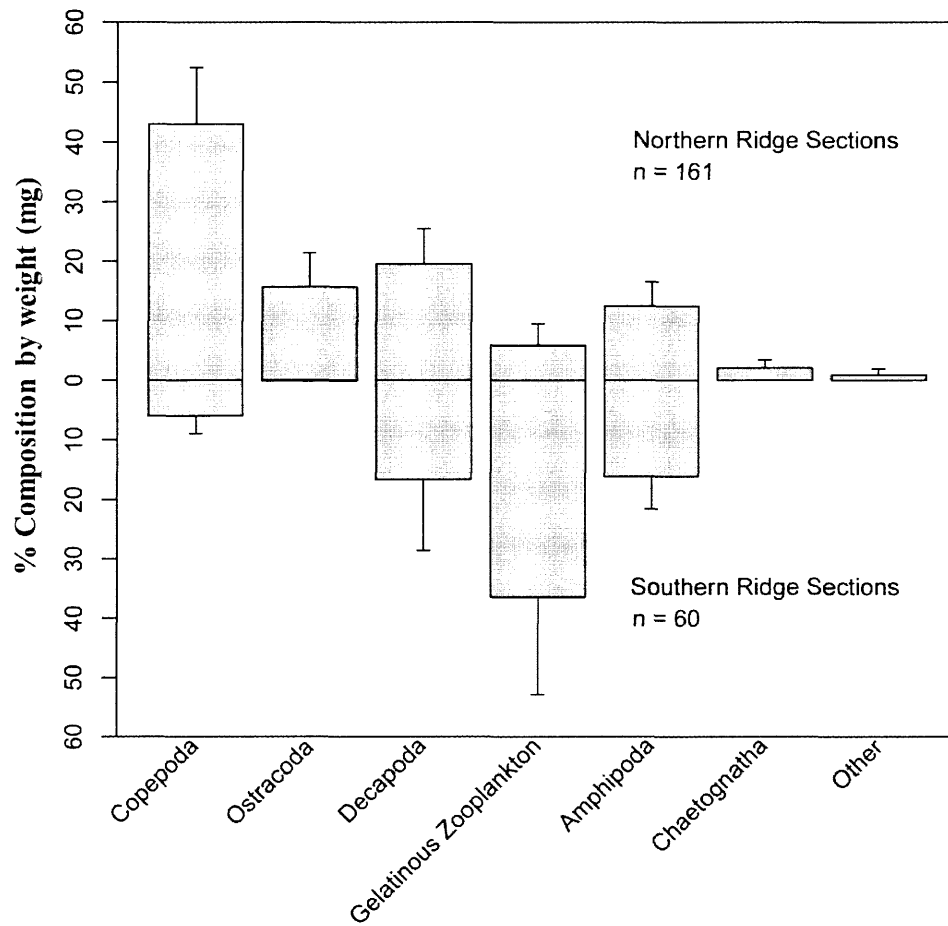
Figure 7. Diet composition (percent wet weight) of *Bathylagus euryops* collected along the northern Mid-Atlantic Ridge relative to northern ridge sections (Reykjanes Ridge and Charlie-Gibbs Fracture Zone; top panel) and southern ridge sections (Faraday Seamount Zone and Azorean Zone; bottom panel). Error bars represent standard error of the percent weight values of each of the prey types relative to the northern and southern ridge sections.

THESIS CONCLUSIONS

Determining distribution and feeding patterns in abundant deep-sea fauna, such as *Bathylagus euryops*, represents a critical component to establishing baseline data for which future studies can compare to. The science of the deep sea has mostly operated under the assumption of stable environments and unchanging situations over large areas (Herring, 2002). However, we now know that the future scenario of climate change will influence all areas of the marine realm. An increase in temperature over the next 100 years, predicted to be between 1.4 and 5.8 $^\circ$ C (IPCC, 2007), will have significant effects on the surface waters of the ocean, which will then be transmitted to depth (Ramirez-Llodra et al., 2010). Furthermore, the expansions of oceanic 'dead zones' will also have severe effects on the distribution and abundance of marine life in the deep sea (Brewer and Peltzer, 2009).

The distributional trends observed in this study highlighted a significant influence of both geographic location and depth on the abundance of *B. euryops*. The likelihood that climate change will influence the distribution of *B. euryops* is high if current trends in elevated oceanic warming and oxygen minimum zones persist. The ontogenetic vertical migration that was postulated in the present study is one such mechanistic process that will be greatly affected by the warming of the world's oceans, and in turn, will influence the overall distribution of *B. euryops* in the North Atlantic. As outlined in this study, it is likely that the ontogenetic migration to the meso- and bathypelagic zones is preceded by the hatching of eggs in the epipelagic zone. The continued warming of temperatures in the surface waters of the North Atlantic may therefore expose the eggs and larvae of *B. euryops* to an expanded geographic range of lethal temperatures. Considering the importance of depth on the distribution of *B. euryops*, another important ramification of climate change is the expansion oxygen minimum zones in the deep pelagic realm. The decline in oxygen in the deep pelagial is a result of lower

sea-surface oxygen concentrations, reduced ventilation of the meso- and bathypelagic zones from ocean warming (Diaz et al., 2008; Stramma et al., 2008), and local eutrophication events, all of which lead to an expansion of oxygen minimum zones (Brewer and Peltzer, 2009). The impact of these oxygen minimum zones may impose a physiological strain on *B. euryops* in areas in the water column where they are most abundant. These physiological strains would likely impair performance of *B. euryops* and would require energy that would otherwise be used for locomotion, predation, reproduction, or dealing with other environmental stressors (Brewer and Peltzer, 2009).

Smith et al. (2008) reviewed the potential impact of climate change on deep-sea taxa and concluded that organisms in the deep sea are highly vulnerable to temporal and spatial perturbations in food availability and other environmental conditions. The deep sea relies mostly on the downward flux of surface primary production and thus is often considered a food limited environment. Changes in the quality and quantity of production in the epipelagic zone may therefore have pronounced effects on deep-sea communities (Smith et al., 2008). For example, one of the potential major consequences of climate change for *B. euryops* is a distributional and abundance shift of arguably its most important food item, *Calanus finmarchicus*. Beaugrand et al. (2003) predicted that in the North Atlantic, a shift in the distribution and abundance between the northern *C. finmarchicus* and the southern *Calanus helgolandicus* can be expected. As temperature warms, the boundary between the two shifts north and where their distributions overlap, *C. helgolandicus* becomes comparatively more important (Drinkwater, 2005). Results from this study have illustrated that the life cycle of *C. finmarchicus* appears to be linked with trends in the feeding ecology of *B. euryops*. If a profound distributional and abundance northward shift occurs for a major prey group of *B. euryops*, it is certainly plausible that climate

change will negatively affect the feeding ecology of *B. euryops*. While these predictions remain highly uncertain, I believe they are a reasonable approximation of how climate change will influence *B. euryops* throughout the mid-oceanic North Atlantic Ocean.

Overall, the consequence of the disturbance of deep-sea ecosystems is relatively unknown and difficult to predict. However, the result of continued and widespread disturbances would most certainly be severe and have long term effects on deep-sea fauna. The shear abundance and biomass of *Bathylagus euryops* along the northern Mid-Atlantic Ridge, and the subsequent distributional and feeding patterns observed in this study indicate that this species plays an important role in the ecosystem of the mid-oceanic North Atlantic. *Bathylagus euryops* is an important prey item for commercially fished species like orange roughy, Greenland halibut, and alfonsino (Mauchline and Gordon, 1984; Chambers and Dick, 2007; Horn et al., 2010) and the findings in this study can help in the management of these fishes that are highly vulnerable to overfishing. Furthermore, the patterns observed in this study can be used to ultimately predict future implications of environmental variability on the distribution and feeding ecology of *B. euryops*, which can have cascading effects on both prey and predator populations.

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