TAXONOMY AND ECOLOGY OF THE DEEP-PELAGIC FISH FAMILY MELAMPHAIDAE, WITH EMPHASIS ON INTERACTIONS WITH A MID-OCEAN RIDGE SYSTEM

by

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This dissertation was prepared under the direction of the candidate's dissertation advisor, Dr. Tracey Sutton, Department of Biological Sciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

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Much of the world's oceans lie below a depth of 200 meters, but very little is known about the creatures that inhabit these deep-sea environments. The deep-sea fish family Melamphaidae (Stephanoberyciformes) is one such example of an understudied group of fishes. Samples from the MAR-ECO (www.mar-eco.no) project represent one of the largest melamphaid collections, providing an ideal opportunity to gain information on this important, but understudied, family of fishes. The key to the family presented here is the first updated, comprehensive key since those produced by Ebeling and Weed (1963) and Keene (1987). Samples from the 2004 MAR-ECO cruise and the U.S. National Museum of Natural History provided an opportunity to review two possible new species, the *Scopelogadus mizolepis* subspecies, and a *Poromitra crassiceps* species complex. Results show that *Scopeloberyx americanus* and *Melamphaes indicoides* are new species, while the two subspecies of *Scopelogadus mizolepis* are most likely only one species and the *Poromitra crassiceps* complex is actually several different species of *Poromitra.*

Data collected from the MAR-ECO cruise provided an opportunity to study the distribution, reproductive characteristics and trophic ecology of the family Melamphaidae along the Mid-Atlantic Ridge (MAR). Cluster analysis showed that there are five distinct groups of melamphaid fishes along the MAR. This analysis also supported the initial observation that the melamphaid assemblage changes between the northern and southern edges of an anti-cyclonic anomaly that could be indicative of a warm-core ring.

Analysis of the reproductive characteristics of the melamphaid assemblage revealed that many of the female fishes have a high gonadosomatic index (GSI) consistent with values found for other species of deep-sea fishes during their spawning seasons. This may indicate that melamphaids use this ridge as a spawning ground.

Diets of the melamphaid fishes were composed primarily of ostracods, amphipods, copepods and euphausiids. *Scopelogadus* was the only genus shown to have a high percent of gelatinous prey in their digestive system, while *Melamphaes* had the highest concentration of chaetognaths.

This work presents data on the ecology and taxonomy of the family Melamphaidae and provides a strong base for any future work on this biomass-dominant family of fishes.

TAXONOMY AND ECOLOGY OF THE DEEP-PELAGIC FISH FAMILY MELAMPHAIDAE, WITH EMPHASIS ON INTERACTIONS WITH A MID-OCEAN RIDGE SYSTEM

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

OVERVIEW

The deep sea (waters below 200 m) is the planet's largest habitat at around 92% of the total volume of Earth's oceans (Haedrich 1997). Although this environment is vast, knowledge about the deep sea is minuscule in comparison to what we know about coastal environments. In the deep sea, light is attenuated rapidly leaving the environment in a constant state of near or total darkness, depending on the depth (Merrett and Haedrich 1997; Gage and Tyler 1999; Herring 2002). In this dark environment the water is much colder (-1 to 4°C) than the surface and the pressure can reach more than 800 times the surface pressure (Sverdrup *et al.* 1963; Randall and Farrell 1997; Gage and Tyler 1999; Herring 2002). The stresses applied by the low temperatures, high pressures and low ambient light conditions have given rise to special adaptations in the organisms found in this environment. Deep-sea organisms usually have delicate, watery tissue with low muscle concentration and often show low respiratory and enzyme activities to conserve energy between meals, which can often be few and far between (Ebeling and Weed 1963; Ebeling and Calliet 1974; Gartner *et al.* 1997).

THE MID-ATLANTIC RIDGE

The Mid-Atlantic Ridge (MAR) is a unique habitat in the deep sea. The ridge is a series of seamounts, or underwater mountains, that were formed by the separating of

continental plates. The MAR-ECO study area (the northern MAR) encompasses the area between the Reykjanes Ridge south of Iceland to the Azores (between 36°42'W - 25°57'W and 59°46'N - 38°37'N). The peaks of the ridge system rise to within 1000 m of the surface, in stark contrast to the surrounding abyssal plains. The continuity of the ridge is broken in an area called the Charlie-Gibbs Fracture Zone (between 35°00'W - 32°00'W and 52°30'N - 52°00'N), which is a transverse fault in the otherwise linear MAR (Fig. 1.1). Sea surface temperatures correspond to a wide range of habitats from the sub-polar to the sub-tropical (Fig. 1.2). Vertical thermal and salinity profiles show some vertical mixing (Fig. 1.3). The MAR has been shown to be an area of strong vertical mixing associated with increased upwelling (Mauritzen *et al.* 2002; Søiland 2008). Chlorophyll A maximums occur North of the Sub-Polar Front and South of the Azorean Front, the stations near the latter associated with a deep lying chlorophyll maximum around 85-105 m depth (Macedo *et al.* 2000; Pérez *et al.* 2003; Gaard *et al.* 2008; Opdal *et al.* 2008; Vecchione *et al.* 2010).

It has been shown that seamounts and ridge systems are areas of high micronekton and demersal fish biomass (Fock *et al.* 2002; Genin 2004). The MAR could provide areas of high primary production due to so-called "seamount effects" (Dower and Mackas 1996; Haury *et al.* 2000; Genin 2004). One theory as to why fish aggregate around seamounts is that seamounts create localized upwelling, while simultaneously creating anticyclonic vortices from which plankton cannot escape (Dower and Mackas 1996; Mullineaux and Mills 1997; Haury *et al.* 2000). The interactions of the local upwelling and the trapping of plankton by vortices increase localized primary production above the ridge. This increase in primary production and local plankton stocks supports

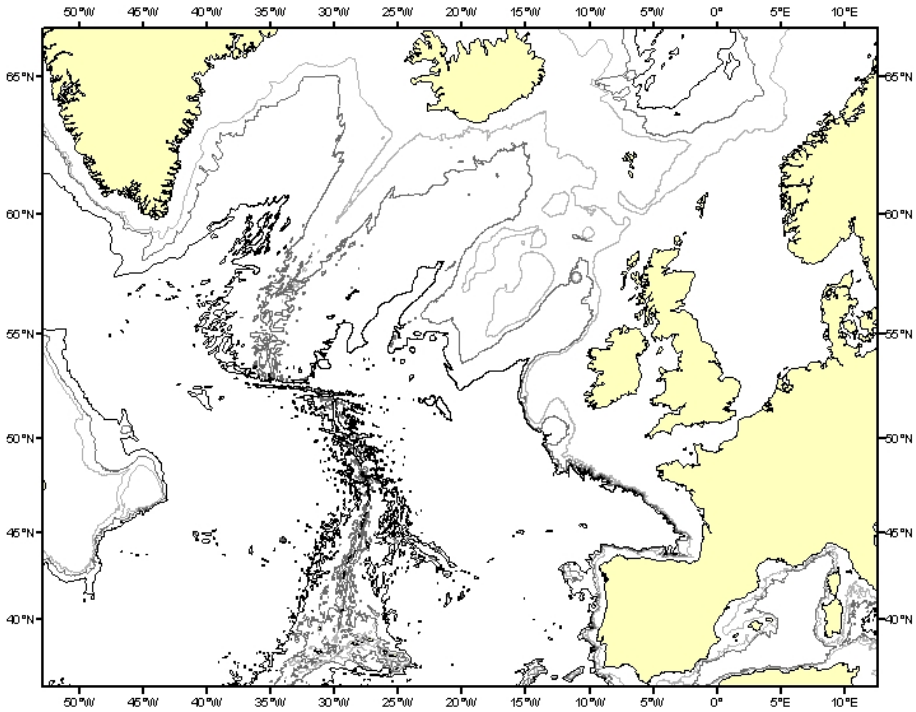

Figure 1.1. The northern Mid-Atlantic Ridge, from Iceland to the Azores including surrounding areas.

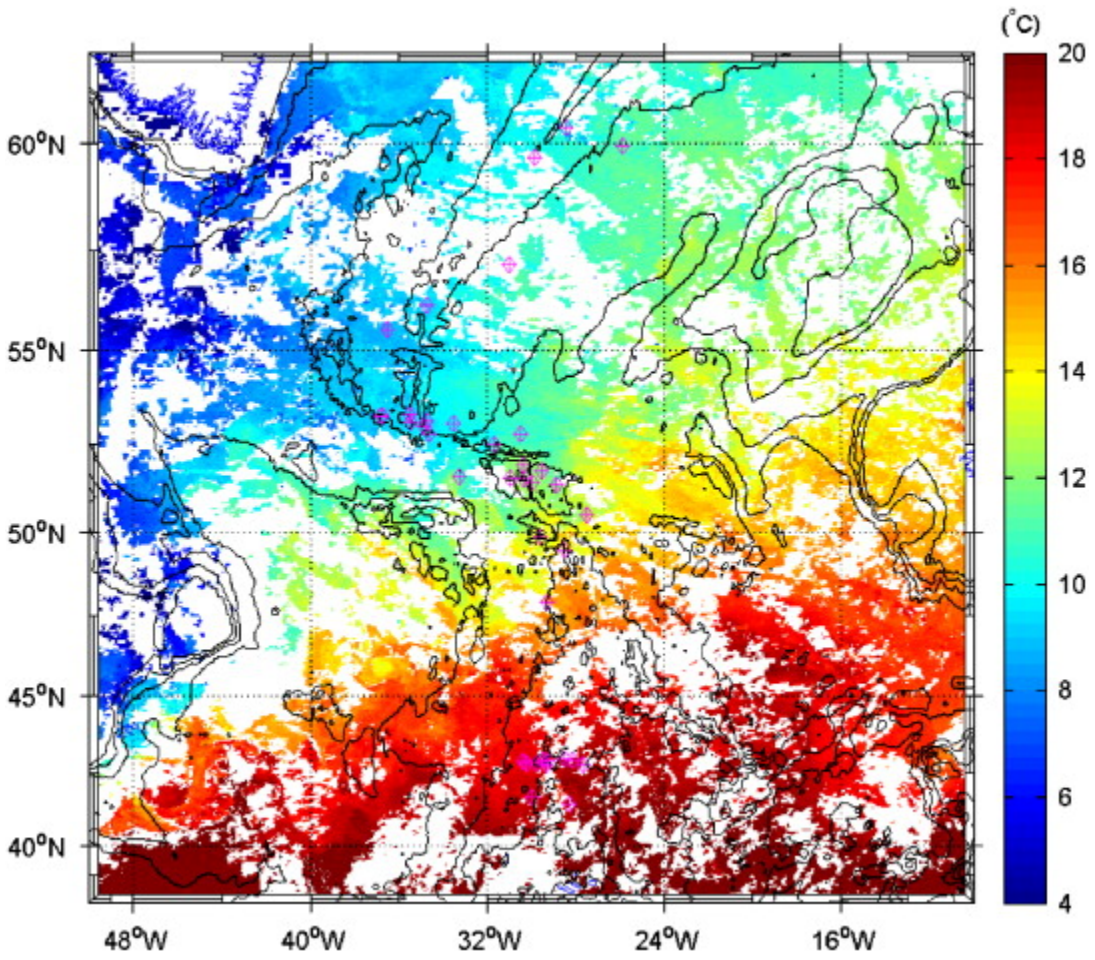

Figure 1.2. Eight-day composite of sea-surface temperature (SST) for June 18-24, 2004. Bottom topography indicated by thin black lines. Color bar scale in °C. Magenta diamonds indicate CTD stations (from Søiland *et al.* 2008).

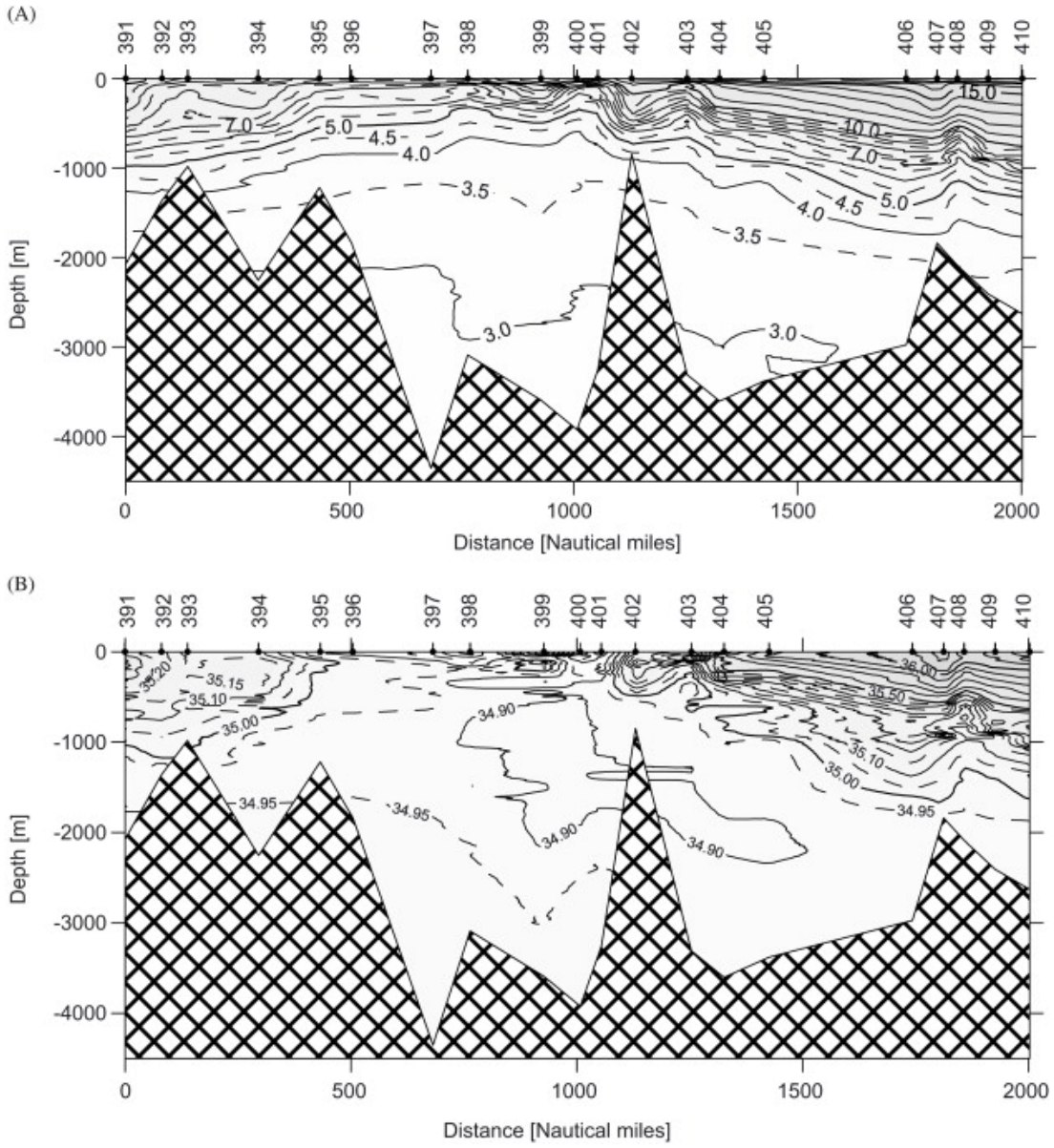

Figure 1.3. (A) Potential temperature (θ) as a function of depth and accumulated great circle distance between CTD stations on leg 1. Contour interval is 0.5 below 10 °C and 1.0 above. Isotherms 5, 10 and 15 °C are drawn as thick lines. Blanked out bottom based on measured depths on CTD stations. (B) Same as (A), but for salinity. Contour interval is 0.05 below 35.5 and 0.1 above. Isohalines 35, 35.5 and 36 are drawn as thick lines. Note that north is to the left (from from Søiland *et al.* 2008).

higher trophic levels all the way to the local nekton stocks (Dower and Mackas 1996).

Another theory explaining the relatively high nekton and plankton biomass along ridge systems is that ridges could act to concentrate vertically migrating prey, which would attract predators thereby increasing their abundance near the ridge (Isaacs and Schwartzlose 1965; Koslow 1997). The theory states that vertically migrating zooplankton and micronekton (small [<10 cm], freely swimming organisms whose swimming movements are still greatly affected by strong currents). get advected over areas that are shallower than their normal diurnal depth distribution, thus topographically trapping them as they try to descend to their normal depths. Ridges have also been shown to be feeding grounds and/or navigational landmarks for large predators such as hammer-head sharks (*Sphyrna)* and sperm whales (*Physeter macrocephalus)* (Klimley *et al.* 2002; Moulins and Würtz 2005; Skov *et al.* 2008). Ridges like the MAR provide a unique ecosystem where the interactions of multiple pelagic and benthic trophic levels can occur over a relatively concentrated area.

MAR-ECO

MAR-ECO is a field project of the Census of Marine Life program, designed specifically to "describe and understand the patterns of distribution, abundance and trophic relationships of the organisms inhabiting the mid-oceanic North Atlantic, and identify and model ecological processes that cause variability in these patterns" (Godø 2004). MAR-ECO provided an opportunity to study the deep-sea environment in the area of a large-scale topographic feature. Sixteen nations have worked together to understand the organisms and processes from the surface layer down to the abyssal zone. The goal of this project is to better understand the many aspects of the benthic habitat of the ridge

system as well as the water column above it. The scientists of MAR-ECO aim to understand how a mid-ocean ridge system such as the MAR may affect the interactions of benthic and pelagic communities, which are usually separated in time and space. A consortium of experts, like the MAR-ECO project, not only allows for focus on specific groups of organisms but their relation to one another and their environment.

THE FAMILY MELAMPHAIDAE

One of the least studied fish families in the deep sea is the Melamphaidae (Order: Stephanoberyciformes), whose lack of distinguishing morphological characters, low sample size of study material, and unstable taxonomic status make it a challenging family to study (Ebeling 1962; Keene 1987). Ebeling (1962) showed that the melamphaids were one of the most abundant families of the deep sea. With this discovery came increasing interest in and study of the family and its individual members. Melamphaids are a family of mesopelagic to bathypelagic fishes, whose adult members are rarely seen at depths shallower than 200 m. Individuals of the family are dark brown to black in color, some with rather large, deciduous scales and all have large cavernous heads with well-defined sensory pores, a blunt snout and minute jaw teeth (Figure 1.2).

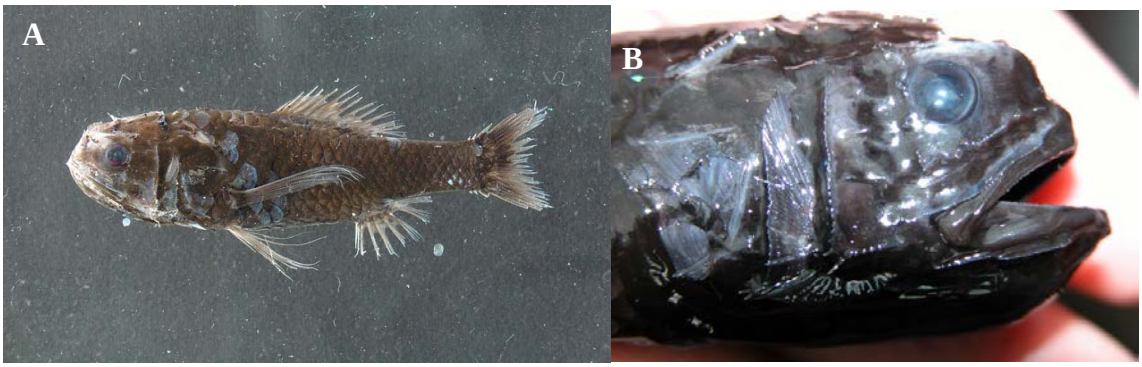

Figure 1.4. *Poromitra capito,* a species of Melamphaidae. A) Full body. B) Head. (Photos: Alexei Orlov and Jaime Alvarez)

Most mesopelagic to bathypelagic organisms have some means of producing light (Nicol 1962; Widder 2001), but melamphaids lack any such bioluminescent organs.

Melamphaid Taxonomy

The family Melamphaidae is one of the most problematic groups of fishes in the deep sea due to the scarcity of published information. Systematically, the melamphaids are considered "lower percomorphs" of the order Stephanoberyciformes (Ebeling 1962; Ebeling and Weed 1973; Moore 1993). The family is divided into five genera (*Melamphaes, Poromitra, Scopeloberyx, Scopelogadus,* and *Sio)* containing about 36 species (Nelson 2006; Kotlyar 2004a). Since the work of Ebeling (1975) and Parin and Ebeling (1980), only Kotlyar (1996; 2004 b-c; 2005; 2008 a-b; 2009 a-c) has published manuscripts regarding melamphaid taxonomy, having produced a book on beryciform and stephanoberyciform fishes and an in-depth treatment of the genera *Scopeloberyx* and *Poromitra*. With the current state of knowledge, identification of members of the family is challenging. A lack of distinguishing characters and fragility of specimens make the melamphaids difficult to study and diagnose. For this study the family Melamphaidae will be resolved taxonomically using recent material (e.g. MAR-ECO samples) and museum collections (e.g. Smithsonian Institution's National Museum of Natural History - Division of Fishes and the Bergen Museum in Bergen, Norway).

Feeding Ecology

Crustacean planktivory and piscivory constitute a majority of the foraging strategies employed by fishes in the deep-sea environment, but the Melamphaidae are an

apparent exception to this rule (Sedberry and Musick 1978; Crabtree *et al.* 1991; Sutton *et al.* 1995). Gartner and Musick (1989) and showed that the diet of one melamphaid, *Scopelogadus beanii*, consisted primarily of gelatinous zooplankton. They found that the majority of the gelatinous contents of the stomachs they studied were species of the family Salpidae (Thaliacea). One problem with gut content analysis studies is that gelatinous prey are rapidly digested into unrecognizable remains and thus can be overlooked (Harbison 1998). Unrecognizable remains may lead to a biased dietary importance placed on both the gelatinous prey and other prey items found in these stomachs. It was previously thought that gelatinous zooplankton offer little nutritional value to predators, and that gelatinous zooplankton were a "dead end" in marine food webs due to the lack of natural predators, and thus energy flow to higher trophic levels (Sommer *et al.* 2002; Nelson *et al*. 2002; Arai 2005). However, recent studies have shown that gelatinous zooplankton could play a more significant role in the diets of marine vertebrates than once believed (Kashkina 1986; Purcell and Arai 2001; Cartamil and Lowe 2004; Houghton *et al.* 2006). Mianzan *et al.* (1996) showed that 5% of the filled guts of 20 species of fish from the continental slope waters off Argentina contained ctenophores and other gelatinous material. Kashkina (1986) and Arai (1988) found that 89 species of epipelagic to mesopelagic fishes include coelenterates or salps in their diet. These findings suggest that gelatinous zooplankton may provide a key link between upper and lower trophic levels in the pelagic food web.

Changes in diet that occur over an individual's lifetime, as well as the changes that occur daily or seasonally with the availability of different prey species, must be considered in any feeding study (Mauchline and Gordon 1985). Feeding periodicity

patterns are difficult to determine for species that consume gelatinous prey due to rapid digestion. It may be that melamphaids feed at a constant rate or randomly throughout the diel cycle. Gartner and Musick (1989) showed no consistent pattern in the number of stomachs containing food over the diel cycle and thus no discernable effect of time of day on feeding rate.

Original theories about feeding in the deep sea stressed the need for an individual to be an opportunistic feeder, eating anything that came across its path because densities of prey in the deep are low when compared to shallow water areas (Ebeling and Cailliet 1974). These theories have been shown to be generalizations that have not been substantiated with data. The diet of most deep-sea fishes can change due to prey availability, the energetic value of the prey, and the sizes of the predator and prey themselves (Ebeling and Cailliet 1974). *Scopelogadus beanii* was believed to be a generalist feeder that fed on a variety of small crustaceans, but recently this idea has been challenged by the discovery that the formerly labeled "unidentified tissues" are important to its diet and most likely some type of gelatinous organism (Gartner and Musick 1989; Gartner *et al.* 1997). It was found that *S. beanii* feeds predominantly on gelatinous prey instead of small crustaceans (Mauchline and Gordon 1984; Gartner and Musick 1989; Gartner *et al.* 1997). A focus of the melamphaid diet component of this study will be to compare the ingested prey species with the available prey field. Relative abundances of gelatinous zooplankton will be calculated based on trawl catches and ROV transects of the ridge. Gelatinous material and counts are currently being handled by other MAR-ECO working groups, whose data were freely shared. A ratio of ingested prey to

available prey will provide information as to whether or not the melamphaid fishes display an opportunistic feeding style.

Reproduction and Growth

In the deep sea the most common population structures are ones having either equal sex ratios or assemblages with more, or larger, females (Clarke 1983). Many meso- to bathypelagic species display some sort of sexual dimorphism, ranging from slight differences in photophore patterns to the extreme size difference between males and females of the ceratioid angler-fishes (Bertelson 1951; Marshall 1979; Clarke 1983). In all cases, it is assumed that these sexual differences evolved to aid in a certain sex (be it male or female) to find a suitable mate. In the case of the melamphaids, it has been reported that their sex ratios are skewed towards having more males than females, and there is no apparent sexual dimorphism (Clarke 1983). Clarke (1983) found that the ratio near Oahu, Hawaii was about 2:1 in favor of males (62-64% males). Clarke (1983) and Clarke and Wagner (1976) are the only studies that have dealt specifically with melamphaid sex ratios, meaning that all sex ratio information on the family comes from a single area off the coast of Hawaii and could be different elsewhere.

It is rare to find populations that have such a male-biased sex ratio (Cocker 1978; Clarke 1983). A strategy of equal sex ratios, or one that is biased towards females, is most common due to the energy allocation needed by a female to produce an egg (Emlen and Oring 1977; Clarke 1983). It is believed that a population with no apparent sexual dimorphism and a higher number of males provides a female of the species a higher success rate in finding a mate by chance alone (Clarke 1983; Baird and Jumper 1995). In order to increase reproductive success, females would need to have access to resources

necessary for reproduction (Emlen and Oring 1977). Since the sex ratio seems to negate the availability of males as a limiting factor to reproductive success, it would seem that access to critical food resources is an important limiting factor that could play a large role in the success of the melamphaid species.

Another interesting trait of the family Melamphaidae is that it contains both "dwarf-" and "normal-sized" species (Keene 1987; Kotlyar 2004c). These "dwarf" species have often been mistaken for juveniles of the "normal sized" species, which make estimations of size at maturity and taxonomy particularly difficult (Keene 1987). It is imperative that "dwarf" species be correctly identified and separated from juveniles of other species. Proper handling of the dwarfism issue will aid in identifying new species, estimating reproductive characteristics, and describing the melamphaid species composition over the MAR.

OBJECTIVES

The goal of this study is to increase our understanding of the family Melamphaidae as it pertains to taxonomy, feeding ecology, and reproductive ecology. Products of this dissertation will be monographs describing species of each melamphaid genus, new species descriptions, as well as clarifying the subspecies issues associated with the genus *Scopelogadus*. Questions that will be answered about their feeding ecology are: 1) what are they eating and how does this vary between species; 2) how much do they eat; 3) are they prey-specific; and 4) is there an ontogenetic shift in diet? Analyses of melamphaid trophic ecology will yield a chapter in this doctoral dissertation as well as a paper that will be submitted for publication.

The sampling techniques employed on the MAR-ECO cruise will also allow for analyses of any changes along a vertical or latitudinal gradient. The multiple cod ends of the Akra trawl (de Lange Wenneck *et al.* 2008) allowed for discrete depth sampling. A vertical comparison of stations will define at which depth strata each species feeds. This becomes important when taking into account the diel vertically migrating layer that is found in the pelagic zones. Information about the migrating, sound scattering layer over the Mid-Atlantic Ridge can be found Opdal *et al*. (2008). Sound scattering layers were sampled both acoustically and with net tows to show the relative depth and composition of the layer (Opdal *et al*. 2008). Analyses of depth strata may provide evidence that certain melamphaid species feed when they are at the same depth as the vertically migrating layer, or that they themselves vertically migrate to feed. If melamphaids are feeding at the same depth strata as the vertically migrating layer, then their gut contents should reflect the species compositions of the layers found by Opdal *et al*. (2008). If melamphaids are not feeding at the same depth as the vertically migrating layer, then the gut contents of the melamphaids will be compared to the MAR zooplankton data. A comparison of geographically differing stations will parse out any effects in diet due to changes in latitude (e.g. changes in surface temperature, water masses, or topography, etc.). Expanded data of the feeding habits of this dominant fish family along the northern MAR will provide better understanding as to the flow of energy through this pelagic food web and the importance of gelatinous zooplankton and ridge systems to pelagic trophodynamics.

The gonads will also be removed during dissection and inspected to answer the following questions: 1) Is the MAR used as a spawning area for the Melamphaidae; 2)

What are the species-specific sizes at maturity for both sexes? The reproductive chapter of the dissertation will cover sizes at maturity, estimates of age, and size frequency distribution in order to understand the ontogenetic make-up of melamphaid fishes over the MAR.

Melamphaids could use the ridge to gather energy for reproductive purposes. As mentioned before, the MAR is an ecosystem with a high local biomass due to various physical features. The concentration of prey could provide the energy necessary for producing gametes and spawning, but it would also increase success by decreasing the search volume for individuals looking for mates (i.e. decreasing the volume from the large pelagic realm down to the more concentrated area above the ridge).

Therefore the objectives of this study are to clarify the taxonomy of the melamphaid family; identify and describe the melamphaid distribution, abundance and biomass along the MAR; describe the reproductive and growth characteristics of the melamphaid fishes; and identify melamphaid prey, their abundance and relative composition of the melamphaid diet.

CHAPTER 2

KEY TO THE SPECIES OF MELAMPHAIDAE

INTRODUCTION

A comprehensive key for the family Melamphaidae has not been produced since the works of Ebeling and Weed (1973) and Keene (1987), which are still the two major works used to identify the species of the family. Since the publication of these works, several new species descriptions have been published but not included in any more recent key to the family. A complete key is the initial step in an extensive research on this family of fishes.

MATERIALS AND METHODS

The keys published by Ebeling (1962), Ebeling and Weed (1963), Ebeling and Weed (1973) and Keene (1987) were used as the framework for a more complete key to the family. Included in this key are the works of Keene (1973), Ebeling (1975), Parin and Ebeling (1980) and Kotlyar (1999; 2002; 2004 a-c; 2005; 2008 a-b; 2009 a-c; 2010), which include several new species descriptions, an annotated checklist of species and monographs on the genera *Scopeloberyx* and *Poromitra*. Supplementary counts, measures and diagnostic characters were gathered from other publications in order to strengthen identifications (Ebeling 1986; Maul 1986; McEachran and Fechhelm 1998; Moore 2002; Moore In Press). Though Kotlyar's works were reviewed and considered,

many of the species described in these works merit further review before they can be included in this key. Initial analyses of Kotlyar's works reveal that most of the species descriptions and morphological characters provided coincide with characteristics of previously established species, while others may be new species, but the limited sample sizes prevent a definitive classification as such. While new species descriptions are handled in Chapter 3, they will not be placed in this key until they have gone through further review. This key represents a combination of previously published works and new morphological observations into a comprehensive key to the family.

KEY TO THE GENERA OF THE FAMILY MELAMPHAIDAE

1a. Scales in a longitudinal series (from nape to caudal base) of 15 or fewer; scales usually lost leaving large, shaggy, ill-defined scale pockets; cheek scales absent; frontal ridges of head smooth; supramaxillary bone absent; pyloric caeca 5..... *Scopelogadus* **Vaillant** 1888

1b. Scales in a longitudinal series (from nape to caudal base) of 20 or more; scales mostly lost, but scale pockets well defined; cheek scales present, though usually lost (scale pockets often discernable); supramaxillary bone present; frontal ridges of head serrate and crest-like or smooth; pyloric caeca 7 or 8..... **2.**

2a. Frontal ridges of head crest-like and serrate; conspicuous spine between nares; ventral border, angle and most of the posterior border of the preopercle serrate; gill rakers on first arch 23-33; cheek scales 3-4 (often lost)..... *Poromitra* **Goode and Bean** 1883

2b. Frontal ridges of head not crest-like, margins smooth; spine between nares absent or inconspicuous; border of preopercle smooth or with few large, widely spaced spines around angle; gill rakers on first arch 13-30; cheek scales 2-3..... **3.**

3a. Combined spiny and soft rays of dorsal fin fewer than 13; branchiostegal rays 7; maxillary ends at a vertical from posterior border of pupil; teeth uniserial; scales without circulion posterior field..... *Sio* **Moss** 1962

3b. Combined spiny and soft rays of dorsal fin 13 or more; branchiostegal rays 8; maxillary extends to vertical from posterior edge of eye or beyond; oral teeth in bands; scales with widely spaced and easily visible circuli, narrowly spaced and barely visible circuli, or without circuli on posterior field..... **4.**

4a. Combined spiny and soft rays of dorsal fin fewer than 16; cheek scales usually more than 2, the anteriormost not modified to form receptacle for end of maxillary; eye diameter 11% of head length; epidermis of head thin and fragile, usuallydamaged and missing, accentuating the head ridges *Scopeloberyx* **Zugmayer** 1911

4b. Combined spiny and soft rays of dorsal fin 17 or more; cheek scales 2, the anteriormost modified to form receptacle for end of maxillary; eye diameter in adults usually more than 11% of head length; epidermis of head usually remains intact and the head is smooth..... *Melamphaes* **Günther** 1864

KEY TO THE SPECIES WITHIN EACH GENUS OF THE MELAMPHAIDAE

Scopelogadus **Vaillant** 1888

1a. Total gill rakers on first arch 25 or fewer, GR(6-8)+(15-18); head length 32-38% SL; body depth 23-27% SL..... *S. mizolepis*

1b. Total gill rakers on first arch 26 or more, GR(8-10) + (18-22)..... **2.**

2a. Dorsal spine 1; caudal peduncle length 27.5-32.7% of SL; rudimentary rakers on fifth arch mostly well formed stubs; gas bladder remnant of rete mirabile and gas gland present; vertebrae almost always 23..... *S. unispinis*

2b. Dorsal spines 2; caudal peduncle length 33.4-38.3% of SL; rudimentary rakers on fifth arch mostly reduced to spinose patches or single spines; gas bladder remnant of rete mirabile and gas gland absent; vertebrae 25-27..... *S. beanii*

Poromitra **Goode and Beane** 1883

1a. Eye tiny, its diameter less than 1/15 (6.7%) head length; dorsal rays 9-10; length of upper jaw slightly more than ½ (50%) head length..... *P. oscitans*

1b. Eye moderate to large, its diameter more than 1/10 (10%) of head length; dorsal rays 10 or more; length of upper jaw less than ½ (50%) head length..... **2.**

2a. Eye large, its diameter more than 1/5 (20%) head length; caudal peduncle depth less than 1/3 (33%) peduncle length; gill rakers fewer than 28..... *P. megalops*

2b. Eye moderate, its diameter less than 1/6 (≈17%) head length; caudal peduncle depth more than 1/3 (33%) peduncle length; gill rakers more than 28..... **3.**

3a. Retrose preopercular spine weakly to moderately developed, its length ½ - ¾ (50-75%) of anal-fin base; upper cheek ridge slanting forward, forming 75-85° angle with horizontal..... **4.**

3b. Retrose spine at posteroventral angle of opercle strong, its length (from base at the cheek angle to its point at the posteroventral edge of preopercle) about equal to length of anal-fin base; upper cheek ridge oriented vertically, forming 90° angle with the horizontal; head spines, ridges, scales relatively hard and strong..... *P. capito*

4a. Dorsal rays 11 or more (rarely 10); gill rakers on first arch 27 or more; upper jaw length less than 19% of SL; total vertebrae 25 or..... **5.**

4b. Dorsal rays 10; gill rakers on first arch 24-25; upper jaw length 19-21% of SL; total vertebrae 25..... *P. crassa*

5a. Dorsal rays III,10-12 (usually III,11); Anal rays I,7-9 (usually I,8); vertebrae 25-27; head length greater than 38% SL; anal fin insertion below 3rd to 5th from last dorsal ray..... **6.**

5b. Dorsal rays III,12-15; Anal rays I,9-11; vertebrae 27-29; head length less than 38% SL; anal fin insertion below 6th to 7th from last dorsal ray..... *P. crassiceps*

6a. Pelvic fin insertion in front of the vertical through the posterior edge of pectoral fin insertion; pyloric caeca 9-11; angular preopercular spine absent or rudimentary; scales in transverse row, from the beginning of dorsal fin insertion to the beginning of anal fin insertion, 7-9 (usually 7-8); total gill rakers on first arch 28-33 (usually 31-32)..... *P. unicornis*

6b. Pelvic fin insertion behind vertical through the posterior edge of pectoral fin insertion; pyloric caeca 8-9; presence of an angular preopercular spine, length of which is 2/3 (66.7%) the length of the base of the anal fin; scales in transverse row, from the beginning of dorsal fin insertion to the beginning of anal fin insertion, 10-11; total gill rakers on first arch 30-34 (usually 32-33)..... *P. gibbsi*

Sio **Moss** 1962

Though Keene (1987) described a possible new *Sio* species, there is only one accepted species in this genus: *Sio nordenskjoldii.*

Scopeloberyx **Zugmayer** 1911

1a. Teeth in bands..... **2.**

1b. Teeth uniserial..... *S. rubriventer*

2a. Total gill rakers on the first arch 17 or less; total spines in dorsal either 2 or 3..... **3.**

2b. Total gill rakers on the first arch 19-25 (more often 20 or 21); 2 or 3 spines in dorsal; gill arch shiny blue in color due to guanine iridophores..... *S. robustus*

3a. Total gill rakers on the first arch 10-13; Pelvic soft rays 6; vertebrae 27-29; number of transversal scale rows from the occipital part of the head to the origin of the caudal fin and from the posterior margin of the posttemporal bone to the origin of the caudal fin 46-53 and 38-45, respectively..... *S. microlepis*

3b. Total gill rakers on first arch 14-17; Pelvic soft rays 7 or 8; vertebrae 25-27; Number of transversal scale rows from the occipital part of the head to the origin of the caudal fin and from the posterior margin of the posttemporal bone to the origin of the caudal fin 28-33 and 23-28, respectively..... *S. opisthopterus*

Melamphaes **Günther** 1864

1a. Total gill rakers on first arch 20 or more; width of largest rakers, near their midsections, subequal to the width of the spaces between rakers; length of longest raker at least 1.33 times eye diameter; gill rakers on lower limb of fourth arch usually 10-13; adults mature at 70-117 mm..... **2.**

1b. Total gill rakers on first arch 19 or fewer; width of largest rakers, near their midsections, not more than ¾ the width of the spaces between rakers; length of longest raker usually less than 1.33 times eye diameter; gill rakers on lower limb of fourth arch usually 7-9; adults mature at 18-134 mm..... **10.**

2a. Pelvic rays I,8; dorsal rays III,14-18; body scales with width of widest grooves between circuli on posterior field only 2-5 times width of narrowest grooves on anterior field; vertebrae 26-30; posttemporal spines absent..... **3.**

2b. Pelvic rays I,7; Dorsal rays III,13-16; body scales with width of widest grooves between circuli on posterior field 3-12 times narrowest grooves on anterior field; vertebrae usually 26-29; posttemporal spines present or absent..... **4.**

3a. Dorsal rays III,17-18; gill rakers on first arch 21-24; body scales with width of widest grooves between circuli on posterior field only 3-5 times width of narrowest grooves on anterior field; vertebrae 29-30; posttemporal spines absent..... *M. microps*

3b. Dorsal rays III,14-16; gill rakers on first arch 19-21; body scales with width of widest grooves between circuli on posterior field only 2-3 times width of narrowest grooves on anterior field; vertebrae 26-27; posttemporal spines absent; juveniles have two distinct pigmentation bands on the caudal peduncle..... *M. ebelingi*

4a. Scales in diagonal series 9-10; scale rows 33-36; body scales without circuli on posterior field; origin of anal fin under or behind second to last dorsal ray; spurs on first haemal arch well developed; posttemporal spines absent..... **5.**

4b. Scales in diagonal series 8; scale rows 30-33; body scales with well developed circuli on posterior field; origin of anal fin under third to fifth from last dorsal ray; spurs on first haemal arch well developed or absent; posttemporal spines present or absent..... **6.**

5a. Opercular scales 8 (usually missing); pectoral rays usually 16; head pores mostly single, on preopercle above angle they number 4-6, on mandible usually 4; precaudal vertebrae 12; dorsal rays III,15-16..... *M. lugubris*

5b. Opercular scales 4 (usually missing); pectoral rays 15; head pores mostly in groups, on preopercle above angle they number 10-11, on mandible 5-7; precaudal vertebrae 11; dorsal rays III,13-15 (usually III,14)..... *M. polylepis*

6a. Body scales with width of widest grooves between circuli on posterior field 3-7 times narrowest grooves on the anterior field; spurs on first haemal arch absent; vertebrae 26-27; head length 40-44% SL; pores on cheek inside angle 4-5; insertion of pelvic fin directly under or slightly before that of pectoral..... **7.**

6b. Body scales with width of widest grooves between circuli on posterior field 10 or 11 times narrowest grooves on anterior field; spurs on first haemal arch present and well developed or absent; vertebrae 27-29; head length 34-40% SL; pores on cheek inside angle 3..... **8.**

7a. Dorsal edge of posttemporal without antrorse spine; total gill rakers on first arch 20-21 (rarely 19 or 22)..... *M. macrocephalus*

7b. Dorsal edge of posttemporal with sharp, antrorse spine; total gill rakers on first arch 22-24..... *M. acanthomus*

8a. Dorsal edge of posttemporal with sharp, antrorse spine; vertebrae 28-29; spurs on first haemal arch well developed; dorsal rays III,15-16; gill rakers 20-24; maximum size 114 mm..... **9.**

8b. Dorsal edge of posttemporal without antrorse spine (inconspicuous rudiment occasionally present); vertebrae 27; spurs on first haemal arch absent; dorsal rays III,14-15; gas-bladder rudimentary; gill rakers on first arch 20-22; maximum size 76 mm..... *M. leprus*

9a. Insertion of pelvic fin slightly behind that of pectoral fins; transverse scale rows from nape and temple to beginning of caudal 32-36 and 28-32, respectively; head length 29.7-37% SL; caudal peduncle length 23.6-29.1% SL; upper jaw length 13.4-15.9% SL; dorsal fin base 20.3-30.3% SL; vertebrae 28-29; dorsal rays III,16 (rarely III,15); Atlantic specimens with well-developed gas-bladder twice length of stomach; gill rakers 20-24; dark brown coloration in formalin..... *M. suborbitalis*

9b. Insertion of pelvic fin slightly in front of that of pectoral fins; transverse scale rows from nape and temple to beginning of caudal 31 and 26, respectively; head length 40.3% SL; caudal peduncle length 23% SL; upper jaw length 17.3% SL; dorsal fin base 31% SL; vertebrae 29; dorsal rays III,15; gill rakers 23..... *M. parini*

10a. Adults mature at 34-106 mm; body scales with width of grooves between circuli on posterior field 2-10 times narrowest grooves on anterior field or with posterior field without circuli; scales in diagonal series 8; pores on cheek inside angle 2-5 (usually 3-4); diameter of eye equal to or noticeably greater than suborbital width..... **11.**

10b. Adults mature at 18-27 mm ("dwarf species"); body scales with circuli equally spaced on all fields; scales in diagonal series 8-11; pores on cheek inside angle 2 (rarely 3); diameter of eye noticeably less than suborbital width..... **18.**

11a. Anal rays I,9 (rarely I,8 or I,10); anal origin under fourth or fifth from last dorsal ray; body scales with width of widest grooves between circuli on posterior field 9 or 10 times narrowest grooves on anterior field; precaudal vertebrae 11; adults mature at 112-134 mm..... *M. laeviceps*

11b. Anal rays I,8 (rarely I,7 or I,9); anal origin under or behind last dorsal ray; body scales with width of widest grooves between circuli on posterior field only 2-5 times narrowest grooves on anterior field or with posterior field without circuli; precaudal vertebrae 11-12; adults mature at 28-106 mm..... **12.**

12a. Either preopercle with well-developed spines, including large antrorse falciform spine at anterior border (*M. spinifer*) or head ridges expanded to reveal flanges of reticulate bone at their margins (*M. eulepis*); body scales with width of widest grooves between posterior circuli 3-5 times narrowest grooves on anterior field; squamation and head epidermis durable, usually mostly intact..... **13.**

12b. Preopercle without well-developed spines; head ridges thin, not expanded to reveal flanges of reticulate bone at their margins; body scales with width of widest grooves on posterior field only 2-3 times narrowest grooves on anterior field or with posterior field without circuli; squamation caducous, rarely more than half intact; head epidermis frequently damaged..... **14.**

13a. Pores on cheek inside angle 4-5; scale rows 31-33 (usually 32); teeth on third pharyngobranchial 25-40; vertebrae 26-28; scales usually partly missing..... *M. spinifer*

13b. Pores on cheek inside angle 3; scale rows 33-36 (usually 34-35); teeth on third pharyngobranchial 45-55; vertebrae 29-30; scales usually intact; maximum size 48 mm..... *M. eulepis*

14a. Anal origin directly under or slightly behind last dorsal ray (by considerably less than width of a scale pocket); gill rakers on lower limb of first arch, including raker at angle, 13-15; depth of caudal peduncle slightly more than 50% of caudal peduncle length..... **15.**

14b. Anal origin well behind last dorsal ray (usually by as much as width of one or one and a half scale pockets); gill rakers on lower limb of first arch, including raker at angle, 11-13; depth of caudal peduncle 50% or slightly less than 50% of caudal peduncle length..... **17.**

15a. Adults mature at 76-106 mm; dorsal rays III,16-17 (rarely III,15 or III,18); total gill rakers on first arch 16-19 (rarely 20); teeth on fourth pharyngobranchial 18-35; vertebrae 28-30; spurs on first haemal arch absent; fin rays, base of pectoral fin, and head never punctulate; scales with circuli on all fields; predorsal length usually less than 42% of SL..... *M. longivelis*

15b. Adults mature at 28-47 mm; Dorsal rays III,14-15 (very rarely III,13 or III,16); teeth on fourth pharyngobranchial 7-18; vertebrae 25-29; short spurs on first haemal arch usually present; fin rays, base of pectoral fin, and head (mainly in front of preopercle) in most young, half-grown and smaller adults very finely punctulate; scales with circuli on all fields or with posterior field without circuli; predorsal length usually more than 42-43% of..... **16.**

16a. Scale rows 32-33; body scales with circuli on all fields; vertebrae 27-29; head usually less than 40% of SL; total gill rakers on first arch 17-20; mandibular pores 5-9..... *M. parvus*

16b. Scale rows 29-31; body scales with posterior field without circuli; vertebrae 25-27; head usually more than 40% of SL; total gill rakers on first arch 14-17; mandibular pores 6-7..... *M. janae*

17a. Body scales with posterior field without circuli; total gill rakers on first arch 14-17 (usually 16-17); length of longest raker subequal to eye diameter; gill rakers on fourth arch distinct knobs or convexities with 7-9 spines (rarely reduced to spinose patches of more than 8 spines each)..... *M. indicus*

17b. Body scales with circuli on all fields; total gill rakers on first arch 14-15; length of longest less than eye diameter; gill rakers on fourth arch reduced to low convexities or patches of 7-20 spines each; dorsal rays III,14-15; vertebrae 25-27..... *M. typhlops*

18a. Anal rays I,9; dorsal rays III,16 (rarely III,15 or III,17); total length of gas bladder twice that of rete and gas gland..... *M. simus*

18b. Anal rays I,7-8; dorsal rays III,14-15 (rarely III,16); total length of gas bladder 3-5 times that of rete and gas gland..... **19.**

19a. Scale rows 35-36; scales in diagonal series 10-11; head length 33-34% of SL; vertebrae 28-29; dorsal rays III,14-15; anal rays I,8..... *M. hubbsi*

19b. Scale rows 30-32 (rarely 33 or 34); scales in diagonal series 8-11; head length 35-39% of SL (rarely 33 or 34%); vertebrae 25-28..... **20.**

20a. Scales in diagonal series 10-11 (rarely 9); vertebrae 25-27 (rarely 28); precaudal vertebrae usually 11; short spurs on first haemal arch present; tooth formula 2-5/2-3..... *M. danae*

20b. Scales in diagonal series 8; vertebrae 27-28; precaudal vertebrae 12; spurs on first haemal arch absent; toot formula 5-7/3-5..... *M. pumilus*

CHAPTER 3

MELAMPHAID TAXONOMY

INTRODUCTION

The family Melamphaidae is one of the most problematic groups of fishes in the deep sea due to the scarcity of published information about the family. Systematically, the melamphaids are considered "lower percomorphs" of the order Stephanoberyciformes (Ebeling 1962; Ebeling and Weed 1973; Moore 1993). The family is divided into five genera (*Melamphaes, Poromitra, Scopeloberyx, Scopelogadus,* and *Sio)* containing about 36 species (Nelson 2006; Kotlyar 2004a). Since the work of Ebeling (1975) and Parin and Ebeling (1980), only Kotlyar (1996; 2004 b-c; 2005; 2008 b-c; 2009 a-c; 2010) has published on melamphaid taxonomy, having produced a book on beryciform and stephanoberyciform fishes and in-depth treatments of the genera *Scopeloberyx* and *Poromitra*. Melamphaids lack distinguishing morphological characters such as photophores and barbels that are used to discriminate most deep-pelagic fishes (e.g., Stomiiformes, Myctophidae, Ceratioidei). Thus, relative to other deep-sea fish taxa, the taxonomic status of the family in terms of species composition and interrelationships is inadequately described, making it a challenging family to study (Ebeling 1962; Keene 1987; Kotlyar 2004 a-b; Kotlyar 2005). For this study the family Melamphaidae will be resolved taxonomically using recent material (e.g. MAR-ECO samples) and museum

collections (e.g. Smithsonian Institution's National Museum of Natural History, Division of Fishes [NMNH], and the Bergen Museum [ZMUB]).

MATERIALS AND METHODS

Museum Samples

Specimens for this study were acquired via loans from the ZMUB in Bergen, Norway and the NMNH Division of Fishes in Washington, DC. The ZMUB specimens were all fish taken from the waters along and above the northern Mid-Atlantic Ridge (from Iceland to the Azores). The NMNH specimens were mostly collected during the "Ocean Acre" program (Brooks 1972; Brown and Brooks 1974) off the coast of Bermuda, originally studied by Keene (1987). Samples from NMNH used for the analysis of *Poromitra* were caught in the North Atlantic off the coast of Guinea and in the South Pacific off the coast of Chile. The samples used to analyze the *Scopelogadus mizolepis* subspecies complex were collected in the South Pacific off the coast of Peru. For specific location, depths and numbers of specimens examined, refer to Appendix 1.

The samples from Norway were used in the trophic analysis of the melamphaids over the Mid-Atlantic Ridge. Though some measures and counts were taken during species identification for the trophic study, high precision measurements were made for this taxonomic study. Thus, the ZMUB material used for this study can be considered supplementary to the NMNH material, which was analyzed in greater detail.

Species Examined

For this study several lots of fish were specifically chosen from the NMNH collection. These specimens were chosen to investigate the work and species reported by

Keene (1987). Specimens that Keene reported as *Melamphaes indicoides* and *Scopeloberyx americanus* were borrowed from the museum. *Scopelogadus mizolepis* subspecies were also studied to clarify their status as subspecies. Specimens from the *Poromitra crassiceps* species complex were also chosen, as they were the only problematic *Poromitra* lots encountered during a brief visit to the NMNH. These lots were selected instead of others to offer an opportunity to investigate taxonomic difficulties in each of the genera (save for *Sio* which was not handled in this study) and an opportunity to handle three different taxonomic problems (new species, a species complex, and a subspecies complex).

Species Identification

An integral part of this study is the production of an updated key for the Melamphaidae. In order to identify each individual to species level, a revised version of the keys in Ebeling (1962) and Ebeling and Weed (1963) was used. Additions to these keys were made based on species descriptions and keys to genera published since 1963. As seen in Chapter 2 of this dissertation, the updated key takes into account the works of Keene (1973), Ebeling (1975), Parin and Ebeling (1980) and Kotlyar (1999; 2004 a-c; 2005; 2008 a-b; 2009 a-c; 2010). This list of works includes new species descriptions, an annotated checklist of species, and monographs on the genera *Scopeloberyx* and *Poromitra*. Various museums around the world house a large number of unidentified melamphaid specimens and species (Appendix 2). Thirty-five of 37 melamphaid species were found to be housed at various museums during a preliminary search through their collections. Amongst this collection there were six lots of “new species,” one lot

containing a “species complex,” 11 lots of uncertain diagnoses (“c.f.”), and 17 lots of unidentified material. Additional counts and measures for *Scopelogadus mizolepis mizolepis, Poromitra crassiceps* and *Melamphaes* species were gathered from Ebeling (1962), Ebeling and Weed (1963), Keene (1987) and McEachran and Fechhelm (1998). These literature values were used to ensure a sufficient field of values against which the museum material could be compared.

Counts and Measures

All counts and measures were taken following Ebeling (1962) and Ebeling and Weed (1963) that were also reused in Keene's unpublished dissertation (1987). All counts and measures were taken from the right side of a specimen. In some cases, specimens were too badly damaged to get all counts and measures from a single side and in these cases a compilation of counts and measures from both sides of the specimen were used. X-rays were not available during this research so vertebral counts were not included. Spine and ray counts were made using stereo-microscopy. Scale counts were estimated, based on number of scale pockets, in cases where scales were missing and/or indiscernible. Measurements greater than 5 mm were made using calipers, while measurements less than 5 mm and measurements of head features were made using a calibrated ocular reticle inside the stereoscope for maximum precision. The reticle was used on the measurements of head features to get a more precise value.

Counts. Counts were made of dorsal spines and rays; anal spines and rays; pelvic spines and rays; procurrent and principal caudal rays; pectoral rays, all except the small bony splint just before the first unbranched ray; scale rows - scales from and including

the mid-dorsal scale at the nape, through all oblique rows, to, but not including, the mid-lateral triangular scale that slightly overlaps the edge of the hypural plate anteriorly; scales in diagonal series - all scales in an oblique series from and including the modified mid-dorsal scale immediately before the first dorsal spine to, and including, a scale of the mid-ventral row near the anus; gill rakers on the first gill arch - all rudiments, stumps and patches of spines; gill rakers on the lower limb of the fourth arch - all rudiments, stumps and patches of spines, excluding those at or above the angle; teeth rows - either uniserial or in bands.

Pores. Head pores can be hard to see individually, especially if the head tissues have been damaged. As a result groups of pores were counted instead of individual pores. After groups were counted, one group was examined in detail to determine how many pores were in each group. Neuromasts of the head canal portion of the lateral line (Fig. 3.1) were used to enumerate groups. Each group of pores is associated with a single neuromast, which is easier to discern and more robust than the pores themselves, meaning neuromasts were more likely to be intact on each specimen. Neuromasts were counted and separated into five groups: 1) mandibular - the (usually four) groups on the ventral aspect of the mandible along the isthmus; 2) cheek - the (usually four) groups of pores between the posterior aspect of the orbit and the cheek ridge; 3) maxillary - the (usually four) groups of pores between the maxilla and the ventral aspect of the orbit; 4) preopercular - the (usually five to six) groups of pores along both the posterior and ventral aspects of the preoperculum; and 5) supraorbital - the (usually five or more) groups of pores between the dorsal aspect of the orbit and the dorsal midline of the skull,

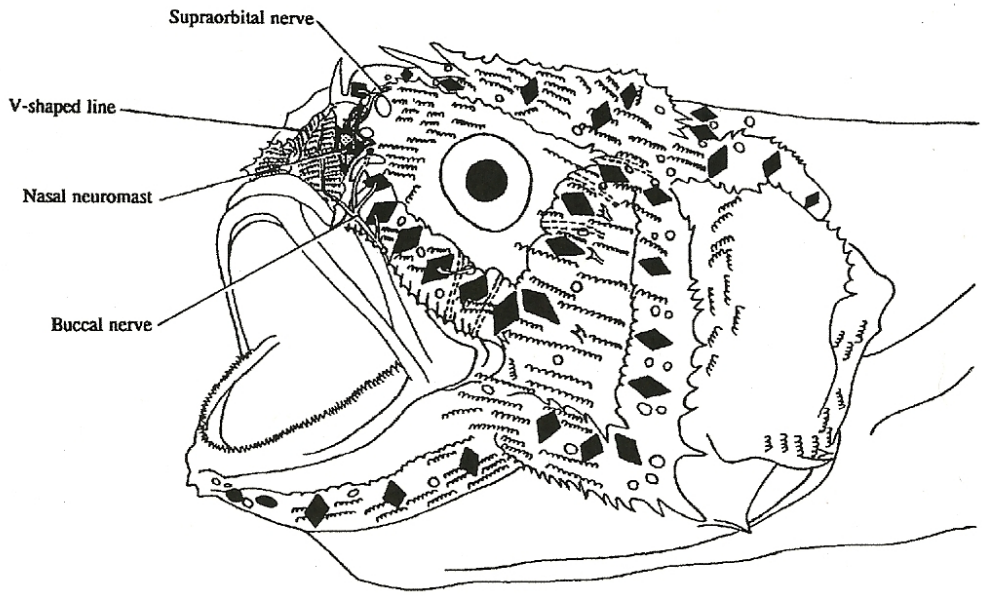

Figure 3.1. Head of *Poromitra capito* in anterolateral view. Neuromasts are shown as black diamonds and open circles are holes in the skin overlying the sensory canals. The zig-zag lines on the cheek and lower jaw indicate rows of free lateral line organs on papillae (from Johnson and Patterson 1993).

running the entire length of the head from the snout to the posterior edge of the operculum.

Measurements. Measurements used in this study are given in Appendix 3 and are defined as follows: standard length (SL) - anterior margin of premaxilla to caudal base; body depth - insertion of pelvic to dorsal margin of body; post-dorsal - base of first dorsal spine to caudal base; end of dorsal to caudal - base of last dorsal ray to caudal base; snout to preopercle - anterior margin of premaxilla horizontally to posterior edge of preopercle; orbit to cheek ridge - posterior margin of bony orbit to posterior edge of cheek ridge; head depth - occiput directly over preopercle to ventral edge of preopercle; interorbital - distance between wide margins of frontal bones directly over middle of eye; length of frontal fossa - anterodorsal edge of frontal knob between the nares to line between posterior extremities of paired ridges on top of head (there is often a visible suture between the frontal and parietal bones on the head crest, which was used as the measuring point); width of frontal fossa - greatest width between the paired ridges on dorsal surface of the head; prepectoral, anterior margin of premaxilla horizontally to vertical through pectoral base; prepelvic - anterior margin of premaxilla horizontally to vertical through the base of the pelvic spine; isthmus to pelvic - midpoint of angle in ventral profile of mandible (marked by the second neuromast from the tip of the lower jaw) to base of pelvic spine; pelvic to anal - base of pelvic spine to base of anal spine; preanal - anterior margin of premaxilla to base of anal spine; anal to caudal, base of anal spine to caudal base; orbit to cheek angle - posteroventral margin of bony orbit to recess between two spinelets at angle of cheek ridge (spinelets are present in all species, though they are more prominent in *Poromitra* species); orbit - greatest horizontal diameter of the

bony orbit; caudal length - posterior edge of anal base to caudal base; caudal width - dorsal edge of caudal peduncle at its mid-length vertically to ventral edge.

Counts and measures are presented following the methods of Ebeling and Weed (1963), Keene (1987), and Kotlyar (2004 b-c; 2005; 2008 b-c; 2009 a-c; 2010). In these works, the ranges of counts and measures are compared to each other without further statistical analyses. The data is presented here in tabular form. In these tables all counts and measures can be analyzed and compared easier to their counterparts in corresponding species. In order to publish this taxonomy chapter, further statistical analyses should be done in to limit any criticism of the results.

RESULTS AND DISCUSSION

***Scopeloberyx* Zugmayer** 1911

Scopeloberyx robustus (Günther 1887)

Description (based on seven specimens, 71.5-82.7 mm SL) -- Dorsal II-III, 10-13 (usually III, 12); anal I, 8-9 (usually I,9); pectoral 12-14 (usually 14); pelvic I, 7-8 (usually I,7); horizontal scale rows 29-33; diagonal scale rows 9-12; total gill rakers on first arch 20-26 (usually 22 or 23); gill rakers on lower limb of fourth arch 10-11 (usually 11); vertebrae 10-11 precaudal +15-16 caudal = 25-27, usually 10+15 (from Keene 1987, based on 17 specimens).

Measurements in % SL-- head depth 23.75-26.64; head length 32.56-36.13; snout to preopercle 18.49-26.05; orbit to cheek ridge 7.19-8.17; orbit to cheek angle 13.16-14.87; interorbital 8.05-10.49; frontal width 8.63-12.10; frontal length 17.37-20.32; fleshy orbit 5.32-6.90; maxilla length 16.45-19.94; body depth 24.74-28.29; postdorsal

34.92-49.96; end of dorsal to caudal 26.40-30.73; prepectoral length 36.77-41.70; prepelvic length 40.13-42.90; isthmus to pelvic 34.46-37.59; pelvic to anal 26.10-29.72; postanal 30.21-33.90; caudal length 22.11-25.41; caudal depth 8.81-11.75.

Head depth approximately 73% of head length. End of maxilla extending beyond vertical through the posterior of the eye by 1.61-3.42% of SL (1.7 to 4.0 times in eye diameter). Head smooth (non-serrate) and lacking a bony "crown" dorsally. Prominent bony ridges and epidermis on head very fragile, often damaged, giving the head a ragged appearance. Vertical preopercular margin straight. Preopercle curves gently through angle and becomes horizontal anteriorly. All margins of preopercle smooth. Upper arm of cheek ridge angles slightly forward at an angle of 83-88° with horizontal arm (Keene 1987). Teeth in bands.

Longest gill filament on first arch 23.08-33.61% of longest gill raker. First gill arch, inside surface of the operculum and the ventral surface of the isthmus all have an iridescent blue color (fixed samples).

Anal insertion under 8^{th}-11^{th} dorsal fin ray. Pectoral fins long, extending past anal fin origin when undamaged. Pelvic fin insertion less than 6% SL behind pectoral fin insertion.

Scales usually missing, but scale pockets often discernable. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 20-26, usually 22 or 23; gill rakers on lower limb of fourth arch 10-11, usually 11; gill filaments on first arch 23.08-33.61% of longest raker; gill arch, inside of operculum and isthmus all with an iridescent blue color; maximum SL of study material 82.65 mm (includes all specimens examined for trophic

study); distance between insertions of the pectoral and pelvic fins less than 6% SL; distance between pelvic and anal fin insertions greater than 26% SL; anal fin insertion under 8^{th}-11^{th} dorsal ray; anal fin elements usually I,9; maxilla extending past posterior margin of fleshy orbit by less than 3% SL; diagonal scale rows 9-12; horizontal scale rows 29-33.

Scopeloberyx americanus (Keene sp. nov.)

Paratypes -- USNM 247399, 33°05' N 64°40' W, 0-1920m, 1; USNM 249714, 32°10' N 64°08' W, 0-1710m, 1; USNM 249736, 32°04' N 63°45' W, 0-1500m, 2; USNM 249738, 32°13' N 63°42' W, 0-3500m, 1; USNM 249782, 32°27' N 64°17' W, 1494-1524m, 1; USNM 249783, 31°57' N 63°47' W, 1488-1555m, 1; USNM 266683, 32°27' N 64°17' W, 1504-1536m, 1; USNM 324745, 800-900m, 1.

Description (based on nine specimens, 17.38-26.69 mm SL) -- Dorsal II-III, 10-12 (usually III, 11); anal I, 7-8 (usually I,8); pectoral 11-17 (usually 14; extreme values most likely due to damage, making individual rays difficult to discern); pelvic I, 7-8 (usually I,7); horizontal scale rows 22-30; diagonal scale rows 9-11; total gill rakers on first arch 19-23 (usually 20 or 21); gill rakers on lower limb of fourth arch 9-10; vertebrae 10 precaudal + 14-15 caudal = 24-25, usually 10+15 (from Keene 1987, based on 16 specimens).

Measurements in % SL-- head depth 21.58-25.92; head length 32.98-38.19; snout to preopercle 24.04-30.34; orbit to cheek ridge 6.77-9.74; orbit to cheek angle 12.27-15.72; interorbital 8.97-12.99; frontal width 10.81-12.49; frontal length 13.98-23.52; fleshy orbit 3.73-7.50; maxilla length 17.54-20.11; body depth 23.53-28.79; postdorsal

44.24-52.08; end of dorsal to caudal 24.76-31.27; prepectoral length 32.69-42.01; prepelvic length 38.77-46.60; isthmus to pelvic 35.77-38.89; pelvic to anal 20.57-26.13; postanal 26.54-31.65; caudal length 17.77-25.35; caudal depth 5.38-11.10.

Head depth about 69% of head length. End of maxilla extending beyond vertical through the posterior of the eye by 3.08-5.85 of SL (1.02 to 1.89 times in eye diameter). Head smooth (non-serrate) and lacking a bony "crown" dorsally. Prominent bony ridges and epidermis on head very fragile, often damaged giving the head a ragged appearance. Vertical margin of the preopercle straight. Preopercle curves gently through angle and becomes horizontal anteriorly. All margins of preopercle smooth. Upper arm of cheek ridge angles slightly forward at an angle of 80-83° with horizontal arm (Keene 1987). Teeth in bands.

Longest gill filament on first arch 11.36-28.57% of longest gill raker. First gill arch does not have iridescent blue color.

Anal insertion from under 8th dorsal fin ray to one scale pocket behind last dorsal ray. Pectoral fins long, extending past anal fin origin when undamaged. Pelvic fin insertion less than 6% SL behind pectoral fin insertion.

Scales usually missing and scale pockets often missing as well. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 19-23, usually 20-21; gill rakers on lower limb of fourth arch 9-10; gill filaments on first arch 11.36-28.57% of longest raker; maximum SL of study material 26.69 mm; distance between insertions of the pectoral and pelvic fins less than 6% SL; distance between pelvic and anal fin insertions less than 26% SL; anal fin insertion from between 8th dorsal ray to one full scale pocket behind last

dorsal ray; anal fin elements usually I,8; maxilla extends past the posterior margin of the fleshy orbit by 3-6% SL; diagonal scale rows 9-11; horizontal scale rows 22-30.

Scopeloberyx Discussion

Scopeloberyx americanus was originally described by Keene (1987), but this work still remains unpublished. Like *S. robustus*, *S. americanus* differs from *Scopeloberyx microlepis* and *Scopeloberyx opisthopterus* in having more gill rakers (19-23 vs. 17 or less) and a smaller distance between pectoral and pelvic insertions (less than 6% SL vs. 7.5% SL or more). The possession of multiple rows of teeth separates *S. americanus* from *Scopeloberyx rubriventer*, as the latter has only a single row of teeth on its upper and lower jaws.

The *S. americanus* paratypes studied for this taxonomic study show characteristics outside the range of *S. robustus*, indicative of a unique species. The most striking difference between the two species is the iridescent blue color associated with the gill arch, inner operculum and isthmus of *S. robustus*. This iridescent tissue is most likely due to guanine iridophores much like the ones found in the integument of squids and cuttlefish (Mirow 1972; Cooper *et al*. 1990). The function of this pigmentation is, as of yet, unknown. *S. americanus* usually has fewer gill rakers on the first (20 or 21 vs. 22 or 23) and the lower limb of the fourth (10 vs. 11) gill arches. Another difference between these two similar species is that the distance (in % SL) between the pelvic and anal fin insertions is smaller in *S. americanus* (20.57-26.13 [23.31] vs. 26.10-29.72 [27.65]). Other differences between these two species are summarized in Table 3.1.

Table 3.1. Counts and measures taken from *Scopeloberyx americanus* and *Scopeloberyx robustus*. Values are displayed as ranges with the mean (for measures) or mode (for counts) following in parentheses. All length/depth measurements listed as %SL. Bold categories represent characters that could be used to differentiate the two species

	S. americanus	*S. robustus*
SL (mm)	17.38-26.69 (24.20)	71.47-82.65 (76.31)
Dorsal spines	II-III (III)	II-III (III)
Dorsal rays	10-12 (11)	10-13 (12)
Anal spines	I	I
Anal rays	7-8 (8)	8-9 (9)
Pelvic spines	I	I
Pelvic rays	7-8 (7)	7-8 (7)
Pectoral rays	11-17 (14)	12-14 (14)
Caudal fin	23-26 (26)	24-27 (24)
Anal origin	Under 3rd from last dorsal ray to one scale behind last dorsal ray	Under 4th from last to 2nd from last dorsal ray
1st rakers	19-23 (20)	23-26 (24)
4th rakers	9-10 (10)	10-11 (11)
Filament	6.25-28.57 (17.68)	18.18-33.61 (26.26)
Scale rows	18-30 (28)	29-33 (29)
Diagonal scales	9-11 (10)	9-12 (9)
Mandibular pores	4	4
Cheek pores	3-5 (4)	3-4 (4)
Maxillary pores	4	3-5 (4)
Preopercle pores	6-7 (7)	6-7 (7)
Supraorbital pores	5-8 (7)	5-10 (9)
Teeth	In Bands	In Bands
Head	Smooth	Smooth
Gill arch color	No iridescent blue	Iridescent blue on arch, inner opercle and isthmus
Supramaxillary	Present	Present
Preopercle	Smooth	Smooth
Maxilla length beyond orbit	3.08-5.85 (4.24)	1.61-3.42 (2.56)
Maxilla length	17.54-20.11 (18.76)	16.45-19.94 (18.39)
Body depth	23.53-28.79 (26.04)	24.74-28.29 (26.91)
Head depth	21.58-25.92 (23.96)	23.75-26.64 (25.14)
Head length	29.96-38.19 (34.80)	32.56-36.13 (34.08)
Postdorsal	44.24-52.08 (48.05)	34.92-49.96 (46.79)
End of dorsal to caudal	24.76-31.27 (27.63)	26.40-30.73 (28.75)
Snout to preopercle	24.04-33.64 (28.55)	18.49-26.05 (23.22)
Orbit to cheek ridge	6.77-9.74 (8.52)	7.19-8.17 (7.50)
Interorbital	8.97-12.99 (10.34)	8.05-10.49 (9.49)
Prepectoral	32.69-42.01 (38.43)	36.77-41.70 (38.98)
Prepelvic	38.77-46.60 (43.47)	40.13-42.90 (41.35)

Table 3.1 *cont'd.*

	S. americanus	*S. robustus*
Isthmus to pelvic	35.77-38.89 (37.39)	34.46-37.59 (36.07)
Pelvic to anal	20.57-26.13 (23.31)	26.10-29.72 (27.65)
Preanal	65.23-78.42 (70.30)	
Postanal	26.54-31.65 (27.78)	30.21-33.90 (31.54)
Orbit to cheek angle	12.27-15.72 (14.40)	13.16-14.87 (13.94)
Frontal width	10.81-12.49 (11.69)	8.63-12.10 (10.20)
Frontal length	13.98-23.52 (17.75)	17.37-20.32 (18.53)
Orbit	3.73-7.50 (5.60)	5.32-6.90 (5.82)
Caudal length	17.77-25.35 (21.50)	22.11-25.41 (23.64)
Caudal depth	5.38-11.10 (9.00)	8.81-11.75 (10.09)

Special attention must be paid to Kotlyar's monograph on the genus *Scopeloberyx* (Kotlyar 2004 b-c; 2005). In these works Kotlyar described several new species of *Scopeloberyx* that have yet to be universally accepted. However, it is necessary to make sure that *S. americanus*, as described above, is unique when compared to those species of Kotlyar. According to the revised key to the species of *Scopeloberyx* (Kotlyar 2005), the closest species to *S. americanus* is *S. maxillaris*. Most of the counts and measurements of the two species seem to match up, the only things that strike me as different between the two is the maximum length (*S. americanus* = 28 mm and *S. maxillaris* = 88 mm) and the position of the anal fin relative to the caudal fin. *S. americanus* appears to have an anal fin that is slightly closer to the beginning of the caudal fin, which could mean that its anal fin is shifted slightly posterior relative to that of *S. maxillaris*. Since no mention is made of the gill arch coloration, more research needs to be done on this subject and the specimens used in Kotlyar's works must be examined for comparative purposes. This subject will be covered again in the "future research" chapter of this dissertation.

***Melamphaes* Günther** 1864

Melamphaes sp. A

Description (based on 1 specimen, 63.22 mm SL) -- Dorsal III, 14; anal I, 10; pectoral 14; pelvic I, 7; caudal 25 (3+9+10+2); total gill rakers on first arch 29; gill rakers on lower limb of fourth arch 12.

Measurements in % SL-- head depth 23.74; head length 38.04; snout to preopercle 27.02; orbit to cheek ridge 7.59; orbit to cheek angle 12.05; interorbital 7.75; frontal width 9.00; frontal length 20.20; fleshy orbit 7.42; maxilla length 19.52; body depth

25.26; postdorsal 50.13; end of dorsal to caudal 27.10; prepectoral length 42.22; prepelvic length 39.83; isthmus to pelvic 33.42; pelvic to anal 22.49; postanal 30.65; caudal length 21.59; caudal depth 8.04.

Head depth approximately 62% of head length. End of maxilla extending only slightly beyond the posterior of the eye by 0.79% of SL (about nine times in eye diameter). Head smooth. Prominent bony ridges and epidermis on head very fragile but mostly intact. Angle of preopercle with at least three short spines connected to each other by preopercular tissue. No spines at cheek angle. Teeth uniserial.

Longest gill filament on first arch 12.72% of longest gill raker. First gill arch does not have iridescent blue color.

Anal insertion under 12th (3rd from last) dorsal fin ray. Pelvic fin insertion less than 5% SL before pectoral fin insertion.

Scales usually missing and scale pockets often missing as well. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 29; gill rakers on lower limb of fourth arch 12; gill filaments on first arch 12.72% of longest raker; head length 38.04% SL; frontal length 20.20% SL; distance between insertions of pectoral and pelvic fins less than 5% SL (pelvic fins insert anterior to pectoral fins); distance between pelvic and anal fin insertions 22.49% SL; anal fin insertion under 3rd from last dorsal ray; anal fin elements I,10; teeth uniserial; head smooth; preopercle slightly serrate at angle; no spines at cheek angle.

Melamphaes indicoides (Keene sp. nov.)

Description (based on five specimens 22.75-51.21 mm SL) -- Dorsal III, 15-16 (usually III, 15); anal I, 8; pectoral 14-15 (usually 14); pelvic I, 7; caudal 25-27 (usually 25); total gill rakers on first arch 20; gill rakers on lower limb of fourth arch 10-11 (usually 10); horizontal scale rows 25-31; diagonal scale rows 5-8.

Measurements in % SL -- head depth 25.23-26.37; head length 29.76-32.44; snout to preopercle 22.18-28.13; orbit to cheek ridge 6.59-8.12; orbit to cheek angle 10.77-13.75; interorbital 11.65-14.90; frontal width 7.03-8.53; frontal length 14.67; fleshy orbit 4.84-7.82; maxilla length 14.90-18.64; body depth 25.71-29.19; postdorsal 50.20-60.95; end of dorsal to caudal 27.38-32.83; prepectoral length 35.77-40.00; prepelvic length 36.91-39.29; isthmus to pelvic 30.95-34.04; pelvic to anal 29.59-34.74; postanal 25.56-30.77; caudal length 19.72-23.21; caudal depth 9.35-10.81.

Head depth approximately 83% of head length. End of maxilla either ending at posterior margin of orbit or extending slightly beyond by 0.44-1.57% of SL (about 8-17 times in eye diameter). Head smooth. Prominent bony ridges and epidermis on head very fragile. All margins of preopercle smooth. Two nearly symmetrical spines at cheek angle. Teeth in bands. Supramaxillary present.

Longest gill filament on first arch 32.89-61.90% of longest gill raker. First gill arch does not have iridescent blue color.

Anal insertion more than a full scale pocket behind last dorsal ray. Pelvic fin insertion less than 5% SL behind pectoral fin insertion.

At least a few scales present on each specimen, but the majority of scales missing and scale pockets often missing as well. Scales lack circuli on the posterior margin. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Scales do not contain circuli on the posterior field; gill rakers on first arch 20; gill rakers on lower arm of fourth arch 10-11; head length 29.76-32.44% SL; distance between insertions of the pectoral and pelvic fins is less than 5% SL (pectoral fins insert anterior to pelvic fins); postanal distance 28.43% SL; anal fin insertion behind the last dorsal ray by a distance of at least one scale pocket; postdorsal distance 27.38-32.83% SL; caudal length 19.72-23.21% SL; anal fin elements I,10; dorsal fin elements I,15-16; Scale rows 25-31 (5-8 in diagonal series); teeth in bands; head smooth; preopercle slightly serrate at angle; no spines at cheek angle.

Melamphaes Discussion

The *Melamphaes* sp. A specimen was problematic. It had no crest-like ridges on the dorsal aspect of its head and no internarial spine, had 17 dorsal fin elements like *Melamphaes*, but also had 29 gill rakers on the first arch and a slightly serrate preopercular angle like a *Poromitra*. I included it with the *Melamphaes* species because of the lack of internarial spine and the smooth head. Also, anal fin insertion and the number of anal fin rays do not coincide with values for many *Poromitra* species. In comparison to other *Melamphaes* species, this specimen had an unusually large number of gill rakers on the first (29) and fourth (12) arches. The preopercle was smooth everywhere except for a few very weak spines at the angle, which is a characteristic of only one species in the genus *Melamphaes* (*Melamphaes spinifer*). This combination of

Poromitra and *Melamphaes* characteristics leaves two possibilities: 1) this specimen represents an undescribed species of *Melamphaes,* or 2) this specimen was a badly damaged species of *Poromitra*. Characteristics described above indicate that this specimen is a *Melamphaes* species whose gill raker counts differ greatly from other *Melamphaes* species. Counts and measures for this specimen are presented in Table 3.2.

Melamphaes indicoides differs from the majority of *Melamphaes* species in having 20 gill rakers and no circuli on the posterior field of the scales. The most similar species to *M. indicoides* is *M. polylepis* which also has 20 or more gill rakers and no posterior circuli on its scales. However, all five *M. indicoides* specimens examined had a gill raker count of 20 on the first arch whereas the *M. polylepis* has a range of 20-23, with an average of 21 gill rakers. Other differences between the two species include the anal origin, diagonal scale rows, head length and caudal peduncle length. Counts and measures are listed in Table 3.2, including all characteristics that could be used to distinguish the two species. The analyses performed in this study and the unpublished descriptions of Keene (1987) suggest that *M. indicoides* and *M. polylepis* are two separate species.

Table 3.2. Counts and measures taken from *Melamphaes indicoides* and the *Melamphaes* sp. A. Included are counts and measures from *Melamphaes polylepis* for comparison (after Ebeling 1962). Values are displayed as ranges with the mean (for measures) or mode (for counts) following in parentheses. Length/depth measurements listed as % SL. Bold categories represent characters that could be used to differentiate *M. polylepis* and *M. indicoides*

	M. indicoides	*M. polylepis*	*Melamphaes* sp. A
SL (mm)	22.75-51.21 (38.17)	12.00-62.00	63.22
Dorsal spine	III	III	III
Dorsal rays	15-16 (15)	13-15 (14)	14
Anal spines	I	I	I
Anal rays	8	7-8 (8)	10
Pelvic spines	I	I	I
Pelvic rays	7	7	7
Pectoral rays	14-15 (14)	15	14
Caudal fin	25-27 (25)	27-29 (28)	25
Anal origin	1 scale or more behind last dorsal ray	Under 2nd from last dorsal ray	Under 3rd from last dorsal ray
1st rakers	20	20-23 (21)	29
4th rakers	10-11 (10)	9-13 (10)	12
Filament	32.89-61.90 (47.69)	N/A	12.72
Scale rows	25-31 (28)	33-35 (34)	N/A
Diagonal scales	5-8 (7)	8-10 (9)	N/A
Mandibular pores	4	N/A	3
Cheek pores	4	N/A	3
Maxillary pores	3-5 (4)	N/A	4
Preopercle pores	6-7 (7)	N/A	6
Supraorbital pores	6-9 (6)	N/A	4
Teeth	In bands	In bands	Uniserial
Head	Smooth	Smooth	Smooth
Cheek	Two spines	Two spines	No spines
Supramaxillary	Present	Present	Present
Preopercle	Smooth	Smooth	Slightly serrate
Posteroventral cheek spine	1.01-1.40 (1.16)	N/A	N/A
Ventral cheek spine	1.40-2.47 (1.89)	N/A	N/A
Maxilla length beyond orbit	0-1.57 (0.76)	N/A	0.79
Maxilla length	14.90-18.64 (16.57)	16.3-18.0 (17.2)	19.52
Body depth	25.71-29.19 (27.25)	25.0-28.2 (26.7)	25.26
Head depth	25.23-26.37 (25.68)	23.1-27.1 (24.9)	23.74
Head length	29.76-32.44 (30.92)	35.0-41.4 (37.5)	38.04
Postdorsal	50.20-60.95 (56.01)	58.1-62.8 (60.7)	50.13
End of dorsal to caudal	27.38-32.83 (30.37)	33.1-36.6 (35.0)	27.10

Table 3.2 *cont'd*

	M. indicoides	*M. polylepis*	*Melamphaes sp.*
Snout to preopercle	22.18-28.13 (24.84)	24.5-27.3 (25.5)	27.02
Orbit to cheek ridge	6.59-8.12 (7.49)	5.6-7.3 (6.4)	7.59
Interorbital	11.65-14.90 (13.15)	10.9-12.7 (11.7)	7.75
Prepectoral	35.77-40.00 (36.97)	35.4-39.6 (37.0)	42.22
Prepelvic	36.91-39.29 (37.75)	36.3-39.9 (37.9)	39.83
Isthmus to pelvic	30.95-34.04 (32.53)	31.2-34.9 (32.9)	33.42
Pelvic to anal	29.59-34.74 (32.74)	26.4-33.2 (30.3)	22.49
Postanal	25.56-30.77 (28.43)	35.6-41.3 (38.1)	30.65
Orbit to cheek angle	10.77-13.75 (12.68)	9.6-11.7 (10.8)	12.05
Frontal width	7.03-8.53 (8.03)	6.6-8.1 (7.5)	9.00
Frontal length	14.67-16.39 (15.79)	13.0-15.8 (14.5)	20.20
Orbit	4.84-7.82 (6.09)	4.1-6.9 (5.0)	7.42
Caudal length	19.72-23.21 (21.21)	26.6-30.7 (28.3)	21.59
Caudal depth	9.35-10.81 (9.92)	9.8-11.9 (10.9)	8.04

Poromitra **Goode and Bean** 1883

Poromitra crassiceps A

Description (based on 1 specimen, 28.82 mm SL) -- Dorsal II, 15; anal I, 10; pectoral 12; pelvic I, 7; total gill rakers on first arch 24; gill rakers on lower limb of fourth arch 13.

Measurements in % SL-- head depth 24.32; head length 39.17; snout to preopercle 31.51; orbit to cheek ridge 11.28; orbit to cheek angle 11.94; interorbital 5.66; frontal width 12.77; frontal length 23.94; fleshy orbit 5.55; maxilla length 16.38; body depth 21.37; postdorsal 50.42; end of dorsal to caudal 23.91; prepectoral length 45.52; prepelvic length 41.67; isthmus to pelvic 32.30; pelvic to anal 18.39; postanal 36.22; caudal length 24.08; caudal depth 7.46.

Head depth approximately 62% of head length. End of maxilla does not extend beyond vertical through posterior of eye. Head smooth, though could be due to damage to specimen. Small, triangular, convex projection between nares. Prominent bony ridges and epidermis on head very fragile. Preopercle slightly serrate at angle. Cheek without spines at angle. Supramaxillary appeared missing. Teeth uniserial.

Longest gill filament on first arch 15.63% of longest gill raker. Gill arch does not have iridescent blue coloration.

Anal insertion under 9th dorsal fin ray (7th from last dorsal fin ray). Pelvic fin insertion 4% SL before pectoral fin insertion.

Scales missing and scale pockets not discernable. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 24; gill rakers on lower arm of fourth arch 13; gill filament on first arch 15.63% of longest raker; pectoral fin insertion less than 4% SL behind insertion of the pelvic fins; distance between pelvic and anal fin insertions 18.39% SL; anal fin insertion under 7th from last dorsal ray; dorsal fin elements II,15; no cheek spines; maxilla does not extend past posterior of eye; postanal distance 36.22% SL; snout to preopercle 31.51; large, flat, convex internarial spine; SL 28.82 mm.

Poromitra crassiceps B

Description (based on 1 specimen, 37.32 mm SL) -- Dorsal III, 14; anal I, 11; pectoral 12; pelvic I, 7; total gill rakers on first arch 31; gill rakers on lower limb of fourth arch 11.

Measurements in % SL-- head depth 24.20; head length 36.71; snout to preopercle 25.96; orbit to cheek ridge 6.65; orbit to cheek angle 12.65; interorbital 8.15; frontal width 14.20; frontal length 23.77; fleshy orbit 6.30; maxilla length 18.22; body depth 23.07; postdorsal 52.60; end of dorsal to caudal 25.54; prepectoral length 38.64; prepelvic length 39.44; isthmus to pelvic 36.23; pelvic to anal 21.38; postanal 36.84; caudal length 25.99; caudal depth 8.65.

Head depth approximately 66% of head length. End of maxilla does not extend beyond vertical through the posterior of the eye. Head with serrate ridges on dorsal margin. Small, triangular, convex projection between nares. Prominent bony ridges and epidermis on head very fragile. Preopercle serrate at angle. Cheek without spines at angle. Supramaxillary present. Teeth uniserial.

Longest gill filament on first arch 24.20% of longest gill raker. Gill arch does not have iridescent blue coloration.

Anal insertion under 9th dorsal fin ray (6th from last dorsal fin ray). Pelvic fin insertion less than 1% SL behind pectoral fin insertion.

Scales missing and scale pockets not discernable. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 31; gill rakers on lower arm of fourth arch 11; gill filament on first arch 24.20% of longest raker; pectoral fin insertion less than 1% SL in front of pelvic fin insertion; distance between pelvic and anal fin insertions 21.38% SL; anal fin insertion under 6th from last dorsal ray; dorsal fin elements III,14; no cheek spines; maxilla does not extend past posterior of eye; postanal distance 36.84% SL; snout to preopercle 25.96% SL; large, flat, convex internarial spine; SL 37.32 mm.

Poromitra crassiceps C

Description (based on 1 specimen, 98.34 mm SL) -- Dorsal III, 11; anal I, 9; pectoral 13; pelvic I, 7; total gill rakers on first arch 31; gill rakers on lower limb of fourth arch 12; horizontal scale rows 27; diagonal scale rows 9.

Measurements in % SL-- head depth 24.93; head length 35.95; snout to preopercle 24.63; orbit to cheek ridge 7.67; orbit to cheek angle 15.80; interorbital 13.92; frontal width 7.04; frontal length 25.14; fleshy orbit 5.47; maxilla length 18.24; body depth 26.29; postdorsal 51.18; prepectoral length 43.14; prepelvic length 43.64; isthmus to pelvic 37.22; pelvic to anal 27.72; postanal 24.92; caudal length 18.54; caudal depth 10.00.

Head depth approximately 69% of head length. End of maxilla extends beyond vertical through the posterior of eye by 3.13% SL (about 1.75 times in eye diameter). Head with serrate ridges on top. Serrate crown with anterior facing spine. Prominent, horn-like spine between the nares. Prominent bony ridges and epidermis on head very fragile. Preopercle serrate at angle. Cheek with three spines at angle. Teeth uniserial.

Longest gill filament on first arch 29.44% of longest gill raker. Gill arch does not have iridescent blue coloration.

Anal insertion under 9th dorsal fin ray (3rd from last dorsal fin ray). Pelvic fin insertion less than 1% SL behind pectoral fin insertion.

Scales missing but scale pockets discernable. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis -- Gill rakers on first arch 31; gill rakers on lower arm of fourth arch 12; gill filament on first arch 29.44% of longest raker; pectoral fin insertion less than 1% SL in front of pelvic fin insertion; distance between pelvic and anal fin insertions is 27.72% SL; anal fin insertion under 3rd from last dorsal ray; dorsal fin elements III,11; 3 cheek spines; maxilla extends past posterior of eye; postanal distance 24.92; snout to preopercle 24.63; Prominent, horn-like spine between nares; SL 98.34 mm.

Poromitra Discussion

The *Poromitra crassiceps* species complex most likely represents three separate species. Each were treated individually herein, as the counts and measures varied widely, and each were compared to ranges of values for known *P. crassiceps* specimens. When this was done (Table 3.3) *P. crassiceps* A has many morphometric values that differ

greatly from the other species of the complex. It had far fewer gill rakers on its first arch than all the other specimens examined, which coincides more with characteristics of *P. megalops* and *P. crassa.* However, *P. crassiceps* A did not have a large enough eye to be considered a *P. megalops* specimen (14.1% Head Length vs. 20% Head Length) and it has 15 dorsal rays vs. 10-12 reported by Keene (1987). It is likely that *P. crassiceps* A is synonymous with *Poromitra crassa.* The gill raker count (24) and the eye diameter both coincide with measurements for *P. crassa.* However, there are also measurements that make assignment of this specimen to *P. crassa* dubious. There are far more dorsal rays (15) than found in *P. crassa* (10) as well as shorter gill filaments (~15% vs. 30-45%) and differing anal insertions (under 7^{th} from last dorsal ray vs. under 2^{nd}-4^{th} from last dorsal ray). The small, convex horn found between the nares of this specimen is most likely the base of a more hornlike spine. Damage to the specimen can explain why an internarial spine and a spiked crown on the head were not observed.

P. crassiceps B and C are closer to the descriptions of *P. crassiceps* found in both the work of Keene (1987) and Kotlyar (2008a). Both specimens have the same number of gill rakers on the first arch (31), which falls within the range of values for *P. crassiceps* established by Keene (1987) and Kotlyar (2008a). However, in "*P. crassiceps* C," the forward facing spine on the crown, the position of the anal fin, the number of rays in the

Table 3.3. Counts and measures taken from *Poromitra crassiceps* A, B and C. Included are counts and measures from *P. crassiceps* reported by Keene (1987) and Kotlyar (2008a) for comparison. Values are displayed as ranges with the mean (for measures) or mode (for counts) following in parentheses. Length/depth measurements listed as % SL. Bold categories represent characters that could be used to differentiate the possible species of this *Poromitra crassiceps* complex

	P. crassiceps A	*P. crassiceps* B	*P. crassiceps* C	*P. crassiceps* (Kotlyar)	*P. crassiceps* (Keene)
SL (mm)	28.82	37.32	98.34	65-130.5	18-187
Dorsal spine	2	3	3	3	3
Dorsal rays	15	14	11	12-13	12-15 (13)
Anal spines	1	1	1	1	1
Anal rays	10	11	9	9-10	8-11 (10)
Pelvic spines	1	1	1	1	1
Pelvic rays	7	7	7	7	7
Pectoral rays	12	12	13	13-14	14-15
Caudal fin	N/A	25	25	N/A	N/A
Anal origin	Under 7th from last	Under 6th from last	Under 3rd from last	Under 6th to 7th from last dorsal ray	N/A
1st rakers	24	31	31	28-30	28-33 (31)
4th rakers	13	11	12	10-12	12-14
Filament	15.625	24.20	29.44	N/A	25-30
Scale rows	N/A	N/A	27	29-31	29-32
Diagonal scales	N/A	N/A	9	8-9	10
Mandibular pores	N/A	3	4	N/A	N/A
Cheek pores	N/A	3	3	N/A	N/A
Maxillary pores	N/A	5	4	N/A	N/A
Preopercle pores	N/A	6	6	N/A	N/A
Supraorbital pores	N/A	4	6	N/A	N/A
Teeth	Uniserial	Uniserial	Uniserial	N/A	Uniserial
Head	Smooth	Serrate	Serrate with forward facing spine	Serrate crown with posterior facing spine	Serrate
Cheek	No spines	No Spines	3 Spines	2-3 spines	N/A
Internarial spine	Large, flat, triangular, convex spine	Large, flat, triangular, convex spine	Distinct horn-like spine	Distinct horn-like spine	Distinct horn-like spine
Supramaxillary	Absent	Present	N/A	Present	N/A
Preopercle	Slightly Serrate	Serrate	Serrate	Serrate	Serrate
Maxilla length beyond orbit	0.00	0.00	3.13	Extends beyond posterior of eye	Extends beyond posterior of eye
Maxilla length	16.38	18.22	18.24	15.5-17.1	N/A
Body depth	21.37	23.07	26.29	26.7-28.6	23.3-29.8

Table 3.3. *cont'd*

	P. crassiceps A	*P. crassiceps* B	*P. crassiceps* C	*P. crassiceps* (Kotlyar)	*P. crassiceps* (Keene)
Head depth	24.32	24.20	24.93	22.1-24.9	N/A
Head length	39.17	36.71	35.95	34.5-37.8	34.3-41.1
Postdorsal	50.42	52.60	51.18	51.5-59.1	52.8-60.4
End of dorsal to caudal	23.91	25.54		26.5-30.6	N/A
Snout to preopercle	31.51	25.96	24.63	N/A	N/A
Orbit to cheek ridge	11.28	6.65	7.67	N/A	N/A
Interorbital	5.66	8.15	13.92	12.9-15.1	N/A
Prepectoral	45.52	38.64	43.14	33.3-39.2	N/A
Prepelvic	41.67	39.44	43.64	39.5-43.5	N/A
Isthmus to pelvic	32.30	36.23	37.22	N/A	N/A
Pelvic to anal	18.39	21.38	27.72	20.3-25.7	N/A
Postanal	36.22	36.84	24.92	37.1-41.5	38.6-42.6
Orbit to cheek angle	11.94	12.65	15.80	N/A	11.7-16.3
Frontal width	12.77	14.20	7.04	N/A	N/A
Frontal length	23.94	23.77	25.14	N/A	N/A
Orbit	5.55	6.30	5.47	5.4-6.6	4.1-5.9
Caudal length	24.08	25.99	18.54	25.1-29.5	24.2-31.5
Caudal depth	7.46	8.65	10.00	9.5-12.4	9.0-12.8

dorsal and anal fins, the number of scale rows and the position of pectoral and ventral fins all indicate that "*P. crassiceps* C" is actually *Poromitra capito.*

Most of the measurements taken from "*P. crassiceps* B" are within the ranges for *P. crassiceps.* The only two characters that are problematic are its lack of cheek spines and the shape of its internarial spine. As in "*P. crassiceps* A" the peculiar shape of the internarial spine is most likely the base of a more horn-like spine that is missing due to damage to the specimen. Damage to the specimen could also explain the lack of prominent cheek spines.

Of the three specimens from the NMNH that were labeled *Poromitra crassiceps*, only one has been confirmed to be *P. crassiceps.* The other two are most likely misidentified *Poromitra* species (*Poromitra crassa* and *Poromitra capito*).

***Scopelogadus* Vaillant** 1888

Scopelogadus mizolepis bispinosis (Gilbert 1915)

Description (based on 12 specimens, 31.11-87.68 mm SL) -- Dorsal II, 10-12 (usually II, 11); anal I, 8-9 (usually I, 8); pectoral 10-14 (usually 12); pelvic I, 6-8 (usually I, 7); horizontal scale rows 12-15; diagonal scale rows 4-6; total gill rakers on first arch 21-24 (usually 24); gill rakers on lower limb of fourth arch 9-11 (usually 11).

Measurements in % SL-- head depth 20.71-28.97; head length 34.74-50.37; snout to preopercle 23.34-29.12; orbit to cheek ridge 3.79-6.93; orbit to cheek angle 8.44-12.66; interorbital 4.47-12.99; frontal width 5.11-10.76; frontal length 14.99-18.64; fleshy orbit 4.49-7.87; body depth 20.52-28.26; postdorsal 50.35-56.70; end of dorsal to caudal 29.60-36.65; prepectoral length 40.14-48.03; prepelvic length 36.94-44.76;

isthmus to pelvic 32.92-51.46; pelvic to anal 15.34-22.17; postanal 32.21-42.69; caudal length 25.08-31.18; caudal depth 6.74-9.45.

Head depth approximately 63% of head length. Head smooth (non-serrate) and lacking a bony crown dorsally. Prominent bony ridges and epidermis on head very fragile, often damaged, giving the head a ragged appearance. Preopercle curves gently through angle and becomes horizontal anteriorly. All margins of preopercle smooth. Teeth uniserial.

Anal insertion under 5^{th}-6^{th} from last dorsal ray. Pectoral fins long, extending past anal fin origin when undamaged. Pectoral fin insertion less than 3% SL behind pelvic fin insertion.

Scales usually missing and scale pockets often reduced to shaggy tissue remnants. Head color dark brown in preservative, body tan to light brown under same conditions.

Diagnosis – Scales large (usually less than 15 in series between the nape of the neck and the base of the caudal fin) and often lost, leaving large shaggy pockets. Gill rakers on first arch 21-24, usually 24; gill rakers on lower arm of fourth arch 9-11, usually 11; maximum size 87.68 mm; distance between insertions of the pectoral and pelvic fins is less than 3% SL; distance between pelvic and anal fin insertions is about 15-22% SL; anal fin insertion under 5th-6th from last dorsal ray; anal fin elements usually I,8; diagonal scale rows 4-6; horizontal scale rows 12-15.

Scopelogadus Discussion

The issue with *Scopelogadus mizolepis bispinosis* is whether or not this is a valid subspecies and what criteria constitutes a subspecies. If *S. m. bispinosis* is not, in fact, a

subspecies then it must be determined if this fish is a completely separate species or a single unified species (*Scopelogadus mizolepis*). In order to make a conclusion on the subspecies status of this fish, one must first look into what the characteristics of a "subspecies" are and a comparison must be made to the other subspecies of this group (*Scopelogadus mizolepis mizolepis*).

A subspecies is defined as two or more subdivisions of a species that cannot interbreed with each other because they are geographically isolated from one another (Ashlock 1991; Coyne and Orr 2004). This means that there is some physical barrier between the subspecies preventing the two populations from mating with one another. If these physical barriers were removed, subspecies would reproduce with each other forming a single species, but, since these barriers exist, they remain as distinct subspecies. Though subspecies often do present some morphological differences, they are defined by their physical separation, not their physical appearance, and that they would and could interbreed if these barriers were removed (Mayr and Ashlock 1991; Coyne and Orr 2004).

In Ebeling and Weed's (1963) work, they described these two subspecies as being slightly morphologically dissimilar but having distributions and depth profiles that intergraded with one another in the Pacific. Ebeling and Weed base their subspecies distinction on morphometric characters and did not discuss any possible physical barriers between the two subspecies that may prevent interbreeding. The fact that their habitat ranges strongly overlap (Ebeling and Weed 1963; Masuda *et al.* 1984; Yang *et al.* 1996; Froese and Pauly 2000) in the Pacific suggests that these two subspecies may be able to intermingle and reproduce with one another. Without physical barriers preventing

interbreeding between these two, it seems less likely that these two are distinct subspecies. If we assume that these two are not subspecies, then it leaves only two possibilities: they are two separate species or they are a single species.

In order to determine whether these are two species or a single species, their counts and measures must be compared. Measures for *"S. m. bispinosis*" were taken from samples obtained from NMNH, counts and measures for "*S. m. mizolepis*" were taken from Ebeling and Weed (1963) (Table 3.4). Ebeling and Weed described an angle between the dorsal and pelvic fins with its apex at the center of the eye, which they used to differentiate *Scopelogadus m. mizolepis* from *Scopelogadus m. bispinosis* (Fig. 3.2). They reported that this angle was able to differentiate 90-100% of the subspecies, using pre-identified specimens as "unknowns." This angle is the major characteristic that Ebeling and Weed use to separate these two "subspecies" along with other secondary characters. This term is used in quotations because the authors use it to designate subspecies and whereas the present study addresses if this angle is sufficient to discriminate two separate species. Although they reported a high success rate using this angle to make definitive identifications, this angle may rely on morphometrics that vary too widely to make this a viable determinant when trying to differentiate between these two subspecies. Eye diameter, predorsal length, prepelvic length, body depth, head length, and body length all play a role in determining this angle. Any variation in these measurements would change the identification angle. If this key characteristic is called into question, other counts and measures must be compared to examine if there is enough difference between the two fish groups to call them two separate species.

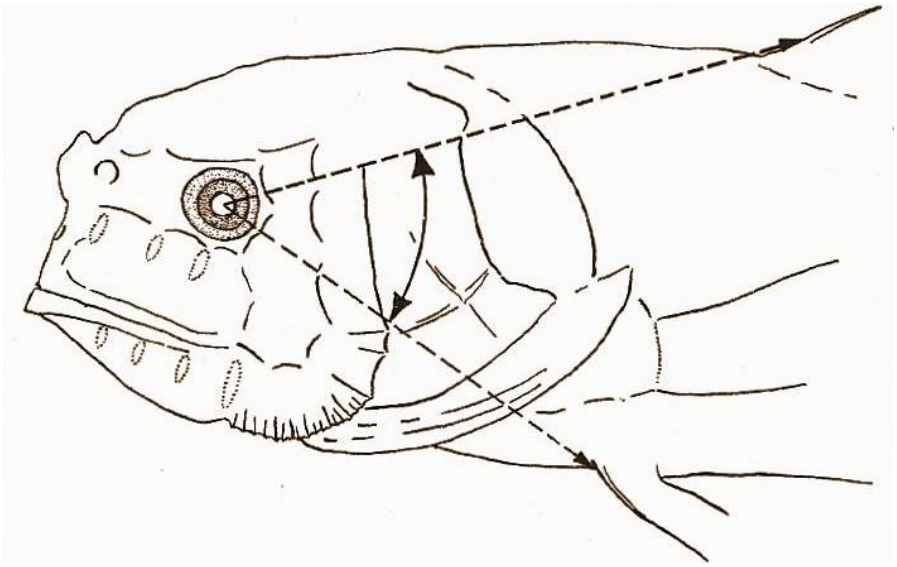

Figure 3.2. Diagnostic angle used by Ebeling and Weed (1963) to distinguish between *Scopelogadus mizolepis* subspecies. Photo from Ebeling and Weed (1963)

When comparing the measurements taken in this study to those of Ebeling and Weed (1963), or when comparing the measurements of both "subspecies" found within this same work, most of the ranges overlap. By taking the range of values that overlap and dividing them by the total range of values for both "subspecies," percentage of overlap can be calculated. For most of the measurements, the values overlap by at least 33% (Table 3.5). This suggests that at least 33% of the time there will be no certainty in the identification of an individual specimen based on a single measurable character. The measurements that overlap the least could be the key characters to determining if these are two species or one. Of these measurements, caudal width, caudal depth, prepectoral length and the angle described by Ebeling and Weed (1963) are the measurements that overlap the least. The hesitancy of accepting the dorsal-to-pelvic angle has already been discussed. Only a single value from a type specimen could be found in the Ebeling and Weed publication for both the prepectoral length and caudal depth. It is hard to evaluate relationships between measurements when full ranges are not available. This is because all of these counts and measures have some inherent natural variance. Thus, more measurements of prepectoral length and caudal depth must be taken to determine the value of using this character in an identification key.

The overlap of the caudal length values is one of the lowest percentages and could be the key to determining if these are two separate species. The fact that these ranges do overlap makes using caudal length problematic when trying to discriminate between two possible species. It does not seem that caudal length alone could be used to accurately identify two separate species. Analyses of type specimens would aid in supporting this

Table 3.4. Counts and measures taken from *Scopelogadus mizolepis bispinosis.* Included are counts and measures from *Scopelogadus mizolepis mizolepis* reported by Ebeling and Weed (1963) for comparison. Values are displayed as ranges with the mean (for measures) or mode (for counts) following in parentheses. Length/depth measurements listed as % SL. Bold categories represent characters that could be used to differentiate the possible species of this *Scopelogadus mizolepis* subspecies complex

	S. m. bispinosis	*S. m. mizolepis* (Ebeling and Weed)
SL (mm)	31.11-87.68 (51.33)	2.00-94.00
Dorsal spine	2	2
Dorsal rays	10-12 (11)	10-12 (11)
Anal spines	1	1
Anal rays	8-9 (8)	8
Pelvic spines	1	1
Pelvic rays	6-8 (7)	7
Pectoral rays	10-14 (12)	N/A
Caudal fin	22-26 (23)	N/A
Anal origin	Under 5^{th}-6^{th} from last dorsal ray	Under 4^{th}-6^{th} from last dorsal ray
1^{st} rakers	21-24 (24)	21-26 (24)
4^{th} rakers	9-11 (10)	N/A
Scale rows	12-15 (15)	10-20
Diagonal scales	4-6 (4)	N/A
Mandibular pores	4	N/A
Cheek pores	3-4 (4)	N/A
Maxillary pores	4-5 (4)	N/A
Preopercle pores	6-7 (7)	N/A
Supraorbital pores	4-6 (5)	N/A
Body depth	20.52-28.26 (24.96)	23-28.9
Head depth	20.71-28.97 (24.42)	26.8
Head length	34.74-50.37 (38.82)	34.4-40.9
Postdorsal	50.37-56.70 (52.74)	56.9
End of dorsal to caudal	29.60-36.65 (32.93)	N/A
Snout to preopercle	23.34-29.12 (26.82)	25.2
Orbit to cheek ridge	3.79-6.93 (5.12)	4.3
Interorbital	4.47-12.99 (9.45)	N/A
Prepectoral	40.14-48.03 (43.19)	36.9
Prepelvic	36.94-44.76 (41.35)	40.6
Isthmus to pelvic	32.92-51.46 (38.86)	36.5
Pelvic to anal	15.34-22.17 (17.66)	22.1
Preanal	57.35-63.14 (61.00)	59.0
Postanal	32.21-42.69 (37.18)	40.5
Orbit to cheek angle	8.44-12.66 (10.33)	9.9-10.8
Frontal width	5.11-10.76 (7.27)	N/A
Frontal length	14.99-18.64 (16.74)	N/A

Table 3.4. *cont'd*

	S. m. bispinosis	*S. m. mizolepis* (Ebeling and Weed)
Orbit	4.49-7.87 (5.62)	3.8-6.8
Caudal length	25.08-31.18 (27.23)	29.0-36.9
Caudal depth	6.74-9.45 (8.40)	12.4

Table 3.5. Percentage overlap of the counts and measures taken from the two *Scopelogadus mizolepis* "subspecies." A) Comparison of the measurements of *Scopelogadus mizolepis bispinosis* taken during this study and the measurements for *Scopelogadus mizolepis mizolepis* reported in Ebeling and Weed (1963); B) Comparison of values for both "subspecies" found in the key to the species of *Scopelogadus* from Ebeling and Weed (1963)

A

	% Overlap
Body Depth	62.77
Head Length	38.57
Orbit to cheek angle	21.33
Orbit	56.76
Caudal Length	18.44

B

	% Overlap
Dorsal-eye-pelvic angle	6.25
suborbital	54.76
body depth	37.86
head length	38.02
filament/raker length	13.51

conclusion, but from the initial analyses of characters and habitat ranges, these two subspecies are most likely just a single unified species.

CONCLUSIONS

This research suggests at least three possible new species (one *Scopeloberyx* and two *Melamphaes*), clarified uncertain identifications of *Poromitra crassiceps,* and presented arguments for synonomizing the *Scopelogadus mizolepis* subspecies into one single species. However, these conclusions need to be supported by more measurements and statistical analyses to limit the amount of scrutiny that can fall on them.

CHAPTER 4

DISTRIBUTION OF THE DEEP-PELAGIC BIGSCALE FISHES (TELEOSTEI: MELAMPHAIDAE) ALONG THE NORTHERN MID-ATLANTIC RIDGE

ABSTRACT

The 2004 MAR-ECO expedition over the northern Mid-Atlantic Ridge aimed, in part, to describe the overlying pelagic macro- and megafauna and their roles in mid-ocean ecosystems. The month-long cruise sampled portions of the ridge between Iceland and the Azores at 36 stations. One of the dominant pelagic fish taxa along the ridge was the family Melamphaidae. Melamphaid species abundance and biomass were examined with respect to depth, altitude above the ridge, and geographic ridge section (Reykjanes Ridge, Charlie-Gibbs Fracture Zone, Faraday Seamount Zone or Azorean Zone). Highest species richness and abundance occurred at depths between 750-1500 m. Some adult individuals were found above 200 m, setting new minimum depth of occurrence records for the family. Large-scale shifts in species composition were observed relative to physical oceanographic features; for example, the genus *Scopelogadus* shifted from *S. beanii* dominance in the North to *S. mizolepis* southward. This shift in species composition is associated with an anticyclonic anomaly, which could indicate a warm-core ring. Multivariate analyses discriminated five distinct assemblages of melamphaids (~ 14% similarity), with depth zone being the major determining factor (describing four of the five groups) and geographical ridge section a less powerful clustering factor (influencing

two of the five groups). Given their high relative abundance and reported consumption of gelatinous prey, the Melamphaidae may represent a significant but poorly known trophic linkage between fishes and gelatinous zooplankton in bathypelagic systems.

INTRODUCTION

The Mid-Atlantic Ridge (MAR) is a vast and unique habitat in the deep sea. The ridge is a series of abrupt topographic features, formed by the separation of continental plates that break up the continuity of the pelagic environment. Ridges and seamounts have been shown to be areas of high biomass, and thus areas of high potential trophic energy, due to so-called "seamount effects" (Dower and Mackas 1996; Haury *et al*. 2000; Genin 2004). In particular, the water column above the MAR has been shown to be an area of increased vertical mixing associated with nutrient upwelling (Mauritzen *et al.* 2002; Søiland 2008). One theory regarding fish aggregation around seamounts is that seamounts create localized upwelling while simultaneously creating anticyclonic vortices in which plankton are entrained (Dower and Mackas 1996; Mullineaux and Mills 1997; Haury *et al.* 2000). The interactions of the local upwelling and the concentrated plankton population may increase primary production above shallow seamounts and ridges, and thus augment higher trophic levels by providing a concentrated food source (see review in Porteiro and Sutton 2007).

Another theory regarding trophic interactions over abrupt topography is that seamounts and ridges could act to concentrate vertically migrating prey, which would support higher biomass of demersal predators (Isaacs and Schwartzlose 1965; Koslow 1997; Fock *et al.* 2002). The theory suggests that vertically migrating zooplankton and/or micronekton are advected over topographic features at night and get trapped or

impinge on ridge/seamount flanks during the downward phase of their diel migrations. Ridges have also been shown to be feeding grounds and/or navigational landmarks for large, highly migratory predators such as great hammerhead sharks (*Sphyrna lewini*), tunas (Scombridae) and sperm whales (*Physeter macrocephalus*) (Klimley *et al.* 2002; Moulins and Würtz 2005; Holland and Grubbs 2007; Skov *et al.* 2008). Ridges like the MAR may represent a unique deep-sea ecosystem where the interactions of multiple pelagic and benthic trophic levels can occur over a relatively concentrated area.

Compared to continental shelves and slopes, and even selected seamounts, very little is known regarding the biology and ecology of mid-ocean ridge systems. MAR-ECO (www.mar-eco.no) is a field project of the Census of Marine Life whose goal is to describe the biodiversity and ecology of organisms of the mid-North Atlantic. Sixteen nations are working together to understand the organisms and processes above the MAR, from the surface layer to the abyssal zone, from Iceland to the Azores. One of the central foci of MAR-ECO is to understand how a mid-ocean ridge system such as the MAR may affect the interactions of pelagic, demersal and benthic communities in the open ocean. The MAR-ECO consortium of expertise in biology, oceanography and engineering not only allows for detailed analysis of specific groups of organisms but also an understanding of their relation to one another and their environment.

Sutton *et al*. (2008) described a biomass maximum of deep-pelagic fishes occurring below 1000 m along the northern MAR (Fig. 4.1). This deep biomass maximum is remarkable as deep-pelagic fishes are usually most abundant in the top 1000 m of the water column (Angel and Baker 1982). Ebeling (1962) showed that the "bigscale fishes" (family Melamphaidae) are one of the most abundant families of the

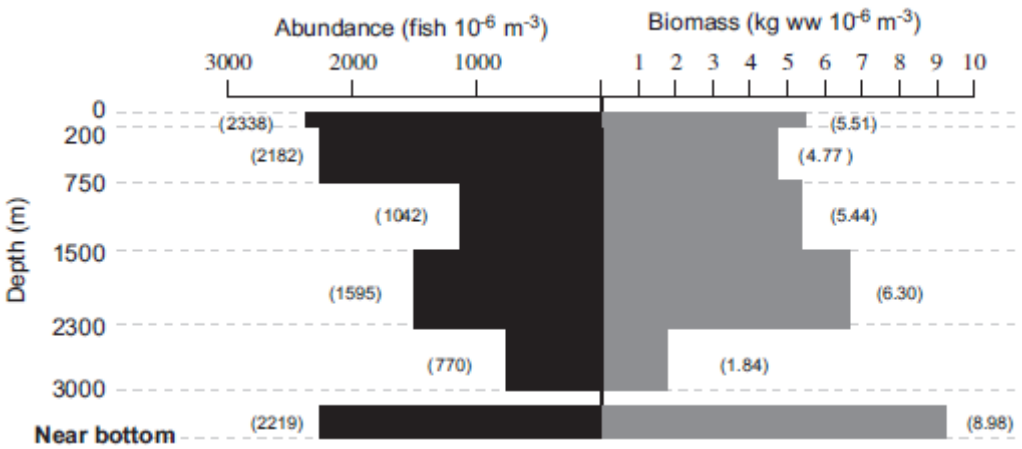

Figure 4.1. Vertical distribution of deep-pelagic fish abundance and biomass over the northern Mid-Atlantic Ridge (Sutton *et al*., 2008).

deep sea, particularly around the 1000-m depth zone. Information on this taxon is extremely scarce for several reasons. First is the overall low sample size of study material due to the historical dearth of bathypelagic sampling. In this paper we present information on the distribution, abundance and biomass of the melamphaid fishes over a mid-ocean ridge system, assess their contribution to the deep (> 1000 m) biomass maximum, and discuss possible reasons for their success in this ecosystem.

MATERIALS AND METHODS

Sample material was collected on Leg 1 of the MAR-ECO cruise aboard the Norwegian research vessel *G.O. Sars* along the northern Mid-Atlantic Ridge (from Iceland to the Azores), beginning 5 June and ending 3 July 2004 (Figure 4.2). The specific goal of the first leg of the MAR-ECO cruise was "to collect data for describing the diversity and distribution patterns of the plankton and nekton of the pelagic ecosystem of the MAR" (Godø 2004).

The northern MAR study area encompasses the Reykjanes Ridge south of Iceland to the Azores (between 36°42'W - 25°57'W and 59°46'N - 38°37'N). The peaks of the ridge system rise to within 1000 m of the surface, in stark contrast to the surrounding abyssal plains. The continuity of the ridge is broken in an area called the Charlie-Gibbs Fracture Zone (between 35°00'W - 32°00'W and 52°30'N - 52°00'N), which is a transverse fault in the otherwise linear MAR (Fig. 4.2).

Several types of mid-water nets (Norwegian macrozooplankton, Åkra and Egersund trawls) were used to collect samples along the MAR. Each net contained a different mesh size that selected for certain-sized nekton (specific details can be found in Table 6.1 and de Lange Wenneck *et al*. 2008). The Åkra and macrozooplankton trawls

were outfitted with multiple cod ends (three and five, respectively), making it possible to sample discrete depth strata.

Eighty-three samples were taken at 17 stations in four geographical regions aligned in roughly a north-south configuration, each station containing five depth zones. Distance between stations varied between 56.25 km and 594.86 km. The samples collected were counted, weighed (wet) aboard-ship on motion-compensating scales, and frozen at sea. The samples were thawed at the Bergen Museum, fixed in a 10% formalin:seawater mixture and stored in 70% ethanol. Specimen taxonomic identity was determined or confirmed at the Bergen Museum prior to use in trophic and gonadal analyses.

Abundance data were compiled and standardized (number of specimens per volume of water sampled, Table 4.1) and spatial distributions represented in graphical form. This abundance data was entered as numbers of individual fish caught per million cubic meters, per species, per station into the PRIMER 6 software package (Clarke and Gorley 2006). Solar Cycle, ridge section, depth zone and proximity to ridge surface (within 200 m or not) were all included as factors for each station. Standardized abundance data were subjected to multivariate analysis routines using the PRIMER 6 software package (Clarke and Gorley 2006) after fourth-root transformation. Fourth-root transformation was necessary to obtain a signal from the other species because of the dominance of *S. beanii*. Bray-Curtis indices were calculated in order to compare the species similarity between samples (Bray and Curtis 1957). The Bray-Curtis matrix then provided the basis for UPGMA (Unweighted Pair Group Method with Arithmetic Mean) cluster analysis to discriminate assemblage groupings (Clarke and Gorley 2006). A

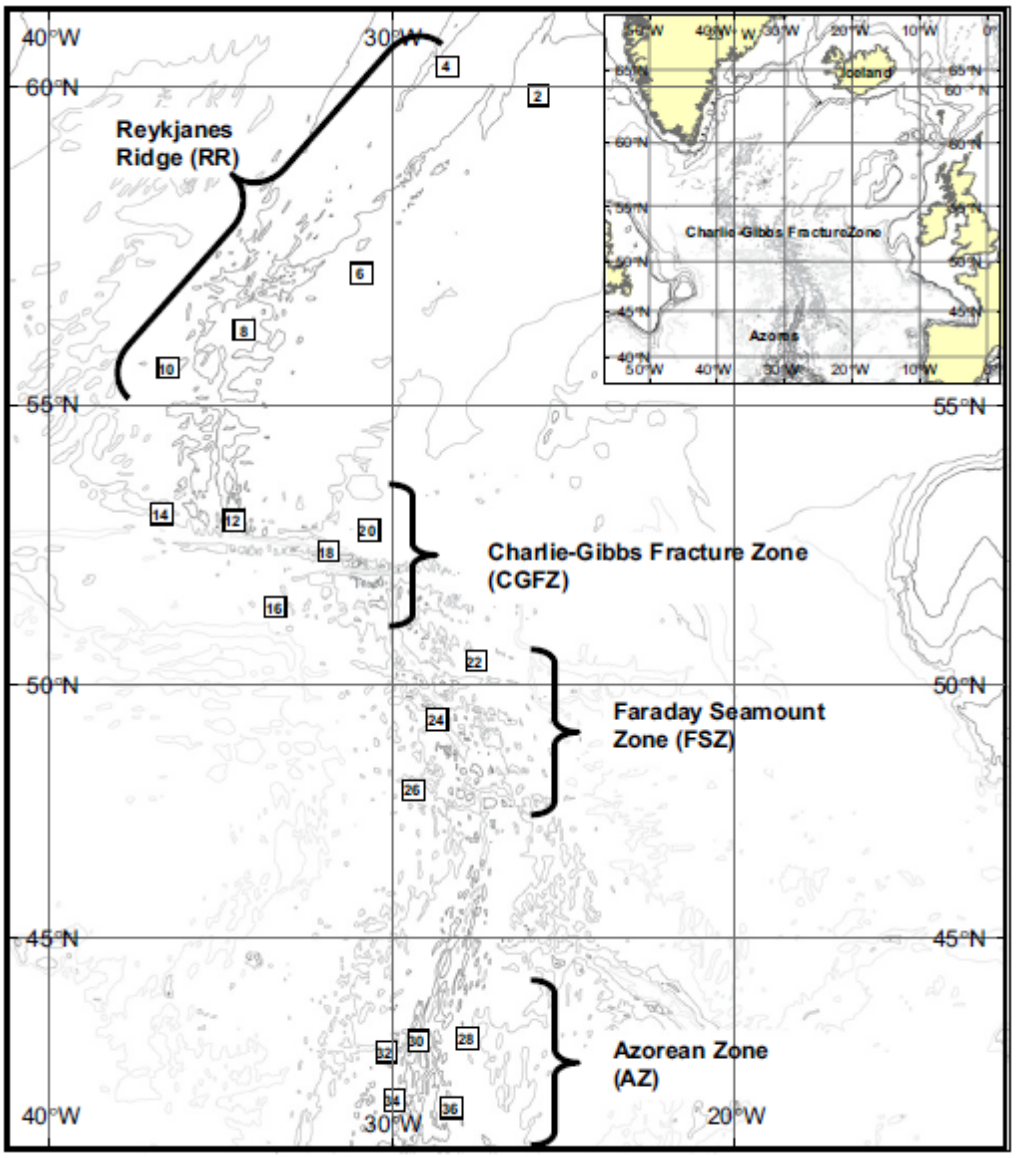

Figure 4.2. Northern Mid-Atlantic Ridge sample sites from Leg 1 of the 2004 MAR-ECO cruise. Each numbered square represents one sampling location containing five depth zones. Diel cycle was not considered in trawl deployment (trawls were taken during both day and night, but with no particular pattern). Sample locations are divided into four geographic regions: Rekjanes Ridge, Charlie-Gibbs Fracture Zone, Faraday Seamount Zone and Azorean Zone.

Table 4.1. Total abundances and wet weights for melamphaid species along the entire length of the MAR, based on krill trawl data. Values have been standardized per million cubic meters of water filtered

Species	Total Number	Total Weight (g)
Melamphaes microps	82.77	451.85
Poromitra capito	31.32	276.65
Poromitra crassiceps	388.93	13576.17
Poromitra megalops	177.41	544.22
Scopeloberyx opisthopterus	104.90	61.55
Scopeloberyx robustus	724.24	3549.5
Scopelogadus beanii	1268.91	22569.43
Scopelogadus mizolepis	174.42	1396.77

similarity profile (SIMPROF) was generated to test the null hypothesis that these sets of samples did not differ from one another in multivariate structure (Clarke and Gorley 2006). Resemblance values are tested against a mean value of 1000 permutations of the random rearrangement of samples, which produces an "expected" similarity profile. The absolute distance (π) between the "actual" and "expected" profiles is the test statistic. The SIMPROF results give a value of $p<0.5$ if π is larger than any of the other 999 simulated values. This probability value was used as evidence of internal group structure (Clarke and Gorley 2006).

A two-way analysis of variance (ANOVA) was run using the R statistical package comparing abundance values across the various depth zones and ridge sections and assessing the ridge section by depth zone interaction (Maindonald 2008; R Development Core Team 2010). Abundance data were fourth-root transformed before use in ANOVA. Residual values were tested using a Shapiro-Wilk test and homogeneity of variances of the response variable (abundance values) was tested using a Bartlett's test of homogeneity (both tests were run using the R statistical package, R Development Core Team 2010).

An analysis of similarity (ANOSIM) was run in PRIMER 6 using the Bray-Curtis data from the cluster analysis. A two-way crossed ANOSIM was used to test whether there was a significant difference amongst and between depth zone groups and ridge section groups. A one way ANOSIM test was run to test whether the group of Southern stations (the stations from sampling site 17) were significantly different from the rest of the stations. Both ANOSIM tests were run using 5000 randomly selected permutations. The critical alpha chosen for these two ANOSIM tests was 0.05.

RESULTS

The four most abundant melamphaid species (*Poromitra crassiceps, Scopeloberyx robustus, Scopelogadus beanii, Scopelogadus mizolepis mizolepis*) accounted for 11.8% of the total biomass and 2.25% of the total number of fishes caught between 0-3000 m along the northern MAR. Highest mean abundance occurred at depths between 750-1500 m (Figure 4.3). Mean biomass was highest between 1500-2300 m (Figure 4.4). Mean biomass and abundance did not show as distinct a change amongst the various ridge sections (Figure 4.5 and 4.6). Post-juvenile and adult specimens of several species (*Poromitra crassiceps, Scopelogadus beanii* and *Scopelogadus mizolepis* representing 10%, 8% and 62% of their total species abundance, respectively) were caught above 200 m at several stations, setting new minimum depth of occurrence records for the family. Though these shallow-living individuals were only single specimens, it is important to note that they are some of the larger melamphaid species, who are not thought to undergo vertical migrations. It is unknown what the cause of this shallow occurrence was, but it has not been observed in any other oceanic environment.

Large-scale geographical shifts in species composition were observed. In the genus *Scopelogadus* species dominance shifted from *S. beanii* north of an anticyclonic eddy described by Søiland *et al.* (2008) to *S. m. mizolepis* along its southern boundary (Figure 4.5). This shift in *Scopelogadus* species composition was further supported by the sample groupings discriminated by cluster analyses.

Cluster analyses discriminated five groupings of melamphaid fishes along the MAR (Figures 4.6 and 4.7). The SIMPROF test showed significance ($P < 0.05$) in

Table 4.2. P values and similarity percentages used to determine the clustering of samples

Similarity (%)	Pi Value	*P* (%)
1.02	2.77	0.1
1.22	2.95	0.1
12.82	3.29	0.1
13.73	2.11	1.1
15.5	3.48	5.7

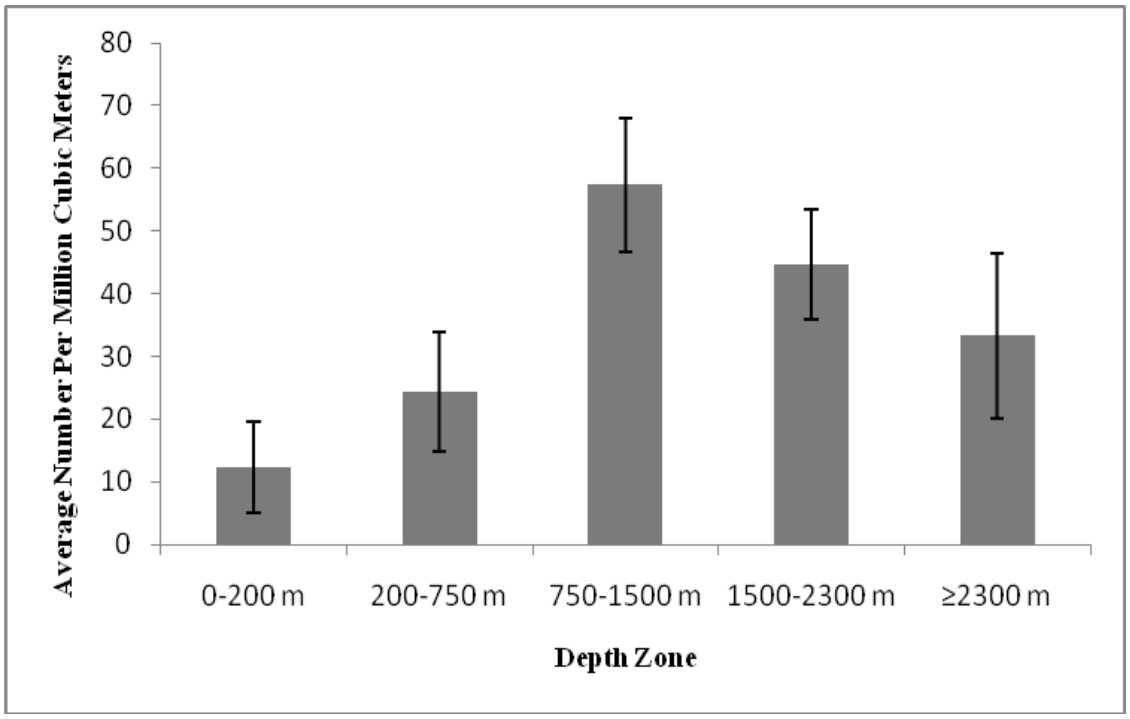

Figure 4.3. Mean abundance (no. 10^{-6} m^{-3}) at each of the five depth zones sampled over the northern Mid-Atlantic Ridge during the 2004 *G.O. Sars* expedition. Error bars are calculated standard error.

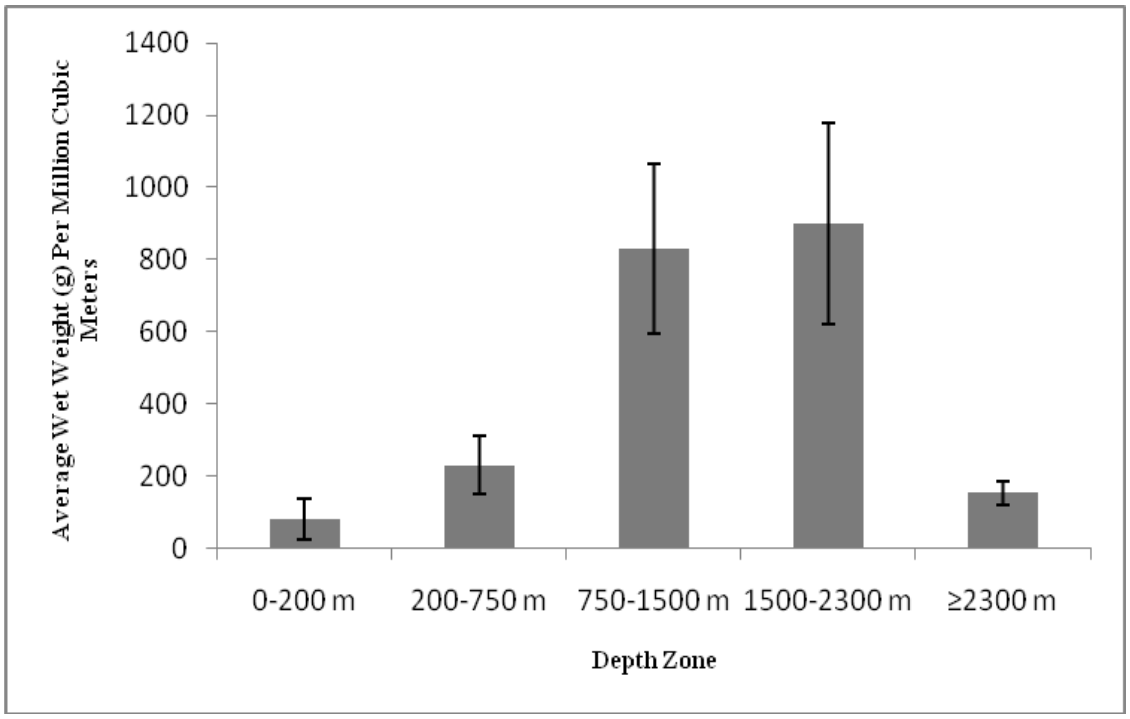

Figure 4.4. Mean biomass (g wet weight 10^{-6} m^{-3}) at each of the five depth zones sampled over the northern Mid-Atlantic Ridge during the 2004 *G.O. Sars* expedition. Error bars are calculated standard error.

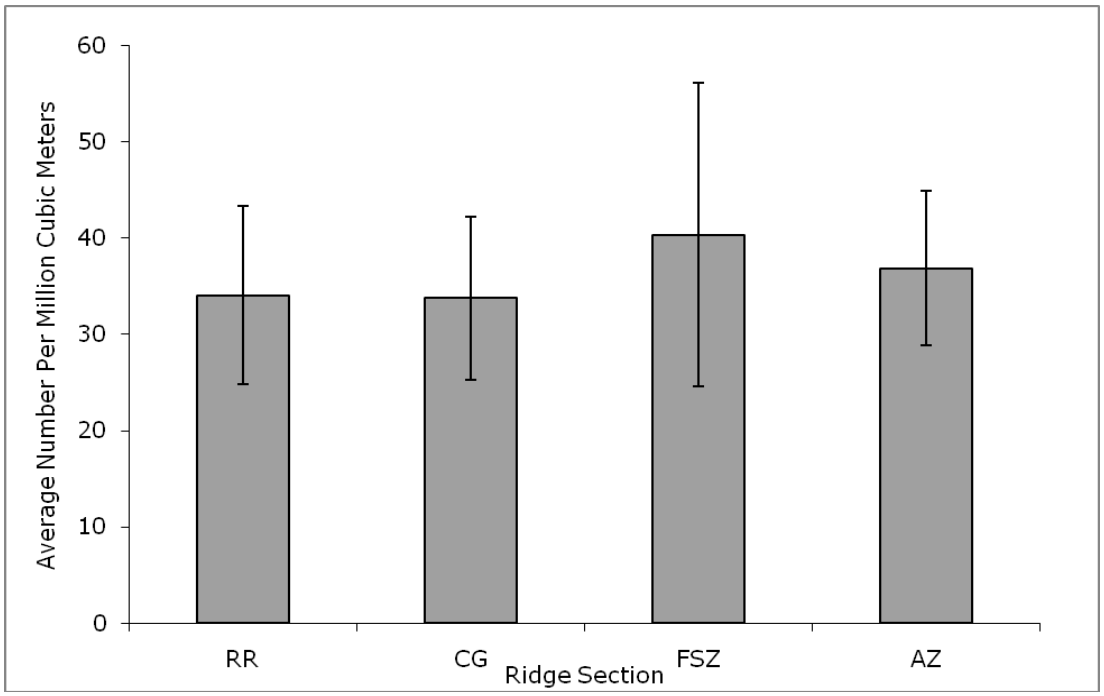

Figure 4.5. Mean melamphaid abundance (no. 10^{-6} m^{-3}) at four geographic regions along the Mid-Atlantic Ridge. RR = Reykjanes Ridge; CG = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azorean Zone. Error bars are calculated standard error.

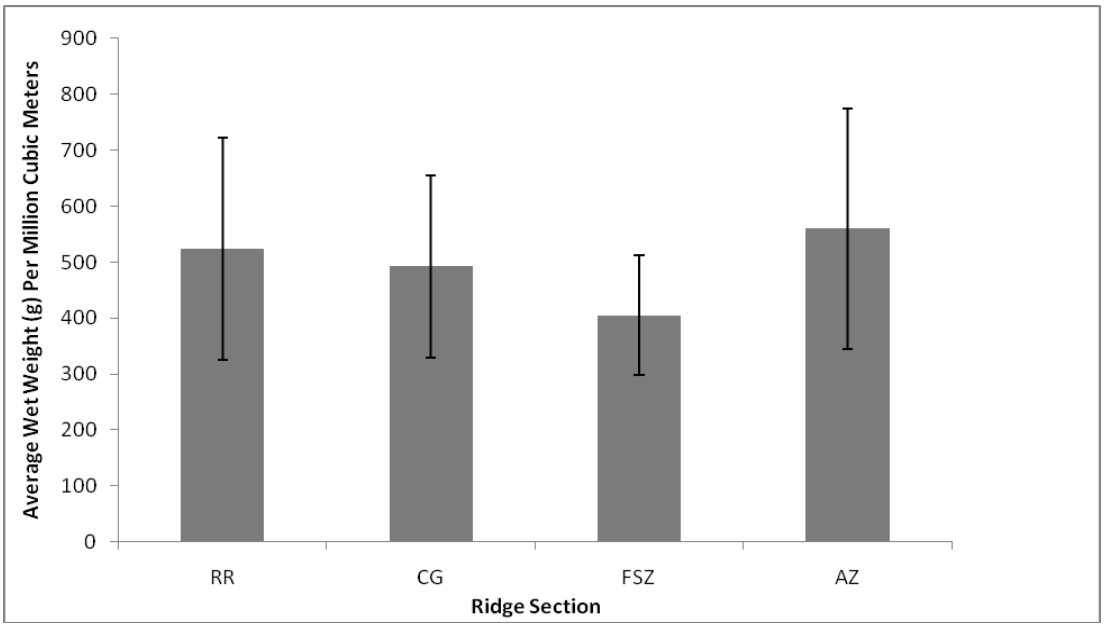

Figure 4.6. Mean melamphaid biomass (g wet weight 10^{-6} m^{-3}) at four geographic regions along the Mid-Atlantic Ridge. RR = Reykjanes Ridge; CG = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azorean Zone. Error bars are calculated standard error.

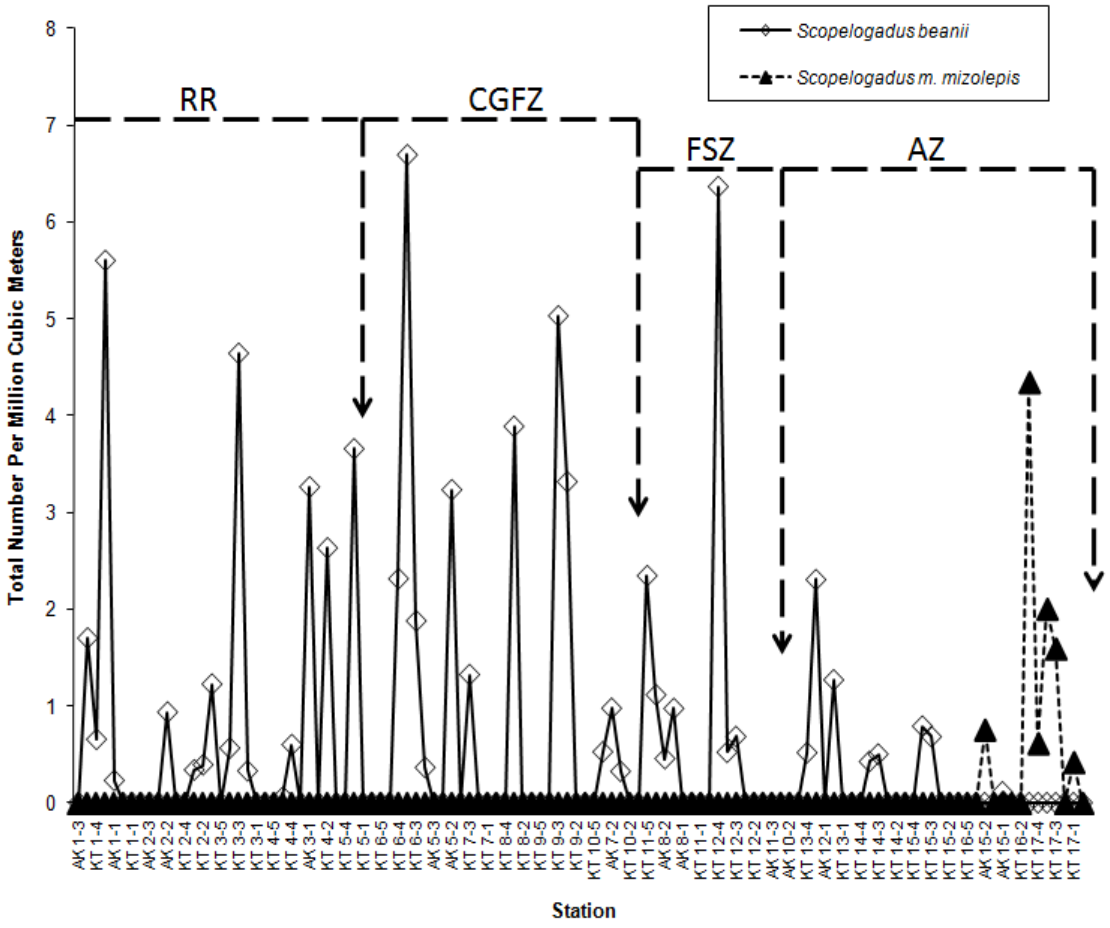

Figure 4.7. *Scopelogadus beanii* and *Scopelogadus mizolepis mizolepis* abundances showing the shift in dominance between *S. beanii* in the north to *S. m. mizolepis* in the south. Samples are listed by trawl numbers (all depths), which trend from North (left) to South (right). RR = Reykjanes Ridge; CGFZ = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azorean Zone.

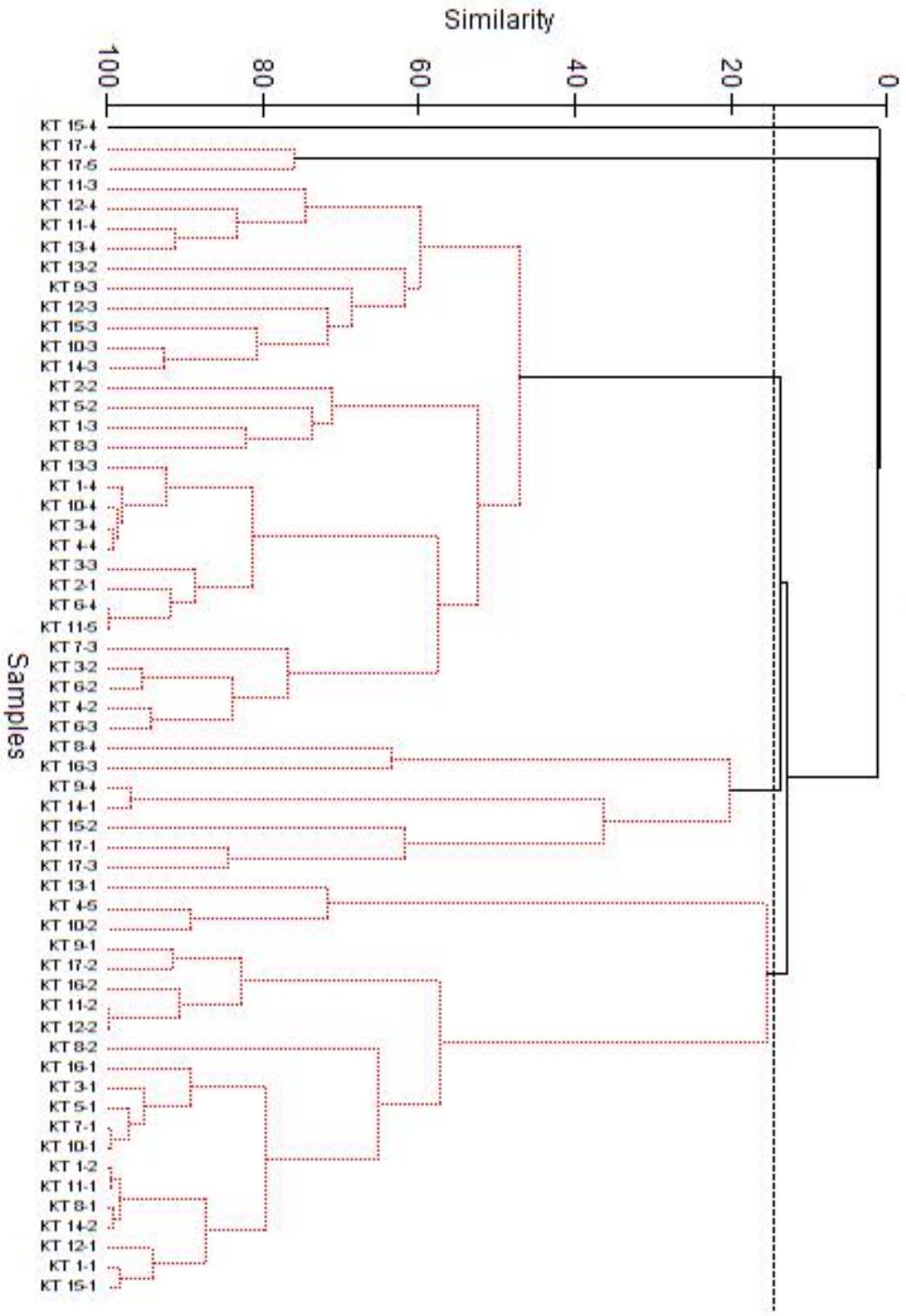

Figure 4.8. A dendrogram produced by the cluster analysis of the Bray-Curtis similarity values of the standardized abundance data. The dashed vertical line represents 14% similarity.

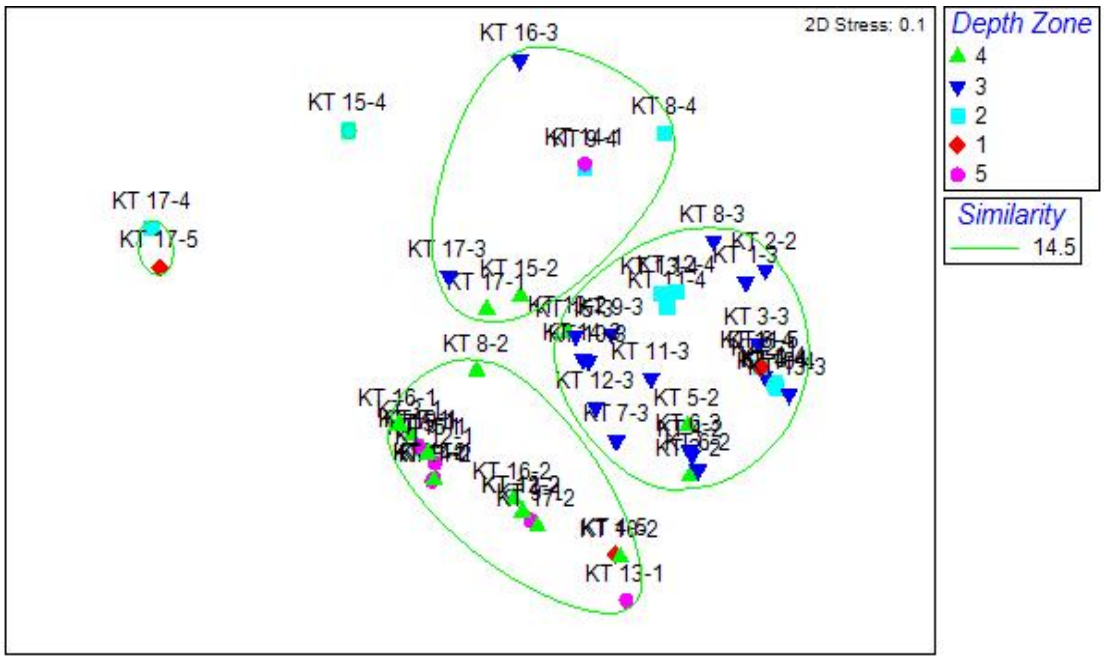

Figure 4.7. Results of multiple dimensional scaling ordination, with classification (cluster analysis) results overlain. Clusters are encircled by a line representing 14.5% similarity between enclosed stations. Symbols represent the five depth zones: 1 = 0-200 m; 2 = 200-750 m; 3 = 750-1500 m; 4 = 1500-2300 m; 5 ≥ 2300 m.

cluster discrimination at approximately 14% similarity (Table 4.2); at higher levels of similarity, there was no evidence of finer-level structure and thus further division of the coarse structure would not be justified or significant. Groups consisted of 1, 2, 21, 28, and 7 samples, respectively. Factor analysis indicated that ridge section, solar cycle (Day/Night), and distance from the ridge surface (close to or far from the ridge surface) were not major determinants of sample grouping. Individual stations were grouped together based primarily on the depth zone. Examination of the species composition of each stations that comprised each group also revealed one or two species dominated each group of stations. The first "Group," a single, shallow Azorean Zone trawl taken during the day, contained only the species *Poromitra capito*. The second Group consisted of two shallow Azorean Zone trawls taken at night that contained only *Scopelogadus mizolepis mizolepis*. Twenty-one trawls comprised the third Group; these primarily fell within depth zones 4 or 5 (sampling depths at or below 1500 m) and contained mainly *Scopeloberyx robustus* and *Poromitra crassiceps*. The largest Group consisted of twenty-eight trawls, mostly from depth zones 2 or 3 (sampling depths of 200-750 m and 750-1500 m, respectively), containing mainly *Scopelogadus beanii* and *Poromitra megalops.* The last of the five Groups represented a collection of samples from a mixture of depth zones, ridge sections and station-specific dominant species, defying easy characterization.

The results of a two-way ANOVA testing the effects of depth zone and ridge section (and their interaction) on melamphaid abundance revealed that depth zone had a significant effect on total melamphaid abundance, while ridge section and the ridge section by depth zone interaction did not (Table 4.3). Tests of normality of the residuals and homogeneity of variance revealed the fourth root transformed data to be both normal

(W = 0.9872, p = 0.5894) and homogeneous (K^2 = 1.6373, df = 3, p = 0.651). ANOSIM tests supported the results of the ANOVA and the cluster analyses. Two-way ANOSIM found that the depth zone groups were significantly different from one another while the ridge section groups were not (Table 4.4). A one-way ANOSIM found that the group of stations north of the anticyclonic anomaly were significantly different in taxonomic similarity than those south of the anticyclonic anomaly) (Table 4.5).

DISCUSSION

Data from MAR-ECO sampling indicate that the family Melamphaidae represents an important biotic component of the Mid-Atlantic Ridge pelagic ecosystem. High abundances and biomass at, and below, 1000 m depth reveal that melamphaids make up a large proportion of the biomass maximum described by Sutton *et al.* (2008). High abundances between 750-1500 m depth coincide with previous estimates of melamphaid habitat ranges (Ebeling 1962; Ebeling and Weed 1963; Keene 1970; Keene 1987; Keene *et al.* 1987). Though species abundance was highest in Depth Zone 3 (750-1500 m), biomass was highest in Depth Zone 4 (1500-2300 m), which suggests that larger melamphaids tend to inhabit deeper water, supporting the findings of Ebeling and Cailliet (1974). With high relative abundance and biomass, melamphaids likely represent an important link in bathypelagic energy flow through this ridge system.

Scopelogadus beanii is found throughout the Atlantic Ocean and has been caught along the entire eastern half of the Atlantic while *Scopelogadus mizolepis mizolepis* has a habitat range between 40°N and 35°S (Ebeling and Weed 1963; Maul 1986; Santos *et al.* 1997; Froese and Pauly 2000; Møller *et al.* 2010; Moore 2002; Moore In Press; Moore *et al.* 2003). Søiland *et al.* (2008) described an anticyclonic anomaly that encircles the crest

Table 4.3. Results of two-way ANOVA testing the effects of depth zone and ridge section on the total melamphaid abundance

	DF	Sum Sq	Mean Sq	F value	Pr(>F)
Section	3	2.721	0.907	0.7896	0.5034
DepthZone	1	28.595	28.5952	24.8954	3.81E-06
Section:DepthZone	3	6.201	2.067	1.7995	0.1545
Residuals	75	86.146	1.1486		

Table 4.4. Results of two-way ANOSIM testing difference in melamphaid abundance within and amongst depth zone and ridge section groups. Pairwise tests compare depth zone groups or ridge section groups to one another. Presented are the significance percentages representing the significance of the difference between two depths or ridge sections. R-statistic represents the amount of overlap or similarity in species composition between two depth zones or ridge sections (R close to 0 indicates strong similarity between groups). Depth zones are as follows: 1 = 0-200 m; 2 = 200-750 m; 3 = 750-1500 m; 4 = 1500-2300 m; 5 = ≥2300 m. Ridge sections are as follows: RR = Reykjanes Ridge; CGFZ = Charlie-Gibbs Fracture Zone; FSZ = Faraday Seamount Zone; AZ = Azorean Zone

TESTS FOR DIFFERENCES BETWEEN Depth Zone GROUPS	
Sample statistic (Global R):	0.443
Significance level of sample statistic:	0.02%
Number of permutations:	5000 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R:	0

TESTS FOR DIFFERENCES BETWEEN Ridge Section GROUPS	
Sample statistic (Global R):	0.075
Significance level of sample statistic:	12.40%
Number of permutations:	5000 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R:	618

Pairwise Tests Depth Zone		
Groups	R Statistic	Significance Level %
4, 3	0.384	0.02
4, 2	0.554	0.02
4, 1	0.654	0.5
4, 5	0.604	0.2
3, 2	0.127	11
3, 1	0.56	5.6
3, 5	0.566	0.1
2, 1	0.424	16.7
2, 5	0.463	1
1, 5	0.5	33.3

Pairwise Tests Ridge Section		
Groups	R Statistic	Significance Level %
RR, CGFZ	0.061	24.2
RR, FSZ	0.246	7.2
RR, AZ	0.153	4.7
CGFZ,FSZ	-0.261	97.5
CGFZ, AZ	0.215	3.5
FSZ, AZ	-0.253	97.2

Table 4.5. Results of one way ANOSIM testing difference in melamphaid abundance between stations found north of an anticyclonic anomaly and south of the same anomaly

Sample statistic (Global R):	0.231
Significance level of sample statistic:	1.10%
Number of permutations:	5000 (Random sample from 5006386)
Number of permuted statistics greater than or equal to Global R:	54

of the ridge between 42°N and 43°N near the site of *Scopelogadus* species replacement. Though eddies are not permanent physical oceanographic features, anticyclonic anomalies such as the one described by Søiland *et al.* (2008) have been shown to be associated with warm core rings (Joyce and Wiebe 1983). Warm core rings have been shown to transport plankton and micronekton beyond their normal habitat ranges (Joyce and Wiebe 1983; Wiebe *et al.* 1985). Warm core rings have been shown to rise from the Gulf Stream current (Joyce and Wiebe 1983; Wiebe *et al.* 1985), which flows just south of the area of this species replacement as well as a branch of the Gulf Stream called the Azores Front. A warm core ring could explain how *S. m. mizolepis* was transported North of its usual habitat range, breaking up the continuous range of *S. beanii*. Distributional characterization based on graphical analysis was further supported by cluster and ANOSIM analyses. Not only did the *S. beanii*-dominant stations cluster together, most of the southern stations, in particular the ones containing *S. m. mizolepis*, also clustered into their own groups. The one-way ANOSIM analysis showed that the species dominance of the stations north of the anticyclonic anomaly were significantly different than the species dominance found in the stations south of the same anomaly. This shift in species composition is consistent with similar shifts in the fish communities along the MAR (Sutton *et al*. 2008). These shifts suggest that a strong current, such as a warm core ring, trapped and transported *S. mizolepis* beyond their usual center of distribution.

The results for the two-way ANOVA, the cluster analysis and the ANOSIM tests all had similar results suggesting that depth zone is the primary permanent factor influencing melamphaid abundances and biomasses along the MAR. Though not

permanent, the anticyclonic anomaly observed by Søiland *et al.* (2008) also represented a major factor influencing species composition near the Azores. The influence of depth zone on melamphaid abundances and biomass coincides with the findings of Sutton *et al.* (2008) and Vecchione *et al.* (2010), who found consistent meso- and bathypelagic fish assemblages running the length of the northern MAR. Deep-sea fish assemblages are not as sensitive to changes in surface characteristics associated with geographical changes (i.e., temperature, salinity, chlorophyll) (Sutton *et al.* 2008; Vecchione *et al.* 2010). Pair this lack of effect from surface change with the relatively unchanging deep-sea environment (Haedrich 1997; Merrett and Haedrich 1997; Gage and Tyler 1999; Herring; 2002 Sverdrup *et al.* 1963; Randall and Farrell 1997) and a ubiquitous, depth specific fish assemblage does not seem anomalous.

Though the focus of this research is the melamphaid fishes found in association with the Mid-Atlantic Ridge, it is pertinent to note the cosmopolitan Atlantic species that do not inhabit, or associate with, the MAR. At least 13 other melamphaid species are known to inhabit all deep Atlantic waters, but were not caught during the MAR-ECO cruise (Maul 1986; Moore 2002; Moore *et al.* 2003; Santos *et al.* 1997; Møller *et al.* 2010; Moore In Press). Some factor is preventing many of the melamphaid species from inhabiting the environment of the MAR and it could be that there are true cosmopolitan species (like those found associated with the ridge) and basin associated species (those not found near the ridge).

Research of the trophic ecology of the family Melamphaidae will be presented in a following chapter. Gartner and Musick (1989) showed that the diet of one melamphaid, *Scopelogadus beanii***,** consisted primarily of gelatinous zooplankton. They found that the

majority of the gelatinous contents of the stomachs they studied were of the family Salpidae (Thaliacea). It was previously thought that gelatinous zooplankton offer little nutritional value to predators, and that gelatinous zooplankton were a "dead end" in marine food webs due to the lack of natural predators, and thus energy flow to higher trophic levels (Sommer *et al.* 2002; Nelson *et al.* 2002; Arai 2005). However, recent studies have shown that gelatinous zooplankton could play a more significant role in the diets of marine vertebrates than once believed (Kashkina 1986; Purcell and Arai 2001; Cartamil and Lowe 2004; Houghton *et al.* 2006). Given the high relative abundance in this survey, and their reported consumption of gelatinous prey, the Melamphaidae may represent a significant basin-scale trophic linkage between fishes and gelata in bathypelagic systems.

CHAPTER 5

GROWTH AND REPRODUCTION OF THE FAMILY MELAMPHAIDAE

INTRODUCTION

In the deep sea the most common population structures are ones having either equal sex ratios or more or larger females (Clarke 1983). Many meso-to- bathypelagic species display some sort of sexual dimorphism, ranging from slight differences in photophore patterns in myctophids to the extreme size difference between male and female ceratioid angler-fishes (Bertelson 1951; Marshall 1979; Clarke 1983). In all cases, it is assumed that these sexual differences represent a trade-off between resource utilization and mate location. In the case of melamphaids, the sex ratio appears to be skewed towards having more males than females, and there is no apparent sexual dimorphism (Clarke 1983). Clarke (1983) found that the ratio near Oahu, Hawaii was about 2:1 in favor of males (62-64% males). Clarke (1983) and Clarke and Wagner (1976) are the only studies that have dealt specifically with melamphaid sex ratios, meaning that all sex ratio information on the family comes from this one area off of Hawaii and could be different elsewhere.

It is rare to find populations that have such a male-biased sex ratio (Cocker 1978; Clarke 1983). A strategy of equal sex ratios, or one that is biased towards females, is most common due to the energy allocation needed by a female to produce ova (Emlen

and Oring 1977; Clarke 1983). It has been suggested that a population with no apparent sexual dimorphism and a higher number of males provides females with a higher success rate in finding a mate by chance alone (Clarke 1983; Baird and Jumper 1995). In order to increase reproductive success, females would need to have access to resources necessary for reproduction (Emlen and Oring 1977). If the unequal sex ratio negates or minimizes male availability as a limiting factor in reproductive success, it would seem that food resource availability would be the limiting factor in the success of the melamphaid species.

A characteristic of the family Melamphaidae is that it contains both "dwarf-" and "normal-sized" species (Ebeling 1962; Keene 1987; Kotlyar 2004c). These "dwarf" species have often been mistaken for juveniles of the "normal sized" species, which makes estimations of size at maturity and taxonomic research particularly difficult (Keene 1987). In order to understand the diversity and ecology of the Melamphaidae, it is imperative that "dwarf" species be correctly identified and discriminated from juveniles of other species. Taxonomic resolution of the dwarfism issue will aid in identifying new species, estimating reproductive characteristics, and describing the melamphaid species composition over the MAR.

MATERIALS AND METHODS

Sample material for the reproductive investigation was collected on Leg 1 of the MAR-ECO cruise aboard the Norwegian research vessel *G.O. Sars* along the northern Mid-Atlantic Ridge (from Iceland to the Azores), beginning 5 June and ending 3 July 2004. The specific goal of the first leg of the MAR-ECO cruise was "to collect data for

describing the diversity and distribution patterns of the plankton and nekton of the pelagic ecosystem of the MAR" (Godø 2004).

The northern MAR stretches from the southern coast of Iceland to the Azores (between 36°42'W - 25°57'W and 59°46'N - 38°37'N). The peaks of the ridge system rise from the surrounding abyssal plains and reach depths above 2000 m. The continuity of the ridge is broken in an area called the Charlie-Gibbs Fracture Zone (between 35°00'W - 32°00'W and 52°30'N - 52°00'N), which is a transverse fault in the otherwise linear MAR (Figure 6.2, following chapter).

Samples were caught using a variety of nets. Each net contained a different mesh size that selected for certain-sized nekton. Macrozooplankton, Åkra, and Egersund trawls were used to collect samples along the MAR, their mouth size and door spread are listed in Table 6.1 (following chapter). Information about each net deployment is found in Appendices 4-8. The Macrozooplankton and Åkra trawls were outfitted with multiple cod ends making it possible to sample discrete depth strata.

The samples collected were frozen at sea, thawed at the Bergen Museum, fixed in a 10% formalin:seawater mixture and then stored in 70% ethanol. Each fish was taken from the ethanol, patted dry and weighed to the nearest 0.01 g to get a post-fixation wet weight. Standard length (the length from the tip of the snout to the end of the caudal peduncle) of each specimen was measured to the nearest 0.01 mm using a pair of calipers. In order to aid in species identification, the first gill arch of each fish was removed from the right side and the gill rakers from this arch were counted.

Dissection

A total of 421 samples, from four genera and eight species were identified and dissected to remove the internal organs. For extraction of internal organs, a "window" was cut in the right side of each fish by making an incision down the ventral midline from the isthmus to the anus. If the body cavity opening was still too small, another incision was made from the beginning of the first incision moving dorsally and through the cleithrum. This window allowed separation of the internal organs from the mesentery sac that attaches the organs to the dorsal and anterior portions of the body cavity.

Once the body was opened, the mesenteries were cut with a pair of spring loaded microdissection scissors. After the excess connective tissue was cleared and the black esophagus was clearly visible, the esophagus was cut at the most anterior point allowing removal of the internal organs (shown in Figure 6.3, following chapter). Cutting the mesenteries was essential to identifying the gender of the fish; if the internal organs were pulled out while the gonads were still attached to the abdominal wall, there was a good chance that they would have torn and be unidentifiable, as they are composed of soft, fragile tissue.

Sex was identified based on the visual description of gonads in the works of Ebeling and Weed (1963), Keene (1970) and Keene *et al.* (1987). These descriptions were largely based on coloration of gonads, which is not a good diagnostic character for specimens stored in alcohol, as the alcohol tends to extract tissue pigmentation. With this in mind, modifications were made to this method in order to accurately identify the two sexes. In general, ovaries were present as a large, yellowish, bilobed organ attached

directly to the dorsal side of the straight portion of the intestine. Ovaries were generally attached in such a manner that they lay close to or touched the surface of the intestine and are attached to the intestine by a short, thick duct for ejecting eggs. Often ovaries were so gravid that the membrane encasing the eggs would easily tear, releasing the spherical eggs.

Testes were present as two distinct, small, white organs separated from the straight portion of the intestine. The testes lay closer to the posterodorsal aspect of the stomach than the intestine proper. They were attached to the intestine and the posterior surface of the stomach by a fragile connective tissue sheet and to the cloacae by long, thin tubes.

An exception to this descriptive characterization occurred in the genus *Melamphaes*. The male and female gonads in these species were both white in color and both were almost always two separate and distinct organs (much like the male gonads in all other genera). Male and female gonads were still distinguishable by relative size, shape and orientation with respect to the straight section of the intestine. Female gonads were long, thick and cylindrical in shape. They lay along the sides of the straight intestine, often being long enough to extend past the posterior third of the stomach; the ends closest to the cloacae were fused together and entered the cloacae through a single duct. The male gonads were short, oval and reniform in shape. Like the male gonads of the other species, they lay well away from the intestine and attached to the posterodorsal aspect of the stomach by a sheet of connective tissue.

Gonads were saved in separate vials of ethanol after initial determination of sex. Gonads were later removed from their vials, patted dry with a paper towel and then

weighed to the nearest 0.001 g. Gonad weight was used along with body weight to calculate Gonadosomatic Index as explained below.

Statistical Analyses

Gonad weight (GW) and total body weight (TW) were used to calculate the gonadosomatic index (GSI) of both the males and females of each species using the formula GSI = (GW/TW)*100 (Ikejima *et al.* 2007*;* Follesa *et al*. 2007; Porcu *et al.* 2010). This standardized value allowed comparison of gonad sizes between size classes. This calculation allowed for an analysis of relative gonad size as related to the size class at which significant gonad growth associated with spawning occurs (Drazen 2002; Figueiredo *et al.* 2003; Walmsley *et al.* 2005; Follesa *et al.* 2007). Since specimens for this study were gathered from a single month, seasonality was removed as an explanatory variable and it was assumed differences in GSI were directly related to size class and not some combination of size and time of year. For this test only female GSI's were used since ovaries, and the eggs contained within them, traditionally show a more pronounced size increase than testes during spawning (D'Onghia *et al.* 1999; Follesa *et al.* 2007). The size at first spawning was interpreted as the size where the GSI shows a significant increase.

In order to compare GSI and size, specimens were pooled into 5-mm size classes (Figueiredo *et al.* 2003). Because some of the 5-mm size classes only had a single replicate within them, several of these had to be grouped together (species, size classes and total N found in table 5.1). This method did not give a specific size-at-maturity but did provide a small, reliable range within which each species begins to focus energy

Table 5.1. Ranges in standard length (mm) for the size classes associated with each melamphaid species studied, including the total number of fishes within each size class.

Species	Size class	Total N
Melamphaes microps		
	80.00-94.99	4
	95.00-99.99	16
	100-109.99	15
Poromitra crassiceps		
	85.00-119.99	3
	120.00-124.99	3
	125.00-129.99	5
	130.00-134.99	9
	135.00-139.99	7
	140.00-144.99	2
Scopeloberyx robustus		
	35.00-59.99	5
	60.00-64.99	4
	65.00-69.99	20
	70.00-79.99	10
Scopelogadus beanii		
	35.00-44.99	4
	45.00-59.99	4
	60.00-64.99	3
	65.00-69.99	2
	70.00-74.99	4
	75.00-79.99	3
	80.00-84.99	8
	85.00-89.99	11
	90.00-94.99	16
	95.00-99.00	21
	100.00-109.99	8

reserves into spawning Differences among size class groups was tested using a one way ANOVA (Maindonald 2008; Venables *et al.* 2010). These statistical tests were run using the R statistical package and a critical alpha of 0.05 (Maindonald 2008; R Development Core Team 2010). *Melamphaes* and Scopeloberyx data were transformed using a Box-Cox transformation, *Poromitra* data which were left untransformed and *Scopelogadus* data which were "ln" transformed (suggested lambda from Box-Cox were: *M. microps* = -0.4651; *S. robustus* = 0.8720). Normality of residuals was tested using a Shapiro-Wilk test. Homogeneity of variance was analyzed using Levene's test for equality of variances.

Total numbers of males and females were calculated and are displayed in tables and graphs for each species (*M. microps, P. crassiceps, Scopeloberyx robustus, Scopelogadus beanii* and *Scopelogadus mizolepis*) in order to visualize the sex ratios of the assemblage. Sex ratios were tested using the χ^2 test in the R statistical package to indicate a significant difference between the observed sex ratio and the expected sex ratio of an even number of males and females, again using 0.05 as the critical alpha (Hardy 2002; Maindonald 2008).

Length-weight regressions of untransformed data for each melamphaid species are presented in this chapter. Graphs of length vs. weight were created in Microsoft Excel and the trend line function was used to find the line that fit the data set best (trend line with the highest R^2 value). Size differences between sexes were tested using one way ANOVAs. Data were transformed using the Box-Cox method (suggested lambda from Box-Cox were: *S beanii* = 2.3387; *M. microps* = 6.7473; *P. crassiceps* = 5.7078; *S. robustus* = 3.0082). Normality of residuals from the ANOVAs was analyzed using a

Shapiro-Wilk test. Homogeneity of variance was analyzed using Levene's test for equality of variances.

RESULTS

Size and Growth

Standard length and total wet weight were determined for 421 specimens from four genera and eight species (Figure 5.1). Sample size for three species, *Melamphaes ebelingi, Poromitra megalops* and *Scopeloberyx opisthopterus* were deemed insufficient for plotting. Length-weight regressions equations, expressed as power functions, are given in Table 5.2.

Specimens from the genus *Poromitra* represented both the largest and heaviest examined (Table 5.3). Analysis of variance revealed that females were significantly larger than the males in all species (ANOVA tables in Table 5.4). All variances were homogeneous while all residuals except those associated with the comparison of the *Melamphaes* sexes were non-normal, even after transformation (Shapiro-Wilk and Levene's test results in Table 5.5). Comparing SL as a function of species, *Scopeloberyx robustus* was smaller than S*copelogadus beanii, Scopelogadus mizolepis, Poromitra crassiceps,* and *Melamphaes microps* (Fig. 5.2). *Poromitra crassiceps* was larger than *Scopelogadus beanii, Scopeloberyx robustus, Scopelogadus mizolepis* and *Melamphaes microps* (Fig. 5.2).

Reproduction

The sex ratios of *P. crassiceps, S. beanii* and *M. microps* were all significantly different from an even 1:1 ratio of males to females (χ^2 values, df and p-values found in

Table 5.2. Regression equations and R^2 values calculated from the length-weight graphs of each species. WW= Wet Weight (g); SL= Standard Length (mm)

Species	Regression Equation	R^2
S. beanii	$WW = 1E\text{-}06(SL)^{3.4894}$	0.9893
S. mizolepis	$WW = 4E\text{-}06(SL)^{3.2814}$	0.9853
P. crassiceps	$WW = 1E\text{-}06(SL)^{3.4847}$	0.9710
S. robustus	$WW = 3E\text{-}06(SL)^{3.4172}$	0.9559
M. microps	$WW = 2E\text{-}06(SL)^{3.4808}$	0.9881

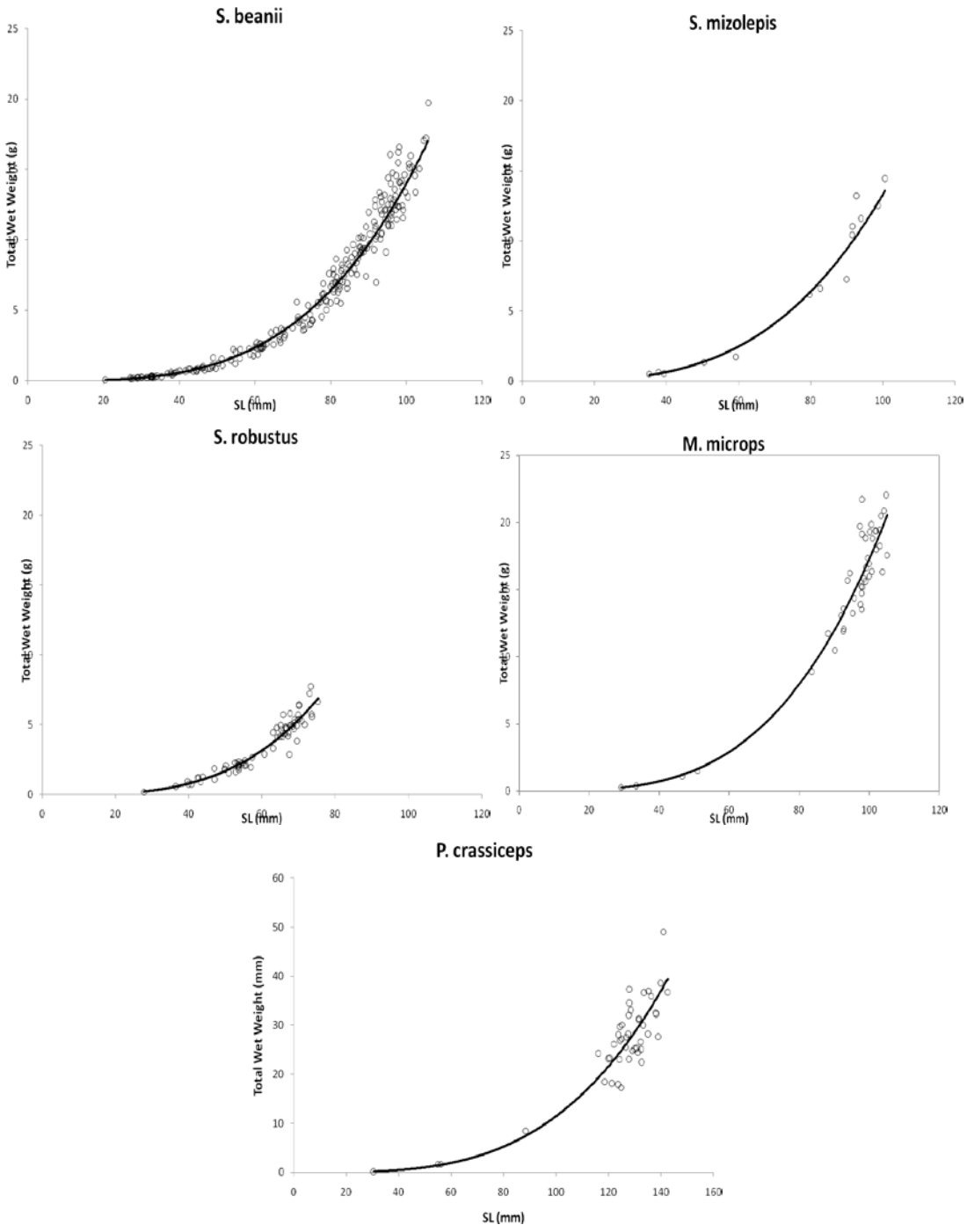

Figure 5.1. Length-weight graphs of five species of melamphaid fishes. The graph of *Poromitra crassiceps* is displayed on an extended scale to accomodate for their larger sizes. Trendlines formed using Excel and represent the lines with the highest R^2 values.

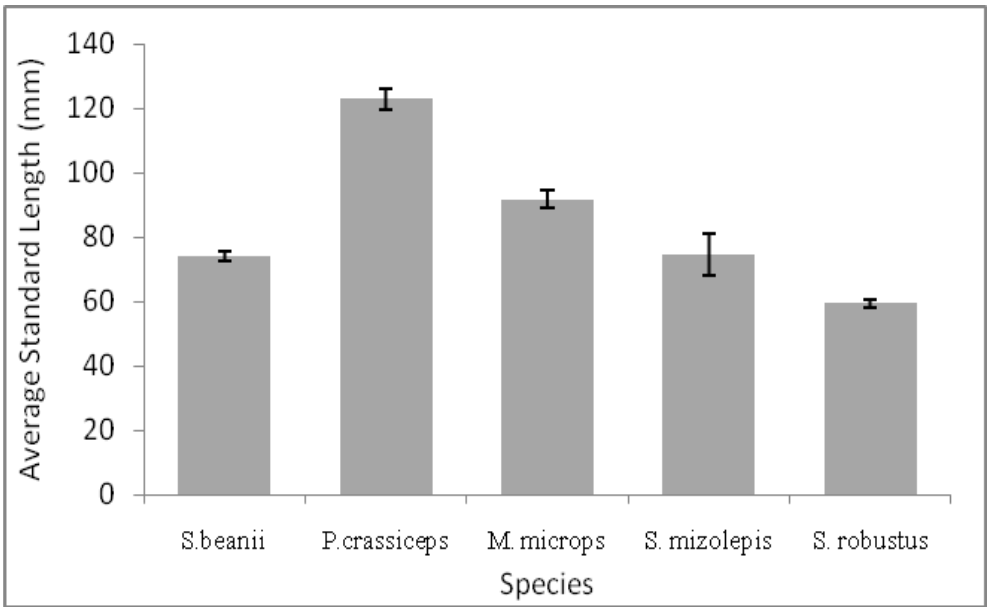

Figure 5.2. Average standard length (mm) for five species of melamphaids. Error bars represent standard error.

Table 5.3. Total numbers, average length, average weight and GSI characteristics separated by species and sex

Species	Sex	Total Number	Average Length	Average Weight	Average GSI	GSI Range
M. ebelingi	Male	4	93.83	12.87	0.17	0.155 - 0.183
M. microps	Female	35	98.93	17.04	4.11	1.663 - 8.778
	Male	8	73.85	8.00	0.27	0.105 - 0.464
	Unknown	2	36.80	0.78	N/A	N/A
P. crassiceps	Female	30	126.42	28.49	2.42	0.269 - 6.375
	Male	16	116.63	22.07	0.49	0.242 - 0.741
P. megalops	Female	1	128.20	29.72	0.92	0.92
S. opisthopterus	Male	2	30.75	0.35	0.20	0.278 - 0.882
S. robustus	Female	39	65.74	4.68	7.30	0.625 - 12.458
	Male	24	50.84	1.81	0.42	0.132 - 0.769
	Unknown	9	54.97	2.81	N/A	N/A
S. beanii	Female	91	82.35	8.85	1.03	0.115 - 6.432
	Male	128	73.92	6.23	0.19	0.021 - 0.476
	Unknown	18	32.38	0.31	0.41	0.41
S. mizolepis	Female	3	90.77	10.10	1.11	0.357 - 2.380
	Male	9	77.35	7.42	0.57	0.027 - 2.188
	Unknown	2	37.15	0.52	N/A	N/A

Table 5.4. Results for ANOVAs run to test if there is a significant difference in standard length (mm) (response variable) between the two sexes for four melamphaid species

Melamphaes microps					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	4.86E+25	4.86E+25	35.235	3.89E-07
Residuals	45	6.20E+25	1.38E+24		
Poromitra crassiceps					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	3.95E+22	3.95E+22	7.3984	0.009245
Residuals	45	2.40E+23	5.34E+21		
Scopeloberyx robustus					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	5.19E+10	5.19E+10	85.864	2.25E-13
Residuals	63	3.81E+10	6.05E+08		
Scopelogadus beanii					
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Sex	1	4.74E+08	474098004	14.188	0.00021
Residuals	229	7.65E+09	33415781		

Table 5.5. Results for Shapiro-Wilk test for normality and Levene's test of homogeneity of variances for ANOVA run on the standard length data of males and females of four melamphaid species

	Shapiro-Wilk normality test		Levene's Test for Homogeneity of Variance		
	W	p-value	Df	F value	Pr(>F)
Scopelogadus beanii					
	0.9678	4.256e-05	1	0.1417	0.707
Melamphaes microps					
	0.9635	0.1481	1	0.0036	0.9524
Poromitra crassiceps					
	0.9316	0.008701	1	2.0398	0.1601
Scopeloberyx robustus					
	0.9073	0.0001362	1	1.3817	0.2442

S. mizolepis and *S robustus* were marginally non-significant (χ^2 = 3, df = 1, p females, ratios, and related percentage of the total population of each sex, as well as the p-values from the χ^2 tests are presented in Table 5.6 and the percentage of females, males and unknowns are presented in Figure 5.3. All specimens of *M. ebelingi*, *P. megalops* and *S. opisthopterus* were left out from analyses of sex ratios as these species were of a single sex only.

Averages and ranges of both male and female GSIs are given in Table 5.3. Females had a notably larger GSI compared to males and also exhibited a wider range of GSIs through the size classes. Gravid ovaries were often the largest organ in the body cavity, fully enclosing the rear of the stomach and the entire intestine. Female *P. crassiceps* (Df = 5, F = 2.0043, P = 0.1160) and *M. microps* (Df = 2, F = 0.0413, P = 0.99596) did not show any significant shift in GSI over the various size classes. Data for *P. crassiceps* and *M. microps* were normal (W = 0.9662, p-value = 0.4617 and W = 0.9438, p-value = 0.07334, respectively) and had homogeneous variances (Df = 5, F = 1.5751, P = 0.2067 and Df = 2, F = 0.1162, P = 0.8907, respectively). In both *S. robustus* (Df = 3, F = 12.585, P = 9.77e-06) and *S. beanii* (Df = 10, F = 9.3938, P = 8.113e-10), GSI did significantly change over the various size classes.

The 60-mm and larger size classes of *S. robustus* all had GSI values that were higher than those reported for smaller size classes (Table 5.7 and 5.8). This suggests that an increased proportion of energy was allocated for producing gonad tissues just prior to and within the 60-mm size class. The 90-mm and larger size classes of *Scopelogadus beanii* differed from the smaller size classes (85-mm and smaller). With respect to mean GSI for the size classes, an upward trend in the values initiated at the 85-mm size class

Table 5.6. Sex ratios for five species of melamphaid fishes represented as percent of total sample population and ratio of males to females. Chi-Square values indicate whether or not the ratios differ significantly from an even 1:1 ratio. df=1 for all χ^2 tests

Species	%Male	%Female	Sex Ratio (M:F)	p-value	χ^2 value
M. microps	17.80%	77.80%	1 : 4.4	3.83E-05	16.9535
P. crassiceps	34.80%	65.20%	1 : 1.9	0.03900	4.2690
S. robustus	33.30%	54.20%	1 : 1.6	0.05878	3.5714
S. beanii	54.00%	38.40%	1.4 : 1	0.01241	6.2511
S. mizolepis	64.20%	21.40%	3 : 1	0.08326	3.00

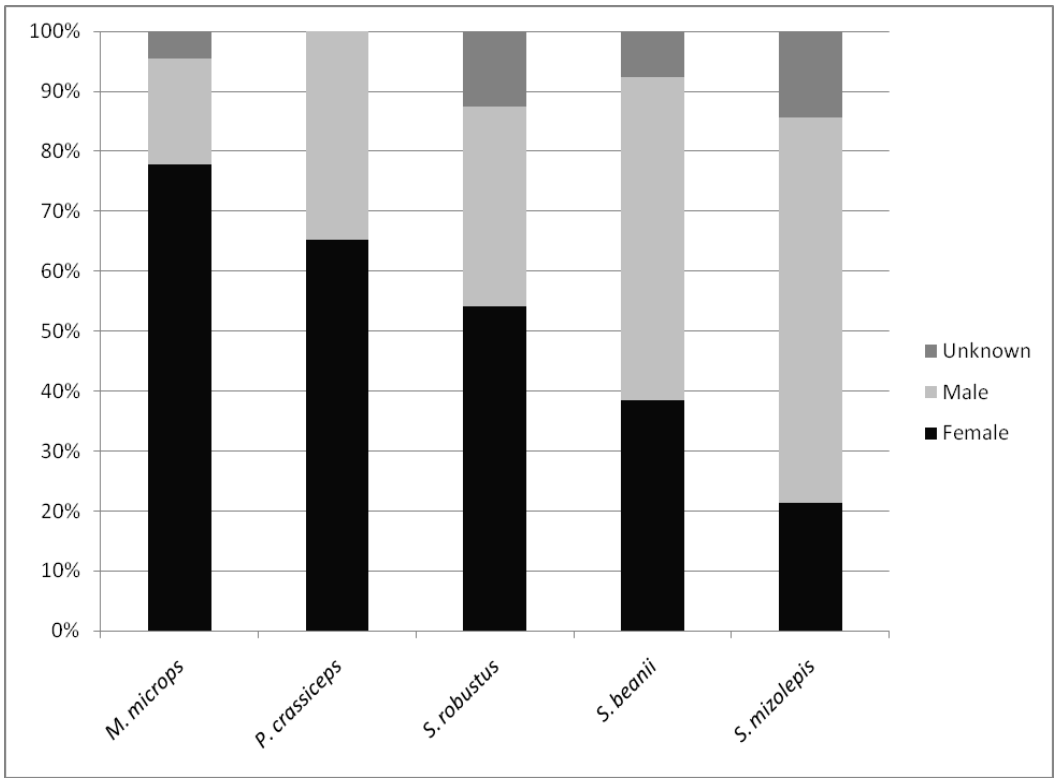

Figure 5.3. Percentage of females, males and unknowns for melamphaid species.

Table 5.7. List of size classes and their associated average GSI for *S. robustus* and *S. beanii*. Numbers in the size class titles indicate the length at which the 5-mm size class begins

Species	Size Classes	Average GSI
M. microps	SL80	2.162162
	SL85	3.967577
	SL90	4.732282
	SL95	4.107973
	SL100	4.192734
	SL105	3.794872
P. crassiceps	SL85	0.427553
	SL115	0.555957
	SL120	0.606602
	SL125	1.426506
	SL130	3.315464
	SL135	3.2946
	SL140	3.356347

Species	Size Class	Average GSI
S. robustus	SL35	1.016949
	SL40	0.625
	SL45	3.756906
	SL50	0.801688
	SL55	0.961538
	SL60	9.816196
	SL65	8.74116
	SL70	6.367295
	SL75	6.069277
S. beanii	SL35	0.483871
	SL40	0.439628
	SL45	0.232963
	SL55	0.530404
	SL60	0.235463
	SL65	0.304293
	SL70	0.350617
	SL75	0.362187
	SL80	0.382227
	SL85	0.521389
	SL90	1.194655
	SL95	1.623465
	SL100	2.002011
	SL105	3.515081

Table 5.8. Detailed ANOVA results for *Scopeloberyx* GSI as explained by size class, including individual size class significance and results from Shapiro-Wilk and Levene's tests.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
SL	3	165.98	55.327	12.585	9.77E-06
Residuals	35	153.87	4.396		

Adjusted $R^2 = 0.4777$

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.3764	0.9377	0.401	0.690579
60-mm Size Class	6.8788	1.4066	4.891	2.23E-05
65-mm Size Class	6.0123	1.0484	5.735	1.73E-06
70- to 75-mm Size Class	4.1512	1.1484	3.615	0.000936

Shapiro-Wilk normality test

W = 0.935 p-value = 0.02606

Levene's Test for Homogeneity of Variance

Df	F value	Pr(>F)
3	1.3304	0.2801

(Tables 5.7 and 5.9). This suggests that more energy begins to be alloted to gonad growth within the 90-mm size class.

DISCUSSION

The length-weight regression equations were all power functions with high R^2 values. These equations compare well with length-weight regressions found in other multi-species studies (Kohler 1994). The form of these equations suggest that melamphaids gain biomass slowly, up to a certain standard length, at which point they rapidly increase biomass. The inflection point is species-specific. Analysis of the length-weight plots and charts of average SL per species show that *S. robustus* is smaller than the other species and that it is one of the "dwarf" species of the family Melamphaidae (Keene 1987). Tests also confirmed that *Poromitra crassiceps* was larger than other species. All species except for the two *Scopelogadus* species exhibited sex ratios skewed towards more females than males. *Scopelogadus beanii* had a significantly larger male fraction. *P. crassiceps, Scopeloberyx robustus* and *M. microps* had significantly larger female fractions. The average female SL of all species was larger than that of the male SL, with the exception of *P. crassiceps*. Populations of fish species having more or larger females are common in the deep sea (Clarke 1983).

The results from *S. beanii* and *S. mizolepis* sex ratios correspond with those of Clarke (1983). This indicates that male-skewed sex ratios may be common to some melamphaid species. The species with the male dominated sex ratio could be region specific. If this is true, each melamphaid species would have separate habitats where they have differing sex ratios. In this case, melamphaids would also have separate

Table 5.9. Detailed ANOVA results for *Scopelogadus* GSIs amongst the various size classes, including individual size class comparisons and results from Shapiro-Wilk and Levene's tests.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
SL	10	34.100	3.410	9.3938	9.77E-06
Residuals	73	26.499	0.363		

Adjusted $R^2 = 0.5028$

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.92525	0.30125	-3.071	0.00299
45- to 55-mm Size Class	-0.19384	0.42603	-0.455	0.65047
60-mm Size Class	-0.6169	0.46017	-1.341	0.18421
65-mm Size Class	-0.26676	0.52178	-0.511	0.61072
70-mm Size Class	-0.12524	0.42603	-0.294	0.76962
75-mm Size Class	-0.13659	0.46017	-0.297	0.76744
80-mm Size Class	-0.09458	0.36895	-0.256	0.79841
85-mm Size Class	0.18137	0.35178	0.516	0.60771
90-mm Size Class	0.8983	0.33681	2.667	0.00942
95-mm Size Class	1.09436	0.32869	3.329	0.00137
100- to 105-mm Size Class	1.6139	0.36895	4.374	3.98E-05

Shapiro-Wilk normality test

W = 0.9862 p-value = 0.5092

Levene's Test for Homogeneity of Variance

Df	F value	Pr(>F)
10	1.4178	0.1897

feeding and breeding locations much like many marine mammals (Boyd et al. 1999; Clapham 2000). These separate feeding and breeding grounds could be species-specific to prevent interbreeding (just like eels and sea turtles have species specific lakes or beaches they use for breeding purposes; Bjorndal *et al.* 1983; Dekker 2000; McClenchan *et al.* 2006).

The high mean GSIs seen in some of the higher size classes of all species analyzed correspond with GSI values seen in other deep-sea fishes during their spawning seasons (D'Onghia *et al.* 1999; Figueiredo *et al.* 2003; Follesa *et al.* 2007; Ikejema *et al.* 2007; Porcu *et al.* 2010). The large GSIs coupled with the amount of fish collected from the larger "size classes," lead to the possibility that the ridge may be a site of aggregation for spawning adult melamphaid fishes.

CHAPTER 6

FEEDING HABITS OF THE DEEP-SEA FISH FAMILY MELAMPHAIDAE ALONG THE MID-ATLANTIC RIDGE

INTRODUCTION

Until recently, gelatinous zooplankton had been seen as an energetic "dead end" in the pelagic food web with little nutritional value to predators (Sommer *et al.* 2002; Nelson *et al*. 2002; Arai 2005). Traditionally, most deep-pelagic fishes were identified as either piscivores or crustacean planktivores (Sedberry and Musick 1978; Crabtree *et al.* 1991; Sutton *et al.* 1995). Recent studies have shown that gelatinous zooplankton have a higher energetic value than once thought and could play a more significant role in marine food webs (Kashkina 1986; Purcell and Arai 2001; Cartamil and Lowe 2004; Houghton *et al.* 2006). Mianzan *et al.* (1996) showed that 5% of the filled guts of 20 species of fish from the continental slope waters off Argentina contained ctenophores and other gelatinous material. Kashkina (1986) and Arai (1988) found that 89 species of epipelagic to mesopelagic fishes included coelenterates or salps in their diet. Gartner and Musick (1989) showed that the diet of one melamphaid, *Scopelogadus beanii*, consisted primarily of gelatinous zooplankton. They found that the majority of the gelatinous contents of the stomachs they studied were species of the family Salpidae (Thaliacea). One explanation as to why gelatinous zooplankton have previously gone unnoticed and understudied could be that gelatinous prey are rapidly digested into unrecognizable

remains and thus can be overlooked (Harbison 1998). Unrecognizable remains would give biased trophic data with an undue emphasis placed on non-gelatinous prey. With an increased knowledge of their energetic contents and their place in the pelagic food web, gelatinous zooplankton could prove to be an important link between upper and lower trophic levels.

Dietary change can occur over an individual's lifetime as well as daily, seasonally or with varying availabilities of certain prey (Mauchline and Gordon 1985). In order to fully encompass a species' dietary preference, all of these factors must be considered. Due to the nature of gelatinous zooplankton, feeding periodicity patterns are hard to determine. Gartner and Musick (1989) showed no consistent pattern in the number of stomachs containing food over the diel cycle and thus no discernable effect of time of day on feeding rate. With one of the largest melamphaid sample sizes in existence, taken over a large area, the MAR-ECO project provides a unique opportunity to observe changes in dietary pattern due to time, age or location.

Early theories about feeding in the deep sea stressed the need for an individual to be an opportunistic feeder, eating anything that they encounter because densities of prey in the deep are low when compared to shallow water areas (Ebeling and Cailliet 1974). These theories were shown to be generalizations by further data and have not been substantiated. The diet of most deep-sea fishes can change due to prey availability, the energetic value of the prey, and the sizes of the predator and prey themselves (Ebeling and Cailliet 1974). *Scopelogadus beanii* (Teleostei: Melamphaidae) was believed to be a generalist feeder that fed on a variety of small crustaceans, but recently this idea has been challenged by the discovery that the formerly labeled “unidentified tissues” are important

to its diet and most likely some type of gelatinous organism (Gartner and Musick 1989; Gartner *et al.* 1997). It was found that *S. beanii* feeds predominantly on gelatinous prey instead of small crustaceans (Mauchline and Gordon 1984; Gartner and Musick 1989; Gartner *et al.* 1997). The melamphaid diet was determined by comparing the ingested prey species with the available prey field. The ratio of ingested prey to available prey provides information as to whether or not melamphaid fishes display an opportunistic feeding style. The large sample size presented here describes the diet of *S. beanii* along the Mid-Atlantic Ridge, as well as the diets of the other biomass dominant species of the family Melamphaidae.

MATERIALS AND METHODS

Sample material for the dietary investigation was collected on Leg 1 of the MAR-ECO cruise aboard the Norwegian research vessel *G.O. Sars* along the northern Mid-Atlantic Ridge (from Iceland to the Azores), beginning 5 June and ending 3 July 2004. The northern MAR stretches from the southern coast of Iceland to the Azores (between 36°42'W - 25°57'W and 59°46'N - 38°37'N). The peaks of the ridge system rise from the surrounding abyssal plains and reach depths above 2000 m. The continuity of the ridge is broken in an area called the Charlie-Gibbs Fracture Zone (between 35°00'W - 32°00'W and 52°30'N - 52°00'N), which is a transverse fault in the otherwise linear MAR (Figure 6.1).

Samples were caught using a series of nets. Each net contained a different mesh size that selected for certain sized nekton (Heino *et al* 2010). Macrozooplankton, Åkra and Egersund trawls were used to collect samples along the MAR, their mouth size and door spread are listed in Table 6.1. Information about each net deployment is found in

Appendices 4-8. The Åkra trawl was outfitted with multiple cod ends making it possible to sample discrete depth strata.

The samples collected were frozen at sea, thawed at the Bergen Museum, fixed in a 10% formalin:seawater mixture and then stored in 70% ethanol. Each fish was taken from the ethanol, patted dry and weighed to the nearest 0.01 g to get a wet weight. Standard length (the length from the tip of the snout to the end of the caudal peduncle) of each specimen was measured to the nearest 0.01 mm using calipers. In order to aid in species identification, the first gill arch was removed from each fish on the right side and gill rakers were counted. Additional measurements of head length and body depth were taken as well as counts of dorsal, anal and ventral fin elements to further support species identification.

Gelatinous Zooplankton Collection

Data on the relative abundance of gelatinous zooplankton were gathered during the same 2004 cruise of the Norwegian research vessel *G.O. Sars*. Estimates of relative abundance for gelatinous zooplankton were collected both by net sampling and *in situ* observations using two ROVs (Hosia *et al.* 2008; Youngbluth *et al.* 2008). An Underwater Video Profiler (UVP) was also used to estimate the relative abundance of macrozooplankton (Stemmann *et al.* 2008). These two visual sampling techniques (ROV and UVP) were employed to augment the trawl data. Trawling for gelatinous zooplankton yields many specimens that are badly damaged and difficult to identify (Hamner *et al.* 1975; Båmstedt *et al.* 2003). For this study, UVP data was used to

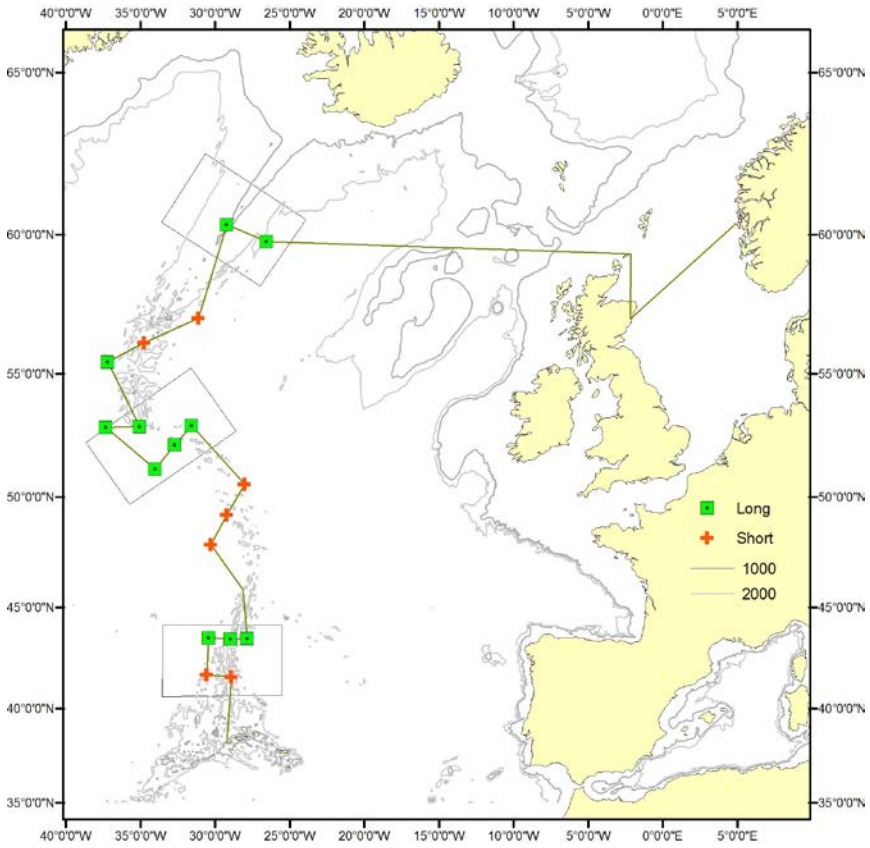

Figure 6.1. Mid-Atlantic Ridge including sample sites and bathymetry. Short and long station information found in Appendix 8. The boxes represent three areas of the ridge (from North to South): Reykjanes Ridge, Charlie-Gibbs Fracture Zone, and Azorean Zone.

Table 6.1. Trawl type broken down by size and door spread (de Lange Wenneck *et al.* 2008)

Trawl Type	Size	Door Spread	Mesh Size
Egersund	90 m – 180 m	150 m	50 mm stretched
Åkratrål	20 m – 35 m	110 m	22 mm stretched
Macrozooplankton	6 m x 6 m^2	N/A	6 mm x 6 mm stretched

estimate larvacean relative abundance in the the plankton in order to prevent error from net catchability and selectivity. Gelatinous zooplankton relative abundance data from the environmental prey field were used, with the findings from gut content analyses, in calculating Ivlev's electivity indices for each species studied.

The UVP is an array of equipment that includes two video cameras (Figure 6.2). The two cameras were synchronized with two stroboscopes to take pictures of zooplankton as they pass through an 8-cm thick, illuminated slab (Stemmann *et al.* 2008). The UVP is programmed to automatically take pictures (at a frequency of 12 Hz) as it descends to 1000 m. Each cast to 1000 m yields approximately 12000 images per camera (Stemmann *et al.* 2008). Physical and chemical properties of the water column were collected by the CTD, fluorometer, and nephelometer (Stemmann *et al.* 2008).

Figure 6.2. The Underwater Video Profiler and its mounted equipment

Dissection

For extraction of the gut contents, a "window" was cut in the right side of each fish by making an incision down the ventral midline from the isthmus to the anus. If the

body cavity opening was still too small, another incision was made from the beginning of the first incision moving dorsally and through the cleithrum. This window enabled separation of the internal organs from the mesentery sac that attaches the organs to the dorsal and anterior portions of the body cavity.

Once the body was opened, the mesenteries were cut with a pair of spring loaded microdissection scissors. After the excess connective tissue was cleared and the black esophagus was clearly visible, the esophagus was cut at the most anterior point allowing removal of the internal organs (Figure 6.3).

Figure 6.3. Internal organs of a melamphaid.

Gut Content Analyses

Identification of non-gelatinous prey items inside the stomachs and intestines was done by analyzing hard parts. Hard parts were taken out of the stomach and intestines and placed on a microscope slide or in separate vials, depending on size. All slides and vials were labeled with the specimen and station numbers. Slides and vials were kept as a personal reference collection for future dietary studies. Identification to the lowest taxonomic level possible was done by examining hard parts for diagnostic characters.

Identification of soft organisms was done by applying a methylene blue dye to the tissues. The dye stained the muscle bands found in the pelagic tunicate prey. If the gelatinous prey was neither Salpida nor Doliolida, then other diagnostic characters (e.g. nematocysts) were used to identify gelatinous prey to the lowest possible taxonomic level. Slides of gelatinous tissues were made in order to search for identifiable microscopic characteristics. Pictures of individual prey items were taken using a camera system mounted on a compound light microscope. These pictures were sent to experts of various zooplankton groups (Ostracods - Dr. Martin Angel, National Oceanographic Institute, Southampton, UK; Fecal pellets - Dr. Deborah Steinberg, Virginia Institute of Marine Science; Amphipods - Dr. Georgy Vinogradov, P.P. Shirshov Institute of Oceanology, Russia) in order to help identify down to the lowest possible level.

Microscopically determined prey data from this research will serve as a "ground-truth" for further molecular prey assessment. Methods for DNA bar-coding are currently being developed as a joint project between Dr. Ann Bucklin and Christopher Sweetman in order to identify gelatinous prey through specific DNA sequences. This molecular work will be the next step of any future trophic research on the family Melamphaidae.

Each stomach was graded on two scales, one that characterized stomach fullness and one that characterized the state of digestion of the items found in the stomach. Since gelatinous prey items are not rigid enough to distend the stomach as it becomes full, the fullness scale was instead based on the amount of space taken up by the prey inside the stomach. The different levels of stomach fullness are: zero = stomach was empty; one = stomach was 1 to 10 percent full; two = stomach was 10 to 50 percent full; three = stomach was 51 to 90 percent full; four = stomach was 90 to 100 percent full or all space

inside the stomach is filled by the prey items. The state of digestion of the prey inside the stomach was based on a scale (similar to the scale found in Albert 1995 and Filiz 2009) from one to three as follows: one = freshly ingested prey that was nearly whole and easily recognizable, two = prey went through some digestion and only parts of it remained intact, three = prey was digested over a longer period of time and was virtually unrecognizable.

Statistics

Ivlev's electivity index was used to measure the amount for selection of a particular prey taxon by each melamphaid species (Hinz *et al.* 2005; Islam *et al.* 2006; Ribeiro and Nuñer 2008). Ivlev's electivity index is defined as:

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)}$$

In the equation r_i represents the proportion of a certain food type consumed and p_i represents the proportion of this food type in the environment (Ivlev 1961; Alwany *et al.* 2003). Ivlev's electivity index relies heavily on both the extent of selectivity and the relative abundance of each prey item in the environment (Jacobs 1974; Gras and Saint-Jean 1982). Indices of selection, such as Ivlev's electivity index, have a series of assumptions inherent in their use. Assumptions of Ivlev's electivity index are (Manly *et al.* 2004):

- The distributions of the available resource units (prey types) do not change during the study period.
- Availability and resource selection probability do not change during the study period

- The population of resource units available to the organisms has been correctly identified
- The subpopulations of used and unused resource units have been correctly identified
- Organisms have free and equal access to all available resource units
- Resource units and organisms are sampled randomly and independently
- All animals have the same available resources
- An animal's selection of a resource is independent of selections made by all other animals

In using Ivlev's electivity index it is assumed that both the sampling methods and the environment sampled meet the above criteria. Information on zooplankton abundances for Ivlev's electivity index was obtained using data produced by other MAR-ECO researchers (Angel 1989; Vinogradov 2005; Gaard *et al.* 2008; Stemmann *et al.* 2008). Prey field information taken from these works must be seen as conservative estimations of average prey abundance along the entire ridge. In order to be used to calculate Ivlev's indices the dietary prey items and the prey field estimations must be standardized so that they are expressed with the same unit (e.g., volume of water sampled).

In order to further quantify which prey items are most important to these fishes, percent occurrence (%O) and percent of total numbers (%N) was calculated as well. Percent occurrence is defined as the ratio of the number of stomachs containing a specific prey item to the total number of full stomachs (Hyslop 1980; Bergstad *et al.* 2010). The formula for calculating percent occurrence is:

$$\%O = \frac{O_i}{O_{tot}} * 100$$

Where O_i = the number of stomachs in which prey category *i* occurs and O_{tot} = the total number of stomachs that contain a prey item (Hyslop 1980; Bergstad *et al.* 2010).

Percent of total numbers is defined as the ratio of the total number of a specific prey item to the total number of all prey items. The equation for calculating the percent of total numbers is:

$$\%N = \frac{N_i}{N_{tot}} * 100$$

Where N_i = the total number of prey item *i* found in all stomachs and N_{tot} = the total number of all prey items in all stomachs (Hyslop 1980; Bergstad *et al.* 2010). Using multiple calculations gives a clearer picture to the melamphaid diet (Hyslop 1980).

Prey items that were identified to species or genus level were treated separately from those prey items that could only be identified to subphylum or class to prevent over-emphasizing the contribution of any particular group or taxonomic level. This method was used for percent occurrence, but for percent of total prey items, individual species were treated separately and within the larger prey categories. This ensured that both the individual species and the larger groups were accounted for when describing their contributions to overall diet.

If it were possible, the Index of Relative Importance would have been calculated (Hyslop 1980; Sever *et al.* 2008; Cortes 1997; Morato *et al.* 1998). Unfortunately, percent weight calculations were not possible. Slides were needed to identify the prey items, making it impossible to individually weigh each item, which is required for analyses of percent contribution to total weight (Hyslop 1980). Volumetric estimates were not possible either, since a very small graduated cylinder would be needed to perceive any change in water volume (Hyslop 1980). In essence, items were too small to be able to identify and weigh individually in any accurate manner. Gelatinous material degrades faster than harder materials, often leaving only a fraction of the animal or a

piece of watery tissue, which lessens their apparent contribution to percent weight calculations (Arai 1988; Harbison 1998; Purcell and Arai 2001). Not being able to produce an accurate estimate for gelatinous prey weights skews weight data towards those prey items that are digested slower (Purcell and Arai 2001).

Intestine data were used to support the stomach data. The prey specimens from the intestine were only used for %N calculations and inclusion in the electivity index. The reason for this is the nature of intestinal data. Stomach data can be used to determine feeding periodicity, percent occurrence and many other qualitative factors about a fish's feeding habits. Stomach contents are assumed to all be taken at relatively the same time. This means that stomach contents can be seen as a "snapshot" of the prey environment, and thus can be compared against time periods, or other such variables in the environment to get a more complete understanding of the fish's diet. On the other hand, it is unknown if the intestinal load is from one stomach-full of food or multiple. It is assumed that all the food in the stomach and intestine represent a 24-h period of feeding (Hopkins *et al.* 1996) but it is unknown if this is true for those deep-sea species that aren't as effected by diel cycles. Intestinal data becomes more confused when taking into account the length of the melamphaid intestine. Long, meandering intestines, such as those found in the melamphaid fishes, are believed to be used by fishes that consume gelatinous prey or phytoplankton (Robison 1984; Harbison 1993; Purcell and Arai 2001). A winding intestine ensures that gelatinous prey stays in the gut longer in order to extract as many nutrients as possible from the prey (Harbison 1993; Purcell and Arai 2001). This means the contents of the intestine could be taken at different times, different locations, different depths, etc. Intestinal prey was also more digested than stomach

contents, which means that these prey items were harder to identify to species level, making more detailed analyses difficult (Hopkins *et al.* 1996). What is definitively known about the prey items in the intestine is that they were ingested at some point. Thus, expressing the total numbers of prey found in the intestine, without any further comparisons or analyses, minimized possible errors in order to best augment the data from the stomach.

RESULTS

In order to determine whether or not enough samples were examined for this trophic study, the number of specimens examined versus the cumulative number of new prey items were plotted. If these rarefaction curves plateau prior to the last specimens examined, this indicates that enough fish were studied to make finding new types of prey items in their stomach increasingly rare. If the graph does not plateau, it indicates that the sample size was likely insufficient. The graphs for the *Melamphaes, Poromitra, Scopeloberyx* and *Scopelogadus* genera are presented in Figure 6.4. Graphs for *Melamphaes, Scopeloberyx* and *Scopelogadus* all showed signs of a long plateau and the trend lines all appeared to level off. The graph for *Poromitra* had a plateau up to the final specimen, which contained three new prey types. The graph ended with an upward trend, indicating that more samples may need to be studied in order to be certain that enough stomachs were examined in order to accurately describe the *Poromitra* prey field. For all other genera, the graphs indicated that enough melamphaid stomachs were examined in order to ensure that the majority of their possible prey types were included in this research.

Melamphaes, *Poromitra*, and *Scopeloberyx* all had around 50% of their stomachs with no prey items inside them. *Scopelogadus*, on the other hand, had only around 27% of its stomachs empty. Of the stomachs that had contents within them, most of the prey items were moderately to fully digested. Very little of the prey items found in the stomachs were freshly ingested or showed little to no digestion.

A total of 306 prey items were found in 421 stomachs. Prey belonged to 40 prey categories (Table 6.2). Intestines contained a total of 827 prey items from 36 prey categories (Table 6.2). The large amount of prey in the intestine supported the idea that intestine data should be included in this study. Prey items in both the stomach and intestine were generally dominated by ostracods, amphipods, and tubes containing oval shaped fecal pellets,. Many of these prey items were not identifiable to species level because of the limited detail left on their bodies after digestion.

The counts for total number of each prey item should be seen as an underestimation. The process of counting total number of each prey item involved counting parts of the animal that occur in a known number on the body (two eyes, one furca, two gnathopods, etc.). Counts for oval pellets should be seen as a severe underestimate. The counts presented here only represent the presence or absence of oval pellets. It was difficult to determine if the multiple pellets all came from one continuous tube (organism) that was damaged during extraction or multiple tubes.

Tables 6.3 through 6.6 present the %N and %O of each prey item for the four genera of melamphaids. Figure 6.6 integrates the percent compositions from the major prey categories for all of the melamphaid genera studied. Oval pellets had high %N and %O in the stomachs and intestines of *Scopelogadus* and *Poromitra*, but were not as

significant in the diets of *Scopeloberyx* and *Melamphaes*. Crustaceans were an important part of all fish diets studied. Amongst the identified crustaceans, amphipods and ostracods had high %N and %O values in all genera except for *Melamphaes*. *Melamphaes* did have a higher concentration of chaetognath hooks in their stomachs and intestines. Figure 6.6 breaks down the larger crustacean group to show that Eucarida (euphausiids and decapods), ostracoda and amphipoda all contributed similar percentages to the total number of crustacea.

Furcae and second antennae were used to identify ostracods as they were often the last remaining pieces of the organism. These body parts indicate that most, if not all, ostracods were from the family Halocyprididae family in the subclass Myodocopa. Pictures sent to Dr. Martin Angel confirmed this assertion. Species indicated in the diets of each melamphaid genera were identified through correspondence with Dr. Angel and ostracod atlases provided in his associated work (Angel 2010). Ostracods represented about 9% of the total prey items found in the stomachs and intestines of all melamphaid fishes and about 18% of all crustaceans (Figure 6.6). Four ostracods were identified to species level while another five were identified to the genus level. The "lattice-work" carapace of *Boroecia borealis* was seen in more than one stomach, making it the most frequent ostracod found. Unfortunately, furcae and second antennae can only narrow observed prey items down to family level.

Amphipods were identified using gnathopods and the telson and uropods of their tail segment. Most species of amphipods were identified from a key (Vinogradov *et al.* 1996) and during a trophic workshop at the Virginia Institute of Marine Science (VIMS) held by Dr. Tracey Sutton. Amphipods made up around 12% of the total prey items

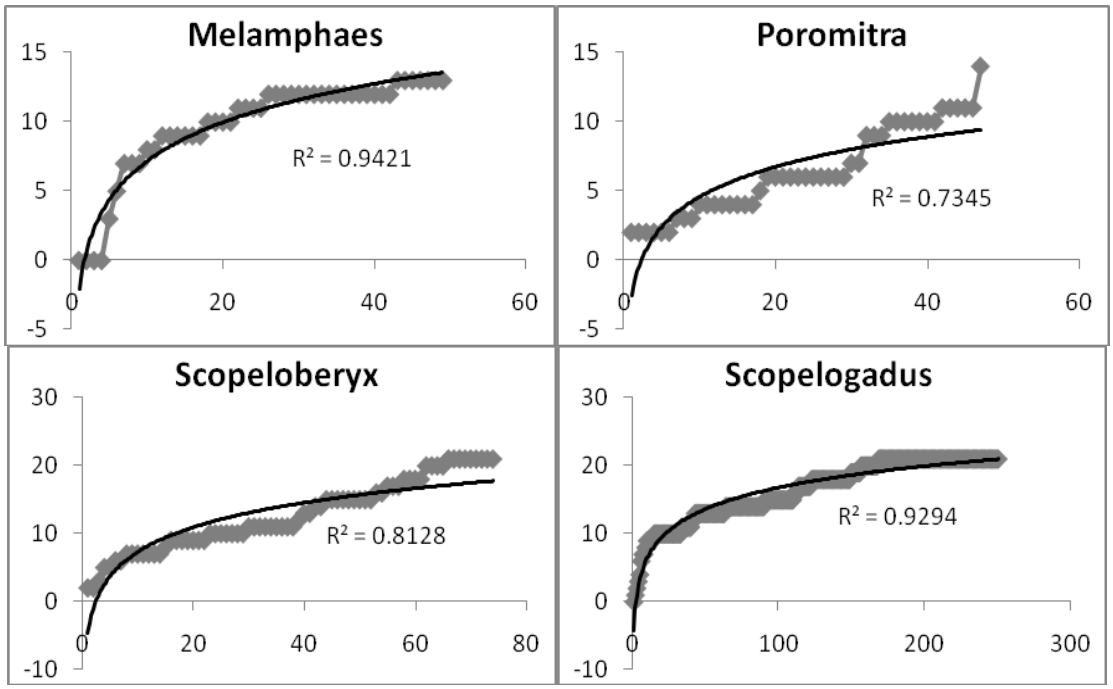

Figure 6.4. Number of stomachs examined versus the cumulative number of prey items found in the stomachs.

Table 6.2. Total stomach and intestine prey items found in all melamphaid species with counts and percent of total number of prey items

Stomach Prey Item	Number	%Total
Larvacean (pellets)	41	13.44%
Copepod pellets	4	1.31%
Scale	3	0.98%
Chaetognath hooks	13	4.26%
Diatoms	2	0.66%
Foram	1	0.33%
Nematocysts	2	0.66%
Spermatophore	1	0.33%
Digenean Trematode	7	2.30%
CRUSTACEAN	58	19.02%
Euphausiid/Decapod/Mysid	21	6.89%
Euphausiid	28	9.18%
Decapod/Mysid	1	0.33%
Decapod	2	0.66%
Caridean	2	0.66%
Copepod	25	8.20%
Calanoid Copepod	1	0.33%
Euchaeta type copepod	1	0.33%
Metridia brevicauda	4	1.31%
Ostracod	36	11.80%
Bathyconchoecia sp.	1	0.33%
Boroecia borealis	2	0.66%
Conchoecissa ametra	1	0.33%
Halocypria/Halocypris sp.	1	0.33%
Halocypris sp.	2	0.66%
Loricoecia loricata	1	0.33%
Orthoconchoecia atlantica	1	0.33%
Amphipod	26	8.52%
Hyperia sp.	1	0.33%
Hyperia spinigera	1	0.33%
Hyperiidean	3	0.98%
Hyperoche sp.	2	0.66%
Lanceola sayana	1	0.33%
Paraphronima gracilis	1	0.33%
Parathemisto abyssocum	1	0.33%
Parathemisto gaudichaudi	3	0.98%
Phronima atlantica	1	0.33%
Phronimella elongata	2	0.66%
Vibilia stebbingi	1	0.33%

Intestine Prey Item	Number	%Total
Larvacean (pellets)	172	20.80%
Tube w/ rhomboid pellets	14	1.69%
Copepod pellets	22	2.66%
Brown Flakes	171	20.68%
Scale	1	0.12%
Chaetognath hooks	22	2.66%
Diatoms	21	2.54%
Mollusc (bivalve)	1	0.12%
Nematocysts	9	1.09%
Juvenile Ophiuroid	1	0.12%
Digenean Trematode	2	0.24%
Nematode	4	0.48%
CRUSTACEAN	127	19.11%
Euphausiid/Decapod/Mysid	27	3.26%
Euphausiid	43	5.20%
Decapod/Mysid	1	0.12%
Decapod juvenile	1	0.12%
Decapod	1	0.12%
Copepod	18	2.18%
Harpacticoid copepod	1	0.12%
Ostracod	61	7.38%
Halocyprid sp.	1	0.12%
Archiconchoeccisa sp.	1	0.12%
Paramollicia sp.	1	0.12%
Amphipod	50	6.05%
Hyperietta sp.	1	0.12%
Hyperiidean sp.	2	0.24%
Paraphronima gracilis	1	0.12%
Parathemisto abyssocum	2	0.24%
Parathemisto gaudichaudi	4	0.48%
Phronima atlantica	7	0.85%
Phronima sedentaria	1	0.12%
Phronimella elongata	1	0.12%
Primno macropa	1	0.12%
Vibilia armata	2	0.24%
Vibilia sp.	32	0.12%

Table 6.3. Stomach contents of *Melamphaes* species with %N and %O for all prey items identified. %N is the total number of a certain prey item divided by all prey items. %O is the number of stomachs containing a prey item divided by the total number of stomachs that contain a prey item. The "total number for group" column represents the total number for those larger taxa (including the species or lower taxon groups handled individually)

Prey Item	Number	Total number for group	%N	%O
Larvacean (pellets)	1		2.04%	3.57%
Chaetognath hooks	10		20.41%	35.71%
Foram	1		2.04%	3.57%
Digenean Trematode	6		12.24%	32.14%
Crustacean	5	31	63.27%	7.14%
Euphausiid/Decapod	2	8	16.33%	14.29%
Euphausiid	5		10.20%	7.14%
Caridean	1		2.04%	3.57%
Copepod	9	10	20.41%	17.86%
Euchaeta type copepod	1		2.04%	3.57%
Ostracod	2		4.08%	3.57%
Amphipod	5	6	12.24%	21.43%
Hyperia sp.	1		2.04%	3.57%
Total	49			

Table 6.4. Stomach contents of *Poromitra* species with %N and %O for all prey items identified. %N is the total number of a certain prey item divided by all prey items. %O is the number of stomachs containing a prey item divided by the total number of stomachs that contain a prey item. The "total number for group" column represents the total number for those larger taxa (including the species or lower taxon groups handled individually)

Prey Item	Number	Total Number for Group	%N	%O
Larvacean (pellets)	3		11.11%	17.65%
Chaetognath hooks	1		3.70%	5.88%
Digenean Trematode	1		3.70%	5.88%
Crustacean	2	20	74.07%	11.76%
Euphausiid/Decapod/Mysid	3	5	18.52%	17.65%
Euphausiid	2		7.41%	11.76%
Copepod	5		18.52%	29.41%
Ostracod	3		11.11%	17.65%
Amphipod	1	7	25.93%	5.88%
Hyperiid	1		3.70%	5.88%
Hyperoche sp.	1		3.70%	5.88%
Lanceola sayana	1		3.70%	5.88%
Parathemisto abyssocum	1		3.70%	5.88%
Phronimella elongata	2		7.41%	5.88%
Total	27			

Table 6.5. Stomach contents of *Scopeloberyx* species with %N and %O for all prey items identified. %N is the total number of a certain prey item divided by all prey items. %O is the number of stomachs containing a prey item divided by the total number of stomachs that contain a prey item. The "total number for group" column represents the total number for those larger taxa (including the species or lower taxon groups handled individually)

Prey Item	Number	Total number for group	%N	%O
Larvacean (pellets)	3		4.76%	6.38%
Chaetognath hooks	1		1.59%	2.13%
Spermatophore	1		1.59%	2.13%
Crustacean	15	58	92.06%	29.79%
Euphausiid/Decapod/Mysid	8	13	20.63%	17.02%
Euphausiid	1		1.59%	2.13%
Decapod/Mysid	1	4	6.35%	2.13%
Decapod	2	3	4.76%	2.13%
Caridean	1		1.59%	2.13%
Copepod	3		4.76%	6.38%
Ostracod	11	16	25.40%	23.40%
Halocypria/Halocypris sp.	1		1.59%	2.13%
Halocypris sp.	2		3.17%	2.13%
Loricoecia loricata	1		1.59%	2.13%
Orthoconchoecia atlantica	1		1.59%	2.13%
Amphipod	6	11	17.46%	12.77%
Hyperia spinigera	1		1.59%	2.13%
Hyperiid	1		1.59%	2.13%
Hyperoche sp.	1		1.59%	2.13%
Paraphronima gracilis	1		1.59%	2.13%
Vibilia stebbingi	1		1.59%	2.13%
Total	63			

Table 6.6. Stomach contents of *Scopelogadus* species with %N and %O for all prey items identified. %N is the total number of a certain prey item divided by all prey items. %O is the number of stomachs containing a prey item divided by the total number of stomachs that contain a prey item. The "total number for group" column represents the total number for those larger taxa (including the species or lower taxon groups handled individually)

Prey Item	Number	Total number for group	%N	%O
Larvacean (pellets)	34		20.36%	28.33%
Copepod pellets	4		2.40%	3.33%
Scale	3		1.80%	2.50%
Chaetognath hooks	1		0.60%	0.83%
Diatoms	2		1.20%	1.67%
Globigerina sp.	1		0.60%	0.83%
Nematocysts	2		1.20%	1.67%
Crustacean	36	120	71.86%	30.00%
Copepod	8	13	7.78%	5.00%
Calanoid Copepod	1		0.60%	0.83%
Metridia brevicauda	4		2.40%	3.33%
Ostracod	20	24	14.37%	15.83%
Bathyconchoecia sp.	1		0.60%	0.83%
Boroecia borealis	2		1.20%	0.83%
Conchoecissa ametra	1		0.60%	0.83%
Amphipod	14	19	11.38%	10.83%
Hyperiidean	1		0.60%	0.83%
Parathemisto gaudichaudi	3		1.80%	0.83%
Phronima atlantica	1		0.60%	2.50%
Euphausiid/Decapod/Mysid	8	28	16.77%	6.67%
Euphausiid sp.	20	20	11.98%	13.33%
Total	167			

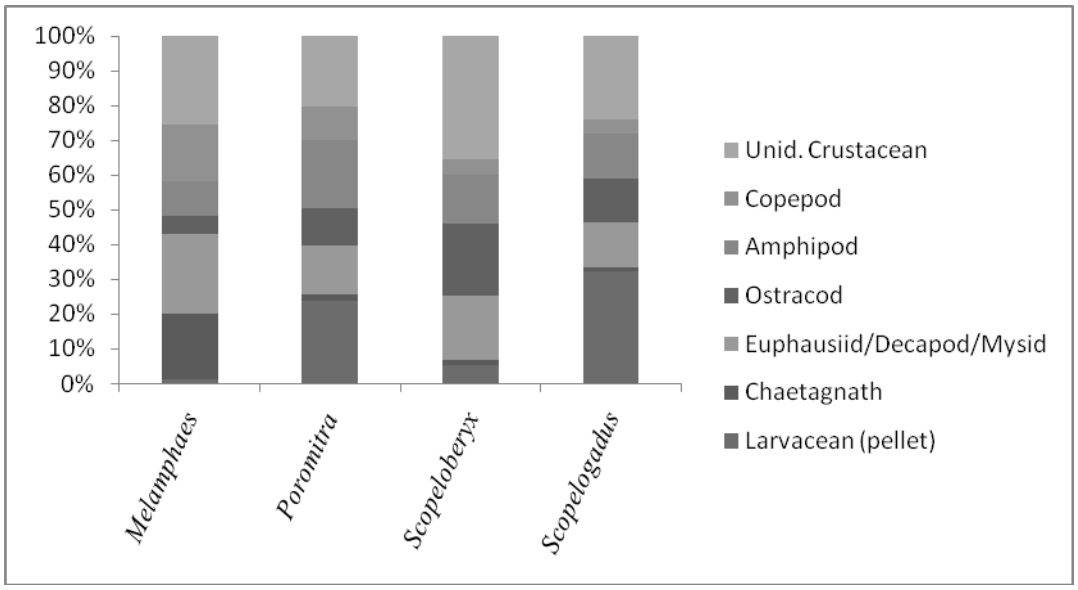

Figure 6.5. Percent composition of melamphaid diet. The categories presented here represent only the most common prey categories found in melamphaid digestive systems.

found in the melamphaid digestive tracts and around 24% of the crustacean prey (Figure 6.6). Eleven distinct amphipod species were identified using the characters described above. Thirty-six other amphipods were identified to genus level. This included one intestine that had 31 organisms that appeared to be a species of *Vibilia* (based on antennae shape). *Phronima atlantica* and *Parathemisto gaudichaudi* had the highest occurrence of all amphipods identified.

The "Euphausiid/Decapod/Mysid" group was the result of finding only setae on a number of slides. These long, slender setae were found in large bundles and are indicative of these "shrimp-like" crustaceans. The "Euphausiid/Decapod/Mysid" group made up around 11% of the total prey found in the melamphaid digestive system and roughly 20% of the total crustaceans. If ommatidia were present, they helped to narrow down the identity of the crustacean in question. More often than not, euphausiid ommatidia were found, or limbs with photophores (another characteristic of euphausiids) were found. Confirmed euphausiids were about 56% of the larger "Euphausiid/Decapod/Mysid" group. Based on size, location, depth and eye shape, the euphausiids found in the diets of melamphaid fishes are most likely small members of the genus *Euphausia* (most likely either *E. tenera* or *E. krefti*). The delicate parts used to identify species of euphausiids were usually damaged, making these identifications problematic. Decapods and mysids were found less frequently but one interesting occurrence was a decapod juvenile found in the intestine of *Melamphaes microps.* Eyes of this item were still on stalks and developing, helping to identify it as both a decapod and as a juvenile. If treated as a large group, these unidentified "shrimp" made up a large portion of the melamphaid diet, with euphausiids contributing the most to this group.

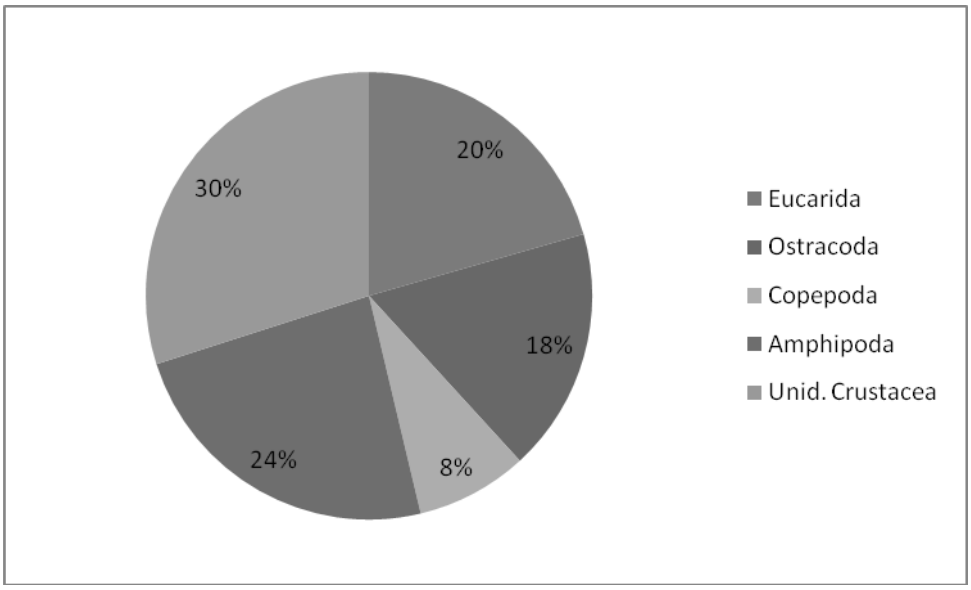

Figure 6.6. Percent composition of each major crustacean group found within the gut.

Copepods were identified by tail and leg segments and body size and shape at the VIMS trophic workshop. Copepods were only 4% of the total prey items and 8% of the crustaceans (Figure 6.6). Only a few full bodied copepods were found and identified as *Metridia brevicauda.* Unfortunately, many of the crustacean prey found in the stomach and intestine had undergone significant digestion, including the copepods. This often would leave unremarkable setae, appendages or molar processes that did not help in identifying these prey items any further. Though it is clear that much of the melamphaid diet consists of crustacean prey, finer level analyses of specific crustacean classes were often difficult.

Fecal pellets also played a large role in the diets of melamphaids. Three separate shapes of pellets were found. According to Wilson *et al.* (2008) oval shaped pellets are most likely the fecal pellets of larvaceans. These pellets were found both free floating in the prey field on the slides or incased in a clear tube that was most likely the remains of the larvacean digestive tract. Larvacean pellets made up around 19% of the total prey items identified but were primarily found in *Poromitra* and *Scopelogadus* digestive tracts. Small circular pellets are produced by copepods and were found in bunches of around 15 or more. Copepod pellets were again found primarily in the *Scopelogadus* diet and comprised about 2% of the total prey items identified. The rhomboid shaped pellets were the least certain as they could be salp pellets or pieces of a larger fish pellet. Rhomboid pellets did not occur quite as frequently as the other two pellet shapes. The large number of stomachs and intestines containing these different shaped pellets indicated that these pellets, or the animals that produced them, are important dietary items for the melamphaid fishes.

As mentioned before, the diet of *Melamphaes* had a higher concentration of chaetognath hooks in their stomach and intestine than any of the other melamphaid species (about 20% of the total prey found in *Melamphaes* digestive systems). Chaetognaths cannot be identified from their hooks (Annelies Pierrot-Bults, personal communication) and must be left as a larger, general prey category.

One of the more difficult prey items to identify (mostly in the intestines) was the unidentified "brown flakes". There are several different possibilities as to the source of these flakes: A.) They could be pieces of a broken up salp pellet [though they do not have the physical features of the pellet described in Wilson *et al.* (2008)]; B.) They could be pieces of calcification from preservative; C.) They could be the severely digested remnants of a larvacean "house"; or D.) They could be the beginnings of the formation of a fecal pellet from the fish itself (though discovery of these brown flakes in the stomach make this the least likely scenario). Whatever they may be, they occurred quite frequently in the intestines of all fishes.

Other prey items occurred less frequently as seen in Table 6.2. Included in this group of lesser prey items are a juvenile ophiuroid, a bivalve, a squid beak, foraminifera, diatoms, scales and nematocysts. Though they are not "prey," digenean trematode and nematode parasites were also found in stomachs and intestines of multiple species of Melamphaidae

DISCUSSION

As discussed in Gartner and Musick (1989) and Gartner *et al.* (1997), *Scopelogadus* does seem to feed on gelatinous zooplankton. Data from this study differs in that it appeared that they eat larvaceans instead of salps. Oval pellets that were most

likely larvacean fecal pellets were found "free floating" and in small clear tubes. This indicates that the fish most likely was eating both the larvaceans and their fecal pellets. The difference seen between these two studies can most likely be attributed to the tendency of gelatinous zooplankton to rapidly wane and bloom (Silver and Bruland 1981; Heron *et al* 1988; Morris *et al.* 1988). *Scopelogadus* most likely takes advantage of a gelatinous bloom and feeds on whichever gelatinous plankton is most abundant in their habitat at that certain time. Though these two studies do differ in the species found in their respective diets, they both agree that gelatinous zooplankton are a major component of the *Scopelogadus* diet (Table 6.7). It is also important to note that the total number of larvaceans was based on presence or absence of their pellets and should be seen as an extreme underestimation of their abundance in the *Scopelogadus* diet. The concentration of these gelatinous zooplankton was probably much higher than the numbers presented here, but there was no sure way to determine whether there was one or more larvaceans when they were encountered. It seems that the largest, most dominant species of melamphaids take advantage of this gelatinous food source and this may contribute to their dominance in the mesopelagic zone.

Another indicator of gelatinous zooplankton in the stomach and intestines of *Scopelogadus* was the presence of copepod pellets. The fact that these pellets occurred in groups, often surrounded by a net of tissue, indicates a gelatinous predator that has used its mucous net to gather pellets of crustaceans (Silver and Bruland 1981). Though these small crustacean pellets do not often descend to the mesopelagic zone as detritus, the evidence of clustered pellets such as this indicate that a gelatinous intermediary may be

Table 6.7. Electivity (E) of each species for 4 major prey groups. Negative number indicate that the melamphaid does not select that particular prey item (values closer to -1 means that the melamphaid actively selects against that item); positive numbers indicate that the melamphaid actively selects that prey item (the closer the value is to +1, the stronger the selection)

	Melamphaes E	Poromitra E	Scopeloberyx E	Scopelogadus E
Appendicularian	-0.68	0.59	0.03	0.69
Copepod	-0.60	-0.72	-0.83	-0.87
"Shrimp"	0.30	0.11	0.34	0.10
Chaetognath	0.84	-0.08	-0.08	-0.40

extremely important in the sinking of energy into deeper waters (Silver and Bruland 1981; Robison *et al* 2008).

Certain amphipods have been shown to be symbiotically connected to gelatinous zooplankton (Laval 1980; Gasca and Haddock 2004). Though amphipods generally associate with salps and not larvaceans, there is still a possibility that some of these amphipods were ingested along with larvaceans (Madin and Harbison 1977; Harbison *et al.* 1977; Gasca and Haddock 2004). The fact that amphipods occurred in the diet of the smaller melamphaids (that did not contain a high number of larvacean pieces) indicates that these fishes at least feed on independent amphipods to some degree. These crustaceans (amphipods included) can be seen as supplementary diet for *Scopelogadus* (Gartner and Musick 1989; Gartner *et al.* 1997; Houghton *et al.* 2006). Though it has been shown that gelatinous prey does contain high tissue density and nitrogen content (Heron *et al.* 1988), data suggests that *Scopelogadus* may be a focused gelatinous zooplanktivore employing an opportunistic supplementary diet (Gartner and Musick 1989; Gartner *et al.* 1997).

Though it is common to find relatively high amounts of euphausiids, decapods and mysids in the diets of mesopelagic fishes (Sameoto 1988; Shreeve *et al.* 2009; Bergstad 2010), the high ostracod and low copepod composition was unusual (Sameoto 1988; Shreeve *et al.* 2009; Bergstad 2010). If more than just a few unremarkable appendages were left in many of the slides, I would predict that the numbers of amphipods and "shrimp" (euphausiids, decapods and mysids) would be even higher than they appear. More "shrimp" and amphipods would make the low number of copepods even more remarkable. In conjunction, the high amount of chaetognaths in the diet of

Melamphaes is not common amongst deep-sea fishes and is more commonly the prey of smaller predators such as polychaete worms (Rakusa-Suszczewski 1968; Jordan 1992; Feigenbaum 1979). It is also important that the parasites (Digenean trematodes) found in the stomachs of some melamphaids (in particular the *Melamphaes* species) have been shown to have chaetognath intermediaries, suggesting that the melamphaids were infected by these parasites upon eating chaetognath prey (Pearre 1979). All of this indicates that melamphaids feed on more than one underutilized food source (gelatinous zooplankton, ostracods and chaetognaths).

The dominance of the melamphaid fishes over the Mid-Atlantic Ridge is most likely due to the fact that they have filled some vacant niches in the ridge's ecosystem. The diet of the melamphaids indicates that their success may be due to their ability to feed on prey items that not many other higher level predators are using. By feeding on ostracods, gelatinous zooplankton and chaetognaths (and supplementing this diet with more traditional amphipods and "shrimp") melamphaids limit their interspecific competition for food and increase their survivability in this unique environment.

CHAPTER 7

SYNTHESIS AND FUTURE RESEARCH

INTRODUCTION

The goal of this dissertation was to provide much needed information on a poorly studied, but dominant family of fishes from the Mid-Atlantic Ridge. Trophic data, reproductive data and growth data were analyzed to better understand the ecology of an important deep-pelagic fish family. The data collected here represents the largest collection of information on this family of fishes in over 20 years, and is the first insight into their interactions in a pelagic ecosystem over a mid-ocean ridge system. This final chapter aims to summarize the data and information that has been collected during this dissertation research, as well as incorporate areas where more research is needed.

TAXONOMY AND SYSTEMATICS

Key to the Species

The key to the species of fishes in the family Melamphaidae represents the first comprehensive key in over 20 years (Ebeling 1962; Ebeling and Weed 1963; Keene 1987). This key incorporates species descriptions that have been published since the last key and, as of yet, have not been included in a full key to the family. The key also represents an amalgamation of counts and measures used in several different keys, in order to better understand what physical characteristics differentiate the species of the

family. Finally, it also incorporates corrections to existing ranges of counts and measures based on personal research and species identifications.

It is important to note that as this key was being constructed, research on individual genera is being done by Kotlyar in Russia (Kotlyar 2004 a-c; 2005; 2008 a-b; 2009 a-c, 2010). It was decided not to include the new species described in these works because they have not been analyzed nor scrutinized fully. Kotlyar's works do not include statistical analyses of taxonomic characters and often are limited to a type specimen to compare against larger collections of established species. This is not to say that Kotlyar's works are incorrect, just that more time and review needs to be done regarding these new species in order to confidently include them into a comprehensive key.

New Species and Taxonomy

This dissertation described two possible new species that coincide with the unpublished descriptions by Keene (1987). *Scopeloberyx americanus* and *Melamphaes indicoides* were both included in Keene's Ph.D. dissertation, but since they were not published, these species are still classified as undescribed. These species have specific physical characteristics that separate them from the other closely related species of the family. On the other hand, *Scopelogadus mizolepis* subspecies were reduced to a single species. That these two supposed subspecies have overlapping habitat ranges and lack differing characteristic counts and measures suggest that they are most likely morphotypes of a single species.

The descriptions of the fishes examined from the National Museum of Natural History follow the same format as the descriptions found in Keene (1987) and the Kotlyar

works (2004 a-c; 2005; 2008 a-b; 2009 a-c; 2010). In order to validate the possible new species, more analysis must be done to the data comparing the counts and measures of the new species with the established species. Another important future step in this taxonomic research will be to analyze the new species described in the works of Kotlyar (2004 a-c; 2005; 2008 a-b; 2009 a-c; 2010). In these publications, Kotlyar describes several new species. I have done an initial comparison of these new species to the established species and the results were equivocal. Some of these "new species" could very well be valid but others appeared to represent extensions of the existing character ranges for accepted species.

Since this study only looked at some of the numerically dominant fishes of the family there still is a need for taxonomic research on the rest of the species of the genera *Poromitra, Melamphaes* and *Scopeloberyx* genera. *Sio* was not looked at in this study because, though Keene discussed this genus from the Ocean Acre off Bermuda, it is mostly a Pacific species. Keene (1987) described a new *Sio* species in his unpublished dissertation, which indicates that this genus must undergo a review in any future taxonomic research as well. Many more taxonomic issues and complications still remain to be studied within the melamphaid species (Appendix 2).

DISTRIBUTION

The abundance and biomass data analyzed for this dissertation revealed that the melamphaid fishes represent a large percentage of the deep biomass maximum described by Sutton *et. al.* (2008). The top four most abundant melamphaid fishes comprise about 11% of the total biomass and about 2% of the total number of fishes caught between 0-3000 m along the MAR. These results indicate that the melamphaid fishes are not only

an important contributor to a unique deep biomass maximum but also an important component of the MAR ecosystem.

Melamphaid fishes were most abundant between 750-1500 m. The melamphaid biomass maximum occurred 1500-2300 m which coincides directly with the deep biomass maximum described by Sutton *et al.* (2008). The offset of the melamphaid biomass maximum from their abundance maximum indicates that larger fish are found at a slightly deeper depth than smaller fishes and "dwarf" species, which confirms the data found in Ebeling and Cailliet (1974). The data collected for this dissertation represented a unique opportunity to study the melamphaid assemblage over the MAR at discrete depth intervals, but condensing the size of the depth ranges studied would aid in identifying the precise depths of the melamphaid abundance and biomass maxima.

Cluster analysis revealed that there were five distinct groups of melamphaid fishes along the MAR. These groups were distinguishable from one another at about 14% similarity. Groups were characterized by depth zone and species, which further supports the findings of Ebeling and Cailliet (1974) who said that different-sized species can be found at different depths.

Species composition shifted dramatically from the northern border to the southern border of the anticyclonic anomaly described by Søiland *et al.* (2008). This observation was supported by the results of the cluster analysis, which found the assemblages on the southern border of this anomaly to be distinct from those north of it. Though eddies are not a permanent feature, they could suggest the presence of a warm core ring (Joyce and Wiebe 1983). Warm core rings have been shown to trap and transport plankton and micronekton (Joyce and Wiebe 1983; Wiebe *et. al* 1985). A warm core ring could have

transported *Scopelogadus mizolepis* beyond its usual distribution center and into the habitat range of *Scopelogadus beanii*.

Future research studying biomass and abundances along the MAR during different months is still needed. Large scale shifts in melamphaid distribution relative to seasonal changes would provide details on the seasonal shifts in abundance and biomass. Coupling these shifts with changes in GSI would provide a better understanding of what role the MAR plays in the life-cycle of the melamphaid fishes

Comparisons to other locations would provide a better understanding of how these abundance and biomass values relate to those from other areas. Specifically, studies directly off the MAR, to the east and west of the ridge would give a direct comparison for the values found along the ridge. If the MAR is truly an aggregation point for the melamphaids then it would be expected that abundance and biomass values along the ridge would be higher than those on either side of the ridge. Another very interesting comparison could be to study these fishes in a similar environment in the Pacific Ocean, particularly along the East Pacific Rise and the Pacific-Antarctic Ridge (and all the smaller ridge sections associated with this system). Though not similar in all aspects, a comparison to a Pacific mid-ocean ridge system could be invaluable in understanding what role ridge systems play in melamphaid assemblages. This comparison would also allow for a better understanding of just how unique the MAR is to all other pelagic ecosystems.

Studying other locations would also allow for further analysis of melamphaid "grouping" in certain ecosystems. The current study showed that melamphaids grouped based on depth and species and it is possible that these groups would be widespread at the

specific depths. If cluster analyses reveal that assemblage structure in these new study areas differs from that found along the MAR, what factors bring about this difference? Do the depth zones associated with each species shift downwards or upwards in non-ridge associated ecosystems? Multivariate analyses of various assemblages would lead to a better understanding of what factors induce melamphaid species to form different assemblage groups as well as what contrasting characteristics of distinct ecosystems cause changes to the generalized assemblage patterns found in this study.

REPRODUCTION AND GROWTH

Statistical tests revealed that *Melamphaes microps* and *Poromitra crassiceps* had sex ratios significantly skewed towards having more females than males, while *Scopelogadus beanii* had a ratio significantly skewed towards males. The *S. beanii* sex ratios were the expected result given the data collected by Clarke (1983). However, sex ratios like those found in *M. microps* and *P. crassiceps* populations agree with what are considered "normal" sex ratios of the deep sea (Clarke 1983). All species except for *P. crassiceps* had significantly larger females than males, which also is considered typical for deep-sea environments such as the MAR (Clarke 1983). Specimens of a particular species with unidentified sex were significantly smaller than males and females of the same species, except in *Scopeloberyx robustus*.

Tests revealed that *P. crassiceps* was significantly larger than all other species and that *S. robustus* was significantly smaller than all other species. The results for *S. robustus* confirm that this species is one of the "dwarf" species of the family Melamphaidae. However, all species did show similar growth curves and length-weight regression equations. Regression equations for the melamphaid fishes are similar to

those found in other multi-species studies (Kohler 1994). These length-weight regressions represent a significant contribution for future research on possible predators of melamphaids or to estimate melamphaid biomass in other populations.

S. robustus and *S. beanii* showed a significant relationship between female Gonadosomatic Index (GSI) and size. Using Tukey tests comparing each size group to one another, it was determined that *S. robustus* begins significant gonad growth within the size class beginning at 55 mm and *S. beanii* begins significant gonad growth at 85 mm. The high GSI's for the larger individuals of all species are comparable to values found for other deep-sea species during their spawning season (D'Onghia *et al.* 1999; Figueiredo *et al.* 2003; Follesa *et al.* 2007; Ikejema *et al.* 2007; Porcu *et al.* 2010). This suggests that the individuals of the larger size classes had gonads that are ripe for spawning.

Finally, comparisons to melamphaid fishes in other ecosystems would allow for a better understanding of the reproductive information presented in this study. Comparison to an open pelagic system would be beneficial, in particular a study of the reproductive characteristics from areas east or west of the ridge. Until other data can be collected from other areas, the data presented in this dissertation represent an invaluable significant reference point for any future studies concerning the family Melamphaidae.

TROPHIC ECOLOGY

Studies located at differing ecosystems would provide data that could be compared to trophic data found in this study. In particular, comparisons of *Scopelogadus*' diet fluctuates with different gelatinous zooplankton. Much larger *Poromitra* specimens were stored at the Bergen Museum, but not analyzed in this study due to hesitance of

destruction. A study of these larger *Poromitra* would provide information about whether these larger fishes utilize the available gelatinous zooplankton more than their smaller counterparts.

The next step in completing a pelagic food web is to identify which predators eat melamphaids. This would give a better view of how energy flows through this family of fishes and their contribution to a pelagic food web. This work established that melamphaids seem to be important in importing energy from the upper pelagic zones, but these fish then contribute back to larger pelagic predators of the photic zone (*Thunnus* sp., Istiophoridae, etc.) or disseminate their nutrients amongst higher level deep-sea predators. Initial information on trophic levels based on stable isotope data have been produced for melamphaids as well as other deep sea fishes (Stowasser 2009; Hoffman and Sutton 2010). Initial results show that melamphaids have an isotopic trophic level of around 3.8 (based off the molar ratio of $\delta^{13}C$: $\delta^{15}N$), which is consistent with values for mesozooplanktivores such as the melamphaids (Keough *et al.* 1996; Hoffman and Sutton 2010). Further investigation into the stable isotopic ratios of the melamphaid fishes could provide further information into their trophic relationship to the benthic environment of the ridge or the surrounding pelagic environment (Stowasser *et al.* 2009). Insight into the nutrient flow to and through the melamphaid fishes could give further information on their utilization and uptake of the nutrients provided by their prey and their position in the pelagic food web along the MAR.

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APPENDICES

APPENDIX 1

Listed below are the specimens examined from the two museum collection. Those lots denoted with a USNM prefix are from the Natural Museum of Natural History collection in Washington, DC and those listed with a ZMUB prefix are MAR-ECO samples from the Bergen Museum in Bergen, Norway. Samples are listed with catalog number followed by latitude and longitude of the station where the samples were caught, the depth of the trawls and the number of fish examined from each lot. For uncataloged MAR-ECO samples their MAR-ECO ID number is listed (ME number) followed by the station number, latitude and longitude, depth of trawl, size range and number of specimens.

Melamphaes sp. -- USNM 317188, 34°10' N 75°27' W, 2908-2919m, 1.

Melamphaes indicoides -- USNM 249739, 32°25' N 64°14' W, 0-760m, 1; USNM 249740, 32°08' N 63°55' W, 0-660m, 1; USNM 249741, 32°11' N 64°00' W, 0-780m, 1; USNM 249742, 32°14' N 64°20' W, 0-800m, 1; USNM 249743, 32°10' N 63°53' W, 0-760m, 1.

Melamphaes ebelingi -- ZMUB 17476, 52°58' N 34°38' W, 815-1750m, 1; ZMUB 17478, 52°45' N 35°57' W, 1800-2015, 3.

Melamphaes microps -- ZMUB 17471, 60°21' N 28°25' W, 850-1260m, 1; ZMUB 17472, 60°18' N 28°25' W, 744-1302m, 2; ZMUB 17474, 56°17' N 34°31' W, 800-1050m, 1; ZMUB 17476, 52°58' N 34°38' W, 815-1750m, 3; ZMUB 17478, 52°45' N 35°57' W, 1800-2015, 22; ZMUB 17481, 51°22' N 33°28' W, 236-678m, 1; ZMUB

17484, 52°33' N 31°53' W, 805-1774m, 4; ZMUB 17485, 52°54' N 30°35' W, 820-1837m, 5; ZMUB 17486, 50°24' N 27°30' W, 1810-2370m, 4; ZMUB 17492, 42°41' N 30°12' W, 800-1800m, 1; ZMUB 18613, 53°05' N 34°36' W. 680-1181m, 1.

Poromitra crassiceps -- ZMUB 18577, 56°19' N 34°23' W, 0-173m, 1; ZMUB 18613, 53°05' N 34°36' W. 680-1181m, 1; ZMUB 18662, 52°45' N 35°57' W, 1800-2015m, 3; ZMUB 18756, 50°21' N 27°31' W, 850-1800m, 1; ZMUB 18776, 49°34' N 28°24' W, 1528-2338m, 1; ZMUB 18792, 49°17' N 28°40' W, 1800-2230m, 2; ZMUB 18795, 49°15' N 28°41' W, 800-1800m, 2; ZMUB 18839, 42°54' N 27°45' W, 2202-2295m, 1; ZMUB 18842, 42°53' N 27°44' W, 1; ZMUB 18861, 42°49' N 27°50' W, 1810-2400m, 11; ZMUB 18918, 42°47' N 29°28' W, 810-1800m, 1; ZMUB 18937, 42°41' N 30°12' W, 800-1800m, 8; ZMUB 18983, 41°34' N 29°55' W, 1800-2000, 13.

Poromitra crassiceps complex -- USNM 296985, 07°32' N 20°54'W, 0-1300m, 1; USNM 301324, 34°00' S 80°36' W, 0-4914m, 1; USNM 301326, 41°05' S 74°54' W, 0-603m, 1.

Poromitra megalops -- ZMUB 18918, 42°47' N 29°28' W, 810-1800m, 1.

Scopeloberyx americanus (paratypes)-- USNM 247399, 33°05' N 64°40' W, 0-1920m, 1; USNM 249714, 32°10' N 64°08' W, 0-1710m, 1; USNM 249736, 32°04' N 63°45' W, 0-1500m, 2; USNM 249738, 32°13' N 63°42' W, 0-3500m, 1; USNM 249782, 32°27' N 64°17' W, 1494-1524m, 1; USNM 249783, 31°57' N 63°47' W, 1488-1555m, 1; USNM 266683, 32°27' N 64°17' W, 1504-1536m, 1; USNM 324745, 800-900m, 1.

Scopeloberyx opisthopterus -- ZMUB 18842, 42°53' N 27°44' W, 1; ZMUB 18929, 42°43' N 30°13' W, 1800-2300m, 1.

Scopeloberyx robustus -- USNM 341553, 25°21' N 91°02' W, 1725-1750m, 1; USNM 380330, 5°30' S 16°28' W, 0-1900m, 2; USNM 380331, 1°04' N 18°22' W, 0-2100m, 2; USNM 380332, 7°32' N 20°54' W, 0-1300m, 2; ZMUB 18689, 52°32' N 31°49' W, 1821-2800m, 10; ZMUB 18753, 50°24' N 27°30' W, 1810-2370m, 6; ZMUB 18877, 42°49' N 27°53' W, 829-1770m, 6; ZMUB 18929, 42°43' N 30°13' W, 1800-2300m, 46; ZMUB 19009, 41°30' N 28°27' W, 1980-2042m, 2.

Scopelogadus beanii -- uncataloged samples: ME 0099, 8, 56°19' N 34°17' W, 1249-1330m, 87.34-98.73mm, 8; ME 0107, 4, 60°19' N 28°21' W, 200-850m, 38.54-93.50mm, 26; ME 0417, 2, 59°54' N 25°45' W, 370-750m, 38.12-94.59mm, 40; ME 5511, 26, 47°50' N 29°13' W, 600-825, 20.37-48.13mm, 32; ME 6203, 18, 52°34' N 31°58' W, 0-743m, 54.23-105.15mm, 97; ME 7597, 36, 41°14' N 28°14' W, 800-1800m, 46.27-105.75mm, 5; ME 7613, 34, 41°31' N 29°55' W, 800-1800m, 95.70-98.10mm, 2; ME 14533, 20, 52°51' N 30°33' W, 0-806m, 48.99-91.42mm, 9; ME 14595, 56, 51°45' N 29°33' W, 1872-1950m, 46.20-102.16mm, 18.

Scopelogadus mizolepis bispinosis -- USNM 398145, 10°35' S 83°32' W, 0-750m, 12

Scopelogadus mizolepis mizolepis -- uncataloged samples: ME 6203, 18, 52°34' N 31°58' W, 0-743m, 59.14-100.57mm, 10; ME 7613, 34, 41°31' N 29°55' W, 800-1800m, 35.10-39.20mm, 3; ME 14533, 20, 52°51' N 30°33' W, 0-806m, 50.38mm, 1.

APPENDIX 2

Notable museum specimens of the Melamphaidae available for monographic research. Acronyms: MCZ – Museum of Comparative Zoology, Harvard, Department of Ichthyology; SIO – Scripps Institution of Oceanography Marine Vertebrates Collection; USNM – Smithsonian National Museum of Natural History, Division of Fishes; CMarZ – Census of Marine Zooplankton (2006 Sargasso Sea cruise); NHM – Natural History Museum, London; ZMUB – Zoological Museum, University of Bergen. Highlighted rows are those lots yet to be adequately identified. Names in bold represent valid species

Species	MCZ	SIO	USNM	CMarZ	NHM	ZMUB	Total
Melamphaes acanthomus		66	4				70
Melamphaes cf acanthomus		1					1
Melamphaes atlanticus					5		5
Melamphaes beanii			3		15		18
Melamphaes bispinosus			1		4		5
Melamphaes cavernosus			2				2
Melamphaes cristiceps		4	1		5		10
Melamphaes danae	37	21	1				59
Melamphaes ebelingi	2		11				13
Melamphaes eulepis	22	13	8				43
Melamphaes eurylepis					1		1
Melamphaes frontosus	2						2
Melamphaes hubbsi	130		16				146
Melamphaes indicus	6	3					9
Melamphaes janae	39	104	18				161
Melamphaes janops	4						4
Melamphaes laeviceps	1	109					110
Melamphaes cf laeviceps		1					1
Melamphaes laeviceps (?)		3					3
Melamphaes leprus	7		2				9
Melamphaes longivelis	24	38	23				85
Melamphaes cf longivelis		1					1
Melamphaes lugubris		416	204				620
Melamphaes macrocephalus		39	1				40
Melamphaes maxillaris	2						2
Melamphaes megalops					9		9
Melamphaes microps	6	6			15	255	282
Melamphaes mizolepis					28		28
Melamphaes niger					1		1
Melamphaes nigrofulvus	1				1		2
Melamphaes nordenskjoldii					12		12
Melamphaes nycterinus		3	1				4
Melamphaes opisthopterus					4		4
Melamphaes parini							0
Melamphaes parvus		178			1		179
Melamphaes polylepis	76	36	38				150
Melamphaes cf polylepis		1					1
Melamphaes pumilus	2258	9	394				2661
Melamphaes robustus					20		20
Melamphaes simus	675	264	18		1		958
Melamphaes cf simus		13					13

Melamphaes spinifer	1	88					89
Melamphaes suborbitalis	88	14	25			7	134
Melamphaes cf suborbitalis		5					5
Melamphaes triceratops					2		2
Melamphaes typhlops	144	1	89		1	1	236
Melamphaes unicornis			1		1		2
Melamphaes (?) sp.		1					1
Melamphaes sp.	631	322	133		6		1092
Melamphaes n. sp.		1					1
Melamphaes TBD				21			21
Poromitra capito	369	6	136		18	58	587
Poromitra crassa			2				2
Poromitra crassiceps	131	658	133		8	215	1145
Poromitra crassiceps (complex)	4						4
Poromitra 'crassiceps' A	4						4
Poromitra cf crassiceps		23					23
Poromitra gibbsi							0
Poromitra megalops	258	10188	61		15	82	10604
Poromitra oscitans	18	192	23				233
Poromitra cf oscitans		1					1
Poromitra unicornis							0
Poromitra sp.	37	11	53		2		103
Poromitra species G	7						7
Scopeloberyx microlepis	90	76	11		1		178
Scopeloberyx nigrescens	90						90
Scopeloberyx opercularis	8		2				10
Scopeloberyx opisthopterus	1042	713	141		32	11	1939
Scopeloberyx opisthopteryx		1					1
Scopeloberyx robustus	292	945	79		14	239	1569
Scopeloberyx cf robustus		1					1
Scopeloberyx rubriventer	2				1		3
Scopeloberyx n. sp.		69					69
Scopeloberyx n. sp. B		1					1
Scopeloberyx sp.	90	97	80				267
Scopeloberyx species A	123						123
Scopelogadus beanii	846	37	36		5	2152	3076
Scopelogadus bispinosus		25072					25072
Scopelogadus microlepis					1		1
Scopelogadus mizolepis	5	501	115		22		643
Scopelogadus mizolepis bispinisus		3					3
Scopelogadus mizolepis bispinosus	9	3	66		1		79
Scopelogadus mizolepis mizolepis	801	335	138		1	96	1371
Scopelogadus unispinis		8	10				18
Scopelogadus unispinus		6					6
Scopelogadus sp.	6	62	97				165
Sio nordenskjoldii	25	11	68		9		113
Sio sp.	7						7
Sio species K	5						5

APPENDIX 3

The following abbreviations represent the measurements taken in Chapter 3 of this dissertation. These abbreviations are used in the following pictures to better describe how these measurements were taken. Abbreviations were taken from Kotlyar (2004b) to ensure consistency in naming conventions. Those not listed in Kotlyar (2004b) were designed in order to separate these abbreviations from the existing ones. Figure A is a close-up of a *Melamphaes sp.* head taken from Ebeling (1962) and contains all the finer head measurements described below. Figure B is a full body image of *Poromitra oscitans* taken from Ayling and Cox (1982) showing half the full body measurements. Figure C is a full body image of *Scopeloberyx opisthopterus* taken from Ebeling (1986) showing the remaining full body measurements.

SL = Standard length

H = body depth

hc = head depth

pD_1 = postdorsal distance

pD_2 = end of dorsal to caudal

c = head length

or = orbit to cheek ridge

lff = length of frontal fossa

aD = Predorsal distance

aP = prepectoral distance

aV = prepelvic distance

aA = preanal

VA = pelvic to anal distance

pA_1 = anal to caudal

oc = orbit to cheek angle

o = horizontal orbit diameter

lca = caudal peduncle length

h = caudal peduncle depth

PV = pectoventral distance

lmx = maxillary length

sp = snout to preopercle

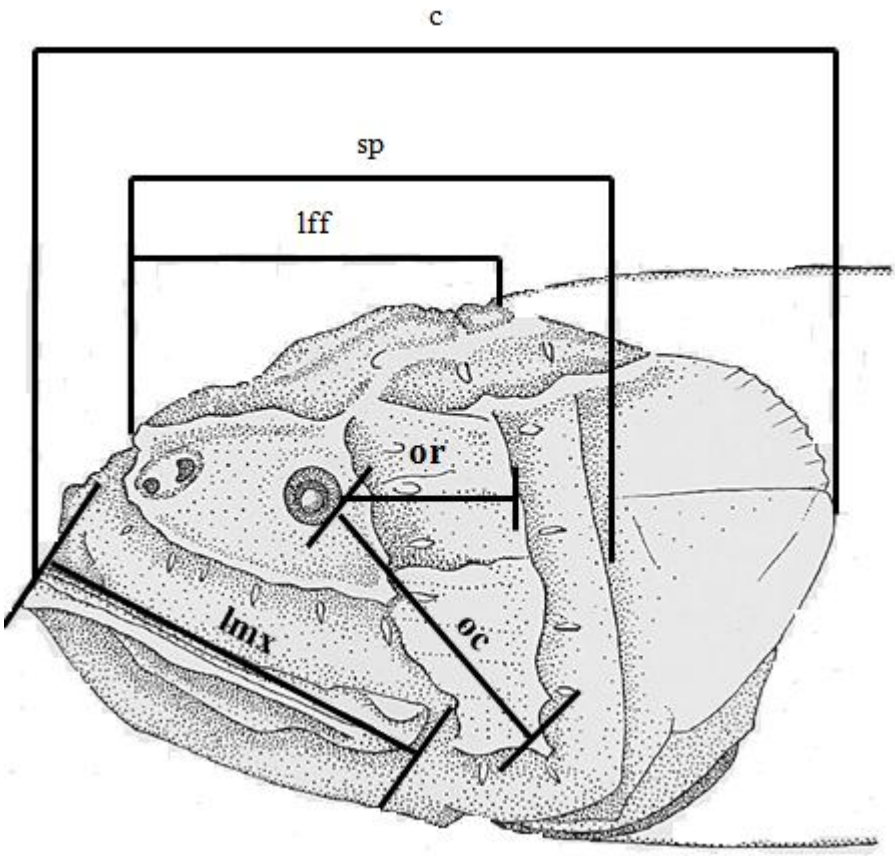


Figure A

Figure B

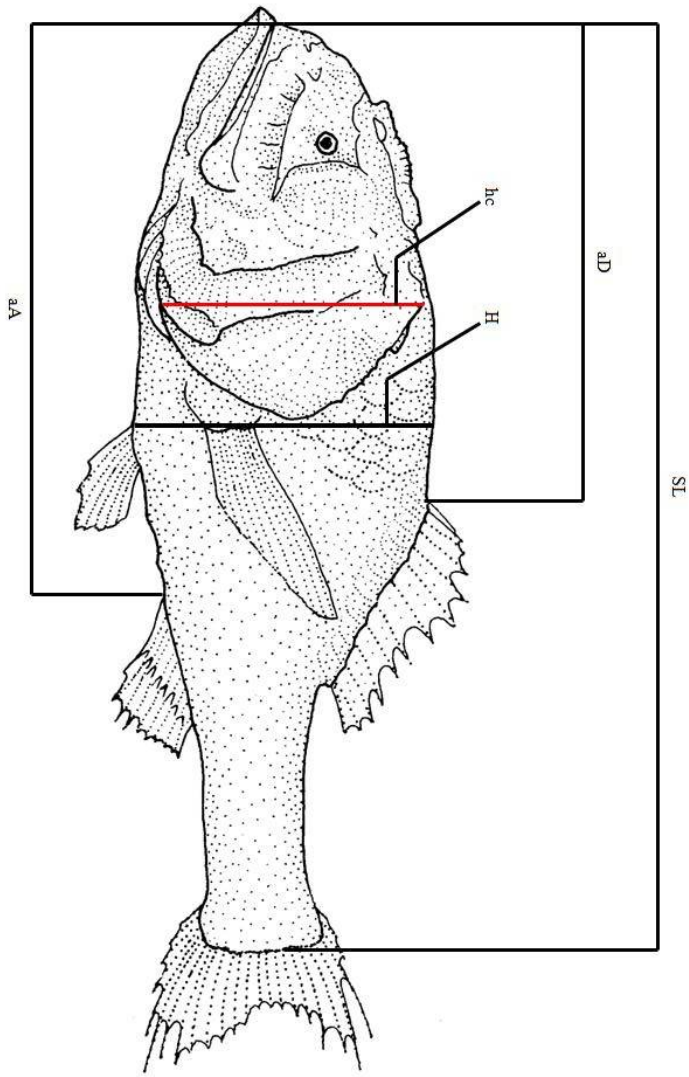
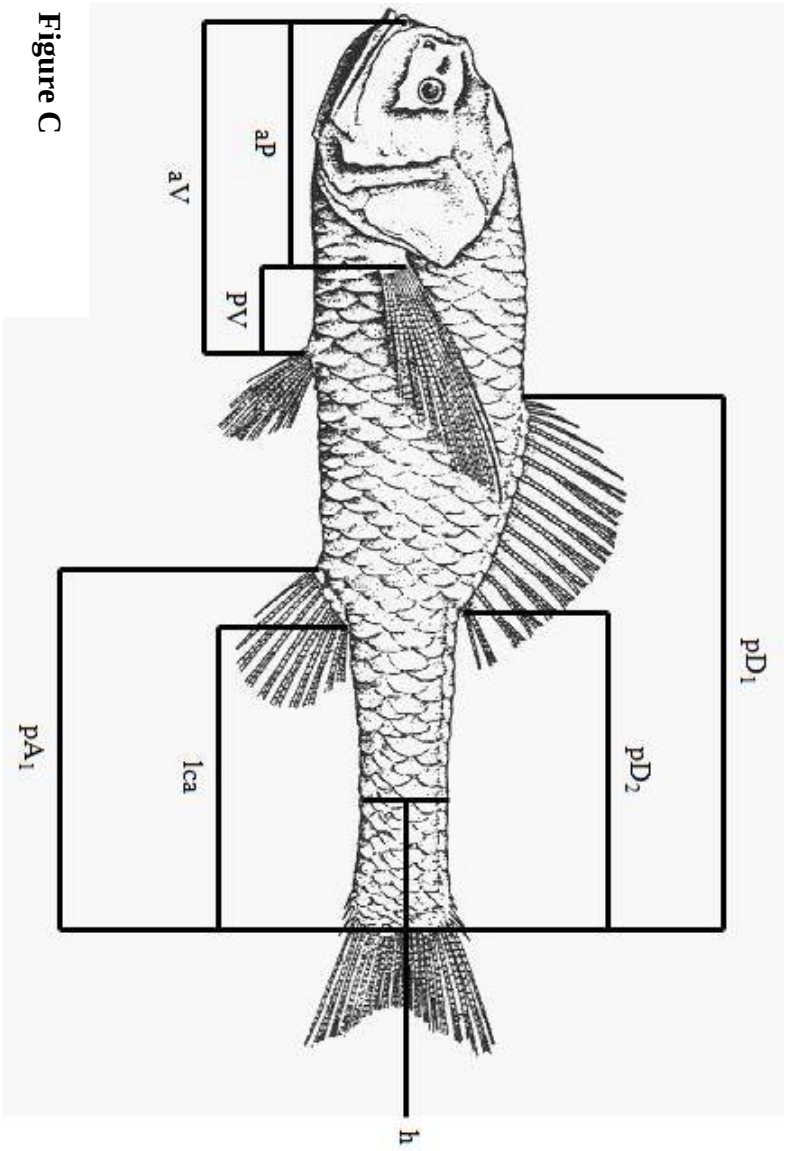


Figure C



APPENDIX 4 (From Sutton *et al*. 2008)

Trawl samples from the 2004 MAR-ECO expedition used for deep-pelagic fish vertical distribution analysis

SS	Net no.	Sample code	Date	Latitude (°N)	Longitude (°W)	Bottom depth (m)	Max trawl depth (m)	Min trawl depth (m)	Depth zone	Solar cycle
2	AK 1-3	1	09-Jun	59.931	25.658	2260	180	0	1	D
2	AK 1-2	2	09-Jun	59.900	25.746	2314	750	370	2	D
2	AK 1-1	5	09-Jun	59.868	25.826	2264	2070	1500	4	D
2	KT 1-5	8	10-Jun	59.927	25.859	2127	200	10	1	ND
2	KT 1-4	3	10-Jun	59.934	25.838	2150	850	200	2	ND
2	KT 1-3	4	10-Jun	59.947	25.804	2187	1550	850	3	ND
2	KT 1-2	6	10-Jun	59.963	25.766	2219	1900	1550	4	N
2	KT 1-1	7	10-Jun	59.970	25.754	2222	2100	1900	bot-3.5	N
4	AK 2-3	9	11-Jun	60.314	28.302	1467	200	0	1	D
4	AK 2-2	11	11-Jun	60.319	28.356	1397	850	200	2	ND
4	AK 2-1	14	10-Jun	60.356	28.421	1419	1260	850	3	ND
4	KT 2-5	10	11-Jun	60.239	28.398	1393	175	5	1	D
4	KT 2-4	13	11-Jun	60.253	28.398	1393	475	175	2	D
4	KT 2-3	12	11-Jun	60.278	28.415	1353	740	475	2	D
4	KT 2-2	15	11-Jun	60.300	28.424	1664	1300	745	3	D
4	KT 2-1	16	11-Jun	60.307	28.428	1501	1330	1300	bot-3	D
6	KT 3-5	17	12-Jun	57.150	31.250	2315	200	0	1	N
6	KT 3-4	18	12-Jun	57.151	31.223	2321	700	200	2	N
6	KT 3-3	19	12-Jun	57.154	31.175	2357	1500	700	3	N
6	KT 3-2	20	12-Jun	57.158	31.127	2344	2140	1500	4	N
6	KT 3-1	21	12-Jun	57.159	31.116	2309	2170	2140	bot-4	N
8	AK 3-3	22	14-Jun	56.201	34.654	1344	300	0	1	D
8	AK 3-2	24	14-Jun	56.243	34.587	1315	800	300	2	ND
8	AK 3-1	27	14-Jun	56.285	34.513	1219	1050	800	bot-3	ND
8	KT 4-5	23	14-Jun	56.314	34.392	2031	200	0	1	N
8	KT 4-4	25	14-Jun	56.314	34.366	1847	760	200	2	N
8	KT 4-3	26	14-Jun	56.316	34.324	1680	1280	760	3	N
8	KT 4-2	29	14-Jun	56.320	34.275	1552	1330	1280	bot-3	DN
8	KT 4-1	28	14-Jun	56.321	34.266	1651	1335	1328	bot-3	DN
10	KT 5-5	30	14-Jun	55.536	36.558	2026	202	0	1	D
10	KT 5-4	31	14-Jun	55.552	36.560	2104	751	202	2	D
10	KT 5-2	32	14-Jun	55.604	36.569	2144	1920	1500	4	D
10	KT 5-1	33	14-Jun	55.609	36.570	2147	1985	1920	bot-4	D
12	AK 4-3	34	16-Jun	52.861	34.668	3239	293	0	1	D
12	AK 4-2	36	16-Jun	52.913	34.650	2744	800	300	2	D
12	AK 4-1	38	16-Jun	52.959	34.638	2112	1750	815	3	D
12	KT 6-5	35	16-Jun	53.047	34.629	1912	200	0	1	D
12	KT 6-4	37	16-Jun	53.060	34.616	1808	700	200	2	D
12	KT 6-3	39	16-Jun	53.081	34.597	1514	1186	700	3	D
12	KT 6-2	40	16-Jun	53.103	34.581	1636	1460	1186	bot-3	D
14	AK 5-3	41	16-Jun	53.182	36.783	3102	340	0	1	D
14	AK 5-2	43	16-Jun	53.134	36.753	3127	900	340	2	D
14	KT 7-5	42	18-Jun	53.083	36.698	3103	200	0	1	D
14	KT 7-4	44	18-Jun	53.041	36.702	3055	665	200	2	D
14	KT 7-3	45	18-Jun	53.067	36.710	3172	1480	665	3	D
14	KT 7-2	46	18-Jun	53.092	36.721	3130	2300	1500	4	D
14	KT 7-1	47	18-Jun	53.100	36.724	3153	2530	2300	5	D
16	KT 8-5	48	19-Jun	51.448	33.450	3794	238	36	1	D
16	KT 8-4	49	19-Jun	51.420	33.455	3793	678	236	2	D
16	KT 8-3	50	19-Jun	51.392	33.465	3764	1488	674	3	D
16	KT 8-2	51	19-Jun	51.364	33.474	3710	2248	1496	4	D

SS	Net no.	Sample code	Date	Latitude (°N)	Longitude (°W)	Bottom depth (m)	Max trawl depth (m)	Min trawl depth (m)	Depth zone	Solar cycle
16	KT 8-1	52	19-Jun	51.346	33.478	3688	3008	2239	5	D
18	AK 6-2	56	20-Jun	52.549	31.892	3935	1774	805	4	D
18	KT 9-5	53	20-Jun	52.983	30.771	3131	202	2	1	D
18	KT 9-4	54	20-Jun	52.995	30.790	3100	676	187	2	D
18	KT 9-3	55	20-Jun	53.014	30.821	3106	1502	685	3	D
18	KT 9-2	57	20-Jun	53.034	30.847	3095	2256	1518	4	D
18	KT 9-1	58	20-Jun	53.055	30.867	3070	2527	2256	5	D
20	AK 7-2	61	21-Jun	52.892	30.585	3167	1837	820	3	D
20	KT 10-5	59	21-Jun	52.983	30.771	3131	202	2	1	D
20	KT 10-4	60	21-Jun	52.995	30.790	3100	676	187	2	D
20	KT 10-3	62	21-Jun	53.014	30.821	3106	1502	685	3	D
20	KT 10-2	63	21-Jun	53.034	30.847	3095	2256	1518	4	D
20	KT 10-1	64	21-Jun	53.055	30.867	3070	2527	2256	5	D
22	AK 8-2	67	23-Jun	50.353	27.515	3650	1800	850	3	D
22	AK 8-1	69	23-Jun	50.395	27.497	3604	2370	1810	4	D
22	KT 11-5	65	23-Jun	50.516	27.486	3177	210	36	1	D
22	KT 11-4	66	23-Jun	50.532	27.488	3179	656	227	2	D
22	KT 11-3	68	23-Jun	50.559	27.491	3420	1487	647	3	D
22	KT 11-2	70	23-Jun	50.582	27.492	3520	2301	1774	4	D
22	KT 11-1	71	23-Jun	50.607	27.493	3705	2731	2309	5	D
24	AK 9-2	74	24-Jun	49.250	28.683	2606	1800	800	3	D
24	AK 9-1	76	24-Jun	49.288	28.662	2672	2230	1800	4	D
24	KT 12-5	72	24-Jun	49.590	28.480	3077	211	27	1	N
24	KT 12-4	73	24-Jun	49.567	28.483	3366	665	212	2	N
24	KT 12-3	75	24-Jun	49.541	28.486	3530	1776	666	3	ND
24	KT 12-2	77	24-Jun	49.516	28.485	3494	2338	1528	4	ND
24	KT 12-1	78	24-Jun	49.501	28.485	3589	2768	2314	5	ND
26	AK 10-2	81	25-Jun	47.967	29.510	3517	1746	800	3	D
26	AK 11-3	79	25-Jun	47.796	29.166	3495	250	0	1	D
26	AK 11-2	80	25-Jun	47.810	29.188	3095	603	250	2	D
28	AK 12-2	85	27-Jun	42.814	27.881	2657	1770	829	3	D
28	AK 12-1	86	27-Jun	42.809	27.825	3010	2400	1810	4	D
28	KT 13-5	83	27-Jun	42.813	27.691	2996	138	7	1	D
28	KT 13-4	84	27-Jun	42.828	27.700	2989	691	151	2	D
28	KT 13-2	87	27-Jun	42.883	27.733	2822	2308	1475	4	D
28	KT 13-1	88	27-Jun	42.901	27.743	2890	2202	2295	5	D
30	AK 13-2	91	28-Jun	42.783	29.468	2407	1800	810	3	D
30	AK 13-1	93	28-Jun	42.789	29.389	2492	2390	1800	4	D
30	KT 14-5	89	28-Jun	42.951	29.257	1949	186	36	1	D
30	KT 14-4	90	28-Jun	42.953	29.274	2443	598	175	2	D
30	KT 14-3	92	28-Jun	42.939	29.312	2718	1500	604	3	D
30	KT 14-2	94	28-Jun	42.912	29.306	2828	2283	1480	4	D
30	KT 14-1	95	28-Jun	42.890	29.303	2839	2383	2265	5	D
32	AK 14-2	97	29-Jun	42.678	30.197	2532	1800	800	3	D
32	AK 14-1	99	29-Jun	42.720	30.215	2542	2300	1800	4	D
32	KT 15-4	96	29-Jun	42.442	30.145	2364	675	188	2	DN
32	KT 15-3	98	29-Jun	42.467	30.144	2289	1523	652	3	DN
32	KT 15-2	100	29-Jun	42.492	30.145	2411	2005	1495	4	D
32	KT 15-1	101	29-Jun	42.515	30.148	2287	1828	2031	bot-4	D
34	AK 15-2	104	30-Jun	41.517	29.909	2230	1800	800	3	D
34	AK 15-1	106	30-Jun	41.560	29.924	2335	2000	1800	4	D
34	KT 16-5	102	30-Jun	41.684	29.999	1927	203	0	1	N
34	KT 16-4	103	30-Jun	41.698	29.999	2317	684	205	2	N
34	KT 16-3	105	30-Jun	41.721	29.999	2177	1494	674	3	N
34	KT 16-2	108	30-Jun	41.746	30.002	2154	1887	1490	4	N
34	KT 16-1	107	30-Jun	41.769	30.007	2524	1981	1887	4	N
36	KT 17-5	109	30-Jun	41.486	28.346	2698	180	0	1	N
36	KT 17-4	110	30-Jun	41.489	28.364	2524	729	218	2	N
36	KT 17-3	112	30-Jun	41.494	28.392	2602	1493	725	3	N
36	KT 17-2	115	30-Jun	41.498	28.425	2441	2036	1489	4	N
36	KT 17-1	114	30-Jun	41.499	28.453	2654	1980	2042	4	N
36	AK 16-2	111	1-Jul	41.239	28.238	2616	1800	800	3	D
36	AK 16-1	113	1-Jul	41.295	28.244	2722	2400	1800	4	D

SS = SuperStation (see Fig. 1). Net: AK = Åkra trawl sample; KT = Krill trawl sample. Sample codes are used in later figures for graphical clarity. Depth zones: 1 = 0–200 m; 2 = 200–750 m; 3 = 750–1500 m; 4 = 1500–2300 m; 5 ≥ 2300 m; bot = near-bottom trawl (depth zone of bottom). Solar cycle: D = day; N = night; DN = dusk; ND = dawn. Group no. = assemblage as defined by multivariate analysis.

APPENDIX 5 (From de Lange Wenneck *et al.* 2008)

Station list for the medium-sized pelagic fish trawl (Aakratrawl) during Leg 1 of the 2004 MAR-ECO expedition

Superstation	Local station	Serial number	Date	Latitude (N)	Longitude (W)	Fishing depth (m)	
						Min.	Max.
2	326	1001	09.06.2004	59°52′	25°50′	1500	2070
2	326	1002	09.06.2004	59°54′	25°45′	370	750
2	326	1003	09.06.2004	59°56′	25°39′	0	180
2	326	8002	09.06.2004	59°52′	25°50′	0	2070
4	328	1009	10.06.2004	60°21′	28°25′	850	1260
4	328	1010	11.06.2004	60°19′	28°21′	200	850
4	328	1011	11.06.2004	60°17′	28°18′	0	200
4	328	8003	10.06.2004	60°21′	28°25′	0	1260
8	334	1031	14.06.2004	56°17′	34°31′	800	1050
8	334	1032	14.06.2004	56°15′	34°35′	300	800
8	334	1033	14.06.2004	56°12′	34°39′	0	300
8	334	8001	14.06.2004	56°17′	34°31′	0	1050
12	339	1046	16.06.2004	52°58′	34°38′	815	1750
12	339	1047	16.06.2004	52°55′	34°39′	300	800
12	339	1048	16.06.2004	52°52′	34°40′	0	293
12	339	8000	16.06.2004	52°58′	34°38′	0	1750
14	341	1055	18.06.2004	53°05′	36°43′	340	900
14	341	1056	18.06.2004	53°08′	36°45′	0	340
14	341	1057	18.06.2004	53°11′	36°47′	1060	2792
14	341	8004	18.06.2004	53°05′	36°43′	0	2792
18	346	1071	20.06.2004	52°32′	31°49′	1821	2800
18	346	1072	20.06.2004	52°33′	31°53′	805	1774
18	346	1073	20.06.2004	52°34′	31°58′	0	743
20	348	1079	21.06.2004	52°56′	30°38′	1850	2787
20	348	1080	21.06.2004	52°54′	30°35′	820	1837
20	348	1081	21.06.2004	52°51′	30°33′	0	806
20	348	8005	21.06.2004	52°56′	30°38′	0	2787
22	350	1087	23.06.2004	50°24′	27°30′	1810	2370
22	350	1088	23.06.2004	50°21′	27°31′	850	1800
22	350	1089	23.06.2004	50°18′	27°32′	0	780
22	350	8006	23.06.2004	50°24′	27°30′	0	2370
24	352	1095	24.06.2004	49°17′	28°40′	1800	2230
24	352	1096	24.06.2004	49°15′	28°41′	800	1800
24	352	1097	24.06.2004	49°12′	28°43′	0	800
24	352	8007	24.06.2004	49°17′	28°40′	0	2230
26	354	1103	25.06.2004	48°00′	29°34′	1800	2600
26	354	1104	25.06.2004	47°58′	29°31′	800	1746
26	354	1105	25.06.2004	47°57′	29°26′	0	788
26	354	8008	25.06.2004	48°00′	29°34′	0	2600
26	355	1106	25.06.2004	47°50′	29°13′	600	825
26	355	1107	25.06.2004	47°49′	29°11′	250	603
26	355	1108	25.06.2004	47°48′	29°10′	0	250
28	357	1114	27.06.2004	42°49′	27°50′	1810	2400
28	357	1115	27.06.2004	42°49′	27°53′	829	1770
28	357	1116	27.06.2004	42°49′	27°57′	0	800
28	357	8009	27.06.2004	42°49′	27°50′	0	2400
30	359	1122	28.06.2004	42°47′	29°23′	1800	2390
30	359	1123	28.06.2004	42°47′	29°28′	810	1800
30	359	1124	28.06.2004	42°47′	29°32′	0	795
32	361	1125	29.06.2004	42°43′	30°13′	1800	2300
32	361	1126	29.06.2004	42°41′	30°12′	800	1800
32	361	1127	29.06.2004	42°38′	30°10′	50	800
32	361	8010	29.06.2004	42°43′	30°13′	50	2300
34	364	1138	30.06.2004	41°34′	29°55′	1800	2000
34	364	1139	30.06.2004	41°31′	29°55′	800	1800
34	364	1140	30.06.2004	41°28′	29°54′	0	800
34	364	8011	30.06.2004	41°34′	29°55′	0	2000
36	366	1146	01.07.2004	41°18′	28°15′	1800	2400
36	366	1147	01.07.2004	41°14′	28°14′	800	1800
36	366	1148	01.07.2004	41°11′	28°14′	0	800
36	366	8012	01.07.2004	41°18′	28°15′	0	2400

For each superstation, each tow produced depth-stratified catches from three codends. The fourth "net", that sampled the entire depth range of the tow, is the sample derived from the forenet of the trawl.

APPENDIX 6 (from de Lange Wenneck *et al.* 2008)

Station list for large pelagic fish trawl (Egersundtrawl) during Leg 1 of the 2004 MAR-ECO expedition

Superstation	Local station	Serial number	Date	Latitude (N)	Longitude (W)	Fishing depth (m)	
						Min.	Max.
7	332	1025	13.06.2004	57°05′	31°22′	1180	1530
11	336	1039	15.06.2004	55°28′	36°28′	1000	1500
11	337	1040	15.06.2004	55°20′	36°18′	1000	1450
15	342	1057	18.06.2004	52°45′	35°57′	1800	2015
31	360	1199	28.06.2004	42°47′	30°05′	1434	1434

APPENDIX 7 (from de Lange Wenneck *et al.* 2008)

Station list for the macrozooplankton trawl during Leg 1 of the 2004 MAR-ECO expedition

Superstation	Local station	Serial number	Date	Latitude (N)	Longitude (W)	Fishing depth (m)		Filtered volume (m^3)
						Max.	Min.	
2	327	1004	09.06.2004	59°58′	25°45′	1843	2141	35,655
2	327	1005	09.06.2004	59°58′	25°46′	1555	1803	101,738
2	327	1006	10.06.2004	59°57′	25°48′	880	1546	89,929
2	327	1007	10.06.2004	59°56′	25°50′	180	844	54,831
2	327	1008	10.06.2004	59°56′	25°52′	11	174	23,409
4	329	1012	11.06.2004	60°18′	28°26′	1304	1329	29,349
4	329	1013	11.06.2004	60°18′	28°25′	744	1302	91,568
4	329	1014	11.06.2004	60°17′	28°25′	472	729	107,075
4	329	1015	11.06.2004	60°15′	28°24′	172	464	60,264
4	329	1016	11.06.2004	60°14′	28°24′	5	164	19,529
6	331	1020	12.06.2004	57°10′	31°07′	2135	2155	24,013
6	331	1021	12.06.2004	57°10′	31°08′	1493	2124	109,070
6	331	1022	12.06.2004	57°09′	31°10′	834	1476	108,503
6	331	1023	12.06.2004	57°09′	31°13′	171	811	63,655
6	331	1024	12.06.2004	57°09′	31°15′	2	165	28,613
8	333	1026	13.06.2004	56°19′	34°16′	1328	1337	21,338
8	333	1027	13.06.2004	56°19′	34°17′	1249	1330	109,381
8	333	1028	13.06.2004	56°19′	34°19′	762	1244	96,255
8	333	1029	13.06.2004	56°19′	34°22′	169	762	59,937
8	333	1030	13.06.2004	56°19′	34°23′	0	173	22,226
10	335	1034	14.06.2004	55°37′	36°34′	1986	1928	20,110
10	335	1035	14.06.2004	55°36′	36°34′	1489	1997	98,392
10	335	1036	14.06.2004	55°35′	36°34′	744	1480	115,106
10	335	1037	14.06.2004	55°33′	36°34′	189	736	66,332
10	335	1038	14.06.2004	55°32′	36°33′	7	189	21,052
12	338	1041	16.06.2004	53°06′	34°35′	1532	1457	16,885
12	338	1042	16.06.2004	53°06′	34°35′	1179	1529	98,817
12	338	1043	16.06.2004	53°05′	34°36′	680	1181	95,720
12	338	1044	16.06.2004	53°04′	34°37′	206	660	62,196
12	338	1045	16.06.2004	53°03′	34°38′	7	183	22,897
14	340	1049	17.06.2004	53°06′	36°43′	2304	2534	31,768
14	340	1050	17.06.2004	53°06′	36°43′	1496	2284	106,524
14	340	1051	17.06.2004	53°04′	36°43′	665	1478	108,691
14	340	1052	17.06.2004	53°02′	36°42′	175	668	54,945
14	340	1053	17.06.2004	53°02′	36°42′	25	175	19,435
16	343	1058	19.06.2004	51°27′	33°27′	2239	3008	116,674
16	343	1059	19.06.2004	51°25′	33°27′	1496	2248	116,531
16	343	1060	19.06.2004	51°24′	33°28′	674	1488	120,300
16	343	1061	19.06.2004	51°22′	33°28′	236	678	73,743
16	343	1062	19.06.2004	51°21′	33°29′	36	238	20,657
18	345	1066	20.06.2004	52°24′	31°49′	2320	2660	108,037
18	345	1067	20.06.2004	52°25′	31°47′	1444	2316	118,900
18	345	1068	20.06.2004	52°27′	31°46′	702	1440	121,619
18	345	1069	20.06.2004	52°28′	31°44′	177	716	72,010
18	345	1070	20.06.2004	52°29′	31°43′	11	186	33,267
20	347	1074	21.06.2004	53°03′	30°52′	2256	2526	97,829
20	347	1075	21.06.2004	53°02′	30°51′	1518	2256	105,408
20	347	1076	21.06.2004	53°01′	30°49′	685	1502	110,656
20	347	1077	21.06.2004	52°60′	30°47′	188	674	68,308
20	347	1078	21.06.2004	52°59′	30°46′	2	202	18,771
22	349	1082	23.06.2004	50°36′	27°30′	2309	2731	97,861
22	349	1083	23.06.2004	50°35′	27°29′	1774	2301	96,557
22	349	1084	23.06.2004	50°34′	27°29′	647	1487	110,879
22	349	1085	23.06.2004	50°32′	27°29′	227	656	64,547
22	349	1086	23.06.2004	50°31′	27°29′	36	210	15,339
24	351	1090	24.06.2004	49°35′	28°29′	2314	2768	105,943
24	351	1091	24.06.2004	49°34′	28°29′	1528	2338	98,426
24	351	1092	24.06.2004	49°32′	28°29′	666	1776	105,224
24	351	1093	24.06.2004	49°31′	28°29′	212	665	62,181
24	351	1094	24.06.2004	49°30′	28°29′	27	211	21,070
26	Failed tow							

Superstation	Local station	Serial number	Date	Latitude (N)	Longitude (W)	Fishing depth (m)		Filtered volume (m^3)
						Max.	Min.	
28	356	1109	27.06.2004	42°54′	27°45′	2295	2202	353,377
28	356	1110	27.06.2004	42°53′	27°44′	1474	2308	113,381
28	356	1111	27.06.2004	42°51′	27°43′	699	1476	112,869
28	356	1112	27.06.2004	42°50′	27°42′	151	691	69,452
28	356	1113	27.06.2004	42°49′	27°41′	7	138	60,855
30	358	1117	28.06.2004	42°53′	29°18′	2265	2383	91,439
30	358	1118	28.06.2004	42°55′	29°18′	1480	2283	109,229
30	358	1119	28.06.2004	42°56′	29°19′	604	1500	143,030
30	358	1120	28.06.2004	42°57′	29°16′	175	598	51,004
30	358	1121	28.06.2004	42°57′	29°15′	36	186	23,304
32	362	1128	29.06.2004	42°31′	30°09′	2030	1828	93,626
32	362	1129	29.06.2004	42°30′	30°09′	1495	2008	99,716
32	362	1130	29.06.2004	42°28′	30°09′	652	1523	105,441
32	362	1131	29.06.2004	42°27′	30°09′	188	675	60,606
32	362	1132	29.06.2004	42°26′	30°09′	1	195	19,314
34	363	1133	30.06.2004	41°46′	30°00′	1887	1981	93,402
34	363	1134	30.06.2004	41°45′	30°00′	1490	1887	102,346
34	363	1135	30.06.2004	41°43′	29°60′	674	1494	97,902
34	363	1136	30.06.2004	41°42′	29°60′	205	684	56,691
34	363	1137	30.06.2004	41°41′	29°60′	0	203	23,817
36	365	1141	30.06.2004	41°30′	28°27′	2042	1980	85,369
36	365	1142	30.06.2004	41°30′	28°26′	1489	2036	101,932
36	365	1143	30.06.2004	41°30′	28°24′	725	1493	90,335
36	365	1144	01.07.2004	41°29′	28°22′	218	729	58,311
36	365	1145	01.07.2004	41°29′	28°21′	0	180	24,865

Each tow (local station number) had five samples (codends with separate serial numbers).

APPENDIX 8 (from de Lange Wenneck *et al.* 2008)

Activities at point-sampling superstations during Leg 1 of the 2004 MAR-ECO expedition

	Maximum deployment depth (m)
"Long" stations (duration 20 h)	
Towbody (variable depth)	1500
CTD/ADCP (0-bottom)	3000
UVP	1000
Multinet, deployment 1	2500
Multinet, deployment 2	1000
Macrozooplankton trawl	2500
Pelagic fish trawl (Aakratrawl)	3000
"Short" stations (duration16 h)	
Towbody	1500
CTD/ADCP	3000
UVP	1000
Macrozooplankton trawl	2500
Pelagic fish trawl (Aakratrawl)	3000

"Long" stations were shortened half way through the cruise by excluding one of the multinet deployments.