Ecological biogeography of deep-sea fishes within Eastern Canadian and Arctic frontier areas

by © Brynn M. Devine

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Abstract

The lack of deep-sea sampling – particularly through *in-situ* observations - limits our understanding of factors that influence deep-sea fish distributions and the relative importance of different habitats in the deep ocean. Through five research cruises sampling multiple marine ecoregions, data presented in this dissertation offer novel insight into benthic and mesopelagic fish assemblages in the Northwest Atlantic and Canadian Arctic, improving knowledge of fish distributions and their environmental drivers. Over 200 hrs of baited camera video footage were analyzed from remote regions in the eastern Canadian Arctic to detect significant differences in fish and invertebrate assemblages among regions. Patterns were attributed to variations in depth and temperature, and validated the utility of using baited cameras to detect the presence of benthic taxa when deployed over fine-grain sediments, requiring fewer deployments compared to fishing gear. These videos yielded the first fisheries-independent estimates of Greenland shark local abundances in Arctic waters, visually identifying 142 individuals and exploring potential extrapolated densities using an established theoretical abundance model. Remotely-operated vehicle transects along the Flemish Cap and Orphan Seamount covering a distance of 55 km documented over 6,900 fish-habitat observations, comprising at least 45 taxa. Fishes were not randomly distributed, with unique assemblages defined by depth zones and particular complex physical and biological habitats. In the pelagos, fish assemblages are largely shaped by changes in hydrography and large-scale oceanographic features. Examination of over 6,000 fishes collected from mid-water trawls along transects through anti-cyclonic eddies in the North

Atlantic eddy field revealed distinct assemblages inside eddy waters, as well as significant differences between upper- and mid-mesopelagic sampled depths. Together these results contribute new data on fish distributions and habitat associations in three remote, understudied deep environments.

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Co-authorship Statement

The research presented in this dissertation was conducted by Brynn M. Devine under the guidance of her supervisor Dr. Jonathan Fisher and supervisory committee members Drs. Evan Edinger, Paul Snelgrove, and Krista Baker. BMD was responsible for initial development of research ideas, planning and participation in at-sea data collection (2013-2016 *R.V. Celtic Explorer* transatlantic cruises, 2014-2016 *Kiviuq I* Arctic cruises), all video analyses from baited camera and ROV surveys, and catch analysis from trawl surveys. BMD led all planning and implementation of data analyses for all chapters and is lead author on all manuscripts. Dr. Jonathan Fisher (Marine Institute) co-authored Chapters 2-5, provided advice on survey design and analyses, reviewed manuscript drafts, and provided financial support. Laura Wheeland (DFO) co-authored Chapters 2-3, assisted with field work, provided invertebrate video analysis, and reviewed manuscript drafts. Dr. Barbara de Moura Neves (DFO) co-authored Chapter 2, provided substrate composition data for baited camera surveys and reviewed the manuscript draft. Dr. Evan Edinger (Memorial University) co-authored Chapter 4, provided 2010 ROPOS ROV survey data and reviewed the manuscript draft. Dr. Krista Baker (DFO) co-authored Chapter 4, assisted with data analyses and fish identification from ROV video data, and reviewed the manuscript draft. Sheena Fennell (National University of Ireland – Galway) co-authored Chapter 5, assisted with at-sea data collection, provided oceanographic data and advice for eddy analyses, and reviewed the manuscript draft. Daphne Themelis (Bedford Institute of Oceanography) co-authored Chapter 5, assisted with mesopelagic fish identification, and reviewed the manuscript draft.

Publications Arising

The following published articles and manuscripts were produced through this dissertation:

Chapter 2:

Devine B.D., Wheeland L.J., Moura Neves B., Fisher J.A.D. (*In Review- Polar Biology*) Baited remote underwater video estimates of benthic fish and invertebrate diversity within the eastern Canadian Arctic.

Chapter 3:

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Chapter 4:

Devine B.M., Baker K.D., Edinger E.N., Fisher J.A.D. (*In Prep* for Deep Sea Research I) Habitat associations and assemblage structure of demersal deep-sea fishes on the eastern Flemish Cap and Orphan Seamount.

Chapter 5:

Devine B.M., Fennell S., Themalis D., Fisher J.A.D. (*In Prep* for Deep Sea Research I) Influence of warm-core eddies on mesopelagic fish assemblages in the Northwest Atlantic Ocean.

Additional manuscripts:

Devine B.M., Van Guelpen L. (*In Prep* for Journal of Fish Biology) Loss of dentition and gill rakers in adult barracudina *Arctozenus risso* (Perciformes: Paralepididae) in the Northwest Atlantic Ocean.

1 Introduction

Increasing interest in the exploitation of a variety of deep-sea resources has generated concern for potential direct and indirect ecological impacts of human activities in the deep ocean (Ramirez-Llodra et al. 2011; Levin and Le Bris 2015). The deep ocean below 200 m encompasses the largest ecosystem on Earth, constituting 95% of the ocean's volume and supporting substantial total biomass, diversity, and providing a variety of ecosystem and climate services (Danovaro et al. 2017). Despite its size, the deep sea remains one of the least explored environments, with limited information on the biogeography and functional roles of deep-sea taxa. The expansion of human activities in the global oceans creates an urgent need for baseline data from understudied 'frontier' areas to improve our understanding of how these activities may impact local biodiversity and whether these impacts could have cascading effects on trophodynamics and ecosystem services.

However, many challenges inherent to deep-sea sampling can slow progress of deep-sea science, resulting in data deficiencies in many frontier areas worldwide, including data needed to inform policy, management, and conservation efforts to preserve and protect the deep ocean. In response to these information gaps and challenges to monitoring and understanding these areas, my dissertation chapters are linked through the common themes of increasing understanding of ecological biogeography of deep-sea fauna, advances and limitations of deep-ocean sampling, and exploring the diversity and distribution of deep-sea fishes. The following sections provide overviews of these linking themes and how they are addressed within frontier areas off of Eastern Canada.

1.1 Ecological biogeography in the deep ocean

How an organism’s environment shapes its distribution and abundance remains at the core of ecological studies, and combined with species morphology, behaviour, and population dynamics is essential for exploring biogeographic patterns (MacArthur 1984). Unlike many biomes within terrestrial environments, the ocean lacks clear visual demarcations of boundaries between ecoregions or zones. As a result, and combined with reduced accessibility, marine biogeography has been comparatively slow to develop. Some of the earliest attempts at delineating biogeographic boundaries in the ocean used minimum temperature to define patterns in coral and crustacean distribution (Dana 1853). This effort was expanded to include depth zones and latitudinal variations (Forbes 1856), but these works and other notable biogeographic atlases developed into the late 20th century (Bartholomew et al. 1911; Ekman 1953; Briggs 1974) restricted their descriptions of patterns to coastal, shallow oceans, as limited data were available for the deep ocean beyond the sunlit, shelf waters.

In contrast to historical biogeography, which explores how geological and climatic events shaped species distributions over time, ecological biogeography addresses present-day patterns. This discipline examines current species distributions, exploring the abiotic and biotic drivers that regulate spatial patterns of distributions (Cox and Moore 2005; Monge-Nájera 2008; Longhurst 2010). Understanding which factors determine where species live can help predict dispersal patterns or barriers that limit expansion. Ecological biogeography also encompasses studies of biodiversity, distributional patterns, and community structure across spatial scales from within-habitat, local/regional, to global areas. Documenting and understanding the fundamental patterns of habitat distributions and the species they contain can help in conserving present day biodiversity by informing management decisions. Such documentation can also help to identify habitats or species that may be at risk to changes in global climate or increased human activities.

The occurrences of marine organisms are not random. A suite of abiotic and biotic factors acting on multiple spatial scales shape distributional patterns of diversity and abundance. The additional dimension of depth adds complexity to resolving the biogeography of marine organisms, requiring consideration of environmental gradients that influence both horizontal and vertical distributions. Dynamics in physical factors such as light, pressure, temperature, and current speed, combined with properties of water chemistry, density, oxygen saturation, and nutrient concentrations can widely vary and change abruptly in marine environments. As the deep ocean depends almost entirely on food supplied from the euphotic zone, assemblage composition of primary and secondary producers at the surface can directly affect the quantity and quality of food reaching the deep seafloor below (Deuser et al. 1981) and directly shape benthic communities (Gooday 2002; Smith et al. 2013). Seafloor topography and bottom type can influence the distribution of biogenic habitat formers such as cold-water corals and sponges (Guinan et al. 2009; Baker et al. 2012a), which can, in turn, influence patterns of other benthic megafauna. Even in the vast and seemingly static pelagic deep ocean, large-scale oceanographic features such as currents, fronts, eddies, and storms can shape communities (Olivar et al. 2012; Sutton et al. 2013).

Contrary to early beliefs, researchers now widely acknowledge that the deep sea supports relatively high biodiversity which can vary across sampled habitats (Hessler and Sanders 1967; Levin et al. 2001; Rex and Etter 2010). This variation is important given the general positive relationships between diversity and ecosystem functioning that also may be enhanced through greater habitat heterogeneity (Zeppilli et al. 2016). The deep ocean provides a wide range of global ecosystem services, from regulating climate through absorption of carbon dioxide and heat from the atmosphere, to playing a key role in nutrient cycling, primary and secondary production, and the biological pump and sequestration of carbon throughout the deep (Danovaro et al. 2014; Thurber et al. 2014). In these contexts, quantifying species diversity is a crucial step in understanding functional diversity within an ecosystem and subsequently the stability and resilience of these systems to change as well as their relative contribution to global processes.

We have still barely scratched the surface in terms of understanding the biogeographic patterns and community structure of fauna in the deep ocean. As the least explored region on Earth, new species are frequently described from the deep sea, with estimates that these depths could harbour over 1 million undiscovered species (Danovaro et al. 2017). Just as the study of biogeography in the shallow seas clarified numerous patterns of distribution, dispersal, and evolution, and generated theories still tested today, expanding observations and sampling of the deep ocean are needed to extend this coastal work and improve our current knowledge of ecological biogeography in the deep sea.

1.2 Advances in deep-ocean sampling

Our understanding of the deep ocean has changed radically over the past century (Koslow 2007). Long-believed to be a dark, homogenous, desert seascape, we now know the deep sea supports many unique habitats such as hydrothermal vents, cold seeps, haline pools, ridges, and canyons; all of these habitats harbour unique and diverse assemblages of organisms and processes (Danovaro et al. 2014). Life has been documented throughout the deep sea, from temperatures below 0 °C to over 110 °C (Jørgensen et al. 1992), at the greatest depth of the oceans (Nunoura et al. 2018), and >1000 m below the seafloor (Ciobanu et al. 2014).

Historically, extractive techniques have dominated survey methods for deep-sea fauna. Dredging aboard early pioneer oceanography expeditions (e.g. sampling by Michael Sars; H.M.S. Challenger voyage) were paramount in dispelling early notions of a life-less deep sea (Gage 1992). Over time, advancements in fishing gear technologies allowed progressively deeper trawling, capturing a wide variety of species but with potentially devastating impacts on benthic habitats (Jones, 1992; Thrush & Dayton, 2002; Tillin et al. 2006). However, the development of methodologies permitting *in-situ* observations revolutionized deep-sea sampling through records of fine-scale species distribution patterns, habitat relationships, and behaviours not afforded by other sampling techniques (Clark et al. 2016). Although extractive methods remain necessary for the collection of voucher specimens, optical technologies are a preferable survey tool for non-destructive sampling of the deep seafloor and can compliment other acoustic mapping and survey techniques (Jamieson 2016; Bowden and Jones 2016).

Visual exploration of the deep sea began in 1934 with the famous ‘bathysphere’ of Beebe and Barton (Busby 1976). Although submersibles remain in use today, the development and refinement of remote underwater optical technologies has allowed for deeper, longer observations that are recorded to provide archival data. Dr. Maurice Ewing and collegues developed the first remotely triggered underwater camera in the 1940s (Ewing et al. 1967), primarily to study seafloor topography. Great advancements in underwater optics occurred during and after World War II to aid in detection of underwater mines, locating shipwrecks, and including early remotely operated vehicles (hereafter ROVs) prototypes used by militaries to recover torpedoes and other objects on the seafloor (Ewing et al. 1967; Matsumoto and Potts 2011). These advancements were later incorporated into scientific research and continued in the 1960s with the development of the “Monster Camera” at the Scripps Institution of Oceanography in California, a baited deep ocean lander rated to 7000 m that provided valuable insight into never before seen abyssal scavenging communities (Isaacs, 1969; Heezen & Hollister 1971; Isaacs & Schwartzlose 1975).

A variety of scientific and industrial ROVs now operate frequently worldwide (Kelley et al. 2016), and the use of baited remote underwater video (BRUV) surveys for ecological monitoring has steadily increased since the 1990s (Jamieson 2016), largely driven by technological advances, including digitalization of data, improving image quality, miniaturization of data storage, and greatly increased battery capacity (Mallet & Pelletier 2014). These advances improved accessibility to users as platforms that can be readily assembled with inexpensive store-bought items (De Vos et al. 2015; Watson &

Huntington 2016; Bergshoeff et al. 2017). BRUVs can generate many types of data, including characterization of benthic habitats, diversity, body size, behaviour, and the relative abundances and distributions of identified species, and have proven useful for surveying a wide range of ecosystems (Cappo et al. 2003; Yeh & Drazen, 2009; Linley et al. 2015; Terres et al. 2015; Lindfield et al. 2016). However, both BRUV and ROV survey methods offer inherent strengths and weaknesses, with trade-offs regarding cost, accessibility, ship time, and of course which type of data (i.e. stationary deployments versus mobile transects) best addresses the research objectives. Nonetheless, the use of these optical technologies as versatile, non-destructive tools to survey marine environments has gained momentum worldwide, with deployments reported from all continents and all the world's oceans (Mallet & Pelletier 2014; Kelley et al. 2016; Whitmarsh et al. 2016).

Despite these advances we still know more about the surface of the moon than the deep ocean seafloor, and with exploration of < 0.0001% of the deep ocean below 200 m new discoveries occur frequently (Webb et al. 2010). For example, in August 2018 scientists using the deep-sea submersible *Alvin* aboard the *RV Atlantis* discovered an unknown dense reef of cold-water corals spanning over 130 km in length just 250 km off the U.S. East Atlantic Coast (D'Angelo 2018). Discovery of this remarkable feature combined non-extractive techniques including acoustic habitat mapping and ROV surveillance to identify this hidden fragile reef while protecting the integrity of its ecosystems and associated organisms. This recent example highlights the continued value and utility of optical technologies for deep-sea exploration.

1.3 Diversity and distributions of deep-sea fishes

Over one-third of all extant fish families contain species that inhabit the deep sea, with a steady rate of new species discoveries since 1750 (Haedrich and Merrett 1988; Weitzman 1997). The two broad deep-sea environments – the benthic and pelagic realms – harbor an impressive array of fishes with morphological adaptations well-suited to each environment. Dominant deep-sea fish taxa are believed to have appeared early (Jurassic-Cretaceous) within the evolution of modern fishes (Haedrich 1997; Priede 2017), resulting in highly specialized forms and adaptions for success in the deep sea, from complex bioluminescent organs and telescopic eyes, to dramatic alterations in swim bladder, jaw, and teeth morphology.

Knowledge of deep-sea fish diversity and drivers of species distributions has grown steadily over time, although sparse sampling limits understanding of the relative influence and scale of these drivers. The structuring of fish assemblages as a function of depth is well-documented throughout the world's oceans. For example, numerous studies reported differences in demersal fish assemblages between various depth classes from 200 m to 3000 m along continental slopes (King et al. 2006; Menezes et al. 2009; Yeh and Drazen 2009; Williams et al. 2018) and even at abyssal and hadal depths (Linley et al. 2017). Most studies identify depth as the most significant factor in structuring deep pelagic fish assemblages (Sutton et al. 2008; Olivar et al. 2012; Cook et al. 2013), but depth is a proxy for changes in hydrography among water masses and food availability, which may drive vertical patterns of both demersal and pelagic fish assemblages in the deep ocean (Haedrich, 1997; Clark et al. 2010; Sutton 2013).

Temperature, salinity, and other variables that can vary greatly with depth (e.g. light, food availability, and oxygen saturation) can influence fish distributions in the deep sea, and collectively are primary drivers in the upper 1000 m of the ocean (Haedrich 1997). Temperature and salinity are often prominent regulators of marine species distributions, particularly in shallow and coastal environments (Perry and Smith 1994; Martino and Able 2003; Olsson et al. 2012), but as a general rule temperature typically decreases with depth and both become relatively constant through much of the deep ocean (Merrett and Haedrich 1997; Denny 2008). However, exceptions occur along shelf-slope areas where merging water masses can generate dramatic hydrological changes and alter benthic assemblage composition (Bergstad et al. 1999; Menezes et al. 2006), as well as temperature fluctuations at depth attributed to spatial and seasonal variability and circulation dynamics (Merrett 1987; Papiol et al. 2012). The influence of this temperature-depth gradient and special exceptions extend into the pelagic realm, with temperature barriers related to oceanic fronts, eddies, or vertical stratification shaping meso- and bathy-pelagic fish communities in the open ocean (Backus et al. 1969; Sutton et al. 2013).

On the deep seafloor additional habitat factors such as topography, substrate composition, and emergent biogenic structures can influence fish distributions. Noting that only a small percentage of the deep seafloor has been directly observed (Clark et al. 2016), understanding of the role and relative influence of different microhabitats and habitat complexity on deep-sea fish assemblages remains limited. As habitats often become more uniform with increasing depth, the relative importance of local structural habitat may also change when contrasted against low complexity landscapes. In this context, biological habitats such as cold-water corals support unique fish assemblages (Ross and Quattrini 2007), and even species-specific fish associations with microhabitats such as gorgonian (Krieger and Wing 2002; Mortensen et al. 2005; Baker et al. 2012b) and soft corals (Heifetz 2002) have been documented. Physical habitats can also influence distributions, with unique fish assemblages associated with geomorphic features like bedrock outcrops (Baker et al. 2012b) or sediment composition of the seafloor (Ross et al. 2015).

Exploration of small-scale and regional patterns of fish distributions have highlighted the challenge of interpreting deep-sea data to establish large-scale, broad-zonation of assemblages across and between ocean basins (Merrett and Haedrich 1997). While distributions may relate to depth and latitude in one region, other regions indicate no correlation with depth or latitude (Merrett and Marshall 1980) or show a greater influence of depth or temperature (Haedrich and Krefft 1978). Likewise, while some studies reported distinct fish assemblages among cold-water corals (Fosså et al. 2002; Costello et al. 2005; Ross and Quattrini 2007), others found no significant relationship (d'Onghia et al. 2010; Baker et al. 2012b; Biber et al. 2014). These discontinuities highlight the dynamic nature of the deep ocean, and the importance of considering sample size, seasonality, and spatial scale when planning and executing community analyses at depth.

Finally, within an applied research context, effective management and conservation of habitats that may be essential to the sustainability of deep-sea populations and processes requires understanding which environmental drivers determine deep-sea fish distributions and the relative importance of physical, biological, or oceanographic features. We still know little about the overall role of fish biodiversity in deep-sea ecosystems and the relative contribution of species/taxonomic groups to ecosystem functioning. The combination of data limitations and characteristic life history traits of many fishes in the deep ocean (i.e. slow growth and late maturation) make this environment particularly vulnerable to human impacts and changing ocean conditions (Roberts 2002; Glover and Smith 2003; Ramirez-Llodra et al. 2011; Clark et al. 2015). Resolving data gaps in our knowledge of the ecological biogeography of fishes across deep-sea habitats, in concert with the application of non-destructive sampling technologies, will help protect essential fish habitats and conserve deep-sea communities and their ecosystem functions and services.

1.4 Field sampling in frontier areas off Eastern Canada

Despite regional interest in deep-sea fisheries and oil/gas extraction, few scientific surveys have sampled deep-waters of the Arctic and off Eastern Canada compared to other parts of Canada and the North Atlantic (Stuart et al. 2008; Danovaro et al. 2017). As a result, several frontier areas persist within the deep-waters of the Arctic and Northwest Atlantic. During my PhD studies, I participated in four transatlantic cruises and three Arctic surveys to sample deep-sea ecosystems in regions with little to no prior sampling. Data from four of these research cruises (and a collaborative Fisheries and Oceans Canada Remotely Operated Platform for Ocean Sciences [ROPOS] cruise), contributed directly to this dissertation. In this section, I outline the spatial scales and data types used to add new knowledge within Arctic, transatlantic, and Newfoundland and Labrador deep-sea regions (Figure 1.7.1) through collaborative research with industry, international research partners, and federal science agencies.

Limited sampling has occurred through much of the Canadian Arctic, largely due to high-operating costs in remote areas and seasonal inaccessibility. Although a wealth of traditional ecological knowledge of Arctic waters exists within northern communities, much of this information is restricted to shallow and coastal depths that can be accessed with traditional fishing gears, with limited data for deep-waters both offshore and within Canada's eastern Arctic archipelago. Despite these knowledge gaps, increased interest in commercial development in the north (Jacobsen et al. 2018) has led to expansion of exploratory fishing efforts and improved access to deep water habitats. In collaboration with the 100% Inuit-owned fishing enterprise the Arctic Fishery Alliance, I participated in joint exploratory fishing and ecosystems surveys in summers from 2014-2016 in the waters near the Nunavut communities of Arctic Bay (Ikpiarjuk), Resolute (Qausuittuq), and Grise Fiord (Aujuittuq). This mutually beneficial industry partnership provided a platform of opportunity to access data-poor regions in the Arctic for baseline scientific research – including baited camera surveys - while simultaneously providing at-sea catch and bycatch analyses in real time to direct exploratory fishing efforts.

Benthic deep-sea sampling in the waters off Newfoundland and Labrador has historically consisted primarily of extractive survey methods, namely trawling. However efforts to employ non-destructive *in-situ* techniques have slowly increased over the past decade. Among these efforts, a 2010 exploratory research cruise using the ROV ROPOS (Remotely Operated Platform for Ocean Sciences) surveyed the geology and biogeography of deep-sea corals in the Flemish Cap, Orphan Knoll, and Orphan Basin. While video footage from these ROV dives was analyzed for physical substrate composition and characterization of coral habitats (Meredyk 2017; Miles 2018), observations of fishes had not been analyzed. Therefore, my research builds upon this previous work, analyzing videos from the 2010 cruise to document small-scale fish-habitat associations from five dives along the Flemish Cap and Orphan Seamount.

The deep pelagic realm is the world's largest and least-studied ocean frontier (Webb et al. 2016). Efforts by the Mid-Atlantic Ridge Ecosystem (MAR-ECO) research project greatly expanded our understanding of meso- and bathy-pelagic communities along the mid-Atlantic ridge from Iceland to the Azores, but limited sampling in the northeast and northwest Atlantic Ocean basins is dominated by acoustic surveys of mid-ocean depths, with sparse characterization of biodiversity. During my studies I participated in four transatlantic research cruises in collaboration with the National University of Ireland and the Galway Marine Institute of Technology, with the 2015-2016 surveys designed to investigate the physical link between the distribution, density, and composition of the deep-scattering layer in relation to mesoscale eddies in the northwest Atlantic.

1.5 Dissertation outline

My dissertation is comprised of six chapters, including four research chapters presented as stand-alone manuscripts. This introduction (Chapter 1) identifies the themes linking these research chapters, including the variety of factors that can influence the distribution of deep-sea fishes and new methods for sampling deep-sea populations. It also highlights the paucity of information on the ecological biogeography and abundance of deep-sea fishes through much of the deep ocean and within several frontier areas in eastern Canadian waters.

In Chapter 2, I identify benthic ichthyofauna and invertebrate communities observed from deep-water baited camera platform deployments conducted in the waters off Nunavut in the eastern Canadian Arctic Archipelago. I evaluate potential local drivers of assemblage patterns among sampled areas, and explore optimal recording time and taxa detection performance compared to traditional fishing gear-based survey methods. The use of BRUV platforms as versatile, non-destructive tools to survey marine environments has gained momentum worldwide, however, few baited camera surveys have occurred in polar environments. As the first baited camera survey conducted in the waters off Nunavut, I provide new biological information from multiple data-poor regions in the Canadian High Arctic and within the boundaries of Canada's newest and largest proposed marine protected area, the Tallurutiup Imanga National Marine Conservation Area.

Baited camera video can generate a variety of biological and behavioural data, and their application here in the remote waters off Nunavut provides valuable new information on an elusive and ancient top Arctic predator, the Greenland shark. In Chapter 3, I identify spatial patterns in distribution and abundance of this large predator based on video-derived size, sex, and count data, and explore the potential application of existing theoretical abundance models to generate the first fisheries-independent abundance estimates for this species. As this IUCN red-listed “Near Threatened” species occurs frequently as bycatch in northern fisheries, future management plans in the face of increased human impacts in the Arctic require more robust information regarding local populations and distribution.

Small-scale patterns in distribution, composition, and availability of different microhabitats in deep-sea benthic ecosystems can influence species diversity, distributions, and potentially fitness, but the relative importance of different microhabitats - both abiotic and biotic - is poorly understood. In Chapter 4, I explore benthic assemblage patterns of deep-sea slope fishes observed during the 2010 ROPOS survey cruise. I identify factors influencing the distribution and abundance of deep-sea fishes, and examine the relative importance of different physical and biological habitats.

In Chapter 5, I explore the influence of mesoscale, warm-core eddies on the structuring of mesopelagic fish assemblages in the Northwest Atlantic eddy field. These ubiquitous oceanographic features can dramatically affect the physiochemical properties and vertical distribution of seawater in the mesopelagic ocean. While past studies demonstrate that these features alter plankton communities and support a variety of larval fishes, few considered their influence on the biodiversity, abundance, and community composition of late-stage mesopelagic fishes.

I conclude my dissertation with a summary (Chapter 6) of how my research contributes to the broader understanding of deep-sea fishes and communities from these three, data-poor frontiers, and highlight the implication of these findings in the context of the rising impact of climate change and human activities in the deep ocean.

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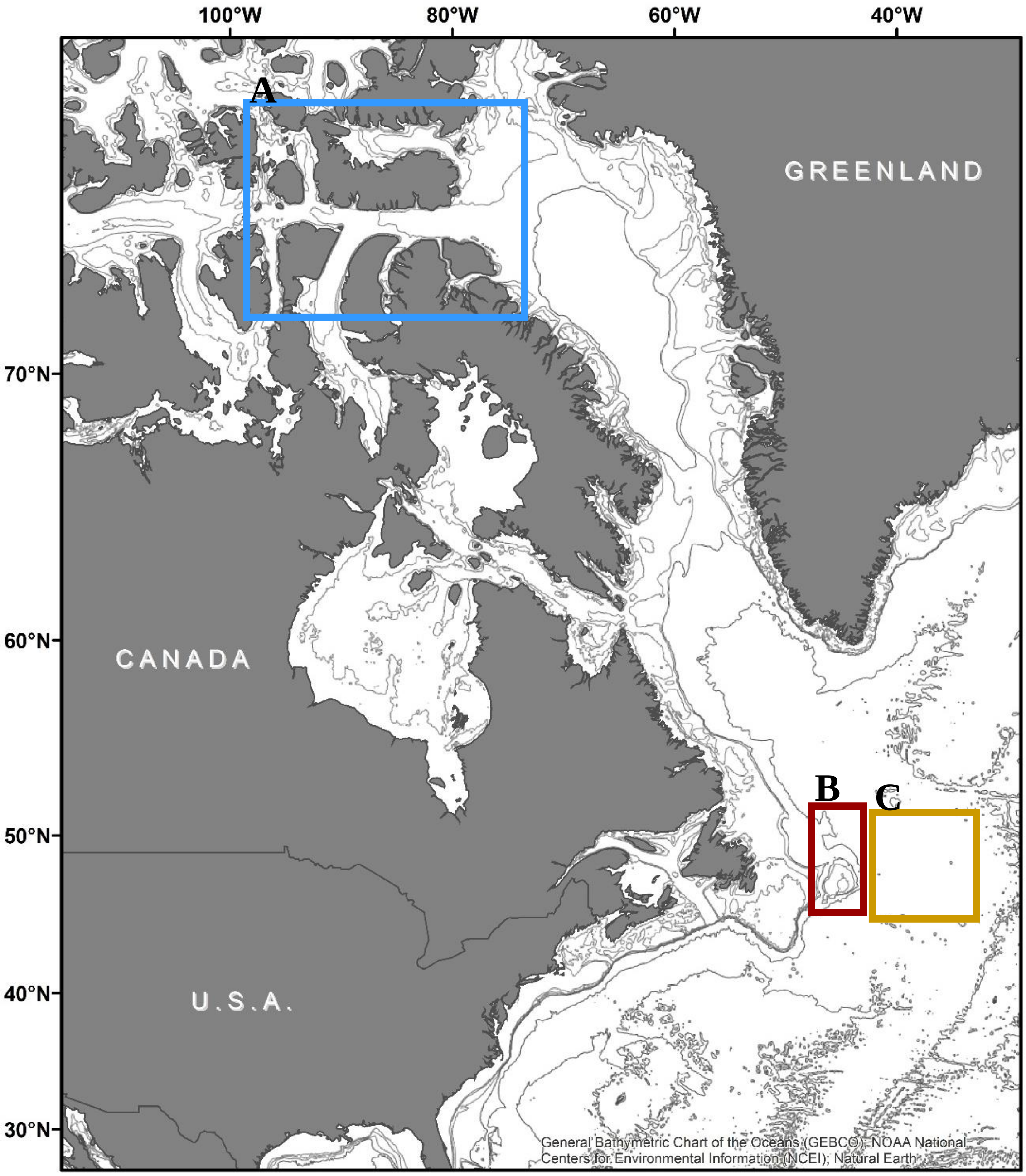
1.7 Figures

Figure 1.7.1 Map showing location of the three frontier areas where chapter studies were conducted, including baited camera surveys within the Canadian Arctic Archipelago (A), ROV surveys along the Flemish Cap and Orphan Seamount (B), and mid-water trawls in the mesopelagic open ocean (C).



2 Baited remote underwater video estimates of benthic fish and invertebrate diversity within the eastern Canadian Arctic

Abstract

The first baited remote underwater video (BRUV) survey was conducted in the Eastern Canadian Arctic, providing new biological information within data-poor regions of interest for marine conservation and potential fisheries development. A total of 31 camera deployments conducted in 2015-2016 aboard an industry fishing vessel during summer exploratory fishing cruises offer new observations in the marine waters of the Qikiqtaaluk (Baffin) Region of Nunavut. In total, 18 invertebrate taxa and 14 fish taxa were observed at the baited camera, with significant differences in assemblages among sites associated with spatial variation in temperature and depth. The Greenland shark *Somniosus microcephalus* and Arctic cod *Boreogadus saida* dominated fish species observations, with brittle stars Ophiurida, amphipods, and chaetognaths dominating the invertebrate community. Comparisons with concurrent fisheries catch data validated the baited camera's ability to comparably detect the presence of invertebrates and fish taxa when deployed over uniform, fine-grain sediment substrates. These results illustrate the utility of low-impact BRUV survey methods to advance understanding of polar marine ecosystems and provide baseline data on spatial patterns of diversity and their drivers.

2.1 Introduction

Effective monitoring and management of Arctic marine speices and ecosystems urgently requires more robust biological information, including distribution and abundance estimates. Ongoing climate change in the Arctic at an unprecedented rate has resulted in warming three times faster than the global average (Hoegh-Guldberg and Bruno 2010; Duarte et al. 2012). These observations and projected future changes in temperature and sea ice extent will undoubtedly impact fauna throughout the region, with high potential to change the structure and functioning of Arctic marine ecosystems (Wassmann et al. 2011; Frainer et al. 2017). The Canadian Arctic has also experienced increases in human activities, as changing sea ice increases accessibility for shipping, tourism, petroleum, and mineral exploitation. Fishing effort is expected to grow as fishers follow boreal species expanding to warming northern waters (Cheung et al. 2010; Christiansen et al. 2014).

Fishing interests within many northern Arctic communities have also grown (Wheeland et al. 2014; Wheeland and Devine 2015; Jacobsen et al. 2018), seeking to explore local waters for resources to expand subsistence fisheries development and potentially join commercial markets. However, as in other emerging fisheries (Anderson et al. 2008), these new fishing grounds are often extremely data poor, with little or no previous sampling in many areas (Coad and Reist 2017). Often these grounds occur in depths beyond the scope of coastal Inuit traditional knowledge. Therefore, broadening our understanding of the biogeography of both commercial and non-commercial species requires enhanced survey efforts in the Arctic in order to establish the baseline data and methodologies necessary to detect ecosystem responses to changing regional climate and human activities.

The large geographic area, seasonal or perennial ice cover, and high operating costs in remote northern regions has constrained fisheries and ecosystem surveys in Arctic marine waters and limited understanding of the spatial distributions, abundances, and functional roles of many species residing in Arctic waters. In the eastern Canadian Arctic, fisheries surveys have largely focused offshore in Davis Strait and predominately target commercial species such as Greenland halibut *Reinhardtius hippoglossoides* and Northern shrimp *Pandalus borealis* (Jørgensen et al. 2011). In contrast, few surveys have been conducted within the Canadian Arctic Archipelago (Mueter et al. 2013), with most occurrence data for fishes within this region derived from early Nordic surveys dating back to the late 1800s (e.g. Videnskaps-Selskab 1913), which biased survey coverage toward southern and coastal regions. Based on these early reports and limited sampling throughout the last century, 207 of the 221 currently known Arctic marine fish species in the Canadian Arctic were reported from Nunavut waters (Coad and Reist 2017). However, the majority of these species lack sufficient data for stock or conservation assessments, with no assessment of roughly 95% of Arctic marine fish species (Christiansen and Reist 2013). Whether additional undocumented taxa occur in these waters and details of their biogeography throughout the region is unknown. The same inherent sampling limitations in the region leave similar knowledge gaps for invertebrate taxa in the Canadian Arctic, with poor understanding of local assemblages, distributions, and relative abundance of Arctic invertebrate species.

An area of particular concern in light of changing Arctic conditions are the waters of Tallurutiup Imanga - the Lancaster Sound region — situated at the eastern entrance of the Northwest Passage, with the broader Lancaster Sound ecoregion extending to encompass the Gulf of Boothia and Jones Sound (Spalding et al. 2007). This significant ecoregion is known to support substantial biomass of Arctic wildlife year round. Many species of Inuit cultural significance and food-security utilize the waterway for vital feeding and nursery grounds, including bowhead, narwhal, and beluga whales, seabirds, polar bears, seals and walruses (Darnis et al. 2012; Laidre et al. 2015; Matley et al. 2015). Many species rely on the productivity of this region in the open water season, when rich plankton blooms coincide with ice-retreat and large schools of Arctic cod *Boreogadus saida* form in near shore waters (Welch et al. 1993; Hannah et al. 2009). Efforts on-going since the early 1980s to establish the Tallurutiup Imanga National Marine Conservation Area (NMCA) seek to preserve these resources and protect ecosystems within this region. In September 2017 the government of Canada defined the boundaries of this prospective NMCA and, pending negotiation, this region could soon become Canada's largest protected area at 109,000 km^2. However, the lack of survey data on benthic ecosystems within this ecoregion leaves a major gap regarding the potential importance of this area to species groups beyond marine mammals and seabirds.

The many established survey methods for fish and invertebrate assemblages each bring inherent strengths and limitations. Historically, extractive techniques have dominated monitoring of fish and other benthic mega-fauna populations, either using records from commercial catch for target and bycatch species assessment, or through fishery-based scientific surveys. However, several issues associated with extractive methods limit their desirability for use in certain circumstances, often resulting in trade-offs between detectability and habitat impacts. Gear selectivity can vary across species and sizes (MacLennan 1992; Fraser et al. 2008), leading to inconsistencies and misrepresentation of local assemblages through false absences in surveys. Fixed fishing gears (e.g. longlines and pots) can provide useful data with reduced impact on benthic habitats, however, gear selectivity can strongly bias toward certain species and/or sizes. In contrast, bottom trawl gears can capture a wide variety of species, but potentially destroy benthic habitats in the process (Jones 1992; Thrush and Dayton 2002; Tillin et al. 2006). For regions harboring sensitive sessile fauna like corals and sponges such impacts are unacceptable. Likewise, some species experience high capture stress and post-capture mortality rates in both mobile and fixed gear types (Gallagher et al. 2014; Barkley et al. 2017), rendering them inappropriate for certain species, including at risk species or populations.

As an emerging complimentary or alternative method to traditional survey techniques, baited remote underwater video (BRUV) surveys for ecological monitoring has steadily increased since the 1990s, largely driven by technological progress improving image quality, storage, and battery capacity (Mallet and Pelletier 2014). Many shallow-water BRUV platforms can now be easily assembled with inexpensive and readily available components (De Vos et al. 2015; Watson and Huntington 2016; Bergshoeff et al. 2017). The use of these optical technologies as versatile, non-destructive tools to survey marine environments has gained momentum worldwide, with deployments to date reported from all continents and all the world's oceans (Mallet and Pelletier 2014; Whitmarsh et al. 2016). Increased use has led to variation in methodology and survey design, including differences in bait type and preparation, camera orientation (horizontal or vertical), soak time, use of a single camera versus stereo-camera designs (Whitmarsh et al. 2016), and modifications to monitor pelagic ecosystems (Bailey et al. 2007; Letessier et al. 2013; Bouchet and Meeuwig 2015; Jamieson 2016). BRUVs can generate many types of data including benthic habitat characterization, species and/or functional diversity, body sizes, swimming speed, and facilitate analyses of habitat associations, animal behaviour such as foraging methods, and the relative abundances and distributions of identified species.

These characteristics have made BRUVs useful in surveying sensitive habitats such as marine protected areas (Cappo et al. 2003; Terres et al. 2015), coral reef habitats (Linley et al. 2015; Lindfield et al. 2016) and other habitats conducive to the low impact nature of BRUVs (Henriques et al. 2002; King et al. 2008; Yeh and Drazen 2009). Evidence suggests that the greatest deterioration in seafloor habitat occurs when bottom fishing first begins (Kaiser et al. 2002). However, given comparatively few commercial fisheries in the Arctic relative to most coastal regions (Christiansen et al. 2014; Stock et al. 2017), many benthic marine ecosystems have been spared the impacts of heavy bottom trawling, and therefore continue to support relatively pristine habitats with significant concentrations of cold-water corals and sponges (Kenchington et al. 2011). Consequently, emerging survey efforts should strive to maintain the integrity of these fragile benthic habitats. Significantly fewer BRUV surveys have occurred in polar environments compared to temperate and tropical regions, with only a few studies from Antarctic (Yau et al. 2002; Smale et al. 2007) and Arctic (Premke et al. 2006) waters. Despite the limited use of BRUVs in polar environments to date, their non-destructive quality, cost-effectiveness, and capability of sampling under seasonal sea ice, offer a valuable method for surveying polar ecosystems.

The goal of our study was to provide new data on fish and invertebrate occurrences and explore patterns of diversity in Arctic marine communities using BRUV survey methods in parallel with traditional fisheries sampling methods within the Eastern Canadian Lancaster Sound ecoregion. We identify benthic fauna to describe local fish and invertebrate assemblages, and compare video-derived diversity estimates to catch data from co-occurring exploratory fishing to assess the feasibility of optical technologies for future ecosystems surveys in the North. Specifically, we use presence-absence information and peak abundance estimates from video data to analyse differences among regions, including assemblage comparisons along depth and temperature gradients. Given expectations of increased fishing efforts in our study areas as fisheries expand north, we validate non-lethal baited cameras as a cost-effective and efficient survey method to improve baseline data for fish and invertebrate communities in remote and deep-water Arctic areas.

2.2 Materials and methods

2.2.1 Exploratory fishing and ecosystem sampling

All data collected were obtained in collaboration with the Arctic Fishery Alliance (AFA), a 100% Inuit-owned fishing enterprise shared by the four Nunavut communities of Arctic Bay (Ikpiarjuk), Qikiqtarjuaq, Resolute (Qausuittuq), and Grise Fiord (Aujuittuq) in northern Canada. This organization invests profits obtained from offshore Atlantic Canadian fisheries (e.g. Atlantic halibut *Hippoglossus hippoglossus*, and *R. hippoglossoides*) into the north through community development, including facilitation of scientific research in conjunction with exploratory fishing efforts conducted in the waters adjacent to these communities. This joint effort strives to explore local waters for potential marine resources that could be developed into small-scale subsistence fisheries, simultaneously providing new insight into benthic marine ecosystems for local traditional knowledge and community outreach. Collaboration of researchers with the AFA supports a mutually beneficial partnership where science can provide at-sea catch analysis in real time to direct exploratory fishing, while the vessel simultaneously offers a platform of opportunity for researchers to access remote regions to collect valuable data from unstudied and/or poorly sampled waters using complementary research methods.

2.2.2 Baited Camera System

A total of 31 baited camera deployments were conducted during August-September 2015-2016 in the Eastern Canadian Arctic aboard the *Kiviuq I*, a 99-ft fishing vessel owned by AFA. Camera deployments occurred in the following regions within the northern Canadian territory of Nunavut: Admiralty Inlet and Adams Sound near the community of Arctic Bay (hereafter ‘Arctic Bay’); central Lancaster Sound*;* southeast McDougall Sound and Barrow Strait near the community of Resolute (hereafter ‘Resolute’)*;* eastern Jones Sound including Starnes Fiord and Grise Fiord (hereafter ‘Jones Sound’); and Scott Inlet (Figure 2.7.1). Bottom temperatures at each camera set were derived from temperature loggers (DST centi-TD Star-Oddi, Gardabaer, Iceland) attached either to the nearest bottom fishing gear set (Resolute and Arctic Bay) or directly to the camera frame (Jones Sound, Scott Inlet). For camera deployments in Lancaster Sound (n=3) where logger data was unavailable, temperature at equivalent depths was taken from CTD (conductivity, temperature, depth) profiler casts aboard the *CCGS Amundsen* in August 2015 (ArcticNet 2015) at locations nearest (<50 nm) to camera deployments.

The baited camera lander consisted of a single high-definition camera with integrated reference lasers (6.24 cm between parallel lasers) and white light source (1Cam Alpha, Aquorea LED; SubC Imaging Inc., Clarenville, Newfoundland and Labrador) mounted onto a weighted aluminium frame tethered to a surface buoy for retrieval. The camera was positioned at the top of the frame, 1.6 m above the seafloor and oriented downward and outward at approximately a 60° angle, with continuous recording at each location (Figure 2.7.2). A bait arm with 6-8 squid (approx. 2 kg) for each deployment was positioned 50 cm above the seafloor and extending toward the field of view. The camera system was deployed similar to a series of fishing pots, with surface buoys leading to anchors on either side of the frame, and 9/16” rope of equivalent length to the deployment depth extending from both sides of the frame and leading to each anchor. This design ensured that the commercial hauler aboard the vessel could retrieve the camera system (Figure 2.7.2).

2.2.3 Video analysis

All fishes were identified to the lowest possible taxonomic level based on morphological characteristics, prevalence of species encountered in nearby fishing catch, and recommendations by regional taxonomic experts. Videos associated with each camera set were observed in full, recording first arrival times for all fish taxa, and enumerated using a measure of peak abundance (n_{max}) calculated as the maximum number of individuals per species/taxa present within a single video image. This approach ensured counting duplicate individuals did not occur. For *S. microcephalus,* where unique markings (i.e. scar patterns, and coloration) made it possible to distinguish and quantify individuals, an additional cumulative measure of local abundance was derived for each deployment (Devine et al. 2018). Fish lengths were estimated using the software ImageJ (Schneider et al. 2012) for all fishes that swam along the seafloor in plane, allowing measurement with the camera reference lasers.

Benthic habitat for each set was characterized using descriptions of surface substrate type based on the Wentworth scale (Wentworth 1922), determined using reference lasers for spatial scale. Given the different grades of fine sediment are not readily distinguishable from video footage, the term ‘fine-grained sediment’ was used to encompass substrate types of clay, silt, and/or sand. For the characterization of invertebrate communities, a one-minute video clip (starting at minute 0) was analyzed at half-hour intervals throughout each camera deployment, identifying all invertebrates to the lowest taxonomic group possible. The number of video intervals within a set depended on set duration, and ranged from 6 to 21 (mean = 15). Deployments or video intervals where water turbidity or an obstruction in the field of view (i.e. rope) impeded a clear view of the seafloor were not included in invertebrate analyses. Sessile organisms typically occurred throughout a video set – unless an outside force disturbed the substrate and/or camera frame, such as the movements of *S. microcephalus*. A one-minute video clip would therefore capture their presence, and subsequent clips allowed detection of more mobile organisms moving in and out of the field of view (e.g. ophiuroids and gastropods). Observations of taxa within each one-minute interval were accumulated throughout the duration of each set in order to characterize the cumulative invertebrate assemblage at each set.

2.2.4 Validation of baited camera data

The identities of fish and invertebrate taxa in the video were compared to those captured in fishing sets conducted in the same area to assess the ability of both gears to quantify local species diversity in the waters adjacent to each community. Catch data for these comparisons were collected during exploratory fisheries efforts by the AFA near the communities of Arctic Bay, Resolute, and Grise Fiord (Jones Sound) (Figure 2.7.1). A total of 104 fixed pot gear fishing sets were completed (n=35 in Arctic Bay, n=31 in

Resolute, n=38 in Jones Sound) using a combination of whelk pots (conical, 94 cm base with 13 cm opening, 1– 2.2 cm mesh, mean 33 pots (range=20-50) per set, average soak time 26.4 hrs (range=15.3-70.5)) and two sizes of shrimp traps (Small: 82 cm L x 32 cm W x 37 cm H, 0.65 cm mesh; Large: 122 cm L x 62 cm W x 36 cm H, 2.4 cm mesh, average 23 traps (range=20-25) per set, average soak time 25.3 hrs (range=11.8-73 hrs)). Limited deployments of longline gear were also used, with a total of 9 sets (n=5 in Arctic Bay, n=1 in Resolute, n=3 in Jones Sound) comprised of ground-line (1.5 cm diameter rope) with gangions placed approximately 1.8 m apart, with an average soak time of 25.9 hrs (range=14.2 – 41.5 hrs). In 2015, longline strings were comprised of 6 tubs of gear (2 tubs of each of sizes 12, 14 and 16 circle hooks), where each tub contained approximately 125 hooks. In 2016, longline strings were comprised of 3 tubs of gear, where each tub contained approximately 125 hooks and size 14 circle hooks used for all tubs. All sets were baited with commercial squid bait, and spanned multiple depths and temperatures in each region. Catch from each set was identified to species, then counted and weighed to derive abundance and biomass per set.

In regions where both fishing and camera deployments occurred (i.e. Arctic Bay, Resolute, and Jones Sound), catch composition from the nearest (<30 km) whelk pot string to each individual camera set was compared to species presence in videos to assess species detectability between baited camera and fixed gear survey methods. This comparison excluded large fish species (i.e. *S. microcephalus*, Arctic skate *Amblyraja hyperborea*, and *R. hippoglossoides*) and invertebrate infauna, because these species could not be captured by the whelk pot fishing gear or on the video footage, respectively. Both whelk pot mesh sizes (1 cm and 2.2 cm) were used in comparisons as species richness did not differ significantly between mesh sizes ($F_{1,24}$=1.87, p=0.18). For broad comparison between extractive fishing-based and non-extractive camera survey methods, pooled species detection for fishes and invertebrate taxa in each region were compared between observations from all camera deployments versus observations from all fishing gear types used in exploratory fisheries (i.e. whelk pots, shrimp traps, and longlines).

2.2.5 Statistical analyses

Similarity in fish and invertebrate assemblages based on location, depth, and temperature was explored using the statistical software PRIMER 7 (version 7.0.10, Primer-E, Plymouth, UK). Analysis of similarity (ANOSIM) tests were performed to compare regions using a Bray-Curtis similarity matrix based on square-root transformed n_{max} values for fish species for comparison between regions, and using presence-absence data for invertebrate taxa from camera sets. Individual, ranked species contributions to both among-region separation and within-region similarities were further quantified through similarity percentage (SIMPER) routines (Clarke et al. 2014).

The number of taxa observed in an area was positively related to the number of video samples from that site (Figure 2.7.3; GLM: Taxa observed = 0 + sample size, poisson distribution; Invertebrates: $p<0.001$, $z = 26.26$, df=24; Fishes: $p<0.001$, $z=13.18$, df=29). Therefore, extrapolation of accumulation curves were computed in EstimateS v.9.1.0 using the Bernouilli product model (Colwell et al. 2012) to generate expected taxa richness for a theoretical sample of 21 video samples at each site, corresponding to the maximum sample size achieved at a single site within the data set. These standardized extrapolated species accumulation curves were generated for fishes and invertebrates for each deployment, and using mean calculated species per sample across all sets to create cumulative curves to determine optimal deployment time necessary to capture diversity. Finally, differences in video-derived fish lengths were explored through an analysis of variance (ANOVA) of means between sampled regions, using post-hoc Tukey tests to examine pairwise mean comparisons.

2.3 Results

Camera deployments ranged from 176 to 615 minutes (Table 2.6.1), with a total of 258 hrs of video footage analysed. Deployment depths ranged from 143 – 304 m near Resolute, 360 – 720 m in Lancaster Sound, 350 – 710 m near Arctic Bay, 233 – 873 m in Jones Sound, and 620 – 802 m in Scott Inlet (Table 2.6.1), corresponding to differences in bathymetry among these regions. Bottom temperatures ranged from -1.2 to +1.1 °C, with warmest sets occurring in the deep waters of Lancaster Sound and in Scott Inlet, and coldest sets in the shallow sub-zero waters surrounding Resolute. Depth explained 61% of variation in bottom temperature across the 31 camera deployments, with water temperature increasing at depth (Figure 2.7.4). Temperature profiles derived from CTD casts taken throughout the survey area indicate the presence of a cold intermediate layer extending from approximately 50 – 200 m in most regions (Table A1; Figure A1). Substrate varied little among deployments, with 77% of sets comprised of uniform, fine-grained sediments. The remaining sets yielded a combination of fine-grained sediments with scattered cobbles or boulders, with the exception of the two sets within Resolute Pass (Sets 10, 14) characterized by pebbles, cobbles, and/or boulders (Table 2.6.1).

2.3.1 BRUV observation summaries

A total of at least 14 fish species were observed at the baited camera, including 2 elasmobranchs and 12 teleosts, representing 12 different families (Table 2.6.2; Figure 2.7.5). *Somniosus microcephalus,* sea tadpole *Careproctus reinhardti,* and *B. saida* were the only species observed actively feeding on the squid bait. *Somniosus microcephalus* was the most frequent species observed in our video footage, with a total of 142 individuals distinguished across 25 sets (Table A2), with no individual observed in multiple camera sets. This species occurred in all sampling locations, though in highly variable abundance. At least 18 individuals occurred in a single set in Admiralty Inlet, in contrast to only 3 individuals near Resolute, all in the two shallowest sets within Resolute Pass (see also Devine et al. 2018).

Environmental associations with the presence and abundance of other fish species/taxa were also apparent (Figure 2.7.6). *Reinhardtius hippoglossoides* was present only in the two deeper deployments in Lancaster Sound (Sets 4 and 7) and one set just outside Scott Inlet (Set 31). For all of these observations, depths were >650 m and bottom temperatures exceeded 1 °C. Similarly, *A. hyperborea* and *C. reinhardti* occurred only in deep sets >450 m in the open waters of Admiralty Inlet near Arctic Bay, Lancaster Sound, and Jones Sound. *Boreogadus saida* was the most abundant teleost and the only species present in all 5 regions, with the highest peak abundance observed in sets within small fiords and inlets (i.e. Grise Fiord and Starnes Fiord in Jones Sound; Adams Sound near Arctic Bay). *Boreogadus saida* occurred in all sets from 200-670 m and was the only species found throughout the full range of temperatures sampled. Sculpins *Cottidae* spp. and Atlantic poacher *Leptagonus decagonus* both occurred only in Arctic Bay and Jones Sound regions, predominately within small fiords at depths 230 – 700 m and temperatures near 0 °C. Eelpouts *Lycodes* spp. and snailfishes *Liparis* spp. occurred at a wide range of depths and temperatures, from shallow sub-zero waters to warmer deep sets, and were the only other teleosts present near Resolute. Although several other species were likely present, morphological traits distinguishing species within the genera *Lycodes* and *Liparis* and family *Cottidae* are exceedingly subtle, precluding identification to species level through video analysis. Rare or uncommon species (i.e. limited observations within the videos) included American plaice *Hippoglossoides platessoides*, fish doctor *Gymnelus* spp., cusk *Brosme brosme*, spiny lumpsucker *Eumicrotremus spinosus*, capelin *Mallotus villosus*, and a single pelagic unidentified fish in Scott Inlet (Set 31).

A total of 18 invertebrate taxa were observed within the camera sets (Table 2.6.3). Amphipods, chaetognaths, and ophiurids occurred in all camera sets. Nephtheid soft corals occurred in all regions and across the full range of sampled depths (112 – 873 m). Despite high catch frequency of the sea pen *Umbellula encrinus* (8 from longlines, 194 from pots/traps combined), this species was present in just a single camera deployment in Jones Sound (Set 24). Actiniarians were common, present in all locations except Resolute, whereas urchins *Strongylocentrotus* spp. occurred only in a single set in Resolute comprised of pebble substrate. Crinoids *Heliometra* spp. occurred in the shallowest sets from Resolute and Lancaster Sound, both with benthic habitats containing pebble or boulders. Asteroidea sea stars occupied a wide range of depths and were present in all regions except Scott Inlet, whereas the basket star *Gorgonocephalus* spp. was present in only a single set from each of Arctic Bay, Resolute, and Jones Sound. The camera was also able to detect the presence of pycnogonid sea spiders in Resolute and Jones Sound, and miniscule holothurian sea pigs of the genus *Elpidia* in several sets within Arctic Bay and Lancaster Sound, despite their small size and cryptic nature. Regarding species of interest for local emerging fisheries, whelk (family: Buccinidae) were present across all five regions, whereas caridean shrimp were present in all regions except Resolute.

2.3.2 Statistical analyses

Extrapolated invertebrate taxa richness within sets ranged from 4 to 11, with an overall median richness of 7 taxa. Taxonomic richness extrapolated within individual sets was not significantly related to depth or temperature, and did not vary significantly among sampled regions (z=-11.127; p=0.76). Extrapolated fish taxa richness ranged from 1 to 6, with an overall median richness of 3. Fish taxonomic richness was also not significantly related to depth or temperature, nor did it vary significantly among sampled regions (z=-16.061; p=0.81). Pooled cumulative proportions of observed taxa for all deployments using mean extrapolated richness values indicated variability in theoretical observation time necessary for maximum species detection between invertebrate and fish taxa (Figure 2.7.7). Extrapolated richness curves to 11 hrs deployment time suggest observation of 90% of invertebrate taxa within the first 3 hrs of deployments; however 90% of fish taxa were not observed until approximately 6.75 hrs (Figure 2.7.7).

Non-metric multidimensional scaling (nMDS) plots using a Bray-Curtis similarity matrix of square-root transformed n_{max} for fishes and presence-absence for invertebrates indicate varying degrees of similarity in marine communities among regions (Figure 2.7.8). ANOSIM analyses of fish peak abundance revealed significantly distinct groups based on region (Global R=0.273, *P*= 0.004). Pairwise comparisons, however, indicate significant differences in assemblages only between Arctic Bay-Scott Inlet (p=0.048), Resolute-Jones Sound (p=0.003), and Jones Sound-Scott Inlet (p=0.033). However, small sample sizes from Scott Inlet (n=2) and Lancaster Sound (n=3) limited power to detect significant differences via permutation tests. SIMPER analysis indicated *S. microcephalus* was the main contributor (33.9-40.2%) to within-group similarities at Arctic Bay, Lancaster Sound, Jones Sound, and it contributed 100% at Scott Inlet. In Resolute, Arctic cod accounted for 83.3% of within-group similarity.

Presence-absence ANOSIM analysis of invertebrate communities between regions indicate significant separation of groups (Global R=0.27, *P*= 0.006). Pairwise comparisons further indicate significant differences in assemblages between Lancaster Sound versus Jones Sound (p=0.038) and Resolute versus Jones Sound (p=0.001). SIMPER analysis indicates that amphipods, chaetognaths, and ophiurids were the three primary contributors to within-group similarities at Arctic Bay, Lancaster Sound, Jones Sound, and Resolute (57.5%, 69.6%, 56.3%, and 79.2%, respectively). At Scott Inlet, amphipods, anemones, and chaetognaths each contributed 25% to within-group similarity, with the lowest overall dissimilarity observed between Lancaster Sound and Scott Inlet regions (28.7%).

Differences in mean lengths between regions were also observed for several fish taxa (Table 2.6.2). Mean lengths of *S. microcephalus* differed significantly among regions ($F_{4,89}$=3.64, p=0.008), primarily due to smaller sharks occurring within Scott Inlet. *Boreogadus saida* sizes were similar between regions, with a slight difference in means observed between Jones Sound and Resolute ($F_{3,151}$=3.162, p=0.02). Significantly smaller individuals of *A. hyperborea* in Arctic Bay compared to other regions ($F_{2,77}$=8.357, p<0.001) contrasted significantly larger mean lengths of *L. decagonus* ($F_{1,7}$=7.663, p=0.027), *Liparis* spp. ($F_{2,5}$=43.49, p<0.001), and *C. reinhardti* ($F_{2,13}$=13.23, p<0.001) observed within Arctic Bay camera sets compared to other regions.

2.3.3 Camera-catch data comparison

Comparisons between small fish species detection at each camera set and catch composition from the nearest whelk pot where the two sampling methods overlapped (near Arctic Bay, Resolute, and Grise Fiord) often show additional species in video estimations of local diversity not present in catch data. Comparing 21 sets of whelk pot fishing and BRUV deployments within 30 km of each other, 14% of species observations occurred in both camera and catch data, 65% of observations occurred only in camera data, and 21% of observations occurred only in catch data (Figure 2.7.9; Figure 2.7.10). Both methods recorded the presence of *B. saida*, *C. reinhardti*, *Cottidae* spp., *E. spinosus*, *Liparis* spp., and *Lycodes* spp.; the video detected the additional presence of a *Gymnelus* spp. and Atlantic poacher that never occurred in corresponding catch data.

In comparing invertebrate composition from these same sets, both methods sampled 49% of taxa; however, only 15% of species observations occurred solely in the camera data, compared to 36% of observations only in catch data (Figure 2.7.9; Figure 2.7.10). Catch proportions (Table 2.6.3) confirm the ubiquity of Ophiurida observed from video sets, as well as the presence of buccinid whelks. The catch data reflected the absence of caridean shrimp in the Resolute videos where shrimp species (primarily *Eualus gaimardi, Lebbus polaris)* represented only 1% of the total catch weight, markedly less than in the Arctic Bay area (17% by weight).

Comparisons of pooled taxa (including large fish and pelagic invertebrates excluded from nearest whelk pot comparisons) for all camera deployments versus all fishing gear sets (i.e. whelk pots, shrimp traps, and longlines) within each region show similar trends for fish and invertebrate detection (Table 2.6.4). For pooled fish taxa comparisons, the camera and catch sampled the same taxa overall across all areas; however, taxa detection differed within each region. In Arctic Bay, 5 camera sets detected the same 8 taxa of fish captured in 40 fishing sets (21 whelk pots, 14 shrimp traps, 5 longlines). Similarly, in Jones Sound 15 camera sets detected 10 taxa compared to 9 taxa from 41 fishing sets (26 whelk pots, 12 shrimp traps, 3 longlines); cameras documented the additional presence of *E. spinosus* and *Gymnelus* spp. whereas longlines captured *R. hippoglossoides* not observed in camera sets at this location. The baited camera did not out-perform the fishing gear in Resolute, with 6 camera sets detecting 4 taxa compared to 7 taxa from 32 fishing sets (21 whelk pots, 10 shrimp traps, 1 longlines). Here the camera also detected the presence of *S. microcephalus* (not present in fishing sets likely due to only a single longline deployment), whereas catch data provided additional observation of *Gymnelus* spp., *Cottidae* spp., *E. spinosus*, and *C. reinhardti*.

Pooled invertebrate taxa comparisons for all camera sets and all fishing gear types for each region detected 17 taxa in both survey methods, with fishing gear detecting the presence of an additional 8-13 taxa in each region (Table 2.6.4). In Arctic Bay, only the camera detected the presence of euphausids, whereas the catch data detected an additional 8 taxa, including *Strongylocentrotus* spp., *U. encrinus*, and *Heliometra* spp. In Resolute all taxa in the video footage were also present in catch data, with the fishing sets detecting an additional 9 taxa, including anemones, holothurians, caridean shrimp, and several infaunal taxa. The highest discrepancy between sampling methods occurred in Jones Sound, with catch data documenting an additional 13 taxa, including *Strongylocentrotus* spp., pennatulid sea pens, *Heliometra* spp., sponges, and the octopus *Bathypolypus arcticus*, while the camera only detected the additional presence of euphausids. Unsurprisingly, video better detected smaller-bodied, pelagic taxa (Amphipoda, Chaetognatha) that were not efficiently captured given the mesh sizes of the fishing gear.

2.4 Discussion

This study presents the first BRUV survey of fishes and invertebrates in the eastern Canadian Arctic, characterizing the benthic environment and taxa of widely ranging sizes within this poorly studied, but rapidly changing, region. The video data described local ichthyofauna, invertebrate communities, and habitat composition, with depth and temperature variations explaining significant differences among sampled regions. Validation of video observations through comparison to proximate fisheries catch data demonstrate the efficiency of baited cameras for species detection, however, cameras performed better for fish observations compared to invertebrate taxa. Overall, these results demonstrate the potential for BRUV surveys as viable method for monitoring species distributions – particularly fishes - in sensitive areas of the North.

Variability in fish and invertebrate assemblage composition among regions likely resulted from differences in depth and temperature, with temperatures increasing with depth. Pairwise comparisons of species contributions to between region similarities using fish peak abundance show lowest dissimilarity between Arctic Bay and Jones Sound (50%). These two regions offer similar temperature and depth ranges, and substrate dominated by soft mud. Lancaster Sound versus Resolute (22%) and Resolute versus Scott Inlet (25%) were most dissimilar. Temperatures were warmest in Scott Inlet and deep sets of Lancaster Sound, whereas sets within Resolute generally sampled shallower, colder habitats, potentially contributing to higher species dissimilarity among regions. Invertebrate assemblages were less dissimilar overall among locations, partly due to the presence of amphipods, chaetognaths, and ophiurids in all sets. Lancaster Sound versus Scott Inlet were the least dissimilar, reflecting similar temperature and depth regimes.

Comparisons of pooled fish taxa for all camera deployments versus all fishing gear sets (i.e. whelk pots, shrimp traps, and longlines) within a region highlight the value of BRUV surveys. Variable detectability over different substrate types presumably explains differences in species presence where the two surveys methods overlapped. Where fine-grain sediment was the dominant substrate type, as in Arctic Bay and Jones

Sound, the baited camera demonstrated equivalent species detection compared to fishing catch. Where rocky substrates occur (Resolute) which may conceal small and cryptic species from view, BRUVs may be less suitable for characterizing species assemblages. However, invertebrate taxa detection in camera observations was notably lower than fishing, possibly because of smaller invertebrate sizes and behaviour. Overall, the camera detected the presence of most mobile invertebrate macroepifauna collected in fishing gear sets, and also detected euphausids that were absent in the catch data. Of the invertebrates only observed within the catch data, 40% were infaunal taxa. Camera detection of invertebrate infauna may be improved by additional camera deployments that could help to detect 'rare' fauna and increase encounters with sessile fauna, or an additional downward-oriented camera or small baited trap at the frame base to improve detection of small, cryptic species. As each string of pot gear samples a substantially larger effective area compared with the camera field of view, the pots likely encounter more species, particularly sessile or slow-moving invertebrates.

The strong detection overlap between methods for fish taxa over uniform, fine-grained sediment bottom, a substrate type that dominated our sampled areas, demonstrates the utility of baited cameras for non-intrusive, ecological assessment of a variety of fauna across many Arctic regions. These results also suggest camera monitoring may require fewer deployments to detect fish taxa adequately within survey areas compared to catch-based surveys, providing a cost-effective method that requires less time than repeatedly deploying and retrieving fishing gear. However, video surveys have inherent limitations, namely lack of access to voucher specimens to confirm identifications to species level, to quantify food-web relationships, or obtain tissue samples for molecular analyses.

Rarefaction curves of extrapolated invertebrate taxa richness indicated that the first video interval (i.e. 30 minutes) characterized an average 65% of the regional taxa diversity, and the first 6 video intervals recorded 90% of the taxa diversity at a site. This results suggests that a set duration of approximately 3 hours reasonably characterizes benthic invertebrate community diversity. Similar curves of extrapolated fish taxa richness suggest a longer set duration in order to assess regional fish communities, with an average 90% of fish taxa diversity observed at sets within approximately 6 hrs. However, curves for fish diversity extrapolated to 11 hrs had not yet reached an asymptote, indicating that deployments exceeding 6 hrs could potentially detect additional species. Deployment times of ≤ 60 minutes characterize a majority of BRUV surveys conducted to date, although many of these shorter deployments targeted depths < 100 m (Whitmarsh et al. 2016). Reduced abundance and potentially diversity at greater depths may require significantly longer soak times and presumably increased replication in order to adequately characterize local assemblages. As such, over 60% of studies conducted to-date sampling below 100 m utilized soak times longer than 90 minutes (Whitmarsh et al. 2016), with many deep-sea studies often exceeding 11 hrs (Jones et al. 2003; Sweetman et al. 2014; Jamieson et al. 2017). The Arctic may host lower diversity compared to lower latitudes (e.g. latitudinal diversity gradient, Rex et al. 1993), therefore polar regions may require longer deployments akin to those needed for deep-ocean diversity characterization. Likewise, the prevalence of non-scavenging species at shallower depths may reduce bait response, potentially requiring more deployments to detect local species, although many species may combine of photo- and chemo-taxis in locating food.

The use of remote underwater video in marine ecology studies has increased with advancements in optical technologies over the last sixty years. These methods offer well-documented advantages (Mallet and Pelletier 2014; Whitmarsh et al. 2016), including a cost effective and efficient sampling method geared toward a low-impact, ecosystem-based approach to species conservation and management. This non-extractive method provides valuable fishery independent data suitable for a wide variety of habitats, depths, and taxa. However, increased popularity has led to diversification of experimental designs. This lack of consistent protocol for methods, variability in bait type and quantity, as well as uncertainty surrounding the area and longevity of attraction currently limit baited camera methods (Harvey et al. 2013; Whitmarsh et al. 2016) that warrant attention from future studies. Despite these issues, BRUVs offer a desirable alternative or compliment to traditional survey methods, with wide success in ecological monitoring of a variety of coastal and deep-sea habitats (King et al. 2008; Jamieson et al. 2009; Mallet and Pelletier 2014; Whitmarsh et al., 2014) and protected areas worldwide (Langlois et al. 2006; Bond et al. 2012; Roberson et al., 2015).

Significantly fewer BRUV surveys have occurred in polar waters compared to temperate and tropical regions, with a few exploratory studies in the Antarctic (Collins et al. 2002; Gregory et al. 2017) and in Arctic waters east of Greenland (Linley et al. 2015). Limited commercial fisheries in the Arctic Ocean (Christiansen et al. 2013; Stock et al.

2017) have spared many benthic marine ecosystems the impacts of bottom trawling, presumably preserving pristine benthic habitats. As northern waters become increasingly more accessible, BRUVs provide an attractive, low-impact method to monitor species distributions in a changing polar environment while maintaining the integrity of these sensitive habitats.

Understanding current ecosystem dynamics, and predicting potential shifts in local assemblages with future change requires further exploration of biogeographical patterns of species distributions. However, such data are exceedingly sparse for much of the Arctic, and particularly for deep-water environments where warmer water temperatures may support northern range expansions of southern species. For many years, warming in the Arctic has exceeded the global average (Hoegh-Guldberg and Bruno 2010; Duarte et al. 2012). Recent studies already report range shifts for marine fishes, with expansion of boreal species and retraction of Arctic fish communities in the Barents Sea (Fossheim et al. 2015), and nearly two-thirds of North Sea marine fishes have shifted in distribution over the past 25 years, with all but one species expanding northward (Perry et al. 2005). Detecting the presence and rate at which such range shifts occur offer a valuable tool for measuring the impact of climate change on local marine communities; however, detecting such changes requires sufficient time-series data – either from long-term scientific monitoring or historical catch data from commercial fisheries.

High operating costs (Mallory et al. 2018), inaccessibility due to seasonal ice coverage, and limited fisheries exploitation in the north likely explain significant gaps in sampling coverage and temporal monitoring throughout much of the Canadian Arctic.

Cost-effective and efficient sampling of BRUVs may provide a suitable conservation-sensitive approach to monitoring Arctic waters and detecting indicators of change. Although previous studies documented most of the fish in our study within the Canadian Arctic, the observation of *B. brosme* in Scott Inlet likely represents a new record for this area, given that current published species lists (Coad and Reist 2017) and online distribution resources (OBIS, Fishbase) lack records for this species beyond Davis Strait. Our camera observations potentially expand the northern record for this fish by over 700 km. With sparse or no previous sampling of fish populations in our study areas, our observations help to extend or fill in major spatial gaps in the range for nearly all species encountered. This contribution demonstrates the utility of optical technologies such as BRUV surveys to monitor marine environments efficiently and detect species shifts in Canada’s changing northern waters.

Many habitat-forming, sessile organisms such as corals and sponges are fragile and slow-growing, so removal by fishing gear may significantly impact local populations (Clark et al. 2016). There should therefore be high incentive to use non-destructive tools – such as remote cameras - in pristine, undisturbed regions throughout the high Arctic, to address critical knowledge gaps while maintaining habitat integrity. Our exploratory fishing surveys utilized only fixed gears (pots, traps), however, these gear types captured a surprisingly high numbers of corals: 202 *U. encrinus* sea pens, 5 *Virgularia* sp. sea pens, 96 Nephtheid soft corals (including 5 *Gersemia rubiformis* colonies), and 18 sponges from 5 longlines, 14 shrimp traps, and 35 whelk pots. Bycatch rates of *U. encrinus* were usually high, as this species frequently occurred in clusters of 5-10 individuals draped on top of each pot/trap, presumably raked off the bottom by rope lines connecting subsequent pots/traps during gear retrieval. Life history studies of this species indicate slow-growth and high longevity; one of our bycatch specimens measured 230 cm and was aged to ~68 years (Neves et al. 2018). High encounter rates of this species suggest that *U. encrinus* and other sensitive cold-water corals (e.g. Nephtheid soft corals) are prone to incidental bycatch in emerging fisheries.

Baited cameras can provide a suite of valuable ecological data, including species composition and distribution, habitat use, size, relative and/or theoretical abundance indices, and could be deployed through the ice in winter months for seasonal surveys in polar environments. With adequate coverage, BRUV surveys could be a useful, non-destructive tool for exploring marine communities, and detecting the presence of cold-water corals, sponges, and other benthic taxa in these unknown regions. More generally, these data show the feasibility of baited cameras for use as an effective monitoring tool, with the ability to address critical knowledge gaps in our understanding of the biogeography of Arctic species in a region experiencing potential fisheries expansion and changing ocean conditions.

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2.6 Tables

Table 2.6.1 Summary of camera set details including location, depth (m), temperature (°C), set duration (minutes), and a qualitative description of the bottom type based on the video footage.

Set	Location	Latitude	Longitude	Depth (m)	Temperature (°C)	Duration (min)	Bottom type
1	Arctic Bay	73.18	-85.68	610	0.3	570	Fine-grained sediment with cobbles
2	Arctic Bay	73.25	-85.71	645	0.3	595	Fine-grained sediment
3	Arctic Bay	73.29	-85.56	671	0.3	587	Fine-grained sediment
5	Arctic Bay	73.00	-85.42	350	0.0	605	Fine-grained sediment with cobbles
6	Arctic Bay	73.03	-85.96	710	0.3	386	Fine-grained sediment
4	Lancaster Sound	74.11	-83.50	677	1.0	615	Fine-grained sediment
7	Lancaster Sound	74.28	-83.37	720	1.0	495	Fine-grained sediment
8	Lancaster Sound	74.37	-88.37	360	-0.2	462	Fine-grained sediment with boulder
9	Resolute	75.10	-97.00	304	-1.2	250	Fine-grained sediment
10	Resolute	74.62	-95.08	112	-1.0	448	Pebble
11	Resolute	74.50	-95.85	209	-1.1	450	Fine-grained sediment with cobble
12	Resolute	74.94	-96.97	264	-1.2	599	Fine-grained sediment
13	Resolute	74.57	-96.35	210	-1.1	414	Fine-grained sediment
14	Resolute	74.66	-95.29	143	-1.1	395	Pebble with boulders
15	Jones Sound	76.31	-82.78	665	0.2	464	Fine-grained sediment
16	Jones Sound	76.24	-82.62	736	0.2	568	Fine-grained sediment
17	Jones Sound	76.50	-82.14	420	-0.1	487	Fine-grained sediment
18	Jones Sound	76.65	-82.42	262	-0.2	570	Fine-grained sediment
19	Jones Sound	76.56	-82.08	352	-0.1	505	Fine-grained sediment
20	Jones Sound	76.38	-81.86	451	0.1	565	Fine-grained sediment
21	Jones Sound	76.36	-81.35	498	0.2	565	Fine-grained sediment
22	Jones Sound	76.30	-81.96	747	0.2	532	Fine-grained sediment
23	Jones Sound	76.12	-82.33	873	0.2	553	Fine-grained sediment
24	Jones Sound	76.02	-81.55	712	0.2	571	Fine-grained sediment
25	Jones Sound	76.09	-82.78	840	0.2	176	Fine-grained sediment
26	Jones Sound	76.08	-83.58	699	0.2	581	Fine-grained sediment
27	Jones Sound	76.30	-83.43	432	0.2	568	Fine-grained sediment
28	Jones Sound	76.45	-83.15	405	-0.1	406	Fine-grained sediment
29	Jones Sound	76.54	-83.17	233	-0.5	447	Fine-grained sediment
30	Scott Inlet	70.89	-71.60	620	1.1	549	Fine-grained sediment with rocks
31	Scott Inlet	71.12	-70.53	802	1.1	570	Fine-grained sediment

Table 2.6.2 Summary of fish taxa camera observations per region, reporting mean n_{max} for each region, total number of measurements taken (n_{TL}), and mean total length (cm) ± standard deviation with length ranges in parentheses below. The * denotes sets where taxa was present but no individuals were measured. Note: As individuals of most species are indistinguishable, length sample sizes do not reflect total number of individuals observed at the camera.

FISH TAXA	**FAMILY**	**Arctic Bay n = 5**			**Lancaster Sound n = 3**			**Resolute n = 6**			**Jones Sound n = 15**			**Scott Inlet n = 2**		
		n_{max}	**n_{TL}**	**Mean ± SD (range)**	**n_{max}**	**n_{TL}**	**Mean ± SD (range)**	**n_{max}**	**n_{TL}**	**Mean ± SD (range)**	**n_{max}**	**n_{TL}**	**Mean ± SD (range)**	**n_{max}**	**n_{TL}**	**Mean ± SD (range)**
Somniosus microcephalus	Somniosidae	1.8	25	254.5 ± 32.0 (195-314)	1.3	7	235.6 ± 47.8 (157 – 286)	0.3	3	281.3 ± 28.3 (264 – 314)	1.3	52	249.5 ± 33.2 (195 – 320)	1	7	198.3 ± 73.8 (131 – 325)
Amblyraja hyperborea	Rajidae	0.2	3	20.4 ± 7.6 (15 – 29)	1.3	49	49.6 ± 11.6 (15 – 80)	0	-	-	0.9	28	44.0 ± 14.6 (10 – 76)	0	-	-
Boreogadus saida	Gadidae	1.4	21	14.0 ± 5.0 (9 – 26)	0.3	25	13.3 ± 2.5 (9 – 19)	0.8	71	13.4 ± 2.5 (8 – 21)	1.6	38	15.4 ± 4.8 (7 – 30)	0.5	-	*
Careproctus reinhardti	Liparidae	0.2	5	20.5 ± 1.5 (19 – 22)	0.3	1	19	0	-	-	0.4	10	13.3 ± 3.2 (10 – 16)	0	-	-
Cottidae spp.	Cottidae	0.4	1	12	0	-	-	0	-	-	0.9	19	17.0 ± 3.9 (9 – 26)	0	-	-
Leptagonus decagonus	Agonidae	0.8	2	22.0 ± 7.1 (17 – 27)	0	-	-	0	-	-	0.8	7	14.7 ± 2.0 (12 – 17)	0	-	-
Liparis spp.	Liparidae	1.0	5	18.1 ± 1.3 (17 – 20)	0	-	-	0.3	2	8.5 ± 2.1 (7 – 10)	0.1	1	7	0	-	-
Lycodes spp.	Zoarcidae	0.8	4	31.3 ± 14.9 (17 – 46)	0.7	1	35	0.2	2	12.0 ± 2.8 (10 – 14)	0.4	5	18.6 ± 5.8 (10 – 25)	0	-	-
Reinhardtius hippoglossoides	Pleuronectidae	0	-	-	0.7	8	47.4 ± 6.7 (40 – 62)	0	-	-	0	-	-	0.5	1	51
Mallotus villosus	Osmeridae	0	-	-	0.3	-	*	0	-	-	0	-	-	0	-	-

Eumicrotremus spinosus	Cyclopteridae	0	-	-	0	-	-	0	-	-	0.1	1	8	0	-	-
Gymnelus spp.	Zoarcidae	0	-	-	0	-	-	0	-	-	0.1	2	16.6 ± 1.9 (15 – 18)	0	-	-
Hippoglossoides platessoides	Pleuronectidae	0	-	-	0	-	-	0	-	-	0	-	-	0.5	2	33.3 ± 7.1 (28 – 38)
Brosme brosme	Lotidae	0	-	-	0	-	-	0	-	-	0	-	-	0.5	1	59
Unknown	Unknown	0	-	-	0	-	-	0	-	-	0	-	-	0.5	-	*

Table 2.6.3 Summary of invertebrate taxa observed from camera deployments within each region, reporting presence or absence for each region (sets combined by region), and the total percent occurrence within all sets (all regions combined) reported for each taxa.

REGION		**Arctic Bay**	**Lancaster Sound**	**Resolute**	**Jones Sound**	**Scott Inlet**	**TOTAL**
Number of sets		5	3	4	11	2	25
PHYLUM	TAXON	(1 = PRESENT, 0 = ABSENT)					% OCCURANCE
Arthropoda	Amphipoda	1	1	1	1	1	100
Chaetognatha	Chaetognatha	1	1	1	1	1	100
Echinodermata	Ophiurida	1	1	1	1	1	100
Cnidaria	Nephtheidae	1	1	1	1	1	68
Echinodermata	Asteroidea	1	1	1	1	0	56
Arthropoda	Caridea	1	1	0	1	1	56
Annelida	Polychaeta	1	1	0	1	1	52
Mollusca	Buccinidae	1	1	1	1	1	48
Cnidaria	Actiniaria	1	1	0	1	1	40
Arthropoda	Euphausidea	1	0	0	1	0	28
Arthropoda	Pycnogonidae	0	0	1	1	0	16
Echinodermata	*Elpidia* sp.	1	1	0	0	0	16
Echinodermata	*Gorgonocephalus* spp.	1	0	1	1	0	12
Bryozoa	Bryozoa	1	0	1	0	0	12
Echinodermata	*Heliometra* spp.	0	1	1	0	0	8
Porifera	Porifera	1	0	1	0	0	8
Cnidaria	*Umbellula encrinus*	0	0	0	1	0	4
Echinodermata	*Strongylocentrotus* spp.	0	0	1	0	0	4

Table 2.6.4 Comparison of species/ taxa observed from camera deployments versus ALL fishing gear used in exploratory fisheries surveys, including whelk pot (WP), shrimp trap (ST), and longline (LL) gears.

Location	**FISHES**		**INVERTEBRATES**			
	Camera	**Catch**	**Camera**		**Catch**	
Arctic Bay Camera = 5 sets Catch= 21 WP, 14 ST, 5 LL	*A. hyperborea* *B. saida* *C. reinhardti* Cottidae spp. *L. decagonus* *Liparis* spp. *Lycodes* spp. *S. microcephalus*	*A. hyperborea* *B. saida* *C. reinhardti* Cottidae spp. *L. decagonus* *Liparis* spp. *Lycodes* spp. *S. microcephalus*	Actiniaria Amphipoda Asteroidea Bryozoa Buccinidae Caridea Chaetognatha	*Elpidia* spp. Euphausidea *Gorgonocephalus* spp. Nephtheidae Polychaeta Porifera Ophiuroidea	Actiniaria Amphipoda Annelida Asteroidea Bryozoa Buccinidae Caridea Chaetognatha Cumacea Elpidia sp. *Gorgonocephalus* spp.	*Heliometra* spp. Myas spp. Nephtheidae Nudibrancha Ophiuroidea Polychaeta Porifera Pycnogonidae *Strongylocentrotus* spp. *U. encrinus*
Resolute Camera = 6 sets Catch = 21 WP, 10 ST, 1 LL	*B. saida* *Liparis* spp. *Lycodes* spp. *S. microcephalus*	*B. saida* *C. reinhardti* Cottidae spp. *E. spinosus* *Gymnelus* spp. *Liparis* spp. *Lycodes* spp.	Amphipoda Asteroidea Bryozoa Buccinidae Chaetognatha *Gorgonocephalus* spp.	Heliometra spp. Nephtheidae Porifera Pycnogonidae Ophiuroidea *Strongylocentrotus* spp.	Actiniaria Amphipoda Annelida Asteroidea Bryozoa Buccinidae Caridea *Gorgonocephalus* spp. *Heliometra* spp. Holothuroidea	Isopoda *Myas* spp. Mytilidae Nephtheidae Nudibrancha Ophiuroidea Polychaeta Porifera Pycnogonidae *Strongylocentrotus* spp.
Jones Sound Camera = 15 sets Catch = 26 WP, 12 ST, 3 LL	*A. hyperborea* *B. saida* *C. reinhardti* Cottidae spp. *E. spinosus* *Gymnelus* spp. *L. decagonus* *Liparis* spp. *Lycodes* spp. *S. microcephalus*	*A. hyperborea* *B. saida* *C. reinhardti* Cottidae spp. *L. decagonus* *Liparis* spp. *Lycodes* spp. *R. hippoglossoides* *S. microcephalus*	Actiniaria Amphipoda Asteroidea Buccinidae Caridea Chaetognatha Euphausidea	*Gorgonocephalus* spp. Nephtheidae Polychaeta Pycnogonidae Ophiuroidea *U. encrinus*	Actiniaria Amphipod Annelida Asteroidea *Bathypolypus arcticus* Buccinidae Bryozoa Caridea Chaetognatha Cumacea *Elpidia* spp. *Gorgonocephalus* spp. *Heliometra* spp.	Isopoda *Myas* spp. Mytilidae Nephtheidae Ophiuroidea Pennatulidae Polychaeta Porifera Pycnogonidae Sipunculida *Strongylocentrotus* spp. *U. encrinus*

2.7 Figures

Fig. 2.7.1 Map of study area showing positions of each baited camera deployment in the five sampled regions of Arctic Bay, Lancaster Sound, Resolute, Jones Sound, and Scott Inlet. Insets show locations of exploratory fishing sets in Resolute (a), Jones Sound (b), and Arctic Bay (c) regions. Gear types include whelk pots (triangles), shrimp traps (squares), and longlines (crosses).

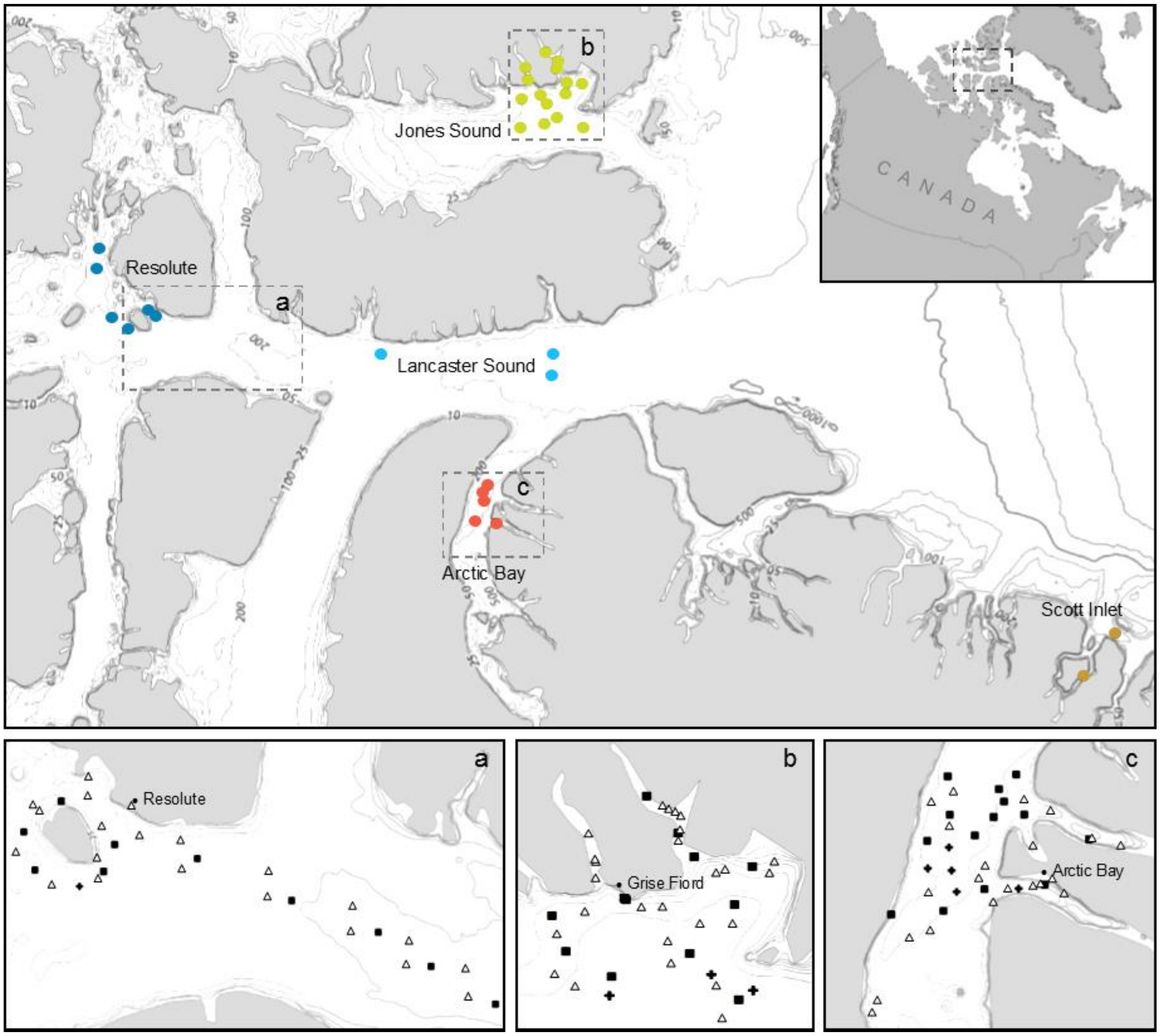


Figure 2.7.2 Diagrams of frame design and deployment configuration. a) Illustration of frame design and dimensions, with camera system components attached. b) Configuration of gear deployment, with camera frame in line with anchors and buoys for retrieval.

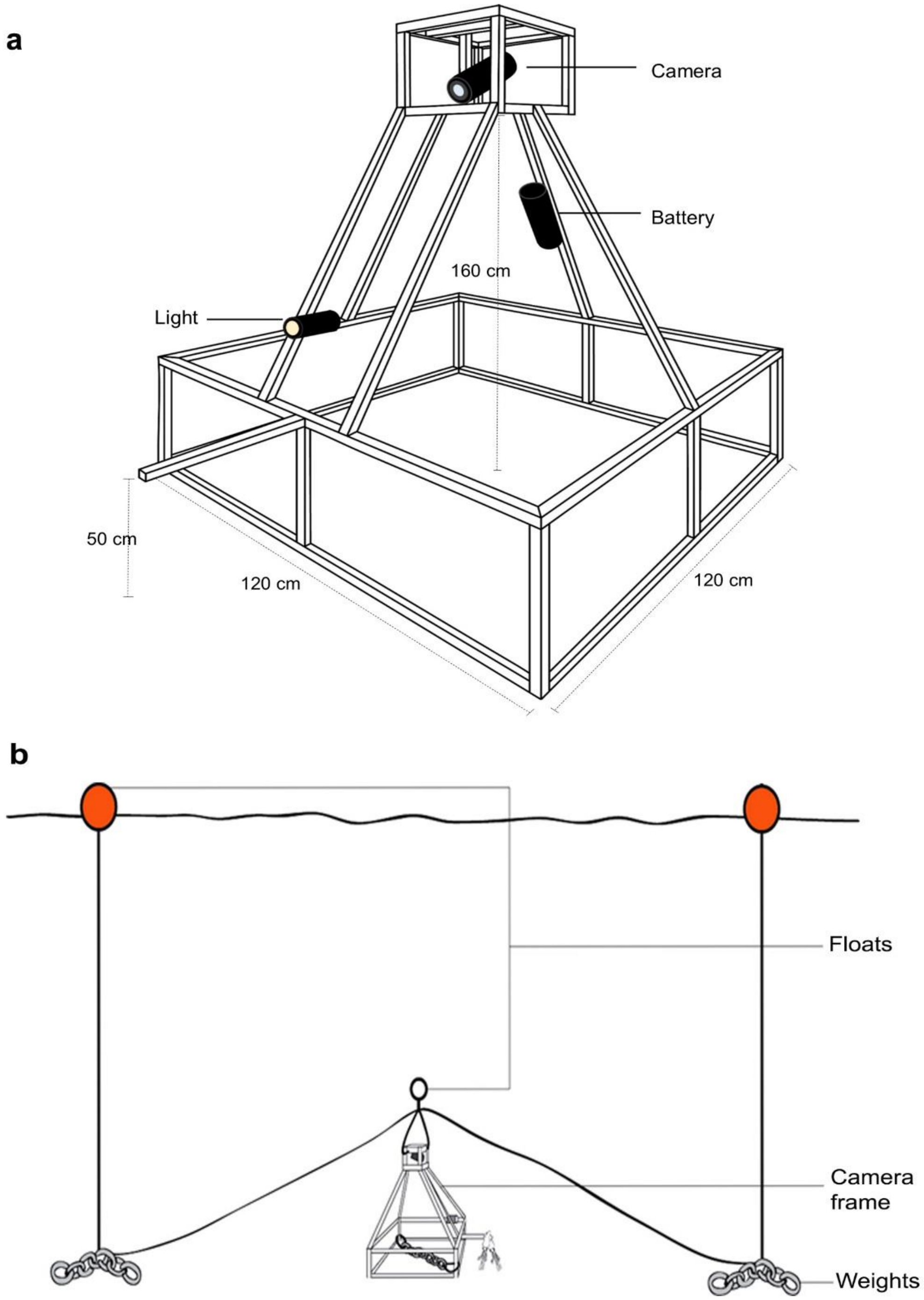


Figure 2.7.3 Positive relationship between number of taxa observed and number of samples per set for fish (closed) and invertebrates (open).

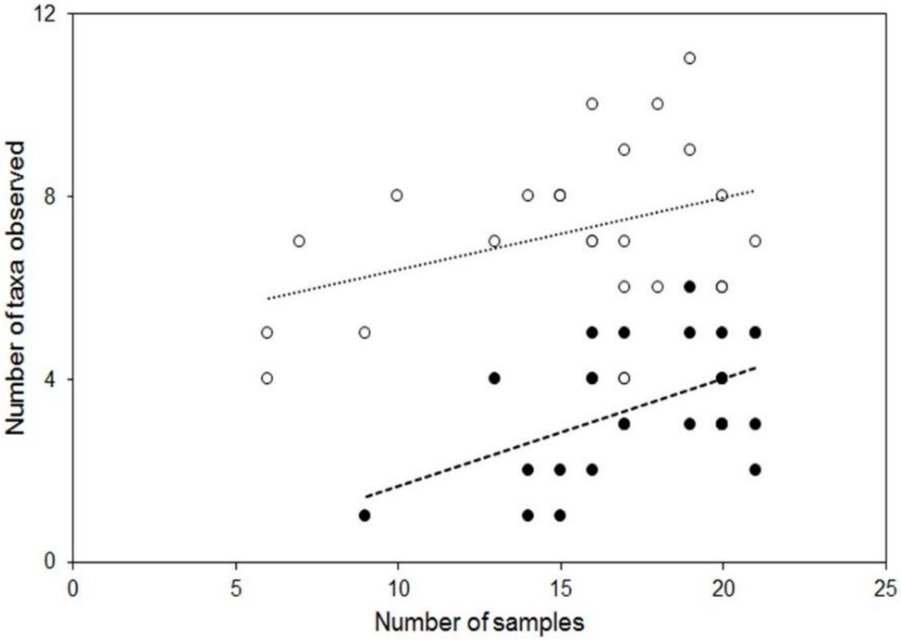


Figure 2.7.4 Bottom depth - temperature relationship across all regions and gear types. All closed symbols correspond to data collected from fishing gear (longlines, pots, traps) sets in Arctic Bay (triangle), Resolute (diamond), and Jones Sound (circle) regions. Open symbols represent camera deployments in these regions. Lancaster Sound (square) and Scott Inlet (cross) regions have camera deployments only.

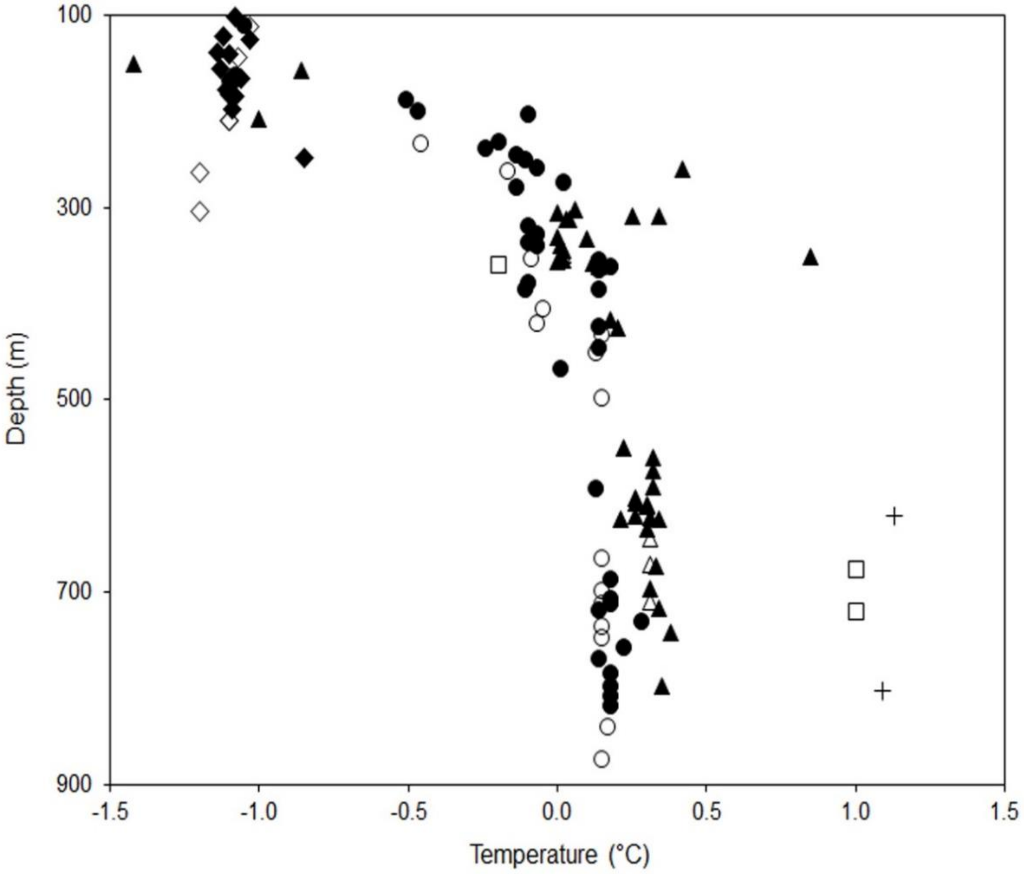


Figure 2.7.5 Images captured by baited camera within the study area: A) *Boreogadus saida*; B) *Somniosus microcephalus*; C) *Careproctus reinhardti*; D) *Reinhardtius hippoglossoides*; E) *Lycodes* spp.; F) *Liparis* spp.; G) *Amblyraja hyperborea*; H) example of rocky substrate in Resolute Pass with crinoid *Heliometra* spp.

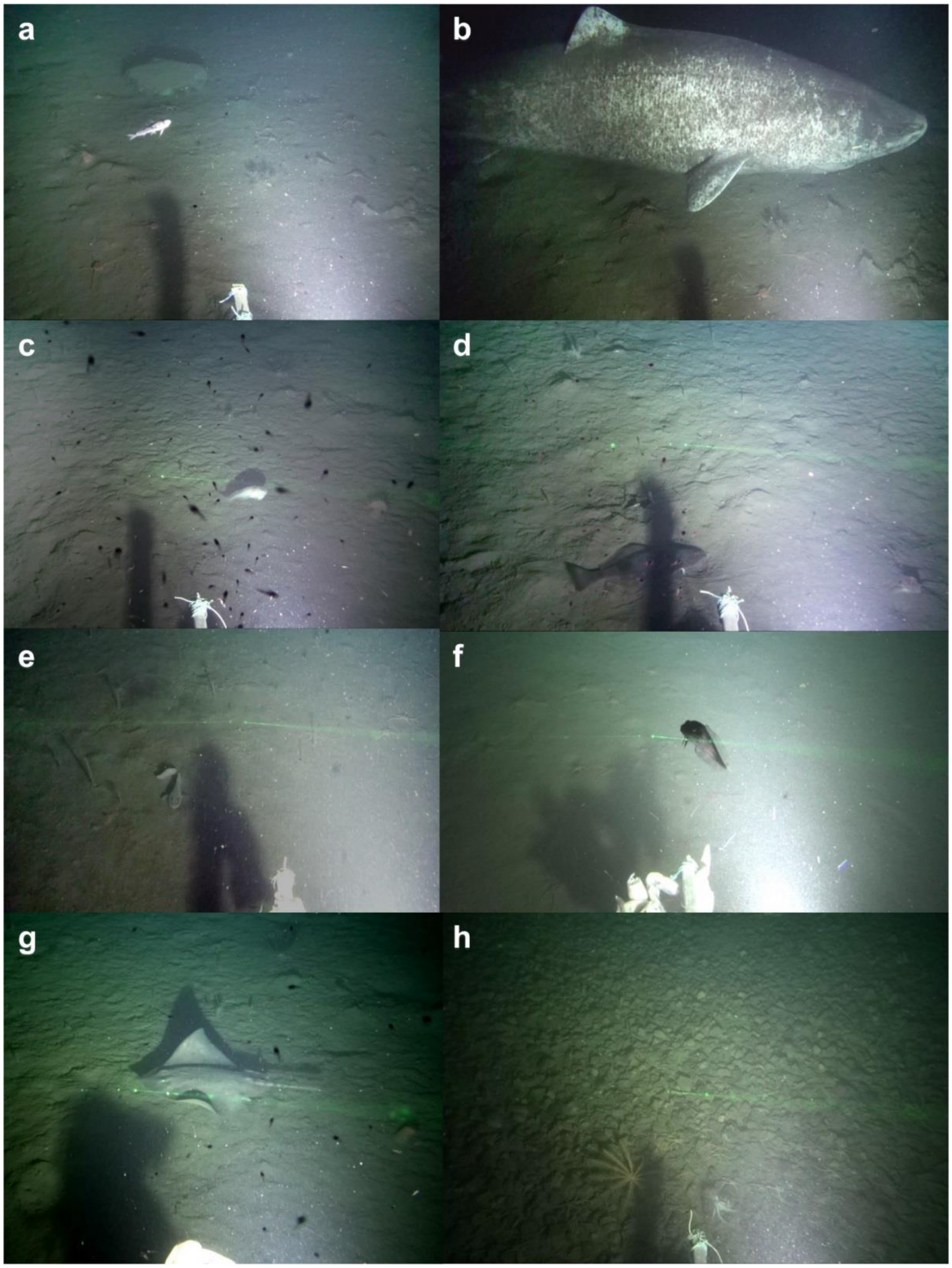


Figure 2.7.6 Depth and temperature ranges for fish observations at each sampling region. Solid bars represent set range for deployments within each region.

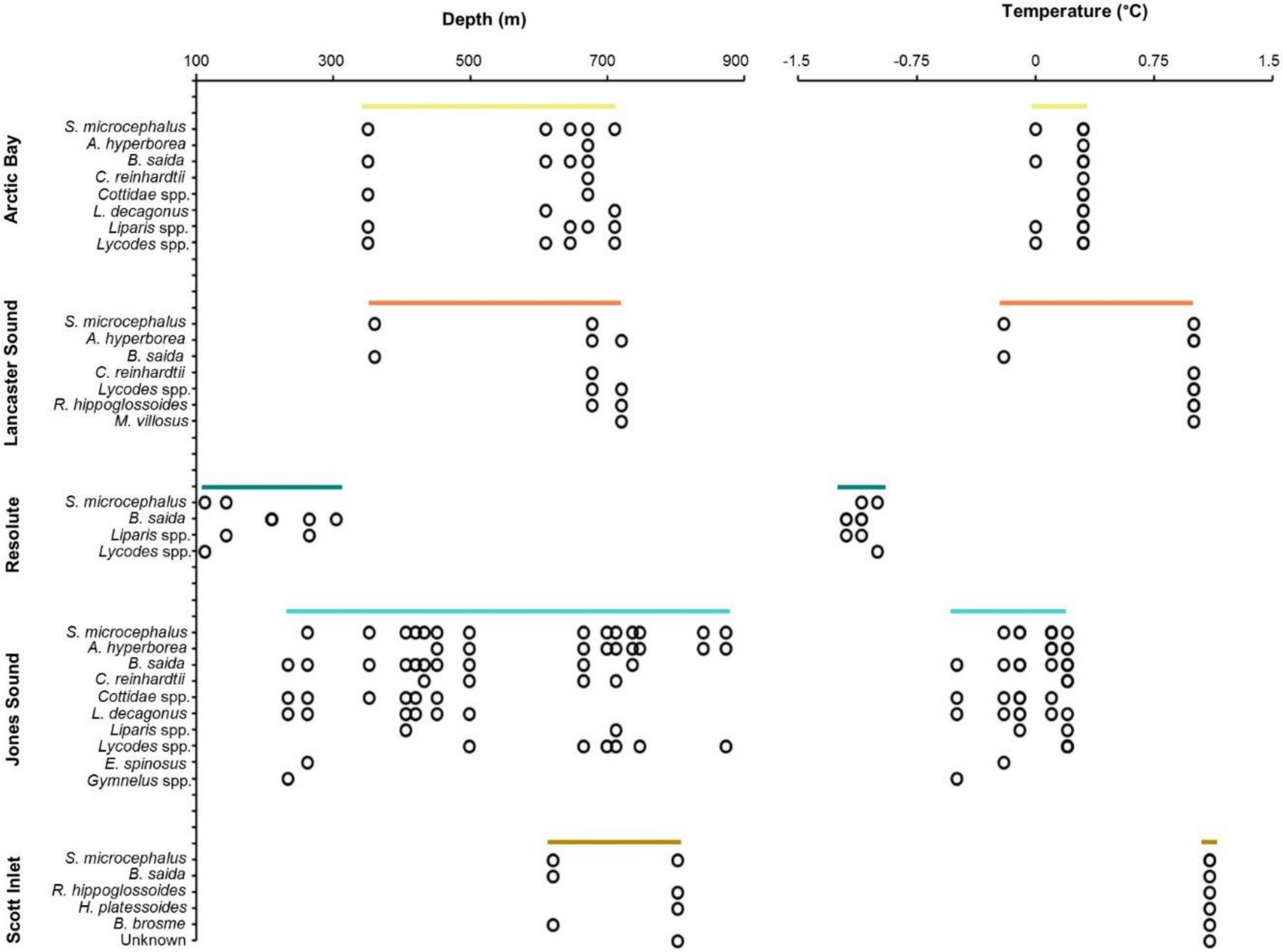


Figure 2.7.7 Combined extrapolated rarefaction curves using mean values for all sets and regions, displayed as cumulative proportion of total observed taxa extrapolated to 21 samples (samples taken at 30 minute intervals) for invertebrate taxa (black line) and fish taxa (grey line) diversity with 95% confidence intervals (dashed lines). Vertical lines denote average time by which 90% of taxa were observed.

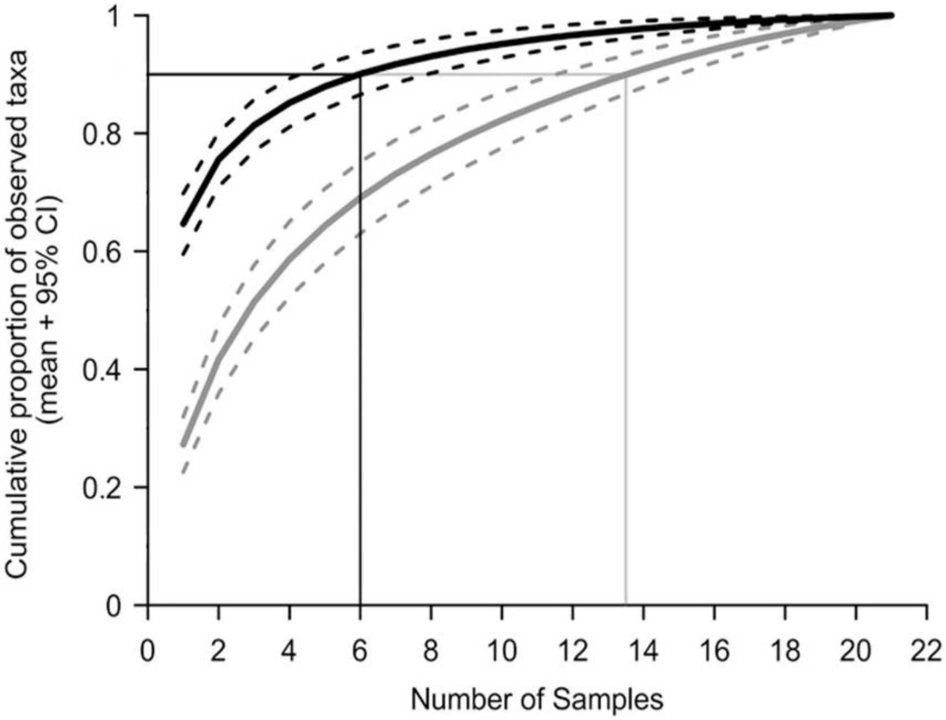


Figure 2.7.8 Non-metric MDS plots of square-root transformed Bray-Curtis similarity matrices of (a) fish Nmax and (b) invertebrate P-A from each region. Dotted lines correspond to 50% similarity for fishes and 75% similarity for invertebrates based on hierarchical cluster analyses.

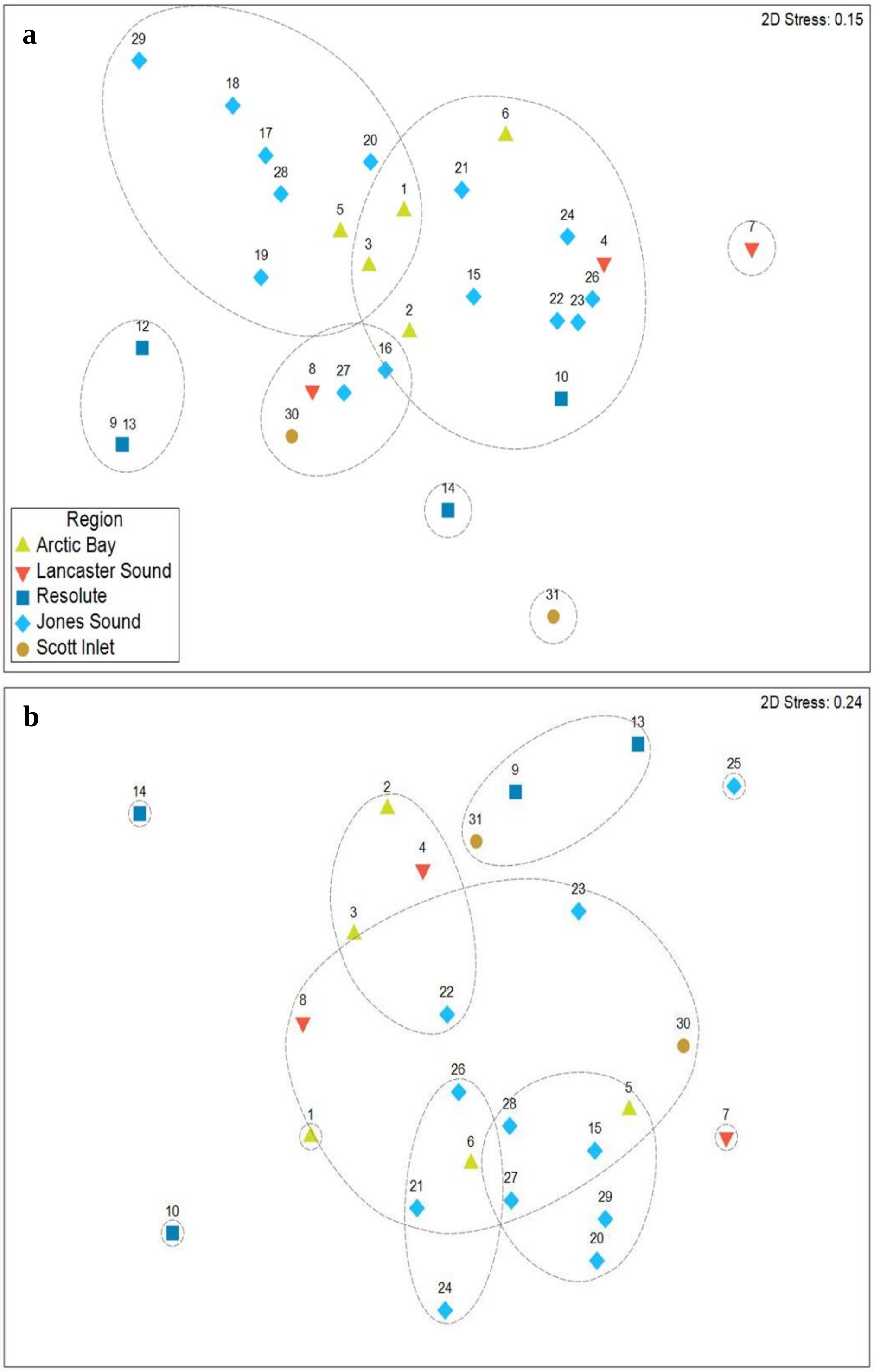


Figure 2.7.9 Mean proportion of fish (circle) and invertebrate (triangle) taxa observed by both the survey methods, by only camera sets, and by only catch data from nearest whelk pot fishing sets across all regions where spatial overlap of the two survey methods occurred (Arctic Bay, Resolute, and Jones Sound).

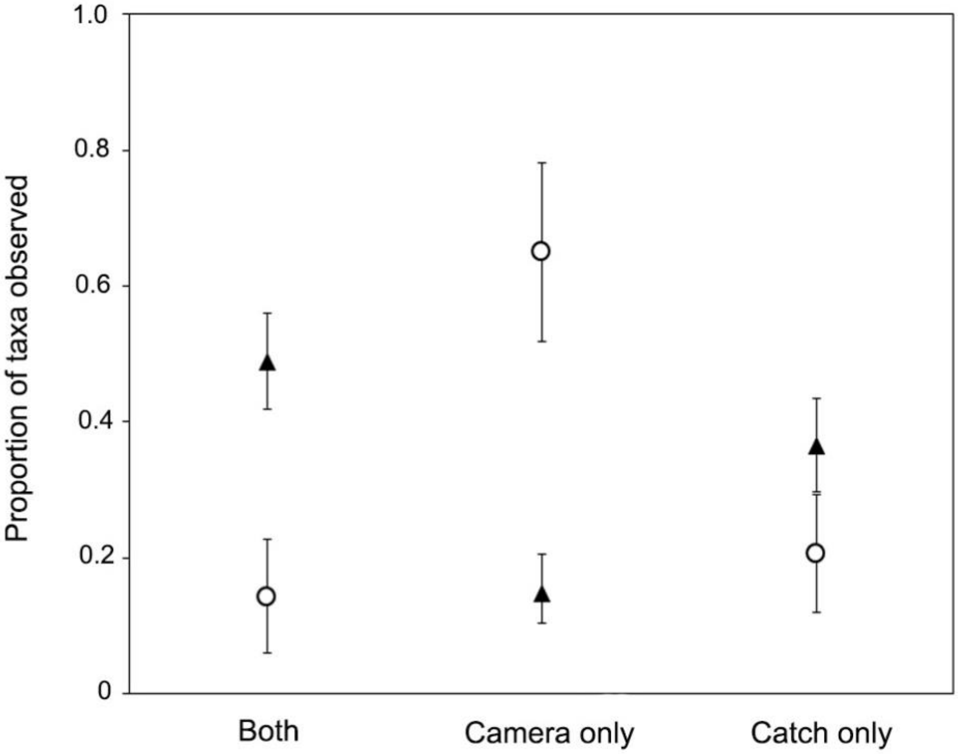
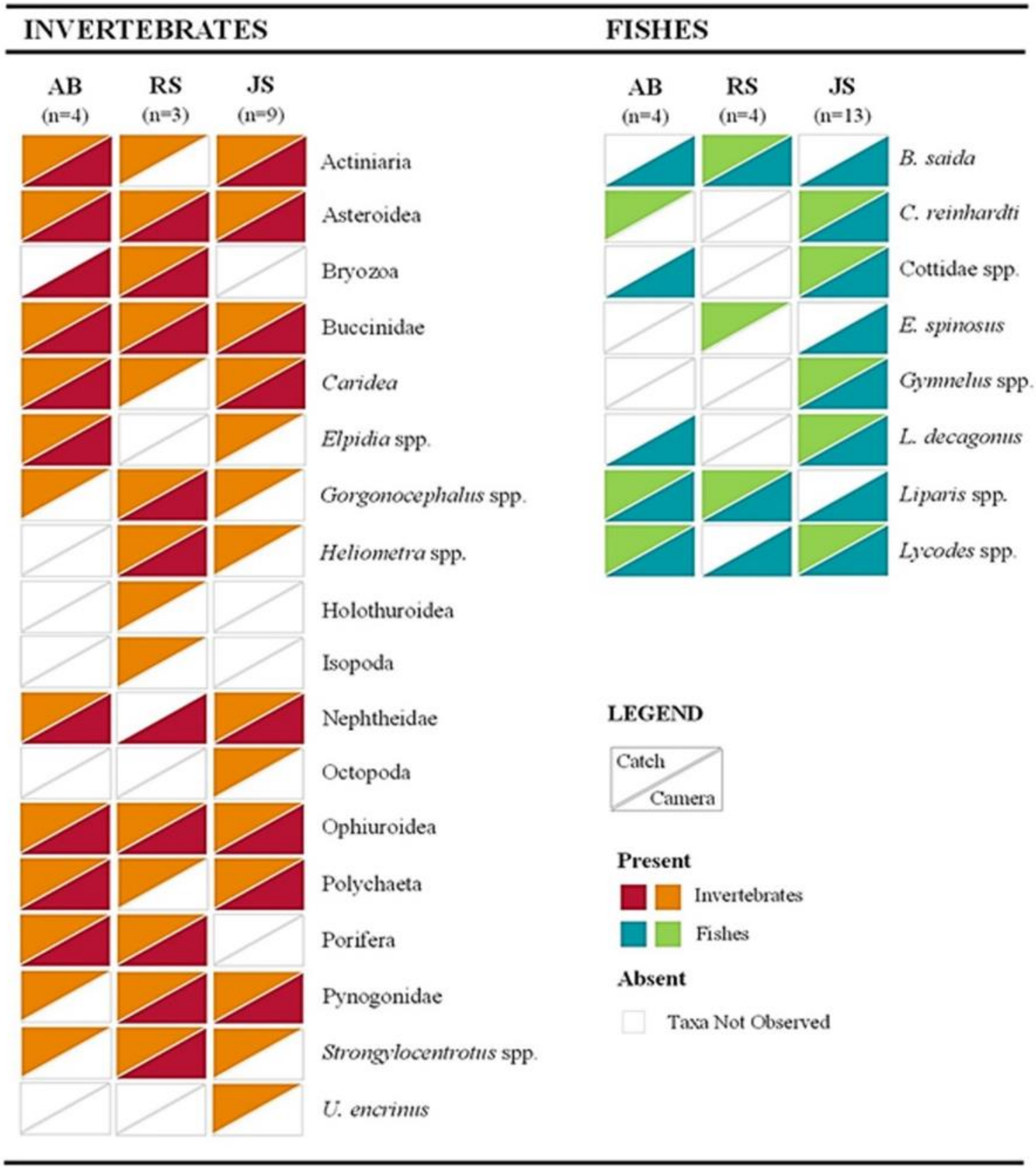


Figure 2.7.10 Fish and invertebrate taxa observed by the camera and nearest whelk pot catch data where the two survey methods overlapped spatially (Arctic Bay, Resolute, and Jones Sound). White indicates when taxa were not observed.



3 First estimates of Greenland shark (*Somniosus microcephalus*) local abundances in Arctic waters

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Abstract

Baited remote underwater video cameras were deployed in the Eastern Canadian Arctic, for the purpose of estimating local densities of the long-lived Greenland shark within five deep-water, data-poor regions of interest for fisheries development and marine conservation in Nunavut, Canada. A total of 31 camera deployments occurred between July-September in 2015 and 2016 during joint exploratory fishing and scientific cruises. Greenland sharks appeared at 80% of deployments. A total of 142 individuals were identified and no individuals were observed in more than one deployment. Estimates of Greenland shark abundance and biomass were calculated from averaged times of first arrival, video-derived swimming speed and length data, and local current speed estimates. Density estimates varied 1-15 fold among regions; being highest in warmer (>0°C), deeper areas and lowest in shallow, sub-zero temperature regions. These baited camera results illustrate the ubiquity of this elusive species and suggest that Nunavut's Lancaster Sound eco-zone may be of particular importance for Greenland shark, a potentially vulnerable Arctic species.

3.1 Introduction

One of very few polar shark species, the Greenland shark *Somniosus microcephalus* is found throughout the cold waters of the North Atlantic and Arctic Oceans (Lynghammar et al. 2013). It is the largest fish in the Arctic and a top predator (Yano et al. 2007; MacNeil et al. 2012; Nielsen et al. 2013), despite anomalously slow swimming speeds (Watanabe et al. 2012) and presumed limited visual acuity as a common host to the corneal copepod parasite *Ommatokoia elongata* (Borucinska et al. 1998). However, the Greenland shark remains a poorly studied species and many aspects of its basic ecology are unknown (MacNeil et al. 2012). Limited life history studies have revealed a remarkably slow growth rate (<1cm yr^{-1} [Hansen 1963]), late maturation timing (mature females > 450 cm [Yano et al. 2007] and ~134 years old [Nielsen et al. 2016]), and Greenland shark currently holds the record for the longest lifespan of any vertebrate species (> 272 years; Nielsen et al. 2016).

Body size (Dulvy et al. 2014) and survival to maturity (Pardo et al. 2016) are key traits of elasmobranchs associated with population extinction risks worldwide. The paucity of data concerning these traits and Greenland shark population dynamics has led to its designation as ‘near threatened’ (Kyne et al. 2017) or ‘data deficient’ (Henriksen and Hilmo 2015) throughout parts of its range; in other areas it remains unassessed (Davis et al. 2013). Therefore an urgent need exists to address major knowledge gaps concerning past, present, and potential future population dynamics (Davis et al. 2013). While some other shark species’ abundance and biomass baselines are being monitored and revised

(Bradley et al. 2017a, 2017b), similar fishery-independent baselines for Greenland shark have not yet been established in any area.

Much of our current understanding regarding the distribution and abundance of Greenland sharks has been obtained from historical commercial exploitation and current bycatch in northern fisheries. Historically, this species was commercially fished for liver oil until 1960 (Castro et al. 1999), with annual catch estimates in the early 20th century ranging from 32,000 to 150,000 sharks in Greenland and Norway (Jensen 1914; Lydersen et al. 2016). The species is still harvested today for human and sled-dog consumption, with mean annual reported landings of 47 t since 1980 (FAO 2016). It is also a bycatch species in northern Canadian fisheries, particularly within Greenland halibut *Reinhardtius hippoglossoides* trawl and gillnet fisheries, with mean annual bycatch rates from 1996 to 2015 in Canada’s NAFO divisions 0AB exceeding 105 t per year (Davis et al. 2013; Fisheries and Oceans Canada 2016). However, in areas of the North Atlantic and Arctic Ocean where directed shark fishing has not occurred – such as the waters of the Canadian Arctic Archipelago – the geographic and bathymetric range of this species remains largely unknown.

Scientific longline surveys are the most common fishery-independent survey method used for sampling shark populations. Relative abundance estimates (e.g. catch per unit effort) provide insights into the spatial and temporal variability in shark abundance and habitat use (Simpfendorfer et al. 2002; Pikitch et al.2005). However, such surveys are not ideal for all species because mortality rates can be high and even capture stress can have adverse effects which may result in reduced fitness and/or delayed post-capture mortality (Campana et al. 2009; Gallagher et al. 2014). Although quantitative estimates of capture mortality rates for Greenland shark have yet to be enumerated, this species is prone to gear entanglement as these large sharks rotate to free themselves from bottom longline gear, and other Greenland sharks are known to depredate conspecifics caught in this way (Idrobo and Berkes 2012). These behaviours could exacerbate stress-related impacts and may increase the likelihood of capture mortality (Davis et al. 2013; Barkley et al. 2016), therefore alternative methods to scientific longlining are needed to quantify Greenland shark abundance and distribution.

Optical technologies are utilized worldwide to survey marine organisms, providing versatile, non-destructive tools to monitor both benthic and pelagic species (Bailey et al. 2007; Letessier et al. 2013; Jamieson 2016). In particular, baited remote underwater video (BRUV) surveys have become increasingly popular as cost-effective and relatively simple survey methods, with high accessibility to users as many BRUVs can be readily assembled with inexpensive components (Watson and Huntington 2016; Bergshoeff et al. 2017). BRUVs have produced results comparable to some traditional fishing gear based survey methods, including longline surveys sampling relative shark abundances (Brooks et al. 2011; Santana-Garcon et al. 2014). BRUVs have also proven useful in surveying sensitive habitats such as marine protected areas (Cappo et al. 2003; Terres et al. 2015), reef habitats (Linley et al. 2015; Lindfield et al. 2015), and other habitats where the low impact nature of BRUVs are deemed favourable (King et al. 2008; Yeh and Drazen 2009). With comparatively fewer commercial fisheries occurring in the Arctic Ocean (Christiansen et al. 2013; Stock et al. 2017), many benthic marine ecosystems have been spared the impacts of bottom trawling, presumably preserving pristine benthic habitats including cold-water corals and sponges. BRUVs therefore provide an ideal method to survey polar marine environments while maintaining the integrity of these sensitive habitats.

BRUVs generate many types of data that can be used to characterize benthic habitats, assess functional diversity, body sizes, and animal behaviours, and quantify the relative abundances and distributions of identified species. Priede and Merrett (1996) demonstrated a significant negative relationship between fish abundances from trawl surveys and arrival time of the first fish to proximately deployed baited cameras for the abyssal grenadier *Coryphaenoides armatus*. This discovery confirmed the validity of a model used to estimate local theoretical abundance from baited cameras using first arrival time, current velocity, and swimming speed (Priede et al. 1990; Priede and Merrett 1996), and has since been applied to other species (Priede et al. 1994; Yau et al. 2001; Cousins et al. 2013). Greenland shark individuals are believed to be non-shoaling, mobile predators, and are known opportunistic scavengers (Dunbar and Hildebrand 1952; Leclerc et al. 2011). Therefore, while the theoretical abundance model was originally developed for an abyssal teleost and not a Selachimorphan, search strategies are presumably comparable between species, although how species-specific differences in olfactory sensitivities may influence theoretical density estimates requires further research (Jamieson 2016). As Greenland shark satisfies these behavioural assumptions for the model, BRUVs may provide a non-destructive and efficient method of generating local population estimates for this poorly understood Arctic predator.

Here we present estimates of Greenland shark local relative abundances within the Canadian Arctic Archipelago using data obtained from baited camera surveys and established models of theoretical abundance using first arrival times and bottom current and swimming speed estimates. We present these estimates in the context of local habitat and oceanographic conditions, relative abundance, and size-and-sex structure of Greenland sharks observed in the waters adjacent to the northern Nunavut regions of Arctic Bay, Resolute, Lancaster Sound, Scott Inlet and Grise Fiord (Figure 3.7.1).

3.2 Materials and Methods

3.2.1 Baited camera

A total of 31 baited camera deployments were conducted in July-September of 2015 and 2016 aboard the 30 m Arctic Fishery Alliance vessel Kiviuq I in the following five regions within the northern Canadian territory of Nunavut: Admiralty Inlet and Adams Sound near the community of Arctic Bay (hereafter 'Arctic Bay'); central Lancaster Sound; southeast McDougall Sound/Barrow Strait near the community of Resolute (hereafter 'Resolute'); eastern Jones Sound including Starnes Fiord and Grise Fiord (hereafter 'Jones Sound'), and; Scott Inlet (Figure 3.7.1). Deployment locations were selected to provide maximum spatial, depth, and habitat coverage throughout each region within the confined range of the exploratory fisheries (largely for Greenland halibut) simultaneously conducted aboard the vessel. Deployment depths varied between sites, ranging from 112 to 850 m (Table 3.6.1) reflecting differences in bathymetry among these regions (Figure 3.7.2a). Bottom temperatures at each camera set were derived from temperature loggers (DST centi-TD Star-Oddi, Gardabaer, Iceland) attached to the nearest bottom fishing gear set conducted at similar depth within Resolute and Arctic Bay regions (2015) or attached directly to the camera frame (2016). At camera deployments in 2015 where temperature loggers were unavailable (i.e. three Lancaster Sound deployments), bottom temperature was taken from CTD (conductivity, temperature, depth) profiler casts performed aboard the CCGS Amundsen in August 2015 (ArcticNet 2015) at similar depths and at locations nearest (<50 nm) to the camera deployments.

The baited camera lander consisted of a single high-definition camera with integrated reference lasers (parallel and spaced 6.2 cm apart) and a white light source (1Cam Alpha, Aquorea LED; SubC Imaging Inc., Clarenville, Newfoundland and Labrador, Canada) mounted to a weighted aluminum frame tethered to a surface buoy for later retrieval. The camera was positioned at the top of the frame at 1.6 m above the seafloor and oriented downward and outward at approximately a 60° angle, with continuous recording at each location. A horizontal bait arm was positioned 50 cm above the seafloor, extended toward the field of view, with approximately 2 kg of commercial grade squid bait (6-8 whole squid) affixed to the bait arm for each deployment.

Within each camera set, arrival times were recorded for the first Greenland shark individual to appear after the camera frame landed on the seafloor, and for each subsequent individual arriving to the baited camera. Individual Greenland sharks were easily distinguished using unique markings (i.e. scar patterns and coloration), length, and sex, which enabled quantification of numbers of individuals observed per set (Figure

3.7.3). Shark lengths were estimated from video still images using the software ImageJ (Schneider 2012) for all sharks that fully entered the field of view and were in line with the camera reference lasers as required for accurate estimates of body size. A general linear model was used to test for differences in length between sexes (Table A3) and location. An additional generalized linear model with a poisson distribution was used to examine the relationship between the total number of sharks observed and parameters of region, first arrival time, duration, and temperature across deployments. All analyses were performed using the statistical software R version 3.3.2 (R Core Team 2015). All methods were carried out under experimental licenses and ethics approval granted by the Department of Fisheries and Oceans Canada and in accordance with experimental protocol approved by the animal ethics committee of Memorial University of Newfoundland.

3.2.2 Abundance estimates

Densities of Greenland shark within the 5 regions were calculated using first arrival time (t_0, seconds), shark swimming speed (V_f, ms^{-1}), and current velocity (V_w, ms^{-1}) based on the following equation originally developed and validated for the abyssal grenadier (Priede et al. 1990):

$$^{(1)} \quad N\ (\#\ \text{individuals km}^{-2}) = 0.3849(1/V_f + 1/V_w)^2 / t_0^{\,2}$$

Estimates of abundance were calculated from averaged first arrival times within region (Priede and Merrett 1996) and using mean measures of swimming speed and current speed. Mean swimming speed for this species was derived from the subset of shark encounters (n=31) where swimming occurred at a consistent rate perpendicular to the camera view, and with lasers passing horizontally along the anteroposterior axis of each shark. No measurements were taken from sharks while approaching the bait, only sharks passing through the field of view at a steady swimming speed. Still images from videos were processed in ImageJ software to measure the speed lasers moved alongside the body, providing inputs to calculate mean swimming speed for the present study. Estimates of bottom current velocity were extracted from the Ocean Navigator portal (http://navigator.oceansdata.ca) using the Regional Ice Ocean Predication System 2016 data set (Dupont et al. 2015; Lemieux et al. 2016). For each set, the location, date, and time of deployment were used as model filters to obtain an average bottom current speed for each set. As we could not measure shark mass, biomass estimates within each region were derived using a length-weight relationship (MacNeil et al. 2012) and our mean shark length per region to calculate estimates of kg km^{-2}.

3.3 Results

Greenland shark was the primary consumer of the bait at the camera and was present in 25 of 31 deployments, but with differing local densities among regions (Table 3.6.1). In total, 142 individuals were identified from the video footage (Figure 3.7.3) and no individuals were observed in multiple camera sets. Sharks were present - and often numerous - in sets near Arctic Bay, with up to 18 individuals present in a single set in Admiralty Inlet (Figure 3.7.1, Table 3.6.1). Observation rates based on the number of individuals sighted per hour were highest in Arctic Bay (mean=1.1 sharks hr^{-1}), similar among Lancaster Sound, Scott Inlet, and Jones Sound (mean=0.5, 0.5, and 0.6 sharks hr^{-1}, respectively), and were lowest in sets near Resolute (mean=0.1 sharks hr^{-1}) with only a few observations (n=3) of sharks in the two shallowest sets within Resolute Pass (Figure 3.7.1). Approximately 75% of sharks were observed at depths from 450 to 800 m (Figure 3.7.2b) and at temperatures from 0 to 0.5 °C (Figure 3.7.2c). A general linear model indicated no significant length differences (n=93 sharks measured) between males versus females (Figure 3.7.4). Overall, no differences in size or sex ratios of sharks were observed among locations ($F_{9, 83}$=1.93, p= 0.06) with the exception of Scott Inlet, which had a significantly higher proportion of small (<150cm) sharks (p<0.01) in the set that occurred within Scott Inlet fiord. Despite body lengths as high as 325 cm, most male and all female sharks were below hypothesised sizes at maturity (Figure 3.7.4).

First arrival times of Greenland sharks to the bait differed among regions, with mean arrival times (± S.D.) longest in Resolute (280 min ± 84) compared to 198 min (± 142) in Jones Sound, 191 min (± 142) in Scott Inlet, and 118 min in both Arctic Bay (± 146) and Lancaster Sound (± 112) (Table 3.6.1). Even prior to estimating local theoretical abundances, there was a negative exponential relationship between first arrival times and total individuals observed ($N = 9.50e^{-0.004t}$, $R^2 = 0.52$, Figure 3.7.5). A generalized linear model also found a significant relationship between total number of sharks observed and first arrival time (z=-3.396, p<0.001) and set duration (z=2.331, p=0.02), but not with region or temperature (p>0.06). Bait was removed by Greenland sharks from Set-1 within 22 minutes of arrival on the seafloor, which may have lessened attraction throughout the deployment, therefore this set was excluded from local abundance calculations.

Swimming speeds derived from 31 measurements across 20 Greenland sharks (TL range 185-314 cm) in this study resulted in a mean swimming speed of 0.27 ms^{-1} (S.D. = 0.07; range 0.15 – 0.42ms^{-1}) and no significant correlation between shark length and speed (r=0.11, p=0.65; Figure 3.7.6). Bottom current speed estimates extracted from a regional ocean model varied between locations, with considerably higher velocities in Lancaster Sound and Resolute (0.1 ms^{-1}) compared to other regions (0.02 - 0.05 ms^{-1}).

Local abundance estimates using mean first arrival times within region, mean swimming speed, and mean bottom current speed within region indicated variable theoretical abundance values between regions. Shark density estimates were higher in Arctic Bay (5.0 individuals km^{-2} and Jones Sound (4.7 individuals km^{-2}) regions compared to waters of Lancaster Sound (1.6 individuals km^{-2}) and Resolute (0.4 individual km^{-2}) (Figure 3.7.7). Local estimates for Scott Inlet were highest (15.5 individuals km^{-2}), but we note that only 2 sets occurred in this region. Estimated local biomass values showed the same rankings as abundances among regions, ranging from 93 to 1210 kg km^{-2} estimated across regions based on numbers and sizes observed (Table 3.6.2).

3.4 Discussion

This study provides the first data and estimates of Greenland shark local and regional abundances independent of fishing and bycatch estimates. This finding is a first step toward fulfilling a major knowledge gap currently preventing assessment of population status needed for the management of this species (Davis et al. 2013).

Theoretical abundance estimates derived from first arrival times of Greenland sharks and total individuals observed both indicate higher concentrations in Arctic Bay, Jones Sound, and Scott Inlet, suggesting these regions may be of particular importance for this species during the summer months. Additionally, camera deployments provided a simple means to collect data on depth, temperature, shark size, and sex distribution in poorly sampled areas within the range of Greenland sharks in Canadian waters.

While Greenland sharks were observed in 80% of camera deployments, spatial variation in their observed and estimated local densities and biomass were associated with co-varying oceanographic conditions. In regions of the Canadian Arctic Archipelago examined, there is a strong summer thermocline, such that water temperatures typically reach minima at intermediate depths (ca. 100-150 m) and become warmer at depth (Michel et al. 2006). Such changes are evident within and among regions, with shark densities peaking at intermediate temperatures sampled (Figure 3.7.2c), and at depths between 450-800 m (Figure 3.7.2b). This may explain the lower number of sharks observed and estimated for waters near Resolute, where average set temperature was -1.1°C and depths below 450 m are unavailable. Although there is variation in sharks observed among sets within regions, with future sampling and a more stratified or systematic spatial coverage, it may be possible to extrapolate to larger areas. In our sampled areas, Admiralty Inlet has an area of 8557 km^2, Lancaster Sound spans 26335 km^2, McDougal Sound covers 4327 km^2 ; Jones Sound is approximately 14,330 km^2. In all of these regions, large areas cover the depth and temperature ranges sampled in this study. Given the opportunistic deployments confined here to the areas of interest to exploratory fishing, the wide-spread occurrences of Greenland sharks across regions highlights their apparent ubiquity, with local abundances influenced by temperature and depth.

Both the sensitivity of our estimated shark densities to model inputs and the need for validation of modeled density estimates are required before such values could be used to estimate population abundances at any spatial scale. In order to demonstrate the effects of first arrival time and current speed, we explored variation in theoretical shark densities across a range of both parameters, and overlaid results from the five regions examined (Figure 3.7.8). The inverse square relationship dictates average t_0 values should be used in abundance models for each region (Priede and Merrett 1996), however the influence of current speed (Figure 3.7.8) emphasizes the need to consider spatial and temporal variation in current speeds (Taylor et al. 2013). The effects of variable swimming speed are equal to those of current speeds in this model, and while we used a fixed swimming speed based on the mean of our observations (0.27 ms^{-1}), our value is within the range of mean reported swimming speed for this species (0.22ms^{-1} to 0.34ms^{-1} based on ultrasonic tracking (Skomal and Benz 2004) and data logging tags (Watanabe et al. 2012), respectively). Replacing our video-derived speed with the only direct measure of speed for Greenland shark (mean = 0.34 ms^{-1}) derived from accelerometer tagging data (Watanabe et al. 2012), the calculated theoretical densities change slightly, decreasing between 0.1 - 0.3 sharks per km^2 among regions.

Further validation of our model results might be achieved through comparisons with data sets within this study and those using other techniques. Within our video analyses, there was a strong positive correlation between the total number of individuals observed and local densities based on first arrival times among 4 of our 5 sampling regions ($r = 0.97$, $p = 0.02$, $n = 4$), with the exception of Scott Inlet where number of individuals observed did not align with theoretical estimates. As one of the two sets in Scott Inlet was characterized by a low mean current speed and quick first arrival time resulting in an unusually high abundance, additional sets are required for more robust density estimates in this region. However, the general correspondence between abundance metrics provides confidence in the theoretical estimates, as the mean number of sharks actually sighted within regions (but not used directly in estimates of local density) corresponds with the proposed abundance values for most regions (Table 3.6.2), but also highlights the need for further studies to determine the necessary sampling effort within regions.

Tagging studies have begun to elucidate movement patterns within the eastern Canadian Arctic (Skomal and Benz 2004; Campana et al. 2015) and other Arctic regions (Fisk et al. 2012; Campana et al. 2015), indicating Greenland sharks are capable of long distance migrations (>1000 km) with excursions between inshore and offshore waters. As these sharks may be highly migratory, seasonal fluctuations in local densities may occur. More camera deployments are needed to examine intra- and inter-annual variability in shark abundance and habitat use. However, even our 31 deployments demonstrate clear differences in relative abundances between regions, and highlight water readily used by Greenland sharks in summer months, including potential nursery areas for small (<150 cm) sharks. Given the recent establishment of the boundaries of what will become the

Lancaster Sound National Marine Conservation Area which encompasses nearly half of our camera deployments, further surveys are essential to characterize spatial variation in local densities and connectivity between broader Arctic regions, and to provide new information for species management both inside and outside of protected areas.

Our findings are revealing in the context of recent life history information and future management potential for this species within the Canadian Arctic. Assuming similar growth rates as individuals sampled from other regions and examined for maturity status (Yano et al. 2007), the males and females we observed may all be sexually immature. While these may be somewhat small (mean 2.48 m, SD = 0.40) relative to mature sharks (Figure 3.7.4), the mean length among 166 sharks of known and unknown sex compiled previously (McClain et al. 2015) was 3.07 m (SD = 0.73). Together, these findings suggest that the vast majority of reported specimens of this species may be juveniles. In addition the use of superficial markings to distinguish individuals provided us with a catalog of over 100 individuals appearing in videos throughout the sampled area. As with other shark species where photo-ID catalogues exist (e.g. white shark *Carcharadon carcharias*, whale shark *Rhincodon typus*), with repeat deployments this information could potentially be used to track individuals throughout their range (Graham and Roberts 2007; Barker and Williamson 2010; Towner et al. 2013). With adequate coverage and seasonality to deployments, BRUV surveys could additionally help to describe movement patterns and site fidelity behaviour which for this species remain largely unknown.

In a comparative context, it is also revealing to examine our Greenland shark video survey results from unexploited regions to estimates of dominant shark local density and biomass from intensively sampled, pristine tropical areas. Recently revised estimates of grey reef shark *Carcharhinus amblyrhynchos* abundance from the protected island of Palmyra have revealed mean shark densities of 21.3 sharks km^{-2} (Bradley et al. 2017a). That estimate is comparable to the upper end of estimated Greenland shark abundances (Figure 3.7.7), illustrating similar densities between these two dominant sharks in their respective tropical and Arctic ecosystems. Estimated biomass of the grey reef shark based on their mean lengths (718 kg km^{-2} at Palmyra; DeCrosta et al. 1984; Bradley et al. 2017b) are lower than Greenland shark estimates within three regions (Table 3.6.2), due to large differences in mean mass per individual. However, total biomass of sharks at Palmyra (Bradley et al. 2017a) greatly exceeds that of any and all Arctic locations, given the presence of multiple shark species at Palmyra. A further comparison of our results to BRUV survey data from the remote tropical island of New Caledonia show surprising similarities in observation rates. There, shark occurrences from 209 BRUV deployments yielded an observation rate of 0.43 individuals hr^{-1} for all 9 reef sharks combined (Juhel et al. 2017), compared to our mean Greenland shark observation rate of 0.56 individuals hr^{-1} from our five Arctic regions. The size and apparent density of Greenland sharks in Canadian Arctic waters conceals the fact that as the only large fish predator they have a unique taxonomic and functional role in Arctic waters compared to shark species in many other areas.

Finally, our results illustrate that in areas explored within the Canadian Arctic Archipelago, Greenland sharks are seemingly widespread and commonly inhabit a wide range of depth and temperature conditions. However, as with other shark species (Dulvy et al. 2014; Pardo et al. 2016), their life history features concomitantly highlight the need for considering Greenland sharks in spatial management and bycatch avoidance plans in this region. In gillnet fisheries targeting Greenland halibut, Greenland shark bycatch was negatively associated with halibut catch, suggesting that where possible, shark avoidance and maximum targeted catch rates may be mutually achievable goals (Cosandey-Godin et al. 2015). Whether similar patterns occur in longline fisheries has yet to be established. Spatial management has multiple approaches and recently, the Lancaster Sound region has been identified by Parks Canada, Nunavut communities, and non-governmental organizations as a priority conservation region and is expected to be designated Canada’s largest area of protected ocean. Our study provides a largely non-invasive means to evaluate marine conservation areas before and after establishment using baited underwater video.

3.5 Literature Cited

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3.6 Tables

Table 3.6.1 Summary of camera deployment details, shark arrival times, number of sharks present in first 250 minutes (approximately half of average set duration) and total number of sharks throughout each duration. Number of individuals was not reported for Set 25 (‘-’) where camera did not remain upright for the entirety of the set so quantification of individuals was not possible; ‘X’s indicate sets were no sharks were observed.

Set	**Region**	**Date**	**Latitude N**	**Longitude W**	**Depth (m)**	**Temperature (°C)**	**Duration (min)**	**First arrival t_0 (min)**	**Sharks in first 250 minutes**	**Total number of sharks**
1	Arctic Bay	21-Aug-15	73.176	-85.679	610	0.3	570	19	4	5
2	Arctic Bay	22-Aug-15	73.245	-85.714	645	0.3	595	4	4	15
3	Arctic Bay	23-Aug-15	73.292	-85.563	671	0.3	587	81	7	18
4	Lancaster Sound	24-Aug-15	74.108	-83.497	677	1.0	615	197	2	8
5	Arctic Bay	25-Aug-15	72.996	-85.417	350	0.0	605	54	4	14
6	Arctic Bay	26-Aug-15	73.026	-85.961	710	0.3	386	332	0	1
7	Lancaster Sound	27-Aug-15	74.276	-83.369	720	1.0	495	X	X	X
8	Lancaster Sound	31-Aug-15	74.369	-88.369	360	-0.2	462	39	5	5
9	Resolute	02-Sep-15	75.101	-96.999	304	-1.2	250	X	X	X
10	Resolute	04-Sep-15	74.625	-95.075	112	-1.0	448	221	1	2
11	Resolute	05-Sep-15	74.497	-95.848	209	-1.1	450	X	X	X
12	Resolute	06-Sep-15	74.941	-96.970	264	-1.2	599	X	X	X
13	Resolute	08-Sep-15	74.574	-96.352	210	-1.1	414	X	X	X
14	Resolute	09-Sep-15	74.662	-95.292	143	-1.1	395	340	0	1
15	Jones Sound	26-Jul-16	76.312	-82.784	665	0.2	464	387	0	3
16	Jones Sound	27-Jul-16	76.238	-82.623	736	0.2	568	191	3	8
17	Jones Sound	28-Jul-16	76.504	-82.143	420	-0.1	487	324	0	3
18	Jones Sound	29-Jul-16	76.649	-82.416	262	-0.2	570	259	0	3
19	Jones Sound	30-Jul-16	76.565	-82.076	352	-0.1	505	87	1	2
20	Jones Sound	31-Jul-16	76.381	-81.857	451	0.1	565	23	6	11
21	Jones Sound	01-Aug-16	76.357	-81.345	498	0.2	565	67	2	7
22	Jones Sound	02-Aug-16	76.303	-81.955	747	0.2	532	37	3	6
23	Jones Sound	03-Aug-16	76.123	-82.333	873	0.2	553	455	0	1
24	Jones Sound	04-Aug-16	76.015	-81.546	712	0.2	571	349	0	3
25	Jones Sound	06-Aug-16	76.086	-82.775	840	0.2	176	134	-	-
26	Jones Sound	07-Aug-16	76.080	-83.582	699	0.2	581	146	1	4
27	Jones Sound	08-Aug-16	76.297	-83.432	432	0.2	568	264	0	8

28	Jones Sound	09-Aug-16	76.448	-83.153	405	-0.1	406	53	3	6
29	Jones Sound	10-Aug-16	76.542	-83.168	233	-0.5	447	X	X	X
30	Scott Inlet	22-Sep-16	70.890	-71.599	620	1.1	549	72	5	6
31	Scott Inlet	23-Sep-16	71.123	-70.530	802	1.1	570	310	0	2

Table 3.6.2 Summary of mean length and associated weights derived from the MacNeil et al.[3] length-weight relationship, theoretical abundances per square kilometer, theoretical biomass per square kilometer, mean number of sharks observed in the first 250 minutes of each deployment, and mean total number of sharks observed in each deployment per region.

Region	**Mean length (cm) ± S.D.**	**Estimated weight (kg)**	**Abundance estimate (#-km^{-2})**	**Biomass estimate (kg-km^{-2})**	**Mean observed in first 250 minutes**	**Mean observed total**
Arctic Bay	254.5 ± 32.0 (n=25)	170.4	5.0	852.0	4	11
Jones Sound	249.5 ± 33.2 (n=52)	160.2	4.7	752.9	1	4
Lancaster Sound	235.6 ± 47.8 (n=7)	133.8	1.6	214.1	2	2
Resolute	281.3 ± 28.3 (n=3)	233.2	0.4	93.3	0	1
Scott Inlet	198.3 ± 73.8 (n=6)	78.1	15.5	1210.6	3	6

3.7 Figures

Figure 3.7.1 Map of baited camera deployments where Greenland sharks were observed, with symbol sizes proportional to the number of individuals distinguished from each set. The ‘X’ indicates sets where no sharks were observed.

NOAA National Centers for Environmental Information (NCEI); International Bathymetric Chart of the Arctic Ocean (IBCAO); General Bathymetric Chart of the Oceans (GEBCO)

Figure 3.7.2 Depth versus temperature relationships for deployments (A) from all regions: Arctic Bay (▴), Lancaster Sound (▪), Resolute (♦), Jones Sound (•), and Scott Inlet (+), with frequency distributions for the number of sharks observed across sampled depths (B) and temperatures (C).

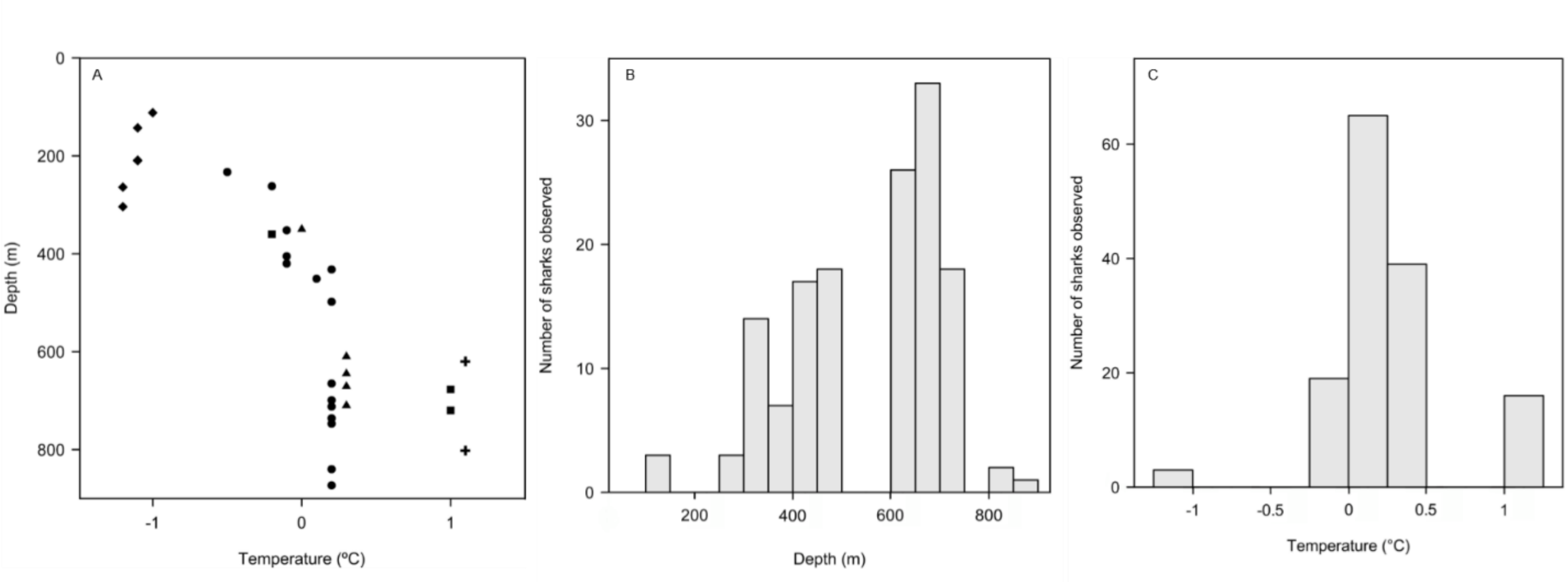


Figure 3.7.3 Images of Greenland sharks attracted to the baited camera: A) Typical size and coloration of sharks observed, showing distinct scar patterns; B) Feeding on squid bait, with multiple sharks within field of view; C) Example of unique scar patterns used to distinguish individuals; D and E) Juvenile sharks <150 cm observed in Scott Inlet.

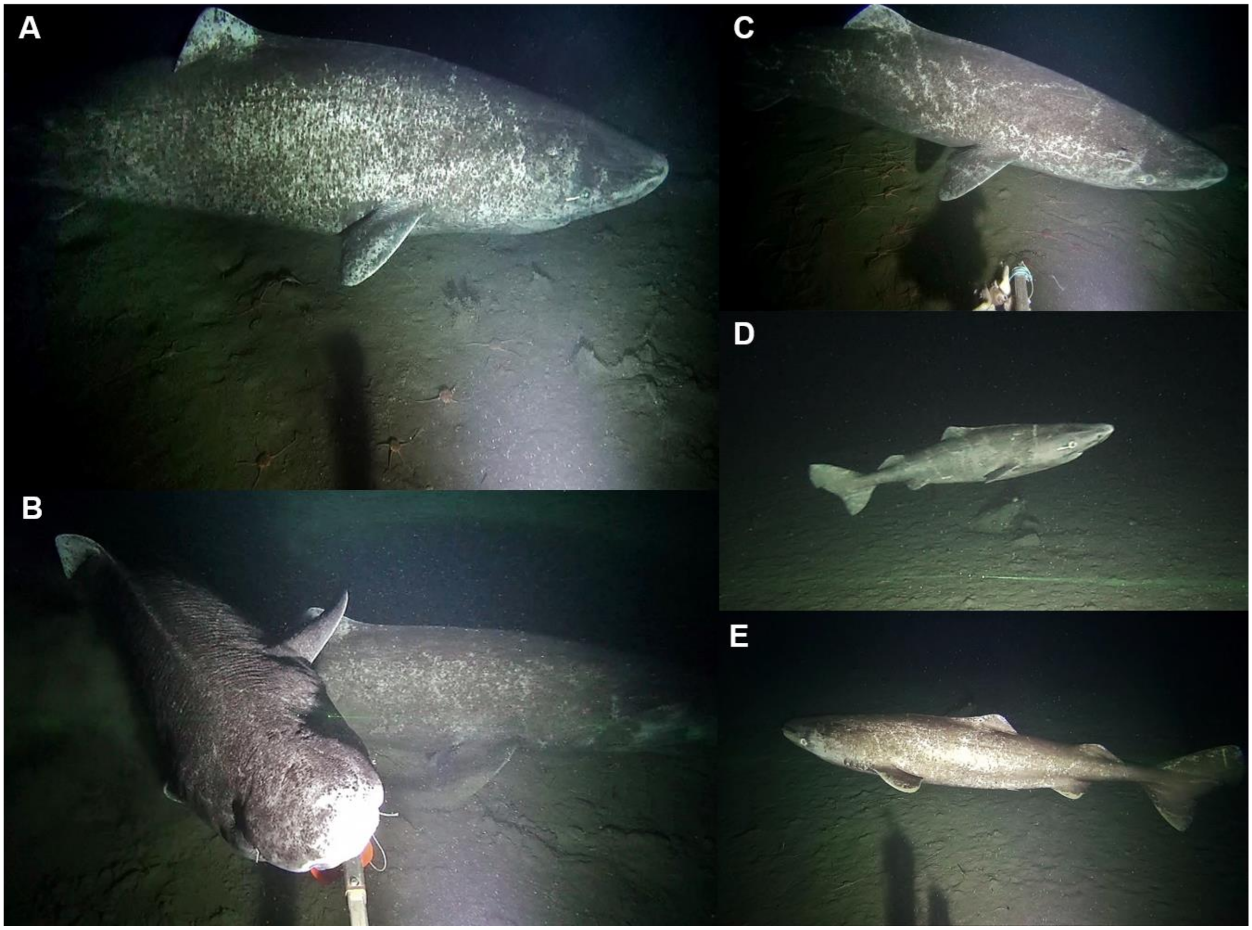


Figure 3.7.4 Length-frequency distribution of Greenland sharks measured from camera footage (n=93), with males (dark grey bars) and females (light grey bars). Dashed lines indicate proposed maturity lengths for both sexes (Yano et al. 2007).

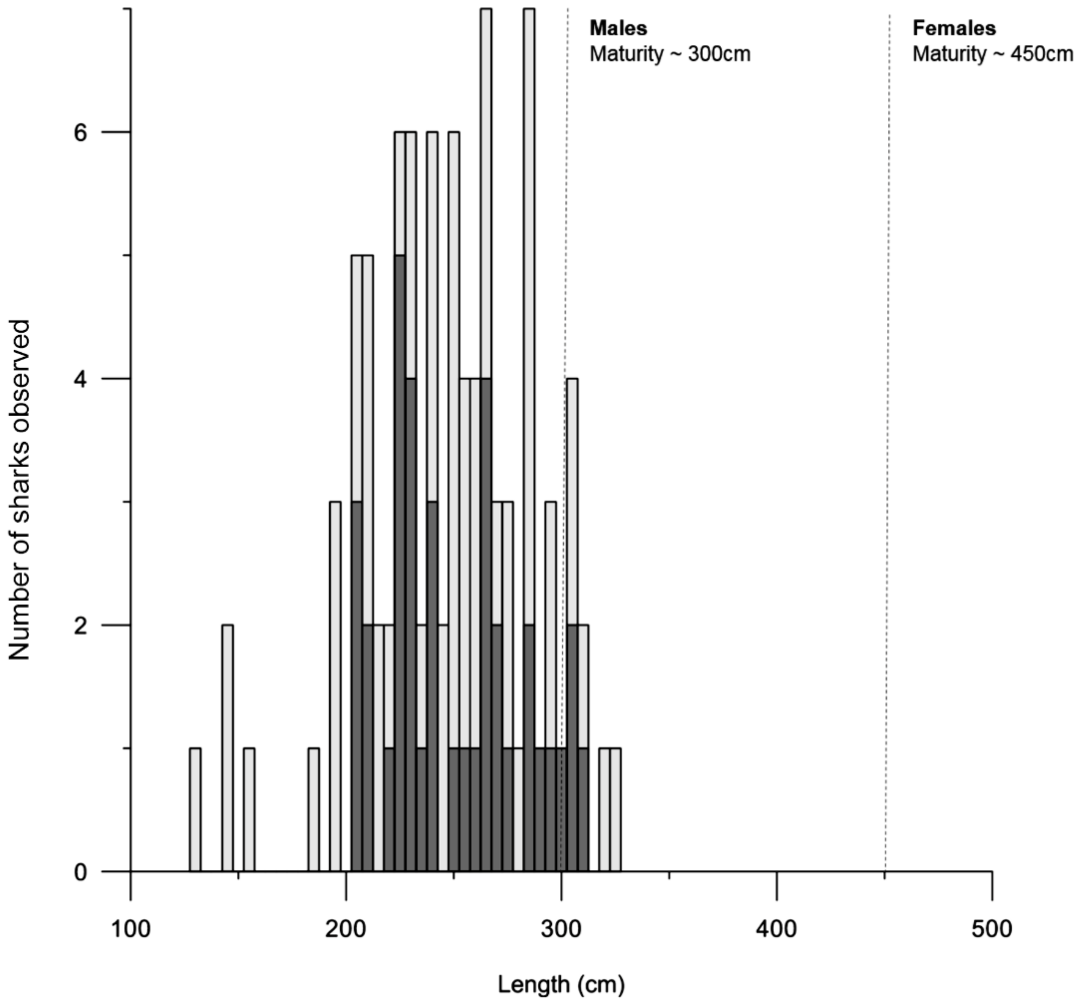


Figure 3.7.5 Comparison of number of individuals observed versus first arrival time of sharks in each camera deployments for all regions: Arctic Bay (▲), Lancaster Sound (▪), Resolute (♦), Jones Sound (•), and Scott Inlet (+).

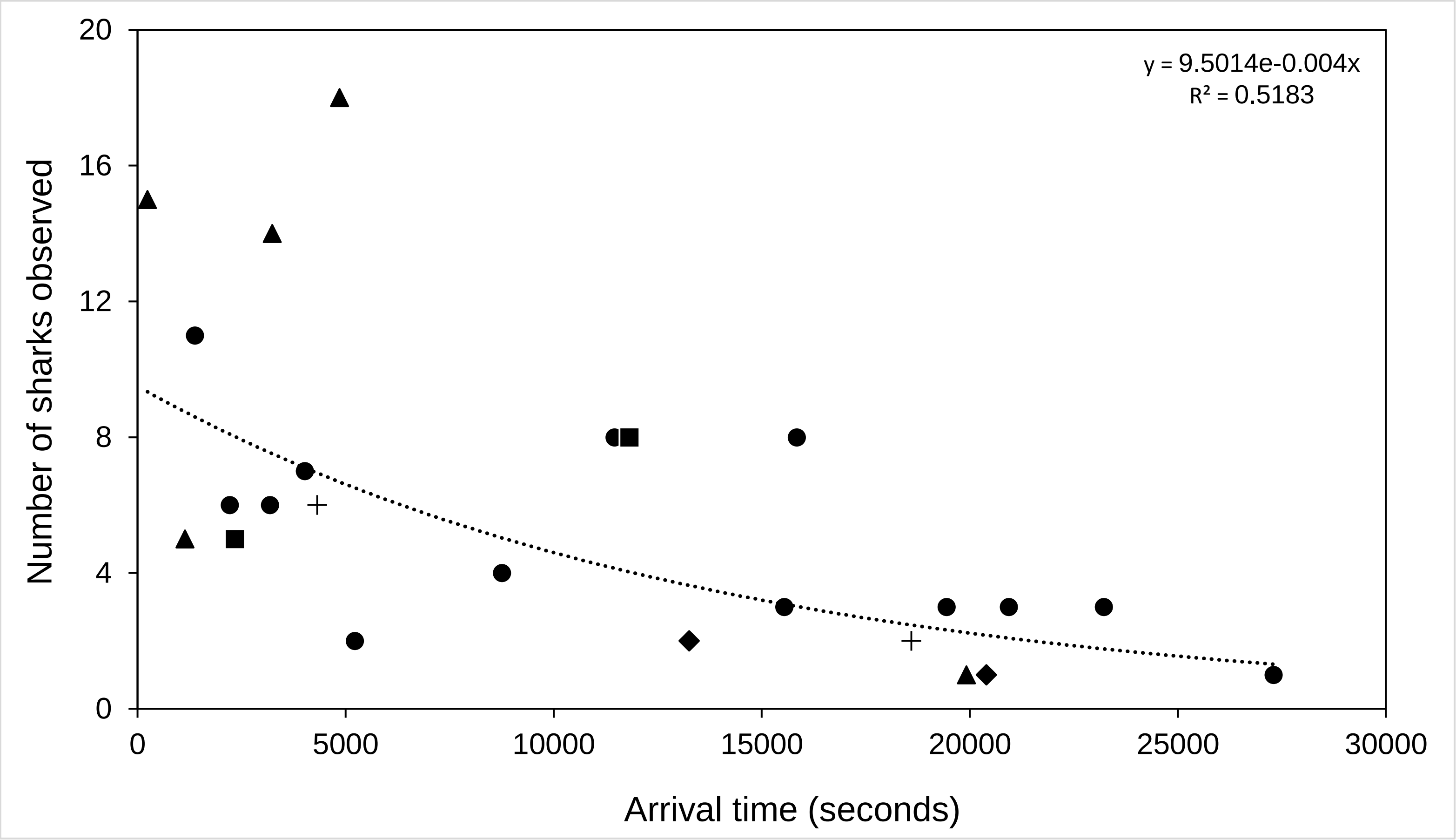


Figure 3.7.6 Comparison of shark length (TL cm) versus swimming speed (ms^{-1}) derived from video measurements (n=31) from 20 individuals. For individuals where multiple measurements were taken, swimming speeds were averaged for each individual. Data of length versus swimming speed from two additional studies have been added for comparison.

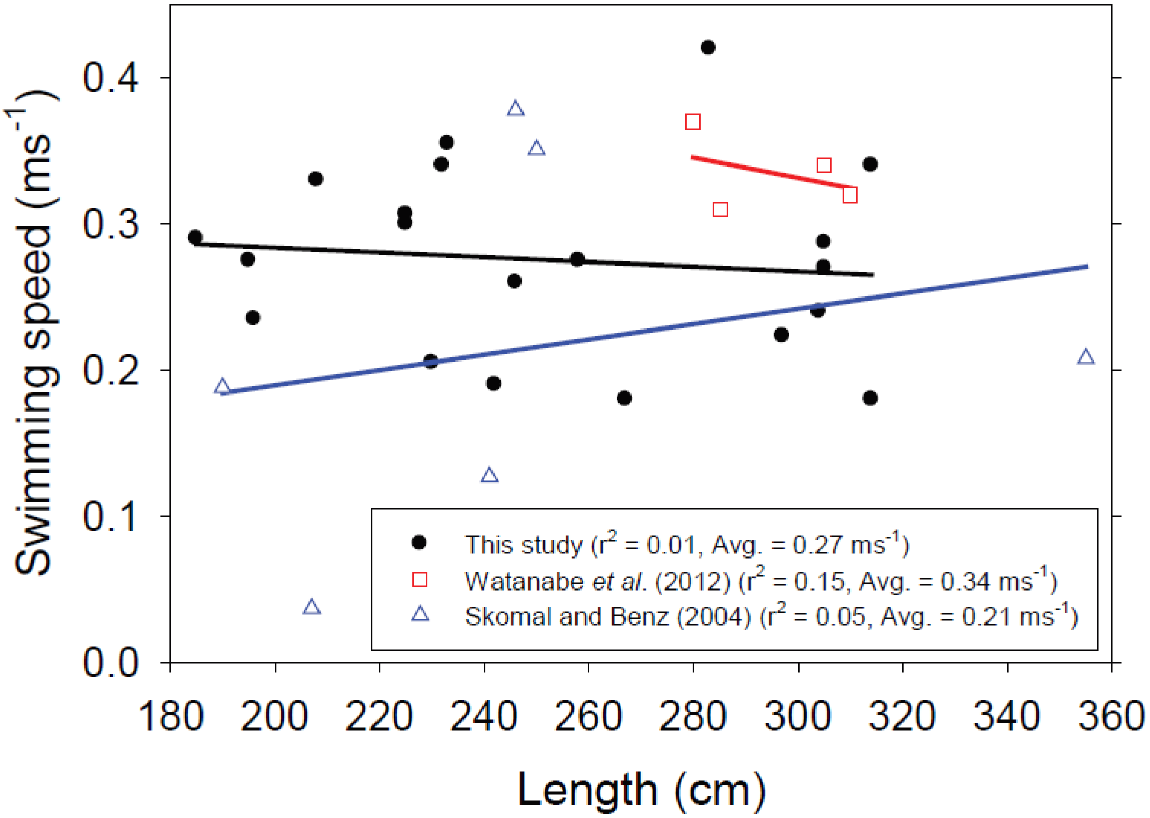


Figure 3.7.7 Comparison of theoretical abundance (▪) and biomass (△) estimates for all five sampled regions. Abundance estimates were calculated using the model validated by Priede and Merrett (1996) using mean first arrival time and bottom current speed estimates within region, and a mean swimming speed of 0.27 ms^{-1} for all regions. Biomass estimates were calculated from an established Greenland shark length-weight relationship (MacNeil et al. 2012) using video-derived mean lengths per region.

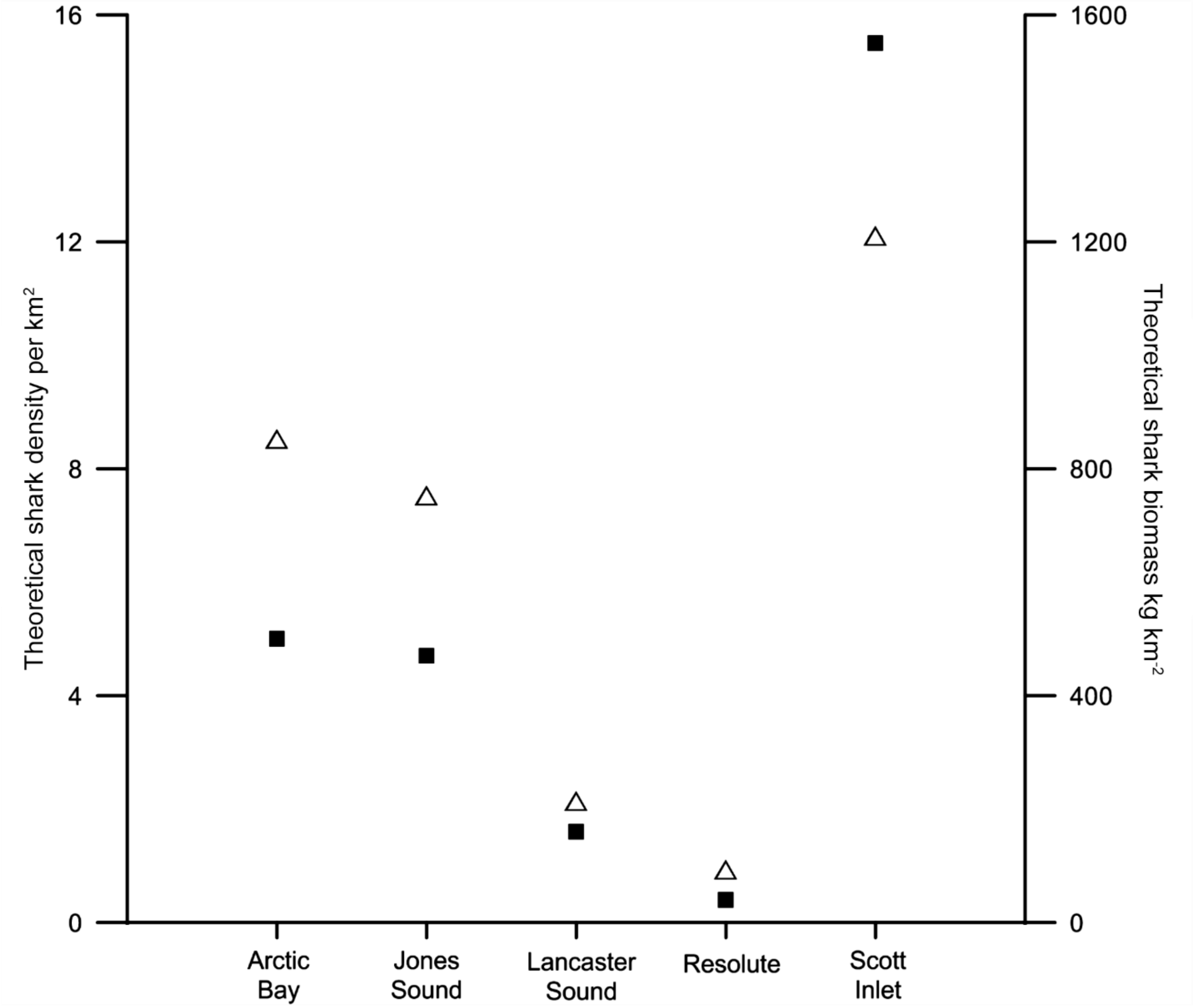
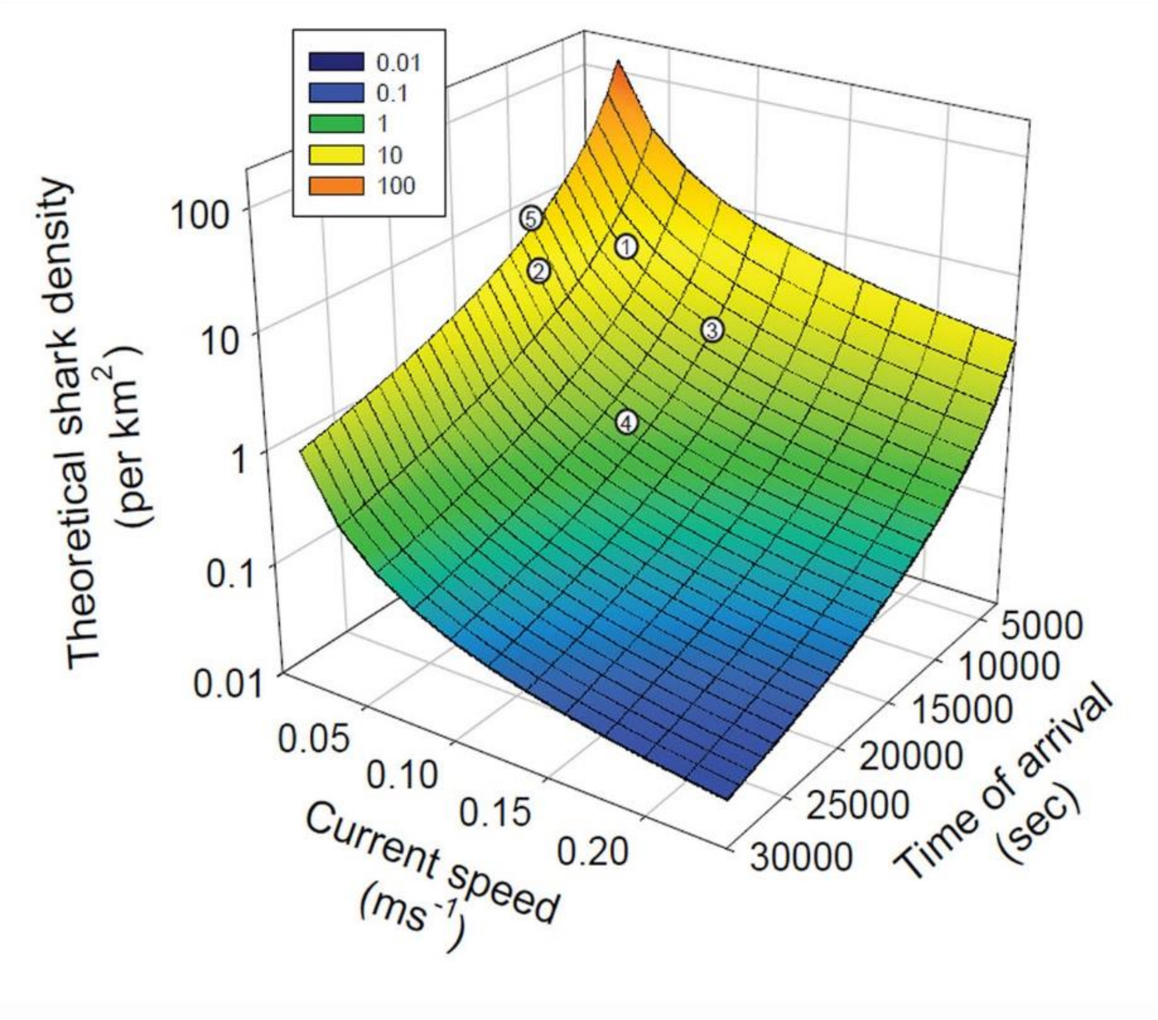


Figure 3.7.8 Surface plot of variation in theoretical shark density as functions of varying mean current speed and mean time of first arrival, using data from five regions and mean swimming speed of 0.27ms^{-1}. Individual numbered points correspond to Arctic Bay ('1'), Jones Sound '2', Lancaster Sound '3', Resolute '4', and Scott Inlet '5'. Note that given current speed and fish swimming speed have the same effect and weighting on the model (see Methods), the effect of current or swim speed can be generalized from this illustration.



4 Habitat associations and assemblage structure of demersal deep-sea fishes on the eastern Flemish Cap and Orphan Seamount

Abstract

Advancements in remote-sampling and optical technologies have considerably improved our understanding of fish-habitat relationships and assemblage structure in the deep ocean through direct observations. The composition and complexity of seafloor habitats can strongly influence species diversity and distributions, but the relative importance of different microhabitats - both abiotic and biotic - is poorly understood. We examined differences in fish species composition and relative abundance between different physical (sediment type and boulder density) and biological (coral and sponge densities) habitat types through *in-situ* observations from remotely-operated vehicle surveys off the coast of Newfoundland, Canada. Fish-habitat relationships were observed across 61 km of seafloor and spanning depths of 875 –3003 m at five dive locations, with additional quantification of fish behaviour and assemblage patterns. Distinct assemblages occurred among depth zones, and biological habitats apparently influenced assemblage structure moreso than physical features. Habitat complexity was also important, with significant differences in assemblages observed in more complex physical habitats (e.g. boulder fields, and outcrops) and complex biological habitats (e.g. sparse corals, and dense corals) compared to less complex areas of fine-grain sediment or locations with no or few corals and sponges present. Our results indicate specific microhabitats and overall

structural complexity of physical and biogenic habitat features may be particularly important to some deep-sea fishes. Until further details of these relationships can be explored, conservation efforts should strive to protect a wide-range of microhabitats to preserve valuable fish habitats in the deep-ocean environment.

4.1 Introduction

Habitat composition, complexity, and heterogeneity can be strong predictors of species diversity and abundance in a variety of marine communities (Menge & Sutherland, 1976; Tews et al. 2004; Gratwicke & Speight, 2005). Benthic habitats provide structure and space for shelter, and can play an important role in feeding and reproduction of demersal fishes (Beck et al. 2001; Teagle et al. 2017), and influence intra- and inter-species interactions and trophodynamics (Diehl 1992; Grabowski & Powers, 2004). Therefore, understanding the relative importance of various benthic habitats to individual species and biodiversity requires establishing habitat-related distributions of fishes. In general, habitat complexity and heterogeneity decrease with depth across continental margins, as variability in substrate types, grain size, food availability, and average epifauna size decline (Levin et al. 2001; Carney, 2005). However, transitional slope habitat between the shelf and margin edge, often punctuated by submarine canyons, sediment flows, and subject to internal tides and eddies, can offer complex and variable habitats beyond the shelf edge (Levin & Dayton, 2009; Buhl-Mortensen et al. 2010). Physical structures, including geomorphological features such as outcrops or canyons and variability in slope and substrate types, can add topographic complexity and heterogeneity across the seafloor. Corals, sponges, and other benthic macrofauna add emergent and biogenic structural complexity to the seafloor, however, physical habitat factors such as sediment composition and current regimes can in turn largely dicate their distributions (Guinan et al. 2009; Baker et al. 2012a). As habitats become more uniform with increasing depth, the relative importance of structural habitat may also change when contrasted against a landscape with fewer features.

Habitat associations for deep-sea fishes are not well-known. The small percentage of the deep seafloor that has been directly observed (Clark et al. 2016) limits our understanding of small-scale patterns in distribution, composition, and availability of different microhabitats in deep-sea benthic ecosystems; as such the role and relative influence of different microhabitats on the distribution and assemblage structure of deep-sea fishes is poorly understood. More frequent direct observation methods reveal a suite of habitat associations of fishes in shallow environments, from obligate associations with particular microhabitats (Munday, 2004; Brooker et al. 2011) to seasonal, diel, and/or life-stage based relationships with particular habitats at multiple spatial scales (Lecchini & Galzin, 2005; Faunce & Serafy, 2006; Hearn et al. 2010). Traditionally, researchers sampled the deep-sea benthos using bottom trawls, providing valuable voucher specimens to explore diversity at these depths and identifying depth-related variables as major drivers in species assemblages (Snelgrove & Haedrich 1985; Merrett & Haedrich 1997; Williams et al. 2001; d’Onghia et al. 2004). However, the spatial resolution (kilometers) and amalgamation of multiple habitats and species in a single tow cannot resolve small-scale patterns in fish-habitat distributions. In contrast, advancements in optical technologies and remotely operated vehicles (ROVs) offer the opportunity to observe *in-situ* habitat associations of deep demersal fishes at a finer scale, and to explore habitat use, assemblage composition, and fish behaviour at depth (Ross & Quattrini, 2007; Anderson et al. 2009; Baker et al. 2012; Milligan et al. 2016). These direct observations are beginning to shed light on fish-habitat relationships in the deep ocean, although many questions regarding temporal variability in habitat use, connectivity between broader habitat patches, and the relative importance of abiotic and biotic habitat factors remain.

Several studies have examined fish-habitat associations using both abiotic and biotic habitat variables, with results suggesting both aspects can influence species assemblages and abundance. On the southern Grand Banks of Newfoundland, Baker et al. (2012b) found geomorphic features such as bedrock outcrops harbour unique fish assemblages and more frequent observations of relatively rare species compared to other habitat types. Substrate or sediment type may also affect fish distributions; pairwise comparisons of various habitat types by Ross et al. (2015) indicated fishes associated with sand substrates differed significantly from fishes in other habitats. Other studies report the role of deep-water corals as important fish habitat, with higher fish abundance and species richness (Costello et al. 2005), and higher densities of larger individuals in cold-water coral habitats (Husebo et al. 2002). Off the coast of Norway, deep-water reefs of *Lophelia pertusa* coral support higher densities of gravid redfish *Sebastes viviparous* (Fosså et al. 2002), suggesting coral habitats may play an important functional role for some fish species.

However, not all studies observed changes in fish abundance and/or assemblage composition in relation to corals (d'Onghia et al. 2010; Baker et al. 2012b; Biber et al. 2014). Auster (2005) found fish communities in dense coral and dense epifauna habitats were functionally similar to those within less complex habitats, and these dense habitats only supported comparatively moderate diversity. Although that study observed high densities of *Sebastes* spp. in areas of dense corals as reported in earlier studies (Mortensen et al. 1995; Fosså et al. 2002), Auster (2005) found no significant difference in densities between regions of dense corals and outcrop-boulder habitats with sparse corals, concluding overall habitat complexity may be a better predictor. However, Krieger and Wing (2002) observed 85% of large *Sebastes* spp. in the Gulf of Alaska associated with coral-covered boulders, despite < 1% of boulders containing corals. Whether species-specific preferences or inter-annual variability in habitat associations explain these discrepancies is unknown and warrants further investigation.

Recent technological advances in accessing deep environments has increased global interest in exploitation of deep-sea resources, with rising prospects for mineral mining and oil exploration (Wedding et al. 2015; Cordes et al. 2016) and commercial fisheries pushing into deeper waters (Morato et al. 2006). Slow recovery rates and high vulnerability to physical disturbances often characterize deep-sea communities (Clark et al. 2015). Bottom impacts from human activities can cause significant redistribution and erosion of sediments (Ewing & Kilpatrick, 2014; Martin et al. 2014) with potentially devastating effects on fragile habitat-forming epifauna (Koslow et al. 2001; Ramirez-Llodra et al. 2011), such as reduced diversity and changes in biomass, abundance, and community composition in areas exposed to physical disturbances (Baker et al. 2009; Clark et al. 2015). For example, many cold-water corals grow at rates of 4 – 25 mm per year, with ages of some gorgonian colonies over 200 years (Sherwood & Edinger 2009) and up to 8,000 years for larger reef systems (Hovland et al. 1998), corresponding to centuries-long recovery rates for damaged reefs (Friewald et al. 2004). Likewise, slow growth, late maturation, and longevity in many deep-sea fishes leaves them particularly vulnerable and slow to recover from disturbances such as habitat degradation and overfishing (Koslow et al. 2000; Cailliet et al. 2001; Baker et al. 2009). Therefore, establishing fish-habitat relationships and the value of particular habitats to fishes in the deep ocean can highlight essential habitats and aid direction of marine protection planning and conservation efforts.

This study opportunistically examined fish-habitat relationships from *in-situ* video data collected during habitat surveys at five locations along the Flemish Cap and Orphan Seamount in the Northwest Atlantic Ocean. We examine patterns in fish occurrence and assemblages in relation to depth, dive location, and habitat classification factors that separate physical topographic complexity and coral and sponge density in an effort to determine whether abiotic or biotic factors best predict fish distributions. These factors are used to explore the overall influence of complexity of habitat on assemblages, and also examine fish behaviour at each observation.

4.2 Materials and methods

4.2.1 Survey design

Benthic habitats and fauna were explored along slopes of the Flemish Cap and the Orphan Seamount located east of the Grand Banks of Newfoundland, Canada (Figure 4.8.1) in July 2010 using the remotely operated vehicle (ROV) ROPOS (Remotely Operated Platform for Ocean Science) (CSSF, 2010). The objective of this cruise was to survey geology and coral distributions given the unique geomorphological history of these seafloor features (Edinger et al. 2011). The Flemish Cap, a circular plateau of continental crust ~58,000 km^2 in area, rises to 140 m depth approximately 600 km east of Newfoundland; the Flemish Pass, which extends below 1000 m depth, separates the Flemish Cap from the Grand Banks shelf (King et al. 1985). Located within a mixing zone of the cold northern Labrador Current and warm southerly Gulf Stream, average water temperatures here typically exceed those on the adjacent northern Grand Banks (Stein, 2007). The Orphan Seamount is a volcanic submarine feature located 620 km north-east of St. John’s, Newfoundland, and approximately 9 km east of the southern portion of the Orphan Knoll. The seamount is roughly 14 km wide at its base, with a depth of 1932 m at its peak (Pe-Piper et al. 2013).

A total of four dives (R1335 – 1337, R1339) were analysed along the south and eastern slopes of the Flemish Cap, and a single dive (R1340) on the Orphan Seamount. As fish distributions were not the survey focus, dive locations were selected based on geological and biological (i.e. corals, sponge) habitats of interest. The location, time, depth, temperature, and orientation of the ROV was recorded at 1-second intervals throughout each dive. Survey depths ranged from 875 to 3003 m, with dive transect distances ranging from 7.7 to 15.6 km (Table 4.7.1).

4.2.2 Video processing

For all analyses, video from the forward-facing colour camera positioned 0.8 m high on ROPOS was used, with white LED lighting and scale reference lasers placed 10 cm apart. All video footage was analyzed using the open-source VLC media player (Version 2.2.6). Location and depth information for each fish observation were acquired from video timestamps on the ROV navigation log. All fish were identified to the lowest possible taxonomic level based on morphological and behavioural characteristics, using video clipsfor consultation with taxonomic experts when necessary. Individuals were identified to species when possible, however several groups were identified only to family level (i.e. Myctophidae and Gonostomatidae) as voucher specimens are needed for further taxonomic resolution. Behaviour was recorded for each fish at first observation, including reaction to the ROV (no reaction, avoidance, and attraction), *in-situ* behaviour (hovering, resting, hiding, and swimming), along with estimated position relative to the seafloor (on bottom <10 cm, off-bottom <100 cm, high-off bottom >100 cm). Positions for fishes associated with vertical habitat (e.g. outcrop) were estimated using the same criteria but in the horizontal plane. To reduce double-counting fish, individuals that approached the ROV from behind were not counted.

Habitats witin the field of view at each fish observation were categorized in two ways using physical factors relating to the substrate composition and topography of the seafloor, and using biological factors relating to coral and sponges densities. Physical habitats included: 1) fine-grain sediments, 2) coarse sediments, 3) coarse sediments with boulders, 4) boulder field, and 5) outcrop. ‘Fine-grain sediments’ and ‘coarse sediments’ were characterized by either finer sediments (sand, silt, clay, or finer gravel) or coarser sediments (pebble, cobble) (Wentworth 1922), respectively, with few <3 boulders (>25 cm) present. ‘Coarse sediments with scattered boulders’ described coarser sediments with scattered (n=3-10) boulders. Habitat with numerous (>10) boulders over fine or coarse sediments defined‘boulder fields’, and regions comprised of vertical, cliff-like structures of exposed bedrock were classified as ‘outcrop’. Biological habitats include 1) absent, 2) sparse corals, 3) sparse sponges, 4) sparse mixed, 8) dense corals, 9) dense sponges, and 10) dense mixed. ‘Absent’ habitats lacked visible corals or sponges present. The term ‘sparse’ describes habitats with <10 colonies, and ‘dense’ habitats were comprised of >10 colonies. ‘Mixed’ refers to presence of both corals and sponges, at the associated density descriptor (i.e. ‘sparse mixed’ contained both coral and sponges at densities <10 colonies). Encrusting corals/sponges were not included in biological habitat density estimates.

Fish observations in relation to species-specific coral or sponge densities were not examined in the present study, although previous studies documented coral and sponges diversity in these regions (Meredyk, 2017; Miles, 2018). These studies showed variable dominant coral taxa and relative abundance among dives. Lowest coral abundance was observed in dives R1335 and R1336 on the southern Flemish Cap, dominated by *Acanella* spp. and *Chrysogorgia agassizii*. Dive R1337 on the eastern Flemish Cap encountered the highest coral concentrations, namely *Anthomastus* spp. and Nephthelidae soft corals, and Isididae corals and *Anthomastus* spp. dominated Dive R1339 (Miles, 2018). The Orphan Seamount (R1340) supported the highest coral diversity, comprised largely of Zoantharian corals, as well as Isididae and Pennatulacea sea pens (Meredyk, 2017). Corals within all dives were predominately small in size (colonies <20 cm) and, although species vary morphologically, they presumably offer similar structure/shelter at these small sizes. Sponges are exceedingly difficult to identify from video data, and the various species have yet to be classified or scored for relative abundance. A vast majority of sponges observed here were small (<10 cm) unidentified, yellow sponges, possibly belonging to the genus *Geodia*, and a limited number of vase-like and glass sponges (Class Hexactinellida).

4.2.3 Data analysis

Multivariate analyses were used to explore differences in fish assemblages within and between depths and both physical and biological habitat types. Fish observations were sorted based on the following depth classes: 1) middle slope <1500 m, 2) lower slope 1500 – 2500 m, and 3) margin edge >2500 m. These groups were selected based on structure of depth zones along continental margins (see Buhl-Mortensen et al. 2010) and to ensure adequate representation of physical and biological habitat combinations within each depth class for comparison. Patterns among location and depth groups were explored by calculating taxa richness and Shannon diversity indices (H’) were calculated for each dive and depth class.

To explore whether physical or biological habitat features better predict fish assemblage composition, two separate assemblage analyses were conducted in PRIMER 7 (v7.0.10, Primer-E, Plymouth, UK; Clarke & Gorley, 2015) using abundance values of each taxa per sample unit, where each sample unit uniquely combined dive, depth class, and physical (or biological) habitat types (see methods in Ross & Quattrini 2007; Baker et al. 2012b). Abundance values of each unique taxa per sampling unit were standardized based on the relative survey distance within each sample unit (i.e. total surveyed distance of each habitat type within each depth class and dive). Fish observations were relatively evenly dispersed along each dive transect (Figures A2-A6), with most observations <100 m apart. Given the uniformity of fish observations, the total distance of each habitat was measured in ArcGIS (ArcMap v10.3.1, ESRI) based on fish observations and associated habitats along each transect, measuring total distance between observation points within each habitat type. Mesopelagic fish taxa (i.e. Myctophidae, Gonostomatidae) were not included in benthic assemblage analyses.

A non-metric multidimensional scaling (nMDS, Kruskal and Wish, 1978) ordination plot and associated group-average linked hierarchical cluster dendrogram were generated based on a Bray-Curtis similarity matrix constructed from fourth-root transformed abundance data that down-weighted dominant species and increased relative influence of rare species. Two-way analyses of similarities (ANOSIM) tested for differences in fish assemblages based on depth class and both physical and biological habitat types to explore which habitat component influenced fish communities most.

SIMPER (similarity percentages) subsequently determined which species contributed most to similarities and dissimilarities between groups.

4.3 Results

A total of 66.4 hrs of bottom video footage was captured, covering a total distance of 55.3 km and spanning depths from 875 – 3003 m (Table 4.7.1) across the five dives. Fine-grain sediment dominated the sampled physical habitat (31.3 km), followed by outcrop (7.8 km) and coarse sediment (7.1 km) habitats (Table 4.7.2). Sponges were the dominant biological habitat feature, with ~60% of the surveyed distance comprised of sparse (19.7 km) and dense (12.7 km) sponge habitats (Figure A7). Survey depth coverage was similar between <1500 m and >2500 m groups (15.2 km and 10.6 km, respectively), with highest coverage at depths between 1500 and 2500 m (29.4 km) (Table 4.7.2).

4.3.1 Species occurrence & habitat specificity

A total of 6,938 fish were observed, representing at least 45 species or unique taxa from at least 19 families and 16 orders (Table 4.7.3; Figure 4.8.2). A majority of individuals were identified to species (n=4,392), with the remaining observations to genus (n=173) or family (n=1,298) level. Macrourids were the most abundant taxa for all dives (n=4,065), comprised of at least 13 species, followed by *Antimora rostrata* (n=993) and unknown mesopelagic fishes (n=867). Rare species included *Apristurus* spp. (n=2), *Histiobranchus bathybius* (n=1), *Lipogenys gillii* (n=2), and *Coelorinchus caelorhincus* (n=1). Six taxa occurred at all five dive locations: *Antimora rostrata*, *Bathysaurus ferox*, *Coryphaenoides carapinus*, *Gaidropsarus* spp., *Hydrolagus affinis*, and *Synaphobranchus kaupi*. Several taxa occurred only in a single dive, inlcuding observations of *Cottunculus sp.* (R1335 only) and *Histiobranchus bathybius* (R1336 only) along the southern Flemish Cap, *Apristurus* spp. and *Neocyttus helgae* on the eastern Flemish Cap (R1337 only), *Coelorinchus caelorhincus* on the northeastern slope of the Flemish Cap (R1339 only), and *Simenchelys parasitica* observed exclusively on the Orphan Seamount (R1340 only). Taxonomic richness was highest in the two shallowest dives (R1335, S= 34; R1337, S=32), followed by R1340 (S=28) and lowest in the deeper waters along the Flemish Cap (R1336, S=24; R1339, S=23). Calculations of Shannon-Weiner diversity indices for dive locations indicate highest diversity at the Orphan Seamount (R1340, H'=2.34), followed by the shallowest dive R1335 (H'=2.18). Diversity indices for the remaining three dives were quite similar, with an average H' index of 1.94 (range=1.93-1.95). Species richness and diversity were highest (S=42, H'=2.21) at depths along the lower slope (1500-2500m) compared to depths of the middle slope (<1500 m; S=32, H'=2.03) and deep seafloor (>2500m; S=20, H'=2.10).

Many species spanned a wide range of sampled depths (Figure 4.8.3), with *Antimora rostrata* (876 – 2969 m), Macrourid sp. 2 (1215 – 2969 m), *Alepocephalus* spp. (1200 – 2890m), *Coryphaenoides carapinus* (1302 – 2969 m), and *Aldrovandia* spp. (1319 – 2924 m) spanning the greatest depth range. Several species were limited to upper slope locations, including *Centroscyllium fabricii* (<1243 m), *Cottunculus thompsonii* (<1215 m), *Caelorinchus caelorhincus* (<1357 m), and *Neocyttus helgae* (<1457 m).

Simenchelys parasitica (>2750 m), *Chaunax* spp. (>2334 m), *Histiobranchus bathybius* (>2323 m), *Lipogenys gillii* (>2171 m), and *Coryphaenoides armatus* (>2090 m) were among the deepest-dwelling species, observed exclusively below 2000m. The deepest species *Coryphaenoides armatus* (3003 m), *Halosauropsis macrochir* (3002 m), and *Bathyraja* spp. (3001 m) occurred at depths >3000 m.

Some species occurred almost exclusively in low complexity habitats (Table 4.7.4) – either fine or coarse sediments with no or few boulders present – including *Centroscyllium fabricii*, *Cottunculus* spp. and *Cottunculus thompsonii*, and all rajids with the exception of a single *Amblyraja jenseni* observed along a bedrock outcrop. *Ophidiidae* and *Neocyttus helgae* also associated with outcrops in high numbers. Sediment grain size was apparently important for some taxa; *Bathysaurus ferox* occurred exclusively over fine-grained sediments whereas *Chaunax* spp. and *Lepidion eques* were only observed over coarse or hard-bottom habitats. Taxa-specific habitat associations were also observed in regard to biological habitat features (Table 4.7.4). Several taxa primarily occurred in areas with no or sparse corals and/or sponges present, including *Polyacanthonotus* spp., *Bathysaurus ferox, Chaunax* spp., and *Aldrovandia* spp. *Neocyttus helgae*, *Lepidion eques*, *Apristurus* spp., *Coelorincus caelorhincus* occurred almost exclusively in dense coral/sponge habitat, whereas *Notacanthus chemnitzii*, *Gaidropsarus* spp., and *Macrourus berglax* occurred in relatively higher numbers in areas of dense coral and/or sponge cover.

4.3.2 Fish behaviour

In response to the approach of the ROV, most fish (n=5,432) exhibited no obvious reaction (Table 4.7.5). No taxon represented by more than two individuals consistently avoided or appeared attracted to the vehicle. *Centroscyllium fabricii* occasionally approached the ROV (~27% of encounters), with those individuals actively swimming toward and often circling the ROV. Mesopelagic fishes (i.e. myctophids, unknown mesopelagic fishes) frequently avoided the ROV, rapidly swimming and colliding with the ROV or the seafloor prior to quickly swimming away. Nearly half of *Hydrolagus affinis* individuals displayed clear avoidance behaviour, as did a small proportion (~12 – 30% of encounters) of some macrourid species. However, individuals of both *H. affinis* and macrourids often hovered relatively high off the seafloor, and therefore potentially had a greater propensity for avoidance behaviour to prevent collision with the moving ROV.

In-situ behaviour of fishes at first observation (Table 4.7.5) indicate a vast majority of individuals either actively swimming (n=3,082) or hovering above the seafloor (n=3,689). Far fewer individuals were observed resting on the seafloor (n=148) or hiding within habitats (n=19). Most macrourids were hovering, with the exception of *Coryphaenoides armatus*, which was almost as likely to be actively swimming (~42%). Several cryptic species, including *Bathysaurus ferox*, *Chaunax* spp., and *Cottunculus* spp., were consistently observed resting on the seafloor. Only *Gaidropsarus* spp. and *Coryphaenoides carapinus* individuals exhibited hiding behaviour by more than 2 individuals within a taxon, which hid beneath overhanging boulders or outcrop ledges, or sheltering within or underneath corals or sponges.

Most fish closely associated with the seafloor (n=3629), as opposed to off-bottom (n=1304) or high off-bottom (n=962). Position relative to the seafloor varied between taxa, both among and within familial groups (Table 4.7.5). Many individuals found predominately or exclusively on-bottom belonged to taxa with morphologies suited to a benthic existence, specifically members of the families *Rajiidae*, *Chaunacidae*, *Psychrolutidae*, and *Bathysauridae*. A majority of individuals in several other taxa also occurred predominately on-bottom, including *Gaidropsarus* spp., *Lepidion eques*, *Ophidiidae*, and *Reinhardtius hippoglossoides*. Taxa observed more frequently not directly associated with the seafloor include all mesopelagic groups (*Myctophidae*, *Gonostomatidae*, and Unknown mesopelagics), *Simenchelys parasitica*, *Lipogenys gillii*, and *Hydrolagus affinis*. Macrourid species differed notably in position, with *Macrourus berglax* and *Nezumia bairdi* nearly exclusively found on-bottom (>95% encountered). *Coryphaenoides carapinus* and *Coryphaenoides rupestris* were also encountered more often on-bottom (~ 80% and 60%, respectively); however, *Coryphaenoides armatus* were observed on-bottom and off-bottom in near equal frequency. Additional variations between closely related species were also observed, namely between notacanthids (~62% *Polyacanthonotus* spp. on-bottom versus ~63% *Notacanthus chemnitzii* off-bottom) and halosaurids (~77% *Halosaurus machochir* on-bottom versus ~56% *Aldrovandia* spp. off- or high off-bottom).

4.3.3 Assemblage analyses

For both physical and biological assemblage analyses, the global ANOSIM indicated significant differences in assemblages between depth groups (physical: R=0.47, *p*=0.001; biological: R=0.45, *p*=0.001), and nMDS plots for both analyses clearly illustrated these differences (Figure 4.8.4). Assemblages also differed significantly between each depth category in pairwise comparisons (R≥0.35, p<0.002). SIMPER results from both habitat assemblage analyses (Table A4-A5) indicate the macrourids *Coryphaenoides carapinus*, *Coryphaenoides rupestris*, and *Macrourus berglax* were the main contributors (cumulative ~35%) to dissimilarity between the middle slope (<1500 m) and both lower slope (1500 – 2500 m; Avg. Dissimilarity: 64.6 – 67.8%) and margin edge (>2500 m; Avg. Dissimilarity: 87.8 – 90.3%) depth groups, driven by higher abundance of *Macrourus berglax* in shallowest depth group and relatively few *Coryphaenoides carapinus* at depths below 1500 m. Dissimilarity between lower slope and margin edge (Avg. Dissimilarity: 63.6 – 67.2%) mainly resulted from higher abundance of *Coryphaenoides armatus* and fewer *Antimora rostata* in the deepest depth class.

Global ANOSIM did not indicate significant differences in assemblages across all physical habitats (R=0.02, *p*=0.40; Table A6). However, pairwise tests showed a significant difference in assemblages between outcrop and fine-grain sediment habitats (R=0.29, *p*=0.032) and boulder field and fine-grain sediments (R=0.23, *p*=0.039), but no differences between other physical habitats. The high relative abundance of *Antimora rostrata* and *Coryphaenoides carapinus* across all physical habitats greatly influenced similarity within groups, with these two species contributing a combined 38 – 71% similarity in each group. The absence of *Halosauropsis macrochir*, myctophids, macrourid sp. 1, and relatively low abundance of *Synaphobranchus kaupi* on boulder fields all contributed to dissimilarity between boulder field and fine-grain sediment habitat. The absence of *Bathysaurus ferox* and relatively low abundance of *Synaphobranchus kaupi*, myctophids, *Halosauropsis macrochir* and higher relative abundance of *Gaidropsarus* spp. and ophidiids on outcrops all contributed to dissimilarity between outcrop and fine-grain sediment habitats.

Among biological habitats, global ANOSIM indicated stronger contrasts in assemblage structure compared to physical habitats, although not at the significance level of $p<0.05$ (R=0.09, $p=0.061$; Table A7). Pairwise tests yielded significant comparisons, including absent versus dense coral (R=0.46, $p=0.008$) and sparse sponge versus dense coral (R=0.37, $p=0.018$) habitats. Again, the high relative abundance of *Antimora rostrata* and *Coryphaenoides carapinus* greatly influenced similarity within biological habitat groups. These two species were the main contributors within most groups, with the exception of *Macrourus berglax* contributing >45% similarity in dense coral habitat. As a result, the relatively high abundance of *Macrourus berglax* in these habitats, along with the lower relative abundance of *Antimora rostrata* and *Synaphobranchus kaupi* contributed the greatest dissimilarity between dense coral habitat and areas with no sponges or corals present. The absence of *Coryphaenoides armatus* and macrourid sp.2 in dense coral habitat and higher relative abundance of *Macrourus berglax* and myctophids and lower abundance of *Antimora rostrata* and *Synaphobranchus kaupi* contributed to dissimilarity between dense corals and sparse sponges habitats.

Some additional comparisons that were statistically non-significant that may be relevant in terms of ecological significance include dense sponges habitat compared to absent (R=0.21, *p*=0.068), dense sponges versus sparse mixed (R=0.22, *p*=0.079), and sparse mixed compared to sparse sponges (R=0.28, *p*=0.075) habitats. Differences between these habitats are attributed to higher relative abundance of species such as *Macrourus berglax, Coryphaenoides rupestris*, and *Gaidropsarus* spp. in dense sponge habitat and lower abundance of taxa found more often associated with less complex habitats (e.g. absent and sparse sponges) including species like *Halosauropsis macrochir*, *Synaphobranchus kaupi*, and *Antimora rostrata.*

4.4 Discussion

We observed distinct fish assemblages between middle slope (<1500 m), lower slope (1500 – 2500 m), and margin edge (>2500 m) depth zones. The influence of physical and biological habitats on assemblages varied, with significant differences in habitats of contrasting topographical relief. This suggests that habitat complexity may be important for some deep demersal fish species. These results also indicated the presence and relative densities of corals and sponges may be a better predictor of assemblage structure compared to physical factors of sediment composition and boulder concentration, suggesting heightened importance of biological habitat structures for some deep-sea fishes.

Multiple studies report the influence of depth on fish assemblage structure throughout the world's oceans. Menezes et al. (2009) reported distinct differences in fish assemblages between upper slope (<800 m) and mid-slope (800 – 1300 m) and lower slope (>1300 m) depths along two seamounts in the northeast Atlantic Ocean. Off of southern Australia, Williams et al. (2018) observed differences in fish assemblages between similar slope depth classes (200 – 3000 m), in addition to changes in biomass, diversity, and density of fishes across depth gradients. Both studies linked vertical changes in assemblage composition with depth and vertical changes in water masses (Menezes et al. 2009) and/or variables associated with unique water masses (i.e. oxygen and temperature) (Williams et al. 2018). Changes in water masses, along with changes in topography and food availability, are identified as the main drivers behind depth-structured demersal fish assemblages (Haedrich, 1997; Clark et al. 2010), with extrapolation to the deep pelagic environment where hydrography and food availability similarly influence vertical distribution of fish species with depth (Sutton, 2013).

Pairwise comparisons indicated distinct assemblages based on both physical and biological habitat types, however, tests for both analyses indicate the importance of overall habitat complexity as an indicator of fish assemblages. The two most topographically complex physical habitats – boulder fields and outcrops - hosted significantly different assemblages compared to less complex substrates. Likewise, density and composition of corals and sponges differed significantly between dense corals versus absent and sparse sponges habitats ($p<0.018$), with a weak and non-significant difference between dense sponges and areas where corals and sponges were absent (*p*=0.068). Dense corals were present in all physical habitat types (Figure A7), and appeared particularly important to some fish species.

In the deep sea where emergent structures can be scarce, coral and sponge colonies can provide topographic relief to otherwise low heterogeneity regions of the seafloor, and they can bolster habitat complexity when present in higher densities. Although complexity may vary with species-specific morphology and size (Buhl-Mortensen et al. 2010), even small sponges such as those observed in the present study likely provide adequate complexity in dense concentrations. Habitat complexity can strongly affect the structure and dynamics of fish communities, with positive relationships between faunal richness and abundance with increased complexity in a variety of marine ecosystems (Luckhurst & Luckhurst, 1978; Gratwicke & Speight, 2005). The presence of structures such as corals and sponges can provide shelter from predators within or adjacent to colonies. These emergent structures can modify near-bed hydrodynamics, altering water flow patterns that may enhance particle entrainment or refuge from currents (Zedel & Fowler 2009; Buhl-Mortensen et al. 2010). By providing shelter and enhanced food supply, as well as potential spawning and nursery habitats, these features may enrich local productivity and improve overall fitness for some species.

Several studies report higher relative abundance of some deep-sea fish species on the deep-water, reef-forming coral *Lophelia* spp., including some commercially important fishes (Fosså et al. 2002; Freiwald et al. 2002; Costello et al. 2005). These corals can form significant structures, with reef sections several hundred meters long clustering to form reef complexes up to 35 km long (Fosså et al. 2005; Buhl-Mortensen et al. 2010). The habitat complexity this species offers differs markedly from non-reef forming corals, with variable relationships between non-reef forming cold-water coral species and fish assemblages. Ross & Quattrini (2007) reported unique fish assemblages associated with cold-water corals along the US Atlantic slope. Others have shown species-specific fish associations with gorgonian corals (Krieger & Wing, 2002; Mortensen et al. 2005) and soft corals (Heifetz, 2002). However, Baker et al. (2012a) found no relationship between corals and fish assemblages, regardless of coral density and colony size. Likewise, based on analyses from over 100 submersible dives off southern California, Tissot et al. (2006) concluded that despite the co-occurrence of fishes and structure-forming invertebrates in the same physical habitats, the two groups were was not necessarily functionallly related. These contradictory conclusions highlight the need for further sampling to determine the level of microhabitat associations and the factors that influence their variability.

As in previous work along the Newfoundland slope waters (see Baker et al. 2012a), we observed two species relatively rare to the region, *Neocyttus helgae* and *Lepidion eques,* in strong association with outcrop and/or boulder habitats. These two species also occurred almost exclusively in areas of high coral density (dense corals or dense mixed), limiting observations to the most physically and biologically complex habitats. Similar studies indicate close association of *Neocyttus helgae* with cold-water corals in the NE Atlantic (Costello et al. 2005; Milligan et al. 2016), potentially utilizing these biological and physical structures for foraging or flow refuge behaviours (Auster et al. 2005). In the NE Atlantic *Lepidion eques* has been found to associate with complex substrates and emergent structures such as solitary corals and gorgonians (Alves 2003; Söffker et al. 2011). Fewer direct observations of *Lepidion eques* exist in the NW Atlantic beyond our study, with limited other western Atlantic ROV surveys (Baker et al. 2012a;

Lepidion sp. from Quattrini et al. 2017) also reporting associations with complex habitats (outcrops, dense corals).

The benefits of using ROVs for non-extractive survey of deep fish populations are far-reaching, preserving habitats and providing *in situ* direct observations of fish-habitat associations. Multiple studies have explored the behaviour of motile fishes in response to the presence of an ROV, reporting that fishes may respond to the presence of light, noise, and water and/or sediment displacement generated by the vehicle (Trenkel et al. 2004; Stoner et al. 2008). In our survey, a majority of individuals did not noticeably react to the ROV, and we observed strong avoidance or attraction behaviours in only in a few taxa. Species-specific attraction or avoidance behaviour has been observed (Lorance and Trenkel, 2006; Baker et al. 2012a), potentially biasing fish observations from ROV surveys. However, a recent study comparing ROV and trawl survey methods reported 20 times more fish observations with ROVs (Ayma et al. 2016). Although this finding does not exclude the possibility of the ‘false absence’ of a species that actively avoids the ROV and remains out of the field of view, Ayma et al. (2016) results in conjunction with issues of catchability and species avoidance also inherent to trawls (Winger et al. 2010) suggest that ROVs may provide a better indication of relative species abundance.

Noting limited knowledge about habitat relationships in the deep sea, variables such as temperature, current regimes, food availability and potentially other unknown factors not explored here could drive small-scale patterns in fish distributions. We considered biological habitat exclusively in the context of corals and sponges, however, several other habitat-forming epibenthic organisms (e.g. stalked crinoids, urchins, and anemones) were also present, although fewer in number. Crinoid beds along the shelfbreak off the coast of western Italy in the Mediterranean Sea support high fish densities, particularly of juveniles and spawners (Colloca et al. 2004). Most research on the role of biotic habitats for fishes in the deep ocean have focused on corals and sponges; whether other epibenthic megafauna may also influence species assemblages requires further study.

Our study surveyed fish during a period of a few weeks within a single year, therefore we cannot preclude the possibility that our observations represent seasonal or life stage based subsets of habitat associations for some species. Some fish rely on specific microhabitats for spawning substrate, as evidenced by the attachment of skate and shark egg cases to gorgonian corals (Ebert and Davis, 2007; Etnoyer and Warrenchuk, 2007) and numerous accounts of teleost egg deposition within a variety of sponges (Barthel 1997; Busby et al. 2012; Chernova 2014). Catsharks (Chondrichthyes: Scyliorhinidae) in particular apparently use a wide variety of benthic invertebrates for egg case attachment (Vazquez et al. 2018), potentially explaining the presence of *Apristurus* spp. only in dense coral habitats. Some researchers have suggested that deep-sea fishes could use these habitats and other structures facultatively, and that fishes associate with habitat structures based on their complexity, regardless of the composition. Auster (2005) found higher densities of *Sebastes fasciatus* over dense coral, dense epifaunal (sponges, anemones), and outcrop-boulder areas, concluding that each of these habitats provided ‘ecologically equivalent’ structures for fishes seeking refuge, minimizing the potential for species-specific physical or biological features. Better understanding of how microhabitats influence the demographics of deep-sea fishes requires surveys of fish-habitat associations spanning a variety of locations and range of available habitat types, both geographically and across seasons and life history stages.

Given our rudimentary understanding of the role of various habitats in the deep sea, habitat conservation should implement an approach to ensure preservation of a wide variety of habitats. Habitat availability presumably affects habitat specialists more than generalists (Swihart et al. 2003), therefore predicting how potential threats to deep-sea habitats might impact fish communities hinges upon understanding how fish communities partition across various microhabitats. Given increased cumulative impacts of human activities in much of the world's oceans (Halpern et al. 2015), and despite limited understanding of habitat extent in the deep ocean, increased global interest in deep benthic resources could potentially alter habitat landscapes in the deep sea (Ramirez-Llodra et al. 2011).

Despite the vulnerability of deep-sea fishes to habitat disturbance and overfishing, efforts to conserve deep-sea habitats in the waters off Newfoundland, Canada have been modest and controversial. As part of Canada's commitment to designate 10% of its waters as marine-protected and conservation areas by 2020, the Northeast Newfoundland Slope Closure Area was announced in December 2017, adding 46,833 km^2 toward this goal. This area spans a range of depths and contains high concentrations of corals and sponges, and while it is closed to all bottom fishing activities, roughly 35% of the reserve remains open to offshore oil and gas exploration (WWF, 2018). Similar regulations exist for other newly designated marine reserves in deep waters within the region, such as the Laurentian Channel Area of Interest in the Gulf of St. Lawrence, where 80% of the 11,619 km^2 remain open to oil and gas exploration and extraction. Although the impacts of infrastructure installation are typically restricted to a localized area (~100 m) surrounding the drill site, impacts from discharges can reach distances exceeding 2 km (Cordes et al. 2016), and impacts of a major spill could extend much farther. Sedimentation and displacement by infrastructure could have severe and persistent impacts on fragile habitats within the area, but whether these effects extend to fish communities is unknown.

4.5 Conclusions

Ensuring protection of essential fish habitats and adhering to ecosystem-based management initiatives requires better knowledge of fish-habitat relationships. We found distinct fish assemblages based on depth and physical and biological habitat factors associated with low and high complexity habitats. Although this study elucidates broad patterns in assemblage structure, more *in situ* research is needed to explore the relative importance of specific biological habitats and if this importance varies seasonally or throughout ontogeny. Until these relationships are identified, management and conservation of deep demersal fish and fisheries requires greater attention to habitat conservation and should strive to preserve a wide range of both physical and biological benthic habitats.

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4.7 Tables

Table 4.7.1 Summary of dive details for 2010 ROV cruise, indicating depth range (m), distance sampled (km), and duration (h) for each dive.

Dive	Date	Depth range (m)	Time on bottom (h)	Distance (km)	Region
R1335	12 July	875 – 1840	13.78	10.0	South Flemish Cap
R1336	13 July	2224 – 2900	11.1	7.7	South Flemish Cap
R1337	14 July	1020 – 2195	16.68	15.6	East Flemish Cap
R1339	17-18 July	1363 – 2463	10.05	10.2	Northeast Flemish Cap
R1340	19-20 July	1870 – 3003	14.8	11.8	Orphan Seamount

Table 4.7.2 Number of fish observations in each physical and biological habitat type, separated by depth groupings. Values in parentheses represent total survey distance in meters of each habitat type.

Habitat type	<1500 m	1500 – 2500 m	>2500 m	Total
Physical				
Fine-grain sediments, no or few boulders	2184 (9957)	1550 (16785)	219 (4549)	3953 (31291)
Course sediments, no or few boulders	448 (2487)	551 (3975)	53 (668)	1052 (7130)
Course sediments, scattered boulders	251 (1253)	321 (3816)	28 (441)	600 (5510)
Boulder field	54 (248)	211 (2160)	25 (1173)	290 (3581)
Outcrop	296 (1259)	612 (2676)	135 (3855)	1043 (7790)
Biological				
No corals or sponges	143 (660)	585 (4848)	164 (2901)	892 (8409)
Sparse corals	17 (87)	135 (1675)	13 (321)	165 (2083)
Sparse sponges	1361 (5059)	1286 (10775)	174 (3879)	2821 (19713)
Sparse mixed	21 (129)	227 (2108)	46 (450)	294 (2687)
Dense corals	176 (748)	112 (790)	-	288 (1538)
Dense sponges	889 (5242)	461 (4573)	58 (2859)	1408 (12674)
Dense mixed	626 (3279)	439 (4643)	5 (276)	1070 (8198)

Table 4.7.3 Number of individuals of each fish taxon observed during the five analysed dives.

Taxa		**R1335**	**R1336**	**R1337**	**R1339**	**R1340**	**Total**
Chimaeridae	*Hydrolagus affinis*	2	1	2	4	1	10
Scyliorhinidae	*Apristurus* spp.			2			2
Etmopteridae	*Centroscyllium fabricii*	17		9			26
Rajidae	*Amblyraja* spp.	3		2	1		6
	Amblyraja jenseni	1					1
	Bathyraja spp.					1	1
	Bathyraja spinicauda			1			1
	Rajella spp.	1	2		1	2	6
	Rajidae (unknown)	1	1	9	1		12
Synaphobranchidae	*Histiobranchus bathybius*		1				1
	Simenchelys parasitica					3	3
	Synaphobranchus kaupi	334	1	57	26	9	427
	Synaphobranchidae (unknown)	9				5	14
Notacanthidae	*Lipogenys gillii*		1	1			2
	Polyacanthonotus spp.	24		1	1	11	37
	Notacanthus chemnitzii	2	1	9	4		16
	Notacanthidae (unknown)			3			3
Halosauridae	*Aldrovandia* spp.	1	4			13	18
	Halosauropsis macrochir	1	49			18	68
	Halosauridae (unknown)			1			1
Alepocephalidae	*Alepocephalus* spp.	16	2			8	26
Gonostomatidae	Gonostomatidae	1		1			2
Bathysauridae	*Bathysaurus ferox*	1	3	2	1	5	12
Myctophidae	Myctophidae (unknown)	14		25	54		93
Chaunacidae	*Chaunax* spp.		5			1	6
Macrouridae	*Coelorinchus caelorhincus*				1		1
	Coryphaenoides armatus		7	2	4	30	43
	Coryphaenoides carapinus	161	146	400	13	123	843
	Coryphaenoides rupestris	402		517	6		925
	Macrourus berglax	180		514	136	4	832
	Nezumia bairdi	93		28	2		123
	Macrourid sp. 1	21	15	3	3		42
	Macrourid sp. 2	10	59	3		2	74
	Macrourid sp. 3		1			4	5
	Macrourid sp. 4	2	3			1	6
	Macrourid sp. 5	3					3
	Macrourid sp. 6	1	1		4	1	7
	Macrourid sp. 7			2			2
	Macrouridae (unknown)	456	176	313	62	152	1159
Moridae	*Antimora rostrata*	242	44	454	200	53	993
	Lepidion eques			5	1	1	7
Lotidae	*Gaidropsarus* spp.	13	1	9	38	2	63
Ophidiidae	Ophidiidae (unknown)	2	2		2	8	14
Oreosomatidae	*Neocyttus helgae*			8			8
Psychrolutidae	*Cottunculus* sp.	1					1
	Cottunculus thompsonii	2		1			3
Pleuronectidae	*Reinhardtius hippoglossoides*	25		27			52
Unknown	Fish unknown (sp. 1)					1	1
	Fish unknown (sp. 2)			1			1
	Fish unknown (sp. 3)	1					1
	Fish unknown (sp. 4)					1	1

	Fish unknown (Anguilliform)	13	3	4	2	5	27
	Fish unknown (mesopelagic)	628	3	160	51	25	867
	Fish (unknown)	17	6	7	1	6	37
Grand total		**2701**	**538**	**2584**	**619**	**496**	**6938**

Table 4.7.4 Relative abundances of fish taxa observed on each physical and biological habitat type, standardized based on the total number of fish observed on each habitat ((Number of Sp.A on Habitat X/Total number of fish observed on Habitat X) * 100).

Taxa		**Physical habitats**					**Biological habitats**						
		FGS	CS	CSB	BF	O	Absent	SS	SC	SM	DS	DC	DM
Chimaeridae	*Hydrolagus affinis*	0.13	0.10	0.33	0.34	0.10	0.22	0.07	0.61	0.34	0.21	0.00	0.09
Scyliorhinidae	*Apristurus* spp.	0.00	0.10	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.07	0.35	0.00
Etmopteridae	*Centroscyllium fabricii*	0.48	0.38	0.33	0.00	0.10	0.22	0.46	0.00	0.00	0.43	0.35	0.37
Rajidae	*Amblyraja* spp.	0.13	0.10	0.00	0.00	0.00	0.11	0.14	0.00	0.00	0.07	0.00	0.00
	Amblyraja jenseni	0.00	0.00	0.00	0.00	0.10	0.00	0.04	0.00	0.00	0.00	0.00	0.00
	Bathyraja spp.	0.00	0.10	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
	Bathyraja spinicauda	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
	Rajella spp.	0.13	0.00	0.00	0.34	0.00	0.45	0.00	0.00	0.00	0.07	0.00	0.09
	Rajiidae	0.20	0.19	0.00	0.69	0.00	0.00	0.21	1.21	0.00	0.21	0.00	0.09
Synaphobranchidae	*Histiobranchus bathybius*	0.03	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00
	Simenchelys parasitica	0.03	0.00	0.00	0.00	0.19	0.11	0.00	0.00	0.00	0.14	0.00	0.00
	Synaphobranchus kaupi	8.17	3.52	2.50	1.03	4.70	9.75	8.44	3.03	0.68	4.40	0.69	2.90
	Synaphobranchidae	0.20	0.19	0.17	0.34	0.19	0.11	0.32	0.00	0.34	0.14	0.00	0.09
Notacanthidae	*Lipogenys gillii*	0.03	0.00	0.00	0.00	0.10	0.11	0.00	0.00	0.00	0.00	0.00	0.09
	Polyacanthonotus spp.	0.68	0.10	0.50	0.00	0.58	0.78	0.78	1.82	1.02	0.00	0.35	0.09
	Notacanthus chemnitzii	0.13	0.48	0.17	0.00	0.48	0.11	0.14	0.61	0.00	0.43	0.69	0.19
	Notacanthidae	0.03	0.10	0.17	0.00	0.00	0.00	0.04	0.00	0.00	0.07	0.00	0.09
Halosauridae	*Aldrovandia* spp.	0.30	0.10	0.50	0.34	0.10	0.45	0.21	1.21	1.36	0.07	0.00	0.09
	Halosauropsis macrochir	1.24	0.67	0.50	0.00	0.86	3.48	0.82	2.42	2.72	0.07	0.00	0.09
	Halosauridae	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.00
Alepocephalidae	*Alepocephalus* spp.	0.33	0.10	0.00	0.69	0.96	1.01	0.50	0.00	0.34	0.00	0.00	0.19
Gonostomatidae	Gonostomatidae	0.05	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.09
Bathysauridae	*Bathysaurus ferox*	0.28	0.00	0.00	0.34	0.00	0.45	0.25	0.00	0.34	0.00	0.00	0.00
Myctophidae	Myctophidae	1.77	1.33	1.00	0.00	0.29	0.45	0.57	2.42	0.00	2.70	1.39	2.52
Chaunacidae	*Chaunax* spp.	0.00	0.10	0.50	0.00	0.19	0.22	0.11	0.00	0.34	0.00	0.00	0.00
Macrouridae	*Coelorinchus caelorhincus*	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
	Coryphaenoides armatus	0.53	0.57	0.83	1.72	0.58	1.35	0.64	1.21	1.02	0.36	0.00	0.28

	Coryphaenoides carapinus	10.88	10.08	16.00	29.31	12.08	21.19	14.36	12.12	32.65	4.76	5.21	4.77
	Coryphaenoides rupestris	10.37	25.86	20.50	6.21	9.78	4.26	12.05	13.94	5.10	15.06	24.65	21.12
	Macrourus berglax	8.10	11.12	14.17	13.10	26.27	1.23	5.92	17.58	7.14	16.97	35.42	24.77
	Nezumia bairdi	2.28	1.33	1.50	0.00	0.96	0.67	1.63	0.61	0.00	3.98	0.69	1.12
	Macrourid sp. 1	0.78	0.29	0.17	0.00	0.67	1.57	0.71	1.21	1.02	0.21	0.00	0.00
	Macrourid sp. 2	1.11	0.76	1.00	0.69	1.34	3.81	1.17	1.21	1.36	0.00	0.00	0.09
	Macrourid sp. 3	0.08	0.00	0.33	0.00	0.00	0.11	0.11	0.00	0.00	0.00	0.00	0.09
	Macrourid sp. 4	0.10	0.10	0.17	0.00	0.00	0.45	0.04	0.00	0.34	0.00	0.00	0.00
	Macrourid sp. 5	0.08	0.00	0.00	0.00	0.00	0.11	0.07	0.00	0.00	0.00	0.00	0.00
	Macrourid sp. 6	0.15	0.00	0.00	0.34	0.00	0.00	0.11	0.00	0.00	0.14	0.00	0.19
	Macrourid sp. 7	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.09
	Macrouridae	14.39	14.07	15.33	24.83	26.65	21.97	19.78	18.79	25.85	11.08	13.89	9.53
Moridae	*Antimora rostrata*	15.08	18.92	15.67	13.79	6.14	12.56	12.41	12.73	13.95	16.69	10.07	19.16
	Lepidion eques	0.00	0.00	0.67	0.00	0.29	0.00	0.04	0.00	0.00	0.00	0.00	0.56
Lotidae	*Gaidropsarus* spp.	0.73	0.86	1.83	1.72	0.86	0.56	0.53	0.61	0.00	2.13	0.69	0.93
Ophidiidae	Ophidiidae	0.08	0.10	0.00	0.34	0.86	0.11	0.25	0.00	0.00	0.36	0.35	0.00
Oreosomatidae	*Neocyttus helgae*	0.00	0.00	0.33	0.00	0.58	0.00	0.00	0.00	0.00	0.00	1.74	0.28
Psychrolutidae	*Cottunculus* spp.	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00
	Cottunculus thompsonii	0.05	0.10	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.07	0.00	0.00
Pleuronectidae	*Reinhardtius hippoglossoides*	0.76	1.43	0.17	0.34	0.48	0.67	0.74	1.21	0.68	0.71	0.00	1.03
Unknown	Fish unknown (sp. 1)	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00	0.00	0.00	0.00
	Fish unknown (sp. 2)	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09
	Fish unknown (sp. 3)	0.03	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00
	Fish unknown (sp. 4)	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.61	0.00	0.00	0.00	0.00
	Fish unknown (Anguilliform)	0.56	0.29	0.33	0.00	0.00	0.56	0.50	0.00	0.34	0.21	0.00	0.37
	Fish unknown (mesopelagic)	18.69	6.27	4.00	2.76	2.88	9.42	15.03	3.64	2.38	17.76	3.13	8.13
	Fish (unknown)	0.71	0.10	0.33	0.00	0.67	1.23	0.64	0.61	0.68	0.28	0.00	0.09

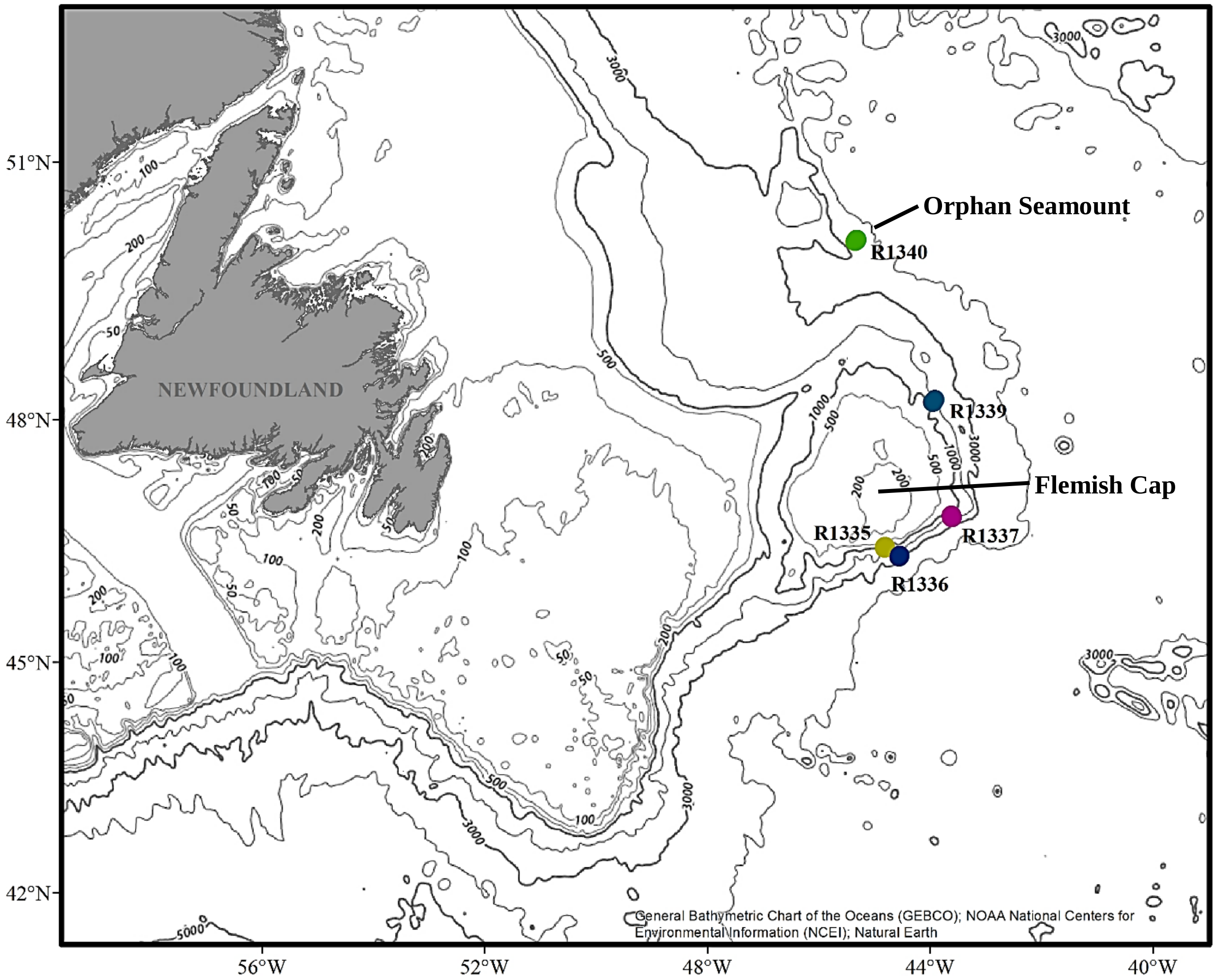
Table 4.7.5 Reaction to the ROV, behaviour, and relative position of individuals for each fish taxa observed during 2010 surveys off Newfoundland, Canada.

Taxa		**Behaviour**				**Reaction to ROV**			**Position**		
		Hiding	Hovering	Restring	Swimming	No reaction	Avoidance	Attraction	On bottom	Off bottom	High off bottom
Chimaeridae	*Hydrolagus affinis*	-	30.0	-	70.0	50.0	40.0	10.0	30.0	30.0	40.0
Scyliorhinidae	*Apristurus* spp.	-	-	-	100.0	50.0	50.0	-	-	-	100.0
Etmopteridae	*Centroscyllium fabricii*	-	-	-	100.0	65.4	7.7	26.9	50.0	34.6	15.4
Rajidae	*Amblyraja* spp.	-	-	66.7	33.3	50.0	50.0	-	100.0	-	-
	Amblyraja jenseni	-	-	-	100.0	100.0	-	-	100.0	-	-
	Bathyraja spp.	-	-	-	100.0	100.0	-	-	100.0	-	-
	Bathyraja spinicauda	-	-	100.0	-	-	100.0	-	100.0	-	-
	Rajella spp.	-	-	-	100.0	66.7	33.3	-	66.7	33.3	-
	Rajiidae	-	-	41.7	58.3	50.0	50.0	-	100.0	-	-
Synaphobranchidae	*Histiobranchus bathybius*	-	-	-	100.0	100.0	-	-	-	-	100.0
	Simenchelys parasitica	-	-	-	100.0	100.0	-	-	-	66.7	33.3
	Synaphobranchus kaupi	-	0.7	-	99.3	88.1	9.1	2.8	37.2	31.4	31.4
	Synaphobranchidae	-	21.4	-	78.6	92.9	7.1	-	28.6	57.1	14.3
Notacanthidae	*Lipogenys gillii*	-	50.0	-	50.0	50.0	50.0	-	-	-	100.0
	Polyacanthonotus spp.	-	51.4	-	48.6	94.6	5.4	-	62.2	29.7	8.1
	Notacanthus chemnitzii	-	25.0	-	75.0	93.8	-	6.3	25.0	62.5	12.5
	Notacanthidae	-	-	-	100.0	100.0	-	-	100.0	-	-
Halosauridae	*Aldrovandia* spp.	-	38.9	33.3	27.8	66.7	33.3	-	44.4	44.4	11.1
	Halosauropsis macrochir	-	89.7	1.5	8.8	94.1	4.4	1.5	76.5	16.2	7.4
	Halosauridae	-	100.0	-	-	100.0	-	-	-	100.0	-
Alepocephalidae	*Alepocephalus* spp.	-	61.5	-	38.5	92.3	7.7	-	25.0	31.3	43.8
Gonostomatidae	Gonostomatidae	-	-	-	100.0	-	-	100.0	-	50.0	50.0
Bathysauridae	*Bathysaurus ferox*	-	-	100.0	-	100.0	-	-	100.0	-	-
Myctophidae	Myctophidae	-	6.5	-	93.5	33.3	57.0	9.7	10.8	39.8	49.5
Chaunacidae	*Chaunax* spp.	-	-	100.00	-	50.0	50.0	-	100.0	-	-

Macrouridae	*Coelorinchus caelorhincus*	-	100.0	-	-	100.0	-	-	100.0	-	-
	Coryphaenoides armatus	-	58.1	-	41.9	86.0	11.6	2.3	41.9	44.2	14.0
	Coryphaenoides carapinus	0.6	89.9	0.2	9.3	86.8	12.7	0.5	79.8	10.6	9.6
	Coryphaenoides rupestris	0.1	77.0	-	22.9	75.4	23.9	0.8	60.2	23.8	16.0
	Macrourus berglax	0.1	83.3	4.3	12.2	96.8	2.8	0.5	94.7	3.4	1.9
	Nezumia bairdi	0.8	85.4	0.8	13.0	96.7	3.3	-	96.7	3.3	-
	Macrourid sp. 1	-	85.7	-	14.3	88.1	11.9	-	83.3	9.5	7.1
	Macrourid sp. 2	-	75.7	-	24.3	71.6	28.4	-	59.5	29.7	10.8
	Macrourid sp. 3	-	100.0	-	-	100.0	-	-	20.0	40.0	40.0
	Macrourid sp. 4	-	83.3	-	16.7	83.3	16.7	-	66.7	33.3	-
	Macrourid sp. 5	-	100.0	-	-	100.0	-	-	100.0	-	-
	Macrourid sp. 6	-	100.0	-	-	100.0	-	-	100.0	-	-
	Macrourid sp. 7	-	50.0	-	50.0	100.0	-	-	100.0	-	-
	Macrouridae	0.2	86.1	0.3	13.5	90.6	9.1	0.3	66.7	13.5	19.8
Moridae	*Antimora rostrata*	-	8.8	0.1	91.1	83.1	11.2	5.7	65.9	27.8	6.3
	Lepidion eques	-	71.4	-	28.6	100.0	-	-	100.0	-	-
Lotidae	*Gaidropsarus* spp.	14.3	14.3	49.2	22.2	95.2	1.6	3.2	96.8	3.2	-
Ophidiidae	Ophidiidae	-	57.1	-	42.9	100.0	-	-	78.6	21.4	-
Oreosomatidae	*Neocyttus helgae*	-	87.5	-	12.5	87.5	12.5	-	25.0	37.5	37.5
Psychrolutidae	*Cottunculus sp.*	-	-	100.0	-	100.0	-	-	100.0	-	-
	Cottunculus thompsonii	-	-	100.0	-	100.0	-	-	100.0	-	-
Pleuronectidae	*Reinhardtius hippoglossoides*	-	-	59.6	40.4	67.3	30.8	1.9	98.1	-	1.9
Unknown	Fish unknown (sp. 1)	-	-	-	100.0	100.0	-	-	100.0	-	-
	Fish unknown (sp. 2)	-	-	100.0		100.0	-	-	100.0	-	-
	Fish unknown (sp. 3)	-	-	-	100.0	-	-	100.0	-	-	100.0
	Fish unknown (sp. 4)	-	100.0	-		100.0	-	-	-	100.0	
	Fish unknown (Anguilliform)	-	18.5	3.7	77.8	77.8	11.1	11.1	44.4	29.6	25.9
	Fish unknown (mesopelagic)	-	1.8	0.2	98.0	27.2	64.4	8.4	18.5	44.5	37.0
	Fish (unknown)	-	50.0	2.6	47.4	86.8	10.5	2.6	35.1	40.5	27.0

4.8 Figures

Figure 4.8.1 Map indicating locations of each of five ROV dives conducted during a 2010 survey of the Flemish Cap and Orphan Seamount off the Grand Banks of Newfoundland, Canada.



General Bathymetric Chart of the Oceans (GEBCO); NOAA National Centers for Environmental Information (NCEI); Natural Earth

Figure 4.8.2 Photos of classified habitat types and fishes observed during 2010 ROV surveys off Flemish Cap and Orphan Seamount: (a) *Antimora rostrata* swimming over fine grain sediments with no corals or sponges present, (b) sparse corals over coarse sediments with scattered boulders, (c) *Chaunax* spp. resting over coarse sediments, (d) dense sponges on outcrop wall, (e) *Centroscyllium fabricii* swimming over sparse sponges, (f) *Coryphaenoides rupestris* in sparse mixed habitat, (g) *Neocyttus helgae* among sparse mixed over coarse sediments, (h) Boulder field with dense mixed, (i) *Macrourus berglax* on bedrock outcrop wall with dense corals.

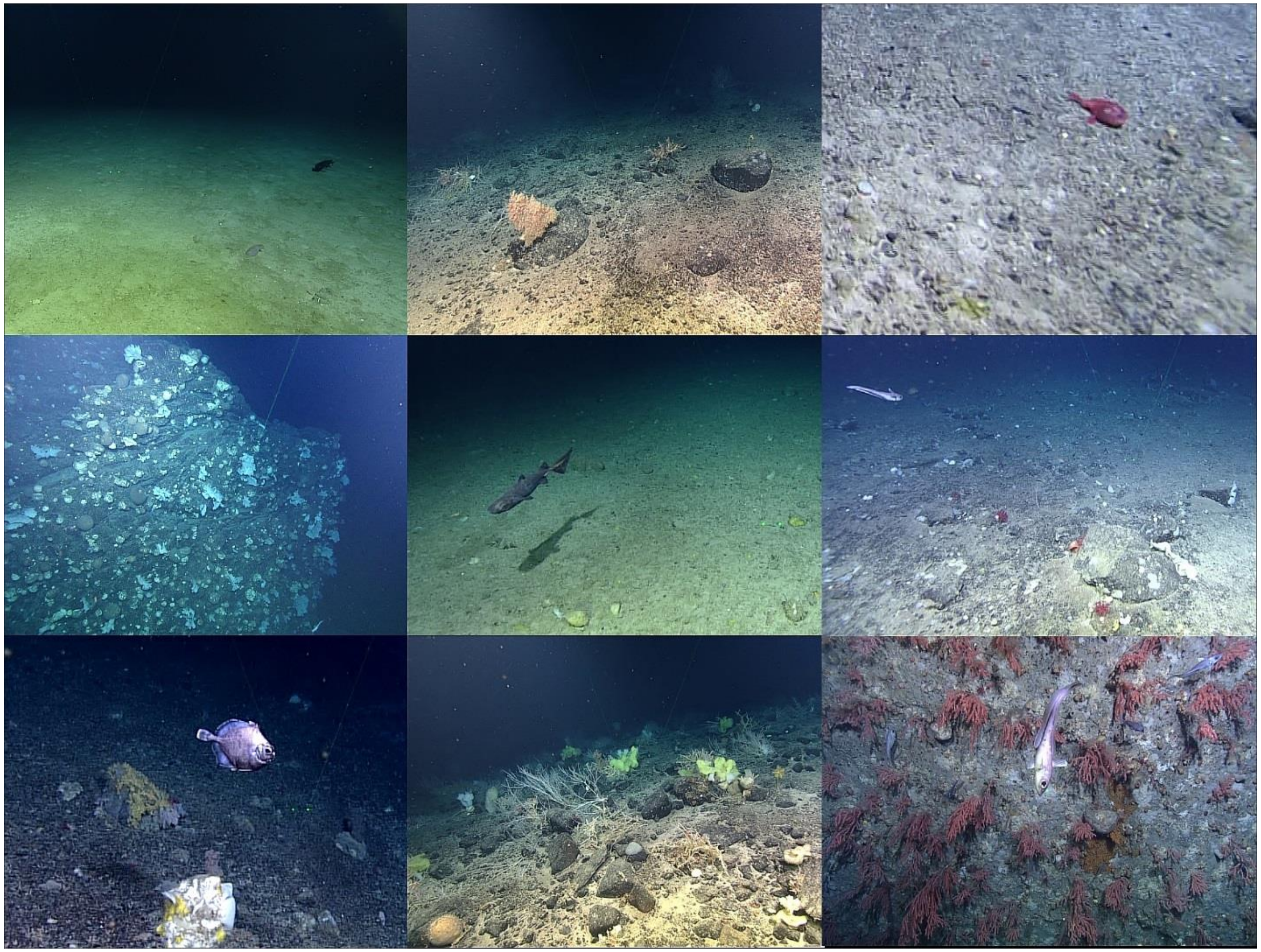


Figure 4.8.3 Depth distribution of fish taxa observed during 2010 ROV surveys off Newfoundland, Canada.

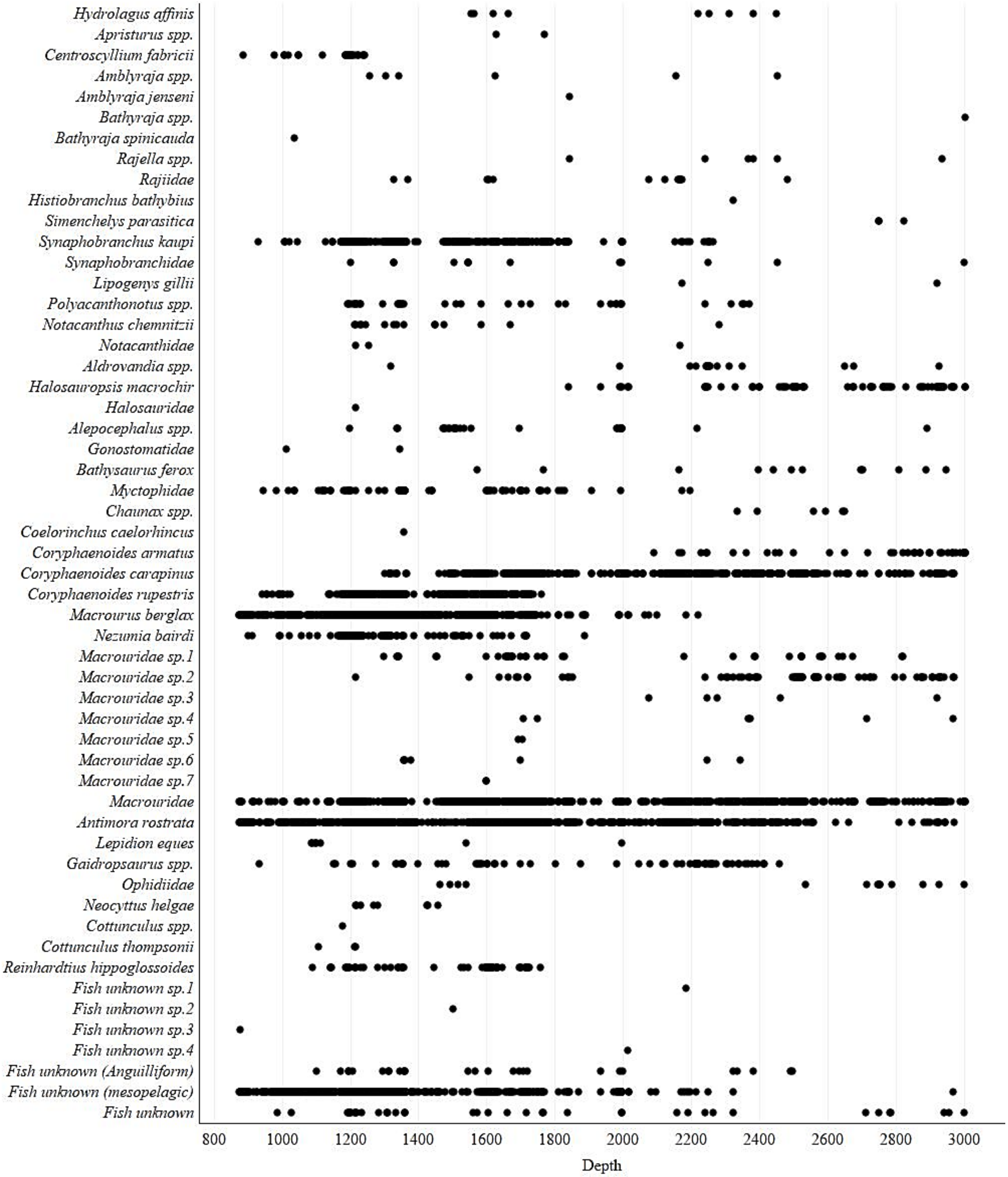
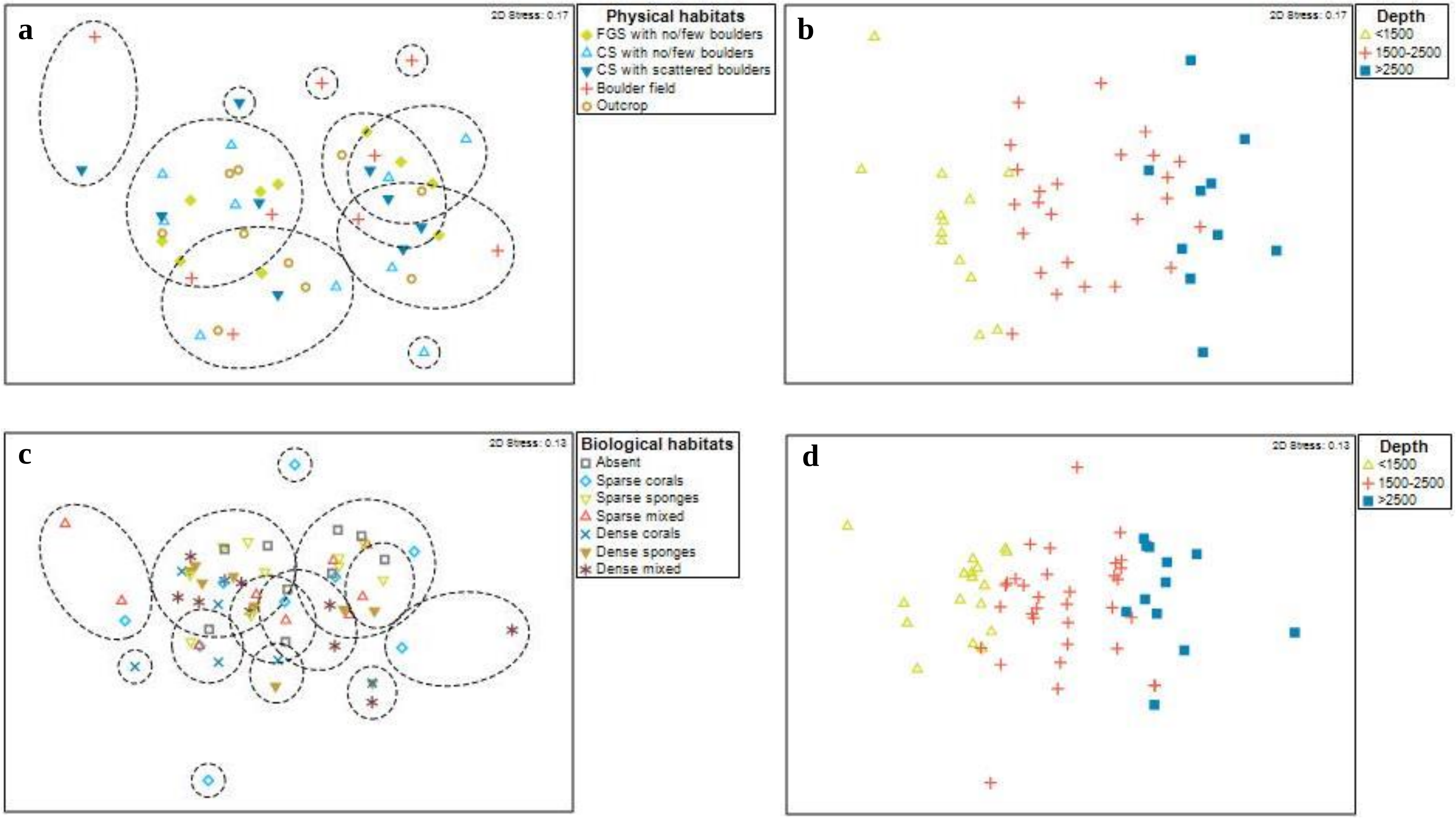


Figure 4.8.4 MDS plots of Bray-Curtis similarity matrices based on fish observations on physical (a) and biological (c) habitats and depth groups based on physical (b) and biological (d) samples. Dotted lines indicate 50% similarities based on dendrogram cluster analyses.



5 Influence of warm-core eddies on mesopelagic fish assemblages in the Northwest Atlantic Ocean

Abstract

Variability in mesopelagic fish assemblages of the deep-scattering layer (DSL) were explored in relation to mesoscale, warm-core eddies in the western North Atlantic Ocean. By combining mid-water trawls and concurrent oceanographic sampling with XBTs (eXpendable Bathy Thermographs) and CTD (conductivity-temperature-depth) deployments aboard the *RV Celtic Explorer* in the Spring of 2015 and 2016, we characterized mesopelagic fish assemblages along multiple transects through eddies identified using satellite-derived regional sea level anomaly data. Sampling yielded a total of 6,091 individual fish specimens, representing at least 111 species across 38 families. The families Myctophidae and Stomiidae were the most speciose taxa in both years, comprising >50% of total catch abundance in each year. Species richness and diversity were significantly higher in deeper fishing sets relative to shallow sets, and were also higher in sets occurring inside warm-core eddies relative to outside the eddy structures. Community analyses indicate significant differences in assemblage structure between both depth (shallow versus deep) and eddy (inside versus outside) groups, with ordination discrimination of 10 pelagic fish assemblages related to both sampled depth and position relative to each eddy. Eddies also harbored more juveniles and rare species, including species with more southerly distributions within the Gulf Stream. Our results indicate

warm-core eddies may play an important role in structuring fish assemblages and dispersion of mesopelagic species.

5.1 Introduction

The mesopelagic environment, comprised of depths between 200 and 1000 m, contains approximately 20% of the global ocean volume. This ‘twilight zone’ plays a crucial role in biogeochemical processes (Davison et al. 2013) and links euphotic surface waters to the aphotic realm below both through settling material (e.g. phytodetritus) and through diel vertical migrations of many mesopelagic organisms spanning multiple depth horizons (Neilson and Perry 1990). These mesopelagic depths support substantial biomass, as evidenced by the ubiquitous presence of an expansive acoustic sound-scattering layer of zooplankton and fishes. First noted during sonar surveys during WWII, this biomass-rich deep-scattering layer (DSL) is sometimes sufficiently dense to be mistaken for the seafloor in early acoustic surveys, and is thus commonly referred to as the ‘false bottom’ (Proud et al. 2017). Mesopelagic fishes comprise the most abundant vertebrates on Earth and a major component of DSLs, with current total biomass estimates of potentially one billion tons (Irigoien et al. 2014). DSLs rarely exceed depths of 1000 m from tropical to sub-polar environments (Magnússon 1996; Fennell and Rose 2015), although some studies report pronounced differences in vertical extent and acoustic backscatter intensity among geographic regions (Proud et al. 2017).

The coupling of physical and biological characteristics are well-known and environmental drivers such as temperature, salinity, and current speed can have a profound impact on the structuring of pelagic marine communities. Oceanographic influences can also shape DSL characteristics, from the physical structure to the composition of the layer. For example, Fennell and Rose (2015) attributed inter-annual variability in DSL density from acoustic backscatter in the North Atlantic Ocean to differences in temperature at depths of 400-600 m, with highest DSL density during years with higher temperatures. Other studies link temperature and DSL density at mesopelagic depths (Proud et al. 2017), although temperature at the sea surface appears insignificant as a driver of temperature below the surface mixed layer. Differences in water masses can also influence species composition, with oceanic fronts creating biogeographic boundaries for some midwater fishes with lesser effects on deeper-dwelling taxa (Sutton et al. 2013). How these taxon-specific influences relate to DSL backscatter intensity is poorly understood as limited data on species composition, size, and associated acoustic target strengths for most mesopelagic fishes constrains understanding how these taxon-specific influences relate to DSL backscatter intensity (Davison et al. 2015).

Mesoscale eddies are transient, circular currents, ubiquitous in the world’s oceans and often propagating along swift ocean currents. Spanning approximately 100 – 200 km in diameter, these kinetic features mix and redistribute water masses, transporting entrained source water into the surrounding ocean, where they can persist for days to years (Chelton et al. 2011). The thousands of mesoscale eddies present globally each day (Faghmous et al. 2015) add dramatic heterogeneity and complexity to open ocean habitats, and strongly influence marine communities (Lévy et al. 2008; Chelton et al. 2011; Wells et al. 2017). These eddies can extend to depths of 5000 m (Rhines et al. 2001), dramatically changing physiochemical aspects of the water column through considerable vertical mixing. Eddies therefore play an important role in transporting heat, salt, and biochemical tracers associated with different water masses (McWilliams et al. 2008; Chelton et al. 2011).

In the North Atlantic Ocean, the fast-moving, western boundary Gulf Stream current transfers heat and water from subtropical regions in the central western Atlantic to the subpoloar region in the northeast Atlantic. It accelerates northward along the eastern coast of the United States until Cape Hatteras at 35°N, where it departs from the coast and flows northeast toward the open ocean. As it rounds the Grand Banks of Newfoundland, changes in bathymetry and interactions with other currents can result in branching meanders. Portions of these swift moving meanders are shed as a closed loop or ring, creating both cyclonic (cold core) and anti-cyclonic (warm-core) eddies. Anti-cyclonic eddies form off the northward meanders of the Gulf Stream, entraining warm water and often traveling eastward across the Atlantic. Conversely, cyclonic cold-core eddies spin off of southward meanders to trap cool coastal waters and typically travel south toward the Sargasso Sea and may be reabsorbed within the Gulf Stream (Saunders, 1971). High primary productivity and plankton biomass typically characterize cold-core eddies, given upwelling of nutrients at the core (Vaillancourt et al. 2003), however, rates of productivity can vary in warm-core eddies depending on the relative depth of the central thermocline/pycnocline (Nelson et al. 1989; McGillicuddy et al. 2007; Chen et al. 2015).

The Gulf Stream produces an estimated 22 anti-cyclonic and 35 cyclonic eddies per year on average (Hogg and Johns 1995). Given many of these structures rank within the upper 90th percentile of global sea level anomalies, eddies derived from the Gulf Stream represent some of the most energetic mesoscale features worldwide (Chelton et al. 2011).

These dynamic mesoscale features can influence pelagic ecosystems across multiple trophic levels, and can strongly influence spatial patterns in marine organisms (Wells et al. 2017). Physical processes within eddies can significantly impact nutrient concentrations and planktonic communities, often with increased plankton abundances and biological production in regions of upwelling and along frontal zones (Doblin et al. 2016; Dufois et al. 2016). Ichthyoplankton assemblages may differ between warm-core and cold-core eddies (Muhling et al. 2007), particularly because eddies retain and aggregate larvae and may act as nursery habitats for eggs, larvae, and juveniles, and also aid in larval transport (Shulzitski et al. 2017; Tiedemann et al. 2018). This concentration of prey may locally enhance fish production (Godø et al. 2012), and aggregations of large marine organisms including turtles (Kobayashi et al. 2011), seabirds (Wellington et al. 2015), cetaceans (Griffin 1999), tunas (Kai and Marsac 2010), and sharks (Gaube et al. 2018) within eddies and along fronts, suggesting these features also support higher trophic levels and apex predators. In addition, eddies may entrain communities from their origin, harboring and dispersing species from source waters to the surrounding ocean. Mesoscale eddies can affect the density and vertical structure of the DSL as species may conform to isoclines present within the feature (Godø et al. 2012; Boersch-Supan et al. 2015; Fennell and Rose 2015). Acknowledging numerous studies of ichthyoplankton composition in relation to eddies (Muhling et al. 2007; Atwood et al. 2010; Contreras-Catala et al. 2012), few studies have explored differences in adult mesopelagic fish assemblages within the DSL along oceanic fronts and eddy systems.

In this study we explore vertical and horizontal variability in fish abundance, size, and assemblage structure in relation to two warm-core eddies in the western North Atlantic Ocean. Oceanographic sampling and sea level anomaly (SLA) data were used to identify targeted eddies, which were then sampled for mesopelagic fishes at different depths with mid-water trawls across a range of proximities to the eddy core, to explore relationships between ichthyofaunal assemblage and physical attributes associated with warm-core eddies.

5.2 Materials and Methods

5.2.1 Study area

Warm-core eddies were sampled in the northwest Atlantic off of Newfoundland, Canada during trans-Atlantic crossings from Ireland to Canada in April of 2015 and 2016 aboard the RV *Celtic Explorer*, a 65-m Irish research vessel with acoustic, hydrographic, and trawl sampling capacity. In 2015, we selected an eddy (hereafter ‘E15’) located approximately 600 km east of the Flemish Cap (between 45-50°N, 35-40°W). In 2016, we seleced an eddy (hereafter ‘E16’) located approximately 400 km east of the Flemish Cap (between 45-50°N, 38-43°W). Surveys included sampling transects across the feature, with oceanographic sampling at pre-defined spatial intervals and biological sampling targeted at areas inside and outside the eddy. Bottom depths at fishing set locations ranged from 4177 to 4583 m with the exception of two sets (9, 10) which occurred over a bottom depth of 3525 m along the southeastern margin of the Flemish Cap.

5.2.2 Hydrographic data collection

Probable anti-cyclonic eddies west of the Mid-Atlantic Ridge were identified each year from satellite sea-surface altimetry data downloaded through CCAR (Colorado Center for Astrodynamics Research). E15 and E16 were selected prior to departure from Ireland, and real-time satellite updates of SLA patterns monitored for several weeks prior to vessel arrival within the study area. Positive and negative altimeter values can facilitate identification of potential eddy features but are not diagnostic and should be integrated with other hydrographic measures. Therefore, we used altimeter values to direct the vessel toward selected probable eddies and confirmed them through *in-situ* oceanographic sampling. Temperature profiles were collected with the Sippican XBT (eXpendable Bathy Thermographs) and the onboard Seabird 911 CTD (conductivity, temperature, depth) system. Both methods collected data to a depth of 1800 m. XBTs were deployed every 50 km during transit to the eddy region, reducing sampling intervals to 2.5 – 10 km near positive altimeter values encountered upon approach to each sampled eddy. CTD casts preceded each fishing set or pairs of fishing sets at the same station. Sea Level Anomaly (SLA) data downloaded from Copernicus Marine Environment Monitoring Service (www.marine.copernicus.eu) were used based on a 0.25 degree gridded data set and anomalies based on a 20 year mean. Eddy centers in the survey area were identified following methods in Chelton et al. (2011).

5.2.3 Fish collection

Fishing sets utilized a herring trawl (40 m x 22 m) with a 10 mm mesh liner, towed pelagically at 3.5 knots for 30 – 45 minutes and fitted with a depth-temperature logger (*DST centi-TD Star-Oddi, Gardabaer, Iceland*) to record depth and temperature during each tow. Fishing sets were designed to sample DSL fauna at a range of proximities to the eddy each year and at ‘shallow’ (200 – 350 m) and ‘deep’ (400 – 650 m) mesopelagic depths. Size, structure, and depth of the DSL was monitored using continuously recorded backscatter coefficient data from the onboard Simrad EK60 acoustic echosounder (18, 38, 120 Hz) with transducer mounted on a drop keel extended 8.8m below sea level. Acoustic profiles of the water column guided selection of fishing depths for each tow in order to target DSL. All tows in 2015 occurred during daylight hours, with 1 set in 2016 occurring at night to target distinct DSL surface layers observed in acoustic profiles (Fennell & Rose, 2015). Following each tow, cod-end samples were processed in the on-board laboratory. All specimens were sorted and identified to the lowest possible taxonomic level, then weighed (to nearest 0.001 kg) and measured (to nearest millimeter, total length) and voucher specimens preserved at -80°C for the remainder of the cruise. Specimens were later preserved in a 10% formalin:seawater solution and deposited at the Atlantic Reference Centre (Huntsman Marine Station, Saint Andrews, NB, Canada) for verification of identifications of select species by regional experts.

5.2.4 Hydrography at fishing locations

Physical variables including temperature and SLA were measured at the location of each fishing set using georeferenced hydrographic data and information retrieved from loggers attached to the trawl. A combination of temperature profiles to a depth of 650 m (deepest fishing depth) and SLA height generated for set locations were used to delineate fishing sets as having occurred ‘inside’ versus ‘outside’ of the eddy for each year. Sets were sorted *a priori* to fish assemblage analyses, and groupings tested through hierarchical cluster analysis using a normalized oceanographic matrix with dissimilarity measured using Euclidean distance. Environmental variables included SLA height at each fishing location and temperature at depths of 10 m, 150 m, 250 m, 350 m, 450 m, 550 m and 650 m. Group-average hierarchical cluster analysis produced a dendrogram which allowed definition of eddy groupings. The edges of the eddy were identified based on changes in the thermocline structure and, in combination with SLA values, used to categorize fishing sets as inside or outside the eddy feature.

5.2.5 Ichthyofauna composition and diversity

Abundance values for each taxa were standardized based on a tow duration of 30 minutes. Biodiversity differences among groups was explored through calculating taxa richness (*R*) and Shannon diversity indices (*H’*) for each tow. Linear regression models assessed differences in indices and set abundance as a function of depth, SLA values, and temperature using the statistical software R v. 3.3.2 (R Core Team). To explore diversity patterns in spatial relation to each eddy, abundance was pooled through the water column and mean diversity indices at each location compared between inside and outside eddy groups using one-way analyses of variance (ANOVA).

5.2.6 Assemblage analyses

The goal of the present study was to examine how fish diversity, abundance, and assemblage composition vary with depth and relative to warm-core eddies. We explored differences in fish assemblages between depth groups and spatial relation to eddies using PRIMER 7 software (Version 7.0.10, Primer-E, Plymouth, UK; Clarke and Gorley, 2015). First, non-metric multidimensional scaling (nMDS, Kruskal and Wish, 1978) plots and group-average hierarchical cluster analyses were conducted based on Bray-Curtis similarity matrices constructed from fourth-root transformed abundance data for each tow and excluding species/taxa present in <5% of samples. Similarity profile analysis (SIMPROF) determined the significance of cluster groups, with permutation testing (1000 iterations) performed to test for differences in multivariate structure between groups.

An analysis of similarity (ANOSIM) tested for assemblage differences based on depth groups of 'shallow' and 'deep' tows. The single tow conducted at night was excluded from depth assemblage comparisons to mitigate potential bias of vertical migration. ANOSIM testing further explored whether assemblages were significantly different 'inside' versus 'outside' each eddy based on objective hierarchical cluster analysis groupings and *a priori* examination of oceanographic variables associated with each fishing set location. For both analyses, where ANOSIM detected significant differences between groups, a SIMPER (similarity percentages) analysis was subsequently used to determine which species contributed most to similarities and differences between groups.

5.3 Results

5.3.1 Oceanography

Temperature profiles generated using XBT and CTD data collected nearest to each fishing set (Figure 5.8.1; Figure 5.8.2) indicated differences in eddy structure and magnitude between years. Typical anti-cyclonic down-welling characterized both E15 and E16, extending the warm mixed-layer to depths in excess of 450 m in 2015 and 650 m in 2016. Oceanographic data collected during each fishing set using loggers attached to trawl gear indicated no significant relationship between fishing depth and temperature during each tow ($F = 1.85_{1, 21}$; $p = 0.19$). SLA values for E15 ranged from -0.20 m to 0.32 m at fishing locations, with a similar range of -0.27 m to 0.34 m observed at sets associated with E16.

Tows were spatially categorized relative to each eddy through a cluster analysis that combined SLA height and temperature profiles at each fishing set location (Figure 5.8.3). SLA heights at the location of each fishing set were considered in conjunction with temperature profiles to determine vertical extent of warm surface waters. Hierarchical clustering of the oceanographic matrix revealed groupings consistent with delineation of sets through comparison of SLA height to temperature at 350 m depth (Figure 5.8.4). In 2015, fishing sets 1-2 and 9-10 occurred outside of E15; SLA heights ≤

-0.001 m in combination with temperatures >10 °C restricted to depths above 300 m characterized all of these sets. Sets 9-10 occurred farthest from E15, and although SLA values were higher than Sets 1-2 (-0.20 m), Sets 9-10 sampled the coldest water, with temperatures just below 4 °C extending beyond 650 m with a cold intermediate layer between 150 and 250 m. Sets 3-8 occurred within the E15, with a mean SLA value of 0.26 ± 0.08 m at these trawl locations. Sets 3-4 occurred near the core of the eddy, indicated by the depressed SLA height of 0.15 m and an extension of warm >10 °C water beyond 450 m. Sets 5-8 occurred along the eddy ring, characterized by high SLA values >0.30 m and a shallower (<300 m) extension of warm waters compared to the core region.

In comparison, E16 displayed overall slightly higher SLA values and deeper warm water extension than E15. Fishing sets 12-13 and 19-23 occurred within the eddy, with mean SLA height of 0.21 ± 0.10 m and temperatures near 14 °C extending below 450 m for most sets within the eddy. Sets 21-22 occurred near the core, with lower SLA heights of 0.10 m compared to 0.17-0.34 m observed at other fishing locations within E16. Trawl deployments in 2016 occurring outside of eddy included Sets 11 and 14-18. Temperature profiles associated with these tows indicate a shallowing of the warm mixed layer depth above 300 m, and a mean SLA value of 0.0 ± 0.14 m. Sets 14-15 were associated with higher SLA values of 0.11 m suggesting tows proximate to the eddy border, however, warmer temperatures >12 °C restricted above 250 m indicated tows outside of E16.

5.3.2 Mesopelagic ichthyofauna

The 23 mid-water trawls collected a total of 6,091 fish (Table 5.7.1; Figure 5.8.2), representing at least 111 species from 38 families and 13 orders (Table 5.7.2). Rare captures were quite common, with 52 species/taxa present in only a single tow and 35 species/taxa represented by only a single specimen. Poor condition of specimens limited identification of 5 taxa to the genus level, and 4 leptocephalus larvae specimens were unidentified. The families Myctophidae and Stomiidae were the most species-rich families, each represented by at least 27 species. Of the other families, only Paralepididae and Sternoptychidae contained at least 5 species.

5.3.3 Relative abundance and biomass

Differences in dominant species were observed between sampling years. In 2015, the myctophid *Benthosema glaciale* was the most abundant species (32% of total individuals). This species, along with confamilials *Myctophum punctatum*, *Notoscopelus kroyeri*, and the barbeled dragonfish *Stomias boa ferox* represented >60% of total fish abundance for Sets 1-10. In contrast, the viperfish *Chauliodus sloani* (16% of total) and the bristlemouth *Sigmops elongatum* (11% of total) dominated Sets 11-23 in 2016. Although overall catch abundance in 2015 exceeded that in 2016 (3877 individuals versus 2213 individuals, respectively) despite fewer fishing sets in 2015, species richness was higher in 2016 with 91 species encountered compared to 60 species in 2015.

Fish biomass was similar between both years, with a total of 30.9 kg from Sets 1-10 (2015) and 31.5kg from Sets 11-23 (2016). Dominant biomass contributors largely reflected abundance patterns, with the addition of a small number of large fishes. In 2015, nearly 50% of the biomass was comprised of the main contributors to total abundance (*Stomias boa ferox*, *Myctophum punctatum*, *Notoscopelus kroyeri,* and *Benthosema glaciale*). However, a single, large lumpfish *Cyclopterus lumpus* also represented ~14% of the total biomass – the same as *M. punctatum*. In 2016, while the two most abundant species –*Sigmops elongatum* and *Chauliodus sloani* – rank second and third highest contributors to total biomass respectively, two large dealfish *Trachipterus arcticus* represent 24% of the total biomass.. Other large fishes including the pomfret *Brama brama*, oarfish *Regalecus glesne*, black gemfish *Nesiarchus nasutus*, and the relatively large myctophid *Lampadena atlantica* also contributed >3% of total biomass.

5.3.4 Vertical zonation with depth

A total of 14 species occurred only in shallow sets at depths between 200 m and 350 m. Over one-third of these were stomiids, with the remainder consisting of bramids, myctophids, and monospecific representatives of the families Paralepididae, Cyclopteridae, Bercidae, and Microstomatidae. In 2015, the myctophid *Benthosema glaciale* largely comprised shallow sets, representing nearly 50% of individuals captured at those depths. Two other myctophids, *Myctophum punctatum* (13%) and *Notoscopelus kroyeri* (12%), along with the hatchetfish *Argyropelecus hemigymnus* (8%) contributed over 80% of shallow species encountered. Shallow sets in 2016 were more speciose compared to 2015. The bristlemouth *Sigmops elongatum* was the dominant species observed in 2016, representing 23% of the total abundance in shallow sets. Other main contributors (>5%) include the viperfish *Chauliodus sloani* (9%) and the lightfish *Maurolicus muelleri* (7%) (Table 5.7.3).

Fifty-seven species/taxa occurred only in deep sets from 400 – 650 m. Myctophids and stomiids comprised over half of the taxa observed, with 15 families found exclusively in deep sets including characteristic groups such as anglerfishes (Himantolophidae, Oneirodidae, Ceratiidae), Synaphobranchidae, Opisthproctidae, Evermannellidae, and Scopelarchidae. In 2015, myctophids *Benthosema glaciale* (22%) and *Myctophum punctatum* (11%), along with the dragonfish *Stomias boa ferox* (12%) largely comprised deep sets. Other species contributing >5% include the myctophid *Notoscopelus kroyeri* (7%), the sawpalate eel *Serrivomer beanii* (6%), and *Chauliodus sloani* (6%). For deep sets in 2016, *Chauliodus sloani* was the most abundant species, representing 18% of total abundance. Similar to 2015 sets, both *Notoscopelus kroyeri* and *Serrivomer beanii* also contributed 7%, with the addition of *Sigmops elongatum* (9%), *Lobianchia gemellari* (9%), *Arctozenus risso* (7%), and the myctophid *Diaphus effulgens* (6%) contributing >40% of total abundance (Table 5.7.3).

5.3.5 Horizontal zonation with eddy structures

The myctophids *Myctophum punctatum*, *Benthosema glaciale*, and *Notoscopelus kroyeri* dominated sets inside the eddy in 2015 and collectively comprised 43% of total abundance from these sets. Sets occurring outside of E15 were overwhelmingly dominated by *Benthosema glaciale*, representing 63% of all individuals, although this value resulted largely from the capture of over 600 *B. glaciale* individuals in Set 1. Other contributing species include *Stomias boa ferox* and *Maurolicus muelleri*, representing 9% and 8%, respectively.

Reflective of overall species abundance in 2016, *Chauliodus sloani* dominated stations both inside and outside of E16. Outside of E16, *Chauliodus sloani* (28%) along with the duckbill eel *Nemichthys scolopaceus* (9%), *Maurolicus muelleri* (8%), *Arctozenus risso* (8%), the pencilsmelt *Microstoma microstoma* (6%), and *Stomias boa ferox* (6%) comprised 65% of the total catch in these sets. Sets occurring inside E16 were dominated by *Chauliodus sloani* and *Sigmops elongatum*, both representing 13% of the total abundance inside. Other top contributing species include the myctophids *Lobianchia gemellari* (8%) and *Notoscopelus kroyeri* (7%), *Arctozenus risso* (7%) and *Serrivomer beanii* (6%).

5.3.6 Eddy-associated fauna

Only 10 species occurred exclusively in sets outside the warm-core eddy in both years (Table 5.7.4). Two species were considered true ‘cold-water’ fishes in the region– the northern wolffish *Anarhichas denticulatus* and the lumpfish *Cyclopterus lumpus*. The remaining 8 species represent 7 families, nearly all distributed widely in both east and west Atlantic Ocean, with the exception of the hatchetfish *Polypinus clarus* known only from the western Atlantic. In contrast, at least 66 species were captured exclusively in tows conducted inside of E15 and E16 (Table 5.7.4). Twenty-one of these species were stomiids, of which over 75% were from the scaleless dragonfish subfamily Melanstomiinae. In addition, twelve families occurred only inside eddies, including the teleosts Aleposauridae, Bercyidae, Caristiidae, Howellidae, and both Stephanobercyiforms, as well as the sole elasmobranch captured, the dalatiid *Squaliolus laticaudus*.

Four unidentified leptocephalus larvae, the only larval forms encountered, occurred both inside and outside of eddy waters. Several juvenile/sub-adults displaying characteristic early life traits (e.g. modified fin structure and coloration) were observed inside eddy waters, with notable species including bramids *Pterycombus brama* (n=1, TL=16.3 cm) and *Taractes asper* (n=1, TL=17.7 cm), the manefish *Caristius groenlandicus* (n=2, TL=7.8 cm, 9.8 cm) and a unique long-finned specimen of the alfonsino *Beryx decadactylus* (n=1, TL= 17.5 cm; see Figure A8; Swinney et al. 1999). Small stomiids also occurred inside eddy-waters, including over 90% of all dragonfishes < 10 cm (n=20), with the exception of 20% of small *Chauliodus sloani* captured outside of the eddies. All *Synaphobranchus kaupi* individuals occurred inside eddies, a majority of which were 12-13 cm (n=9). Despite the presence of adult oarfish *Regalecus glesne* exclusively within eddies, a single juvenile oarfish (TL=27.1 cm) was captured in Set 17 outside of E16.

5.3.7 Abundance, diversity, and species richness

There was no significant difference in overall species richness (S) or diversity (H') between sampled years (S: $F_{1,21}$=0.14, p=0.71; H': $F_{1,21}$=0.99, p=0.33). Regression analyses indicate significant positive relationships between species richness with increasing depth (t=-3.70, p<0.001) and temperature (t=3.05, p=0.007) but not SLA height (*t*=1.17, *p*=0.257). Diversity H' also displayed a significant positive relationship with increasing fishing depth (*t*=2.648, *p*=0.0159) but not SLA height (*t*=2.00, *p*=0.059) or temperature at fishing depths (t=1.24, *p*=0.231) (Figure 5.8.5). Analyses of variance (ANOVA) detected significant differences in mean richness between depth groups (shallow versus deep; F=11.78, *p*=0.0026) and eddy groups (inside versus outside; F=12.11, *p*=0.0024), with higher richness in deeper tows and tows inside eddies. Despite significantly higher mean diversity inside eddies compared to outside (F=13.53, *p*=0.0015), mean diversity did not differ significantly between depth groups (F=4.17, *p*=0.055). Significantly higher total catch abundance per tow in deeper sets (t=2.63, *p*=0.017), but no difference occurred in relation to fished temperatures (t=0.67, *p*=0.501) or SLA heights (t=0.08, *p*=0.934).

5.3.8 Multivariate community analyses

SIMPROF (similarity profile) discriminated 10 fish groups/assemblages at a maximum similarity level of 62% (π=2.55, *p* <0.034), at which (Table 5.7.5; Figure 5.8.6) SIMPER analysis of SIMPROF groups showed average within-group similarity ranging from 49 to 75% (Table A8). MDS points grouped according to SIMPROF minimally overlapped between groups based on two-dimensional representation at a stress level of 0.18 (Figure 5.8.7), which a three-dimensional ordination only moderately improved (stress=0.11), suggesting adequate representation of assemblage structure.

The global ANOSIM test indicated significant differences in assemblages between depth groups (R=0.22, *p*<0.02). A SIMPER analysis showed an average similarity of 35%

between shallow sets. *Notoscopelus kroyeri* and *Nemichthys scolopaceus*, which occurred in high relative abundance in shallower sets, were the two top contributors to group similarity, with a combined contribution of 26%. The average similarity between deep sets was 45%, predominately due to high relative abundance of *Chauliodus sloani*, *Serrivomer beanii*, and *Nemichthys scolopaceus* among deep sets. Average dissimilarity between depth groups was 63%, largely driven by additional species present in deeper tows. Differences between depth groups are attributed to the higher relative numbers of species such as *Serrivomer beanii*, *Stomias boa ferox*, *Diaphus effulgens*, *Melanostomias bartonbeani*, *Chiasmodon niger*, and *Howella sherborni* in deep sets, and higher abundance of species *Macroparalepis affinis* and *Diplospinosus multistriata* in shallow sets.

Global ANOSIM also revealed significant differences in assemblage composition between sets outside versus inside warm-core eddies (R=0.39, p<0.001). SIMPER analysis results showed an average similarity of 41% and 44% among outside and inside groups, respectively. The high abundance and relative ubiquity of *Chauliodus sloani*, *Nemichthys scolopaceus*, *Myctophum punctatum*, and *Notoscopelus kroyeri* in most sets greatly influenced similarity among eddy groups, with these species accounting for 55% of similarity among outside sets and 28% among inside sets. Additional contributors toward >50% similarity inside eddies include *Sigmops elongatum* (7%) and the myctophids *Benthosema glaciale* (6%), *Notoscopelus bolini* (5%), and *Lobianchia gemellari* (5%). Average dissimilarity between eddy groups was 65%, with the absence of *Lampadena atlantica, Diplospinosus multistriata*, *Diaphus rafinesquii*, and

Argyropelecus aculateus, and lower relative abundance of *Benthodesmus elongatus*, *Ceratoscopelus maderensis*, *Diaphus effulgens*, *Lobianchia gemellari*, and *Sigmops elongatum* in sets occurring outside of eddies.

5.4 Discussion

Depth and mesoscale eddies both clearly influenced mesopelagic fish communities, with distinct fish assemblages observed between depth groups categorized as shallow (200 - 350 m) and deep (400 - 650 m), as well as between sets on either side of eddy boundaries defined through hydrographic properties of temperature and SLA height at each fishing location. Several abundant taxa were observed in similar concentrations both inside and outside, such as *Stomias boa ferox* and *Nemichthys scolopaceus*, however, over 60% of all taxa were only captured within warm-core eddies, including several juvenile stages. This pattern suggests large-scale oceanographic features such as eddies may play an important role in shaping pelagic assemblages, including potential entrainment and dispersion of individuals from origin waters, and/or providing aggregative structure in an otherwise low heterogeneity environment.

Past studies document the influence of depth in structuring fish assemblages in both benthic and pelagic environments worldwide. In the North Atlantic, Cook et al. (2013) identified eight distinct deep-pelagic fish assemblages over the Charlie-Gibbs Fracture Zone, with depth as the primary factor distinguishing each group across 4 depth zones between 0 and 3000 m. Extension of sampling to near bottom depths of ~5000 m along the northern Mid-Atlantic Ridge yielded 13 distinct pelagic fish assemblages, with depth as the major factor in explaining community groupings (Sutton et al. 2008). Although these studies and many others sampled a far wider depth range than our study, we nevertheless documented significant differences in assemblages between shallow and deep depth groups, despite the relatively narrow mesopelagic depth range examined.

Through hydroacoustic sampling, several studies reported higher densities of acoustic backscatter and unique DSL profiles within mesoscale eddies (Godø et al. 2012; Béhagle et al. 2014; Rose & Fennel 2015), patterns they attributed to the influence of eddy dynamics on the overall biomass and structuring of pelagic fauna. However, the relative contribution of fishes toward these elevated acoustic densities requires extensive biological sampling and knowledge of species specific acoustic signatures to interpret results beyond higher productivity/food sources inside. Other studies employing extractive survey techniques explored changes in fish assemblage structure in relation to eddies. Given the relevance of mesoscale hydrodynamic processes on larval transport, many past studies focussed on ichthyoplankton, reporting significant influence of mesoscale eddies on larval distribution and assemblage composition (Muhling et al. 2007; Atwood et al. 2010; Holliday et al. 2011; Contrera-Catala et al. 2012; Sanchez-Velasco et al. 2013). Fewer studies have addressed how these features influence adult fish assemblages, but indicate significant differences in abundance and community composition in relation to both cyclonic (Simons et al. 2015) and anti-cyclonic eddies (Brandt 1981). Similar observations have been noted along the boundaries of fronts – other mesoscale oceanographic features, not unlike the boundary edge of eddies – with these fronts acting as a distinct biogeographic barrier for some species, resulting in distinct communities on either side of the boundary zone (Sutton et al. 2013; Netburn and Koslow 2018).

We found distinct fish communities based on pre-defined depth and eddy categories, and identified 10 pelagic fish assemblages. Although only six of these groups contain sets linked to a single pre-defined depth group, nine assemblages link with a single pre-defined eddy group, suggesting eddies played a stronger role in shaping fish communities compared to depth. The only group containing both inside and outside sets (Assemblage B) contained two sets at a depth of 300 m, however, these sets represent the two tows with the lowest catch abundance (<26 individuals), with nearly 80% of within group similarity explained by the presence of *Nemichthys scolopaceus*, *Notoscopelus kroyeri*, and *Myctophum punctatum*. Given the presumably modest difference in environmental conditions between depth groups relative to the magnitude of difference between inside and outside eddy conditions, we expected eddies to be stronger driver of assemblage structure. Although mid-water temperatures and SLA heights used to delineate sets strongly predicted assemblage structure, we cannot exclude the potential influence of other drivers not examined here, such as current speed, oxygen saturation, light, and productivity.

Mesoscale eddies have been proposed as oases for higher trophic marine life, congregating prey and consequently predator concentrations (Godø et al. 2012). A wide variety of both planktivorous and piscivorous fishes were sampled inside eddy waters, from large species like the oarfish *Regalecus glesne* and lancetfish *Alepisaurus brevirostris*, to smaller predators such as the spined pygmy shark *Squaliolus laticaudus*, pearleye *Scopelarchus analis*, barracudina *Sudis hyalina*, and numerous species of stomiid, chiasmodontid, and lophiiform predators. Many fishes inside eddies could be considered Gulf Stream species, with distributions in the western Atlantic spanning from the Gulf of Mexico and Caribbean north to Nova Scotia, Canada. A few species were relatively rare for the study area, representing more tropical to subtropical biota in the West Atlantic, including *Ahliesaurus berryi*, *Taractes asper*, and *Margrethia obtusirostra*, presumably advected north via eddy transport.

Eddies may provide a variety of functions, from enhancing local productivity through vertical mixing to acting as a vehicle for transport and oases across a wide range of life stages and sizes. Lack of knowledge regarding how specific species use these large-scale features limits understanding of how changes or shifts in eddy formations may impact fish populations. Climate change models predict major alteration in marine landscapes, including alteration of current trajectories and ocean circulation (Christensen et al. 2013). In the North Atlantic, the latitude of the Gulf Stream pathway clearly correlates with lagged indices of the North Atlantic Oscillation atmospheric pressure differential, with higher values corresponding to stronger and more northerly paths of the Gulf Stream with a time-delay of 1-2 years. (Taylor and Stephens 1998; Frankignoul and Coëtlogon 2001). Recent decades have seen more positive NAO indices and, while acknowleding natural large multidecadal variations, climate change projection models predict slightly more positive NAO values in the future (Christensen et al. 2013). Shifting trajectories of the Gulf Stream could alter current dynamics in the Northwest Atlantic and potentially change the position and trajectories of eddy-forming meanders.

Understanding and predicting how pelagic assemblages may respond to these climate-related changes hinges upon evaluating how species interact with these features.

Although some studies question the current estimate of 10 billion tons of mesopelagic fishes (Irigoien et al. 2014; Davison et al. 2015), the mesopelagic environment clearly supports a substantial biomass that plays an integral role in marine food-webs, global biogeochemical cycling, and carbon sequestration (Robinson et al. 2010; St. John et al. 2016). As home to a variety of diel migrators that commute to the surface at night to feed and return by day, these animals contribute to vertical carbon flux to deeper water beyond the euphotic zone. This active flux can be significant, accounting for ~ 10-20% of carbon flux below the epipelagic zone and upwards of 70% to below 1000 m (Hudson et al. 2014; Davison et al. 2015). However, not all mesopelagic residents migrate; indeed, migration can vary among species, individuals, life stages, regions, and seasons (Neilson and Perry 1990; Cohen and Forward 2016; Klevjer et al. 2016; Olivar et al. 2018), therefore contributions toward active flux presumably depends on local species composition. The challenge of sampling such an immense and dynamic ecosystem significantly limits knowledge of the composition and distribution of mesopelagic communities worldwide. Recent attempts to delineate worldwide ‘mesopelagic ecozones’ for the first time identify 33 global biogeographic ecoregions (Sutton et al.2017). Although this study provides insight into characteristic regional communities and potential primary drivers within each region, we still know very little about the relative contribution of species/taxon groups to ecosystem services and the overall function of mesopelagic biodiversity.

Multiple studies demonstrate eddies support higher concentrations of early life history stages of many pelagic fish species than surrounding waters (Nishimoto and Washburn 2002; Muhling et al. 2007; Contrera-Catala et al. 2012). This entrainment could benefit some species, enhancing prey concentrations and creating nursery habitat; however, shelf-dependent larvae may suffer if retention results in transport offshore to less favorable habitats or if they experience higher predator concentrations within eddy waters (Bakun 2006). Although our fishing gear was not equipped to target early life stages, several large larvae and juvenile specimens of multiple species were observed. Unsurprisingly, we sampled only four larval fish, however, juveniles were more numerous and observed almost exclusively inside eddies. Although, it is unknown whether these juveniles were actively maintaining position within the eddy in response to favourable food or hydrographic conditions, or simply entrained by strong eddy currents.

The herring trawl used in our study appeared to adequately sample a wide variety of mesopelagic fish species. The combination of a large net opening (fishing circle 330 m) and small cod-end mesh of 10 mm resulted in capture of diverse sizes, from larvae and small fishes <2 cm, as well as both large (i.e. *Regalecus glesne*, and *Trachipterus arcticus*) and fast-swimming species such as black gemfish *Nesiarchus nasutus* and lancetfish *Alepisaurus brevirostris*. Although our sets targeted two relatively narrow depth ranges in the mesopelagic zone, the lack of discrete sampling at specific depth ranges does not preclude possible contamination of shallow species within deep tows captured during haul back. Large MOCNESS (Midwater Opening/Closing Net and

Environmental Sensing System) trawls containing multiple cod-ends would allow more precise sampling of discrete depths in future studies.

As many fishes can repond quickly to changing environmental conditions, assemblages may change in pace with fluctuations in dynamic oceanographic features. Atwood et al. (2010) reported high species richness of ichthyoplankton within core-waters of newly formed eddies in the Gulf of Alaska compared to older formations, suggesting eddy age may affect internal fish assemblages. Propagation timing and location likely also affect species composition, and eddy assemblages may vary greatly depending on the exact origin and timing of departure from the predominant current, in addition to its stability and age. Our study investigated a single eddy within each year, with limited sampling occurring within the span of a week. Although these data provided a valuable snapshot to explore how eddies structure local fish communities, we cannot preclude the potential influence of the timing and frequency of sampling. However, differences in species richness, diversity, and assemblages in core-waters were apparent and consistent with similar studies (Brandt 1981; Muhling et al. 2007; Atwood et al. 2010; Contrera-Catala et al. 2012; Simons et al. 2015).

Greater replication of tows and/or transects both within and between years would allow more comprehensive evaluation of temporal variability in assemblage structure or to explore how inter-annual differences in fish communities and how assemblages change within the same eddy over time. Likewise, the composition and relative abundance of fish species entrained or advected by eddies from shelf-slope source waters could relate strongly to the timing and location of eddy formation, as the presence of species in source waters may depend on seasonality of movements driven by spawning and/or feeding behaviours, and could explain the variability in dominant species between E15 and E16 despite similar sampling location and survey timing. Sampling multiple eddies with different points of origin could provide insight into spatial variability and relative influence of source species on assemblages once eddies depart from coastal waters. As for the potential attraction or aggregation of offshore pelagic species to eddies, the use of tagging technologies for mesopelagic megafauna and additional studies similar to the present could also help identify species consistently associated with eddies and the potential drivers underlying these habitat associations.

5.5 Conclusions

As a site of confluence and overturning of ocean currents and continuous eddy formation, the Northwest Atlantic region is characterized by dynamic hydrography. Based on differences in vertical temperature profiles and SLA values, our study documented distinct mesopelagic fish assemblages relating to both depth and spatial proximity to anti-cyclonic eddies, and both higher abundance and diversity in tows within eddy interiors. Although few studies have examined adult fish communities in relation to mesoscale eddies, these results provide a first look at how such large oceanographic features may shape pelagic communities in North Atlantic eddy fields, and suggest that eddies harbor unique assemblages, aggregate prey and predators, and provide nursery habitat for juveniles of several species.

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5.7 Tables

Table 5.7.1 Set details for the 23 mid-water trawls conducted in 2015-2016, including fishing depth and temperature measured using loggers attached directly to the trawl cod-end, satellite-derived estimates of SLA height at the location of each fishing set, and location of nearest CTD station for each fishing set.

Set	Date	Latitude	Longitude	Fishing depth (m)	Fishing temperature (C)	SLA height (m)	CTD Station	CTD Latitude	CTD Longitude
1	26 Apr 2015	46.922	37.005	357	9.4	-0.200	A	46.868	-37.008
2	26 Apr 2015	46.946	37.006	500	7.6	-0.200	A	46.868	-37.008
3	27 Apr 2015	47.804	37.706	325	12.4	0.148	B	47.776	-37.677
4	27 Apr 2015	47.785	37.681	500	10.4	0.148	B	47.776	-37.677
5	28 Apr 2015	48.434	38.373	300	10.4	0.323	C	48.436	-38.375
6	28 Apr 2015	48.367	38.277	550	7.7	0.323	C	48.436	-38.375
7	29 Apr 2015	48.353	38.764	300	12.4	0.296	C	48.436	-38.375
8	29 Apr 2015	48.306	38.904	650	7.9	0.296	C	48.436	-38.375
9	30 Apr 2015	47.057	42.949	300	3.6	-0.001	D	47.02	-43.02
10	30 Apr 2015	47.057	42.947	500	3.9	-0.001	D	47.02	-43.02
11	14 Apr 2016	49.453	39.210	413	5.5	-0.270	E	49.42	-39.25
12	14 Apr 2016	48.715	40.286	230	12.6	0.205	F	48.69	-40.31
13	15 Apr 2016	48.734	40.253	545	8.9	0.183	F	48.69	-40.31
14	15 Apr 2016	48.362	40.814	275	9.4	0.107	G	48.33	-40.84
15	15 Apr 2016	48.368	40.816	430	8.3	0.107	G	48.33	-40.84
16	15 Apr 2016	48.194	41.039	293	8.2	0.026	G	48.33	-40.84
17	16 Apr 2016	47.755	41.155	283	10.3	0.024	H	47.98	-41.36
18	16 Apr 2016	47.787	41.179	487	7.5	0.024	H	47.98	-41.36
19	16 Apr 2016	47.399	40.304	321	14.6	0.342	I	47.36	-40.01
20	16 Apr 2016	47.402	40.303	540	13.2	0.342	I	47.36	-40.01
21	17 Apr 2016	46.746	39.899	272	14.2	0.100	J	46.73	-39.94
22	17 Apr 2016	46.738	39.896	599	12.3	0.100	J	46.73	-39.94
23	18 Apr 2016	46.376	40.964	585	7.6	0.173	K	46.32	-41.32

Table 5.7.2 Full list of raw abundances of mesopelagic fishes collected from 0 to 650 m during eddy transect surveys in the Northwest Atlantic aboard the *RV Celtic Explorer* in April of 2015 and 2016. Sets are identified as occurring in either shallow (S) or deep (D) depth groups, and occurring either inside (I) or outside (O) of eddies.

Set	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	
Depth Group	S	D	S	D	S	D	S	D	S	D	S	S	D	S	D	S	S	D	S	D	S	D	D	
Eddy Group	O	O	I	I	I	I	I	I	O	O	O	I	I	O	O	O	O	O	I	I	I	I	I	
Taxon																								Total
SQUALIFORMES																								
DALATIIDAE																								
Squaliolus laticaudus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	1	1	7
ANGUILLIFORMES																								
SYNAPHOBRANCHIDAE																								
Synaphobranchus kaupi	0	0	0	0	0	1	0	1	0	0	0	0	6	0	0	0	0	0	0	5	0	1	1	15
DERICHTHYIDAE																								
Nessorhamphus ingolfianus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0	1	0	5
NEMICHTHYIDAE																								
Nemichthys scolopaceus	0	3	1	1	3	44	2	11	5	11	4	8	5	0	12	9	3	6	3	0	0	2	4	137
SERRIVOMERIDAE																								
Serrivomer beanii	0	2	0	0	0	83	0	40	0	18	3	0	5	0	6	9	0	2	0	1	0	1	97	267
Eel leptocephalus larvae	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	4
OSMERIFORMES																								
ALEPOCEPHALIDAE																								
Xenodermichthys copei	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3
BATHYLAGIDAE																								
Bathylagus euryops	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	9	0	5	0	18
Dolicholagus longirostris	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	2	1	5
MICROSTOMATIDAE																								
Microstoma microstoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	25
Nansenia oblita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	2	0	6
OPISTHOPROCTIDAE																								
Opisthoproctus soleatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
PLATYTROCTIDAE																								
Holtbyrnia anomala	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Normichthys operosus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1

STOMIIFORMES																								
GONOSTOMATIDAE																								
Gonostoma atlanticum	0	0	0	0	5	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	8
Gonostoma denudatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0	2	9	29
Margrethia obtusirostra	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Sigmops elongatum	0	0	0	8	1	4	0	29	1	3	0	44	4	0	0	7	0	0	42	71	17	46	17	294
PHOSICHTHYIDAE																								
Vinciguerra attenuate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1	9
STERNOPTYCHIDAE																								
Argyropelecus aculeateus	0	0	44	12	4	7	10	7	0	0	0	0	0	0	0	0	0	0	0	7	7	2	1	101
Argyropelecus hemigymnus	3	1	75	9	40	8	1	1	1	1	0	0	1	0	0	0	3	0	0	3	1	5	0	153
Maurolicus muelleri	3	114	3	0	3	0	5	1	0	0	0	0	0	4	0	0	29	0	0	0	0	0	1	163
Polyipnus clarus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sternoptyx diaphana	0	2	3	1	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9
STOMIIDAE																								
Aristostomias sp.	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Astronesthes gemmifer	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	6	4	12
Astronesthes neopogon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Astronesthes niger	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
Astronesthes sp.	0	0	0	0	0	0	0	0	0	6	0	0	2	0	0	0	0	0	0	1	0	0	0	9
Bathophilus vaillanti	0	0	1	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	8
Bathyphilus metallicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Chauliodus sloani	4	9	3	42	15	71	0	12	0	5	43	0	25	13	1	6	7	39	7	22	11	29	152	516
Echinostoma barbatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Eustomias brevibarbatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Eustomias filifer	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	3
Eustomias leptobolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Eustomias longibarba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Eustomias radicifilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Eustomias sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Eustomias sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Idiacanthus fasciola	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Malacosteus niger	0	0	0	0	0	0	0	6	0	7	0	2	3	0	0	0	0	0	2	5	0	1	2	28
Melanostomias bartonbeani	0	1	0	5	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	5	0	0	3	18
Melanostomias melanops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Melanostomias tentaculatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Melanostomias sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Melanostomias sp.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Melanostomias sp.3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Photonectes margarita	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2
Stomias boa ferox	0	0	0	0	5	92	0	69	4	127	4	0	29	0	8	0	0	0	11	5	1	28	3	386
AULOPIFORMES																								

ALEPISAURIDAE																							
Alepisaurus brevirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
NOTOSUDIDAE																							
Ahliesaurus berryi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Scopelosaurus Lepidus	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	1	5	0	6	0	20
PARALEPIDIDAE																							
Arctozenus risso	1	0	0	0	7	66	0	4	0	1	6	0	13	3	0	1	12	9	4	64	6	27	11	235
Lestidiops affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Lestidiops jayakari	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	3
Macroparalepis affinis	0	0	0	5	0	0	0	0	0	0	0	3	2	0	0	10	0	0	0	0	0	0	0	20
Sudis hyalina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
SCOPELARCHIDAE																							
Scopelarchus analis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
EVERMANNELLIDAE																							
Evermannella balbo	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	5
MYCTOPHIFORMES																							
MYCTOPHIDAE																							
Benthosema glaciale	611	200	0	28	132	108	0	88	0	77	5	4	4	3	0	1	4	0	0	7	6	17	6	1301
Bolinichthys indicus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ceratoscopelus maderensis	0	0	5	6	6	2	0	0	0	0	0	1	2	0	0	0	0	1	5	0	6	1	3	38
Diaphus effulgens	0	2	0	36	4	5	1	4	0	0	0	0	0	0	0	0	0	0	0	41	2	30	17	142
Diaphus holti	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diaphus metapoclampus	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	6
Diaphus rafinesquii	0	0	15	35	40	16	0	5	0	0	0	0	0	0	0	0	0	0	0	13	3	2	0	129
Diaphus sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	15
Electrona risso	1	2	1	4	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	18
Hygophum benoiti	0	0	8	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
Lampadena anomala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Lampadena atlantica	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	14	0	35	0	54
Lampanyctus crocodilus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Lampadena speculigera	0	0	0	0	0	0	0	8	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	11
Lampanyctus alatus?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	16	2	0	0	19
Lampanyctus festivus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	9	1	20
Lampanyctus macdonaldi	0	0	0	0	0	15	0	7	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	50
Lampanyctus photonotus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	13
Lampanyctus pusillus	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Lampanyctus sp.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
Lampanyctus sp.2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Lobianchia gemellari	0	6	2	52	11	10	0	12	0	0	0	0	0	0	0	0	0	0	4	74	2	59	2	234
Myctophum punctatum	9	41	51	95	140	101	5	9	1	7	12	0	1	0	0	1	2	6	0	49	0	0	6	536

Nannobrachium atrum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	7	0	15
Notoscopelus bolini	1	34	27	61	25	10	0	9	0	0	2	0	0	1	0	0	0	1	1	7	5	3	11	198
Notoscopelus caudispinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2
Notoscopelus kroyeri	14	15	34	35	13	102	2	1	5	5	0	1	17	8	0	1	1	2	0	49	0	40	21	490
Symbolophorus veranyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	11
LAMPRIFORMES																								
REGALECIDAE																								
Regalecus glesne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	3
TRACHIPTERIDAE																								
Trachipterus arcticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
GADIFORMES																								
MELANONIDAE																								
Melanonus zugmayeri	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1	0	0	1	0	6
LOPHIIFORMES																								
HIMANTOLOPHIDAE																								
Himantolophus groenlandicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
ONEIRODIDAE																								
Chaenophryne draco	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
CERATIIDAE																								
Cryptosaras couesii	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
STEPHANOBERYCIFORMES																								
MELAMPHIDAE																								
Scopeloberyx robustus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
STEPHANOBERYCIDAE																								
Poromitra capito	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
BERYCIFORMES																								
DIRETMIDAE																								
Diretmus argenteus	0	6	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	10
BERYCIDAE																								
Beryx decadactylus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
SCORPAENIFORMES																								
CYCLOPTERIDAE																								
Cyclopterus lumpus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

PERCIFORMES																							
ANARHICHADIDAE																							
Anarhichas denticulatus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
CARISTIIDAE																							
Caristius fasciatus	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
HOWELLIDAE																							
Howella sherborni	0	0	0	0	0	2	0	7	0	0	0	0	1	0	0	0	0	0	0	15	0	9	0	34
BRAMIDAE																							
Brama brama	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Pterycombus brama	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2
Taractes asper	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
CHIASMODONTIDAE																							
Chiasmodon niger	0	0	0	0	0	0	0	0	0	0	0	0	19	0	1	0	0	0	0	1	0	2	0	23
Chiasmodon juvenile	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	5	0	0	0	0	2	0	8
Pseudoscopelus altipinnis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Pseudoscopelus astronesthidens	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	5	0	9
Pseudoscopelus sp.	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
GEMPYLIDAE																							
Diplospinus multistriata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9	0	4	0	4	18
Nesiarchus nasutus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	4
TRICHIURIDAE																							
Benthodesmus elongatus	1	0	2	2	2	2	0	1	0	0	0	0	3	0	0	0	15	1	4	9	7	4	3	56
Total no. individuals	650	441	277	453	588	758	26	362	18	304	80	68	169	35	29	59	117	71	104	576	91	410	405	6091
Biomass (kg)	1.5	1.2	0.7	2.4	4.6	6.5	0.1	5.0	4.5	4.3	0.5	0.7	2.0	1.5	0.3	0.4	0.3	8.4	0.8	6.0	0.7	6.6	3.1	62.4

Table 5.7.3 Abundances of the most common (>1% total abundance in each group) mesopelagic fish species in shallow sets (200 - 350 m) and deep sets (400 - 650 m). Abundance values have been standardized based on the total number of sets occurring in each depth group.

SHALLOW (200 – 350 m)			**DEEP (400 – 650 m)**		
Species	**Abundance**	**% Total**	**Species**	**Abundance**	**% Total**
Benthosema glaciale	69.18	37.4	*Benthosema glaciale*	44.22	13.6
Myctophum punctatum	19.00	10.3	*Chauliodus sloani*	36.33	11.2
Notoscopelus kroyeri	18.45	10.0	*Stomias boa ferox*	30.42	9.3
Argyropelecus hemigymnus	11.27	6.1	*Myctophum punctatum*	24.61	7.6
Sigmops elongatum	10.18	5.5	*Notoscopelus kroyeri*	22.94	7.0
Chauliodus sloani	6.00	3.2	*Serrivomer beani*	21.92	6.7
Notoscopelus bolini	5.45	3.0	*Arctozenus risso*	16.75	5.1
Argyropelecus aculateus	5.27	2.9	*Sigmops elongatum*	14.94	4.6
Diaphus rafinesquii	5.27	2.9	*Lobianchia gemellari*	11.25	3.5
Maurolicus muelleri	4.27	2.3	*Diaphus effulgens*	10.25	3.1
Arctozenus risso	3.09	1.7	*Notoscopelus bolini*	9.81	3.0
Nemichthys scolopaceus	3.09	1.7	*Maurolicus muelleri*	9.67	3.0
Benthodesmus elongatus	2.82	1.5	*Nemichthys scolopaceus*	8.56	2.6
Microstoma microstoma	2.27	1.2	*Lobianchia gemellarii*	5.22	1.6
Ceratoscopelus maderensis	2.09	1.1	*Lampadena atlantica*	4.33	1.3
Stomias boa ferox	1.91	1.0	*Lampanyctus macdonaldi*	4.17	1.3
			Diaphus rafinesquii	3.86	1.2

Table 5.7.4 Unique taxa of mesopelagic fishes observed exclusively in sets occurring either inside or outside of eddies.

Inside eddy only			**Outside eddy only**
Synaphobranchus kaupi	*Lampanyctus pusillus*	*Aristostomias* sp.	*Trachipterus arcticus*
Alepisaurus brevirostris	*Lampanyctus* sp.1	*Astronectes cyaneus*	*Diaphus holti*
Ahliesaurus berryi	*Lampanyctus* sp.2	*Astronectes niger*	*Diaphus metapoclampus*
Scopelosaurus lepidus	*Nannobrachium atrum*	*Stomias brevibarbatus*	*Microstoma microstoma*
Lestidiops affinis	*Notoscopelus caudispinous*	*Bathyphilus metallicus*	*Opisthoproctus soleatus*
Lestidiops jayakari	*Symbolophorus veranyi*	*Echinostoma barbatum*	*Holtbyrnia anomala*
Sudis hyalina	*Dolicholagus longirostris*	*Eustomias brevibarbatus*	*Anarhichas denticulatus*
Scopelarchus analis	*Nansenia oblita*	*Eustomias filifer*	*Brama Brama*
Beryx decadactylus	*Normichthys operosus*	*Eustomias* sp.1	*Cyclopterus lumpus*
Melanonus zugmayeri	*Pterycombus brama*	*Eustomias leptobolus*	*Polyipnus clarus*
Himantolophus groenlandicus	*Taractes asper*	*Eustomias longibarba*	
Chaenophryne draco	*Caristius fasciatus*	*Eustomias radicifilis*	
Bolinichthys indicus	*Pseudoscopelus altipinnis*	*Photonectes margarita*	
Diaphus rafinesquii	*Pseudoscopelus astronesthidens*	*Idiacanthus fasciola*	
Lampanyctus festivus	*Argyropelecus aculateus*	*Trigonolampa miriceps*	
Hygophum benoiti	*Diplospinosus multistriata*	*Chirostomias pliopterus*	
Lampadena anomala	*Howella sherborni*	*Melanostomias tentaculatus*	
Lampadena atlantica	*Squaliolus laticaudus*	*Leptostomias haplocaulus*	
Lampadena photonotus	*Scopeloberyx robustus*	*Melanostomias* sp.1	
Lampanyctus crocodilus	*Poromitra capito*	*Melanostomias* sp.2	
Lampadena speculigera	*Gonostoma denudatum*		
Lampanyctus alatus	*Margrethia obtusirostra*		

Table 5.7.5 Pelagic fish assemblages identified through multivariate analyses of fishing set species composition and abundances, with representative number of sets belonging to each depth (S=Shallow; D=Deep) and eddy (I=Inside; O=Outside) group and characteristic species/taxa belonging to each group.

Assemblage	Set numbers	Depth group	Eddy Group	Characteristic species
A	12	S	I	*Sigmops elongatum*
B	7, 9	S	1 I, 1 O	*Nemichthys scolopaceus, Notoscopelus kroyeri, Myctophum punctatum, Argyropelecus aculeatus*
C	10, 11, 15, 16, 18	1 S, 4 D	O	*Stomias boa ferox, Nemichthys scolopaceus, Chauliodus sloani, Serrivomer beanii*
D	1, 2, 14, 17	3 S, 1 D	O	*Benthosema glaciale, Maurolicus muelleri*
E	19, 21	S	I	*Sigmops elongatum, Chauliodus sloani, Diplospinosus multistriata, Ceratoscopelus maderensis*
F	5, 6	1 S, 1 D	I	*Myctophum punctatum, Benthosema glaciale, Nooscopelus kroyeri, Gonostoma atlanticum*
G	3, 4	1 S, 1 D	I	*Myctophum punctatum, Notoscopelus bolini, Notoscopelus kroyeri*
H	13	D	I	*Stomias boa ferox, Chauliodus sloani, Chiasmodon niger, Notoscopelus kroyeri*
I	20, 22	D	I	*Lobianchia gemelleri, Sigmops elongatum, Arctozenus risso, Notoscopelus kroyeri, Diaphus effulgens, Astronesthes cyaneus, Chirostomias pliopterus,Nanesia oblita, Nannobrachium atrum*
J	8, 23	D	I	*Serrivomer beanii, Sigmops elongatum, Chauliodus sloani*

5.8 Figures

Figure 5.8.1 Temperature-depth profiles based on CTD data collected from the closest oceanographic sampling station to each fishing station. The legend signifies which profile line corresponds to each of the 23 fishing sets conducted throughout eddies in 2015 (Sets 1-2, 9-10 occurring outside the eddy; Sets 3-8 occurring inside the eddy) and 2016 (Sets 11, 14-18 occurring outside the eddy; Sets 12-13, 19-23 occurring inside the eddy).

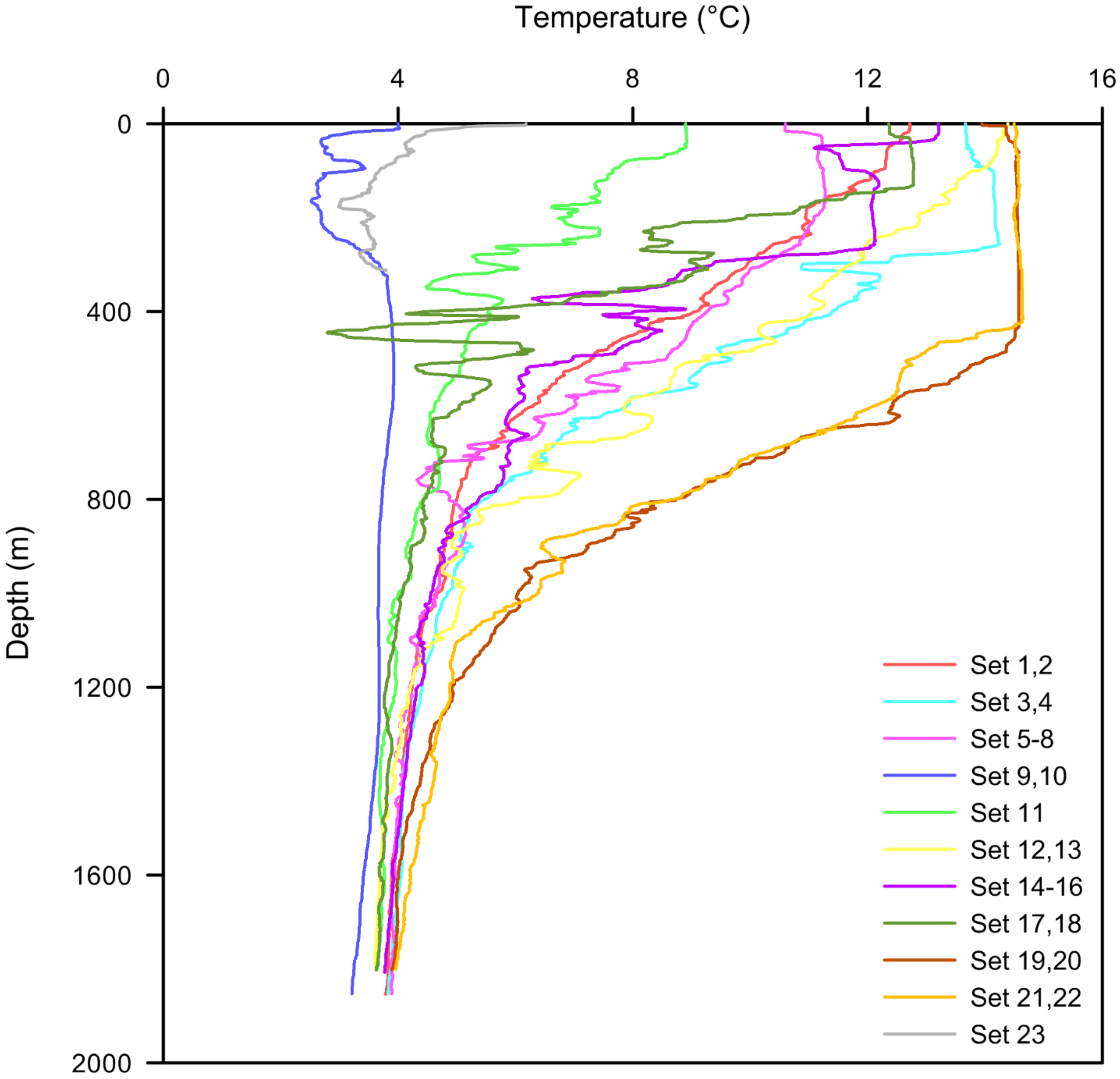
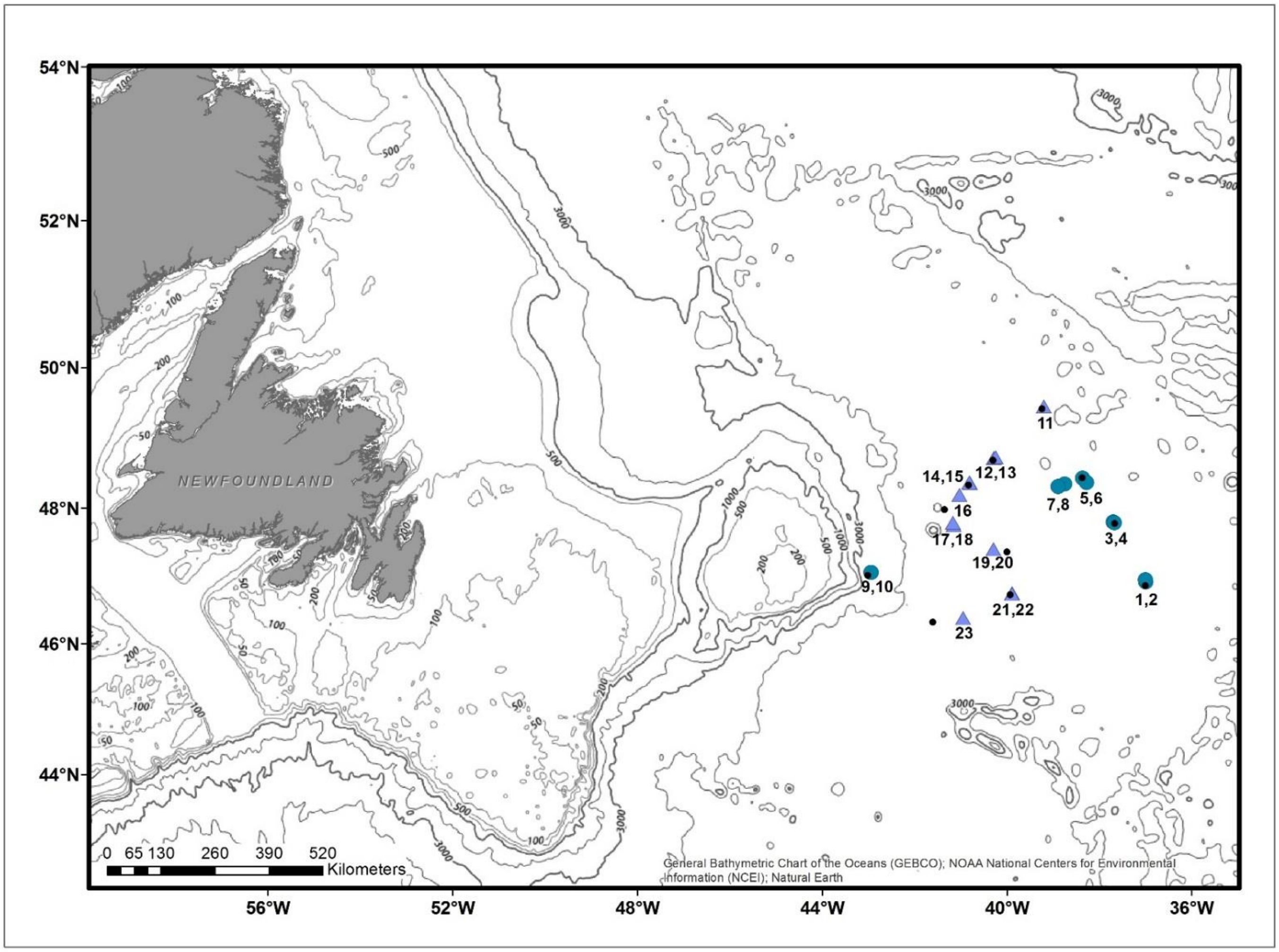


Figure 5.8.2 Map of fishing set locations conducted along eddy sampling transects aboard the *RV Celtic Explorer* in 2015 (•) and 2016 (▲), with black circles signifying CTD station locations.



General Bathymetric Chart of the Oceans (GEBCO); NOAA National Centers for Environmental Information (NCEI); Natural Earth

Figure 5.8.3 Dendrogram created using group average link from clusters using Euclidean distances of normalized environmental variable data of SLA height and temperature values at depths of 10m, 150m, 250m, 350m, 450m, 550m, and 650m from CTD stations nearest to each fishing set, with symbols relating to set locations occurring either inside (▼) or outside (▲) of eddy waters.

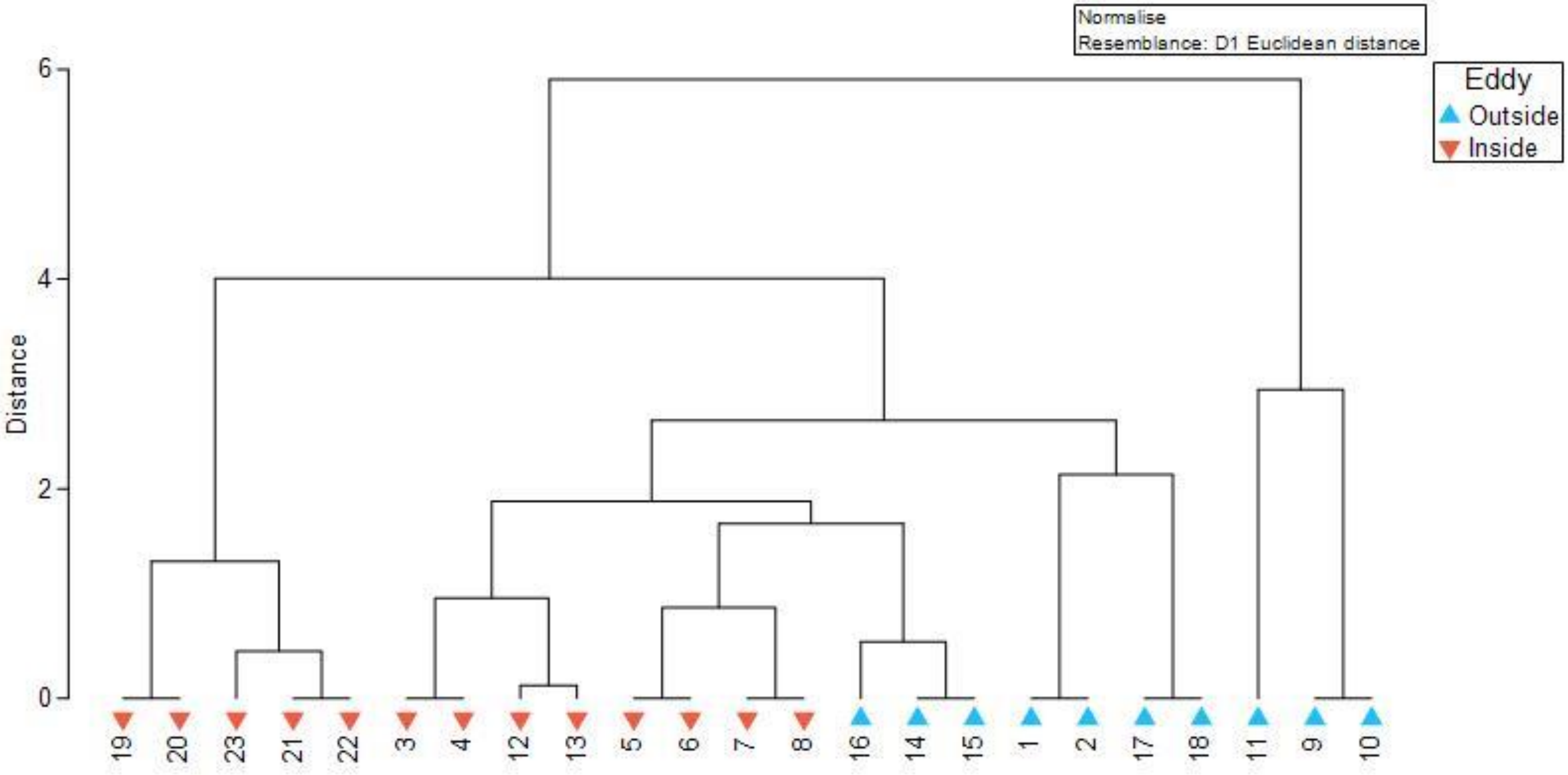


Figure 5.8.4 Separation of fishing sets from both surveyed years based on relationship between satellite-derived SLA heights and temperature at 350 m depth based on CTD profiling nearest to fishing set locations.

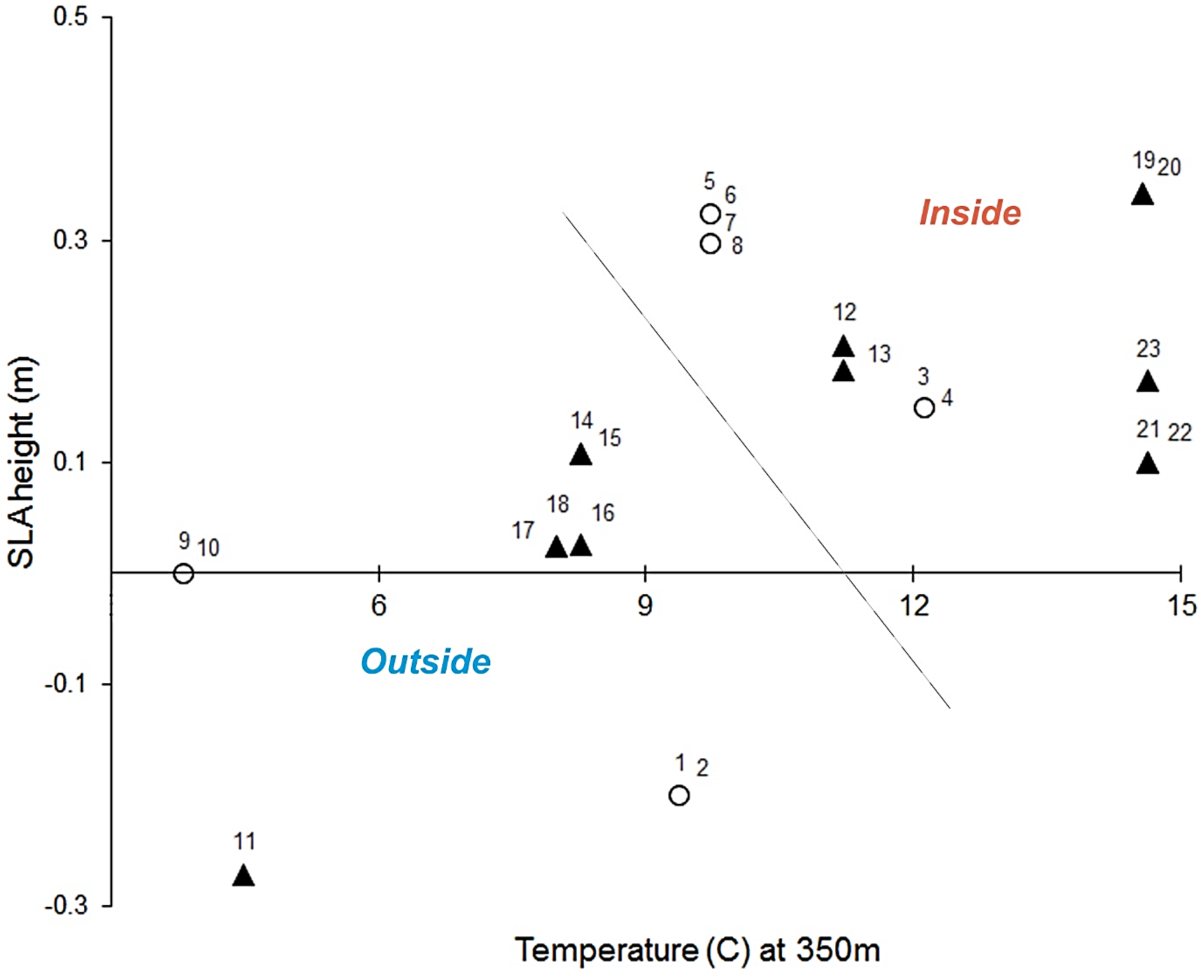


Figure 5.8.5 Relationship between Shannon Diversity (H') values calculated for each fishing set and environmental variables of a) fishing depth, b) fishing temperature, and c) sea level anomaly associated with fishing sets occurring in 2015 (open circles) and 2016 (solid circles) in the Northwest Atlantic. Solid black lines represent linear relationship across both years, and dotted lines corresponding to 2015 (grey) and 2016 (black) sets only.

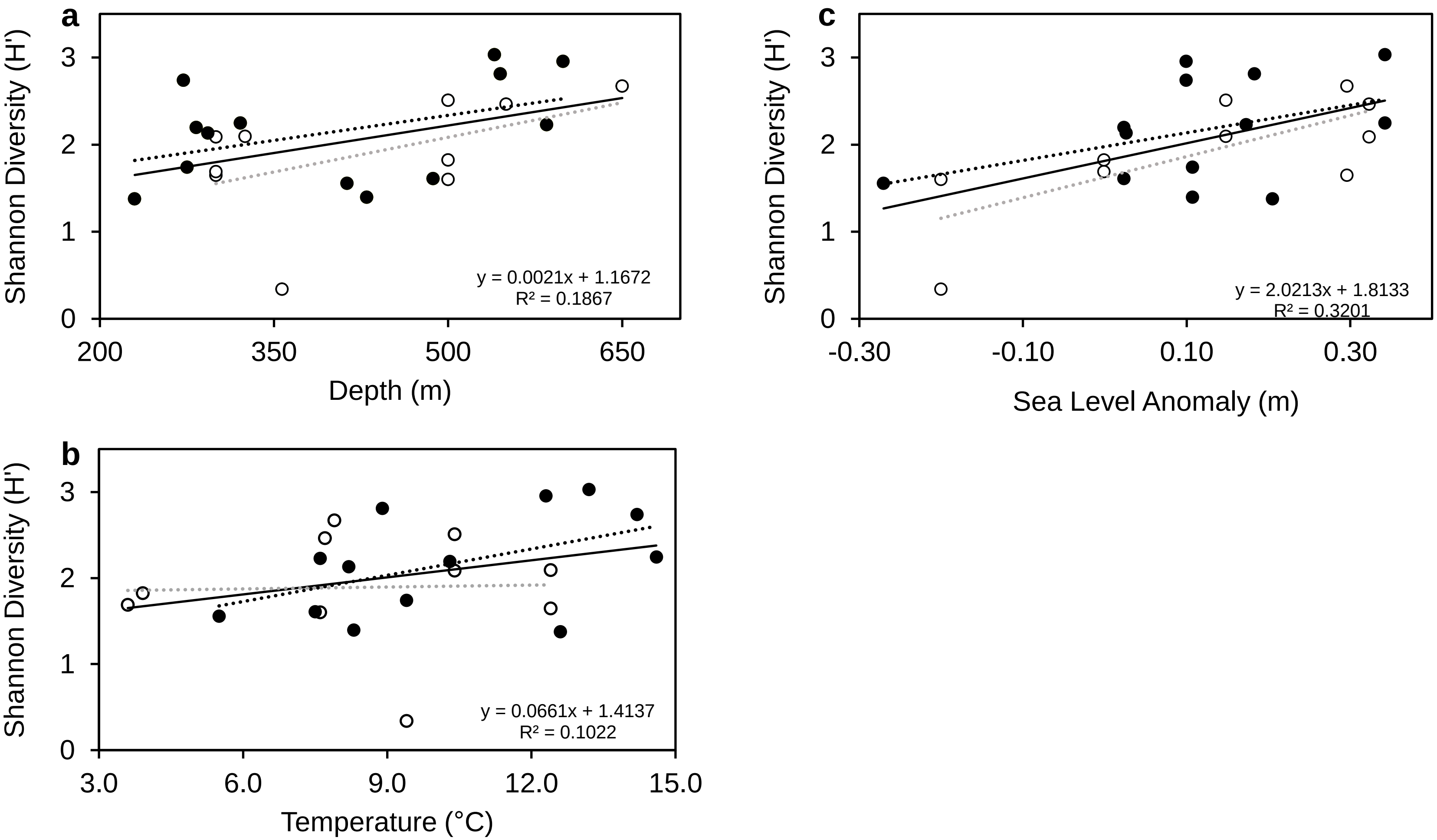


Figure 5.8.6 Dendrogram created using group-average link clustering from Bray-Curtis similarities on standardized fish abundances.

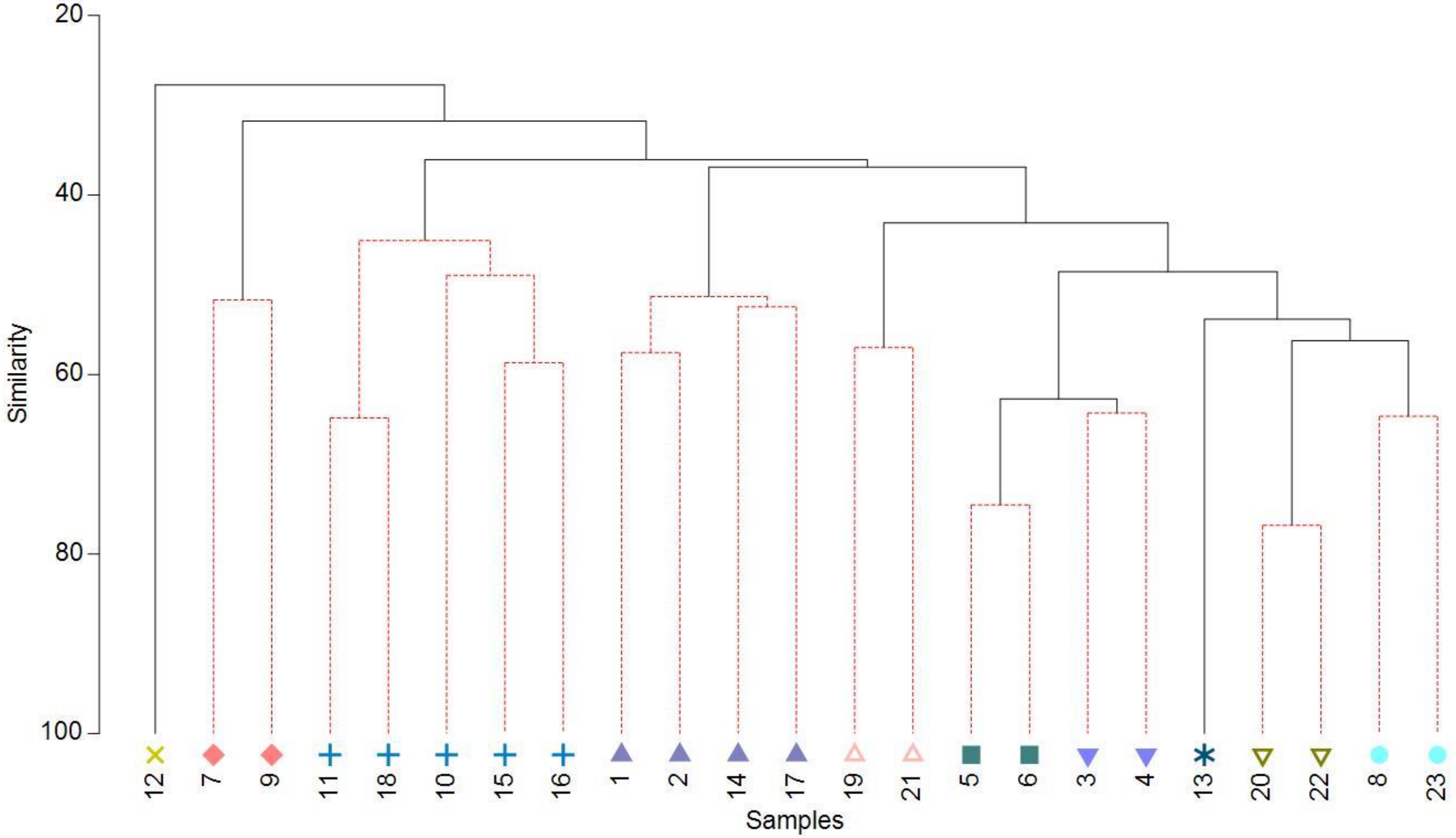
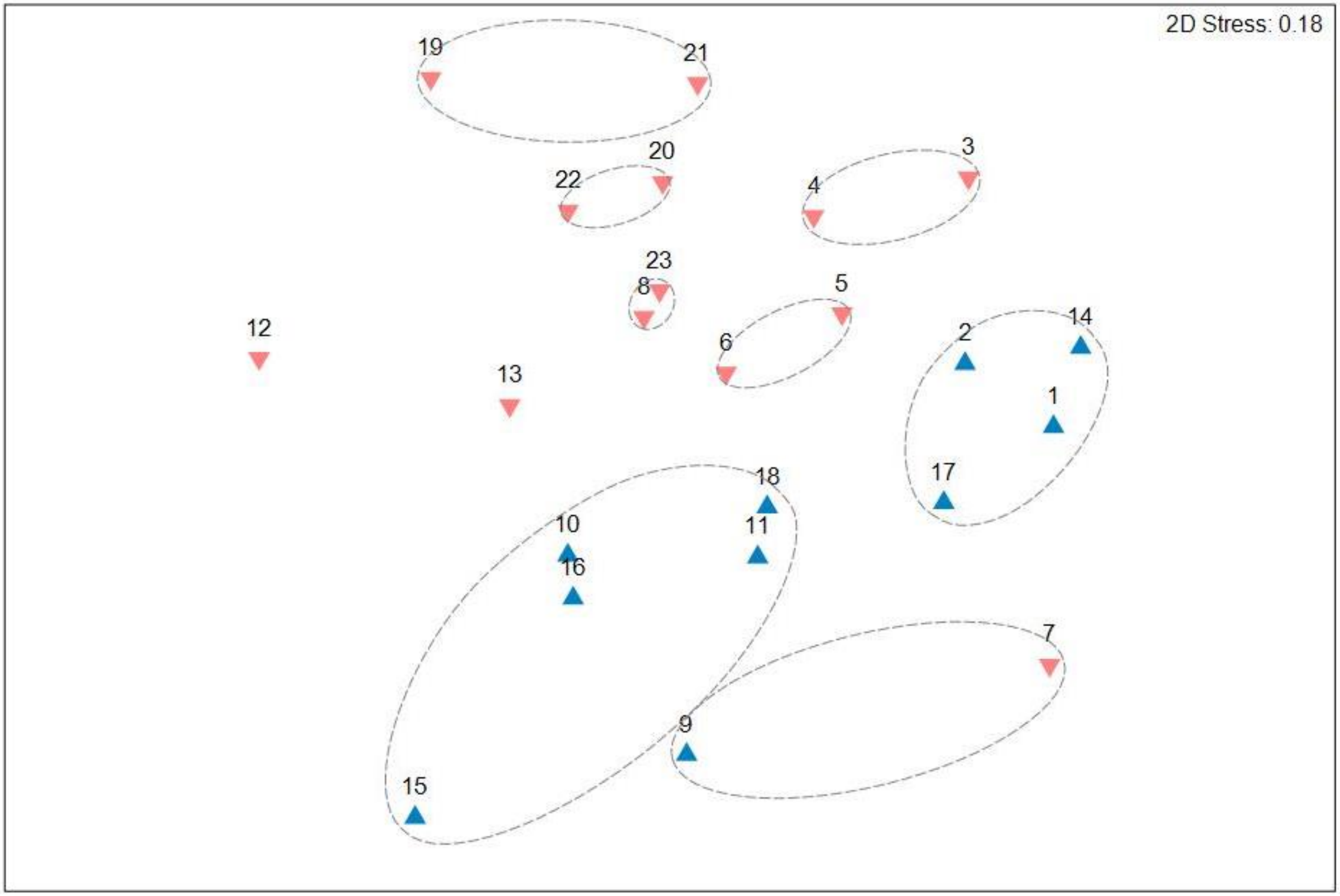


Figure 5.8.7 MDS plot of Bray-Curtis similarity matrix based on standardized abundances of species/taxa observed in at least 5 % of samples. Dotted lines correspond to SIMPROF assemblage groups, with symbols relating to set locations occurring either inside (▼) or outside (▲) of eddy waters.



6 General Conclusions

Technological advancements in recent decades have vastly improved our ability to survey marine environments – particularly in the deep ocean. Improved optics, battery life, and pressure-ratings now provide high-definition images of deep-sea habitats, enabling longer and deeper observations than ever before. Despite these innovations, deep-sea research is still in its infancy compared to shallower marine environments, with relatively little data on the biogeography, ecology, and functioning of deep-sea taxa and ecosystems. Through five research cruises spanning several years and sampling multiple marine ecoregions, data presented in this dissertation offer novel insight into benthic and mesopelagic fish assemblages in the Northwest Atlantic and Canadian Arctic. This work improves our current knowledge of how fishes are distributed and the environmental factors that influence their distributions in these frontier environments.

The use of baited remote underwater video platforms as versatile, non-destructive survey tools has gained momentum worldwide, employed here for the first time in the Canadian High Arctic. Over 200 hrs of video footage enabled description of benthic ichthyofauna, invertebrate communities, and habitat composition in five understudied regions with little or no prior sampling. Significant differences in assemblages among regions were attributed to variations in depth and temperature. Comparisons between video data and catch data from concurrent exploratory fishing validated the utility of the baited camera to detect the presence of invertebrates and fish taxa comparably to catch data when deployed over common deep-water substrates (i.e. fine-grain sediments), requiring fewer deployments than fishing gear. In addition, species accumulation curves contribute valuable new information on optimal recording times for detecting local fauna, providing direction for future survey methodology.

These baited camera deployments also proved valuable as a new tool for surveying the largest Arctic fish and elusive top predator, the Greenland shark. Greenland shark, currently regarded as the longest-lived vertebrate (Nielsen et al. 2016), remains a poorly studied species, with many unknown aspects of its basic biology (MacNeil et al. 2012). This dissertation reports the first fisheries-independent estimates of local abundances in Arctic waters, using visual identifications of 142 individuals and exploring potential extrapolated densities using an established theoretical abundance model (Priede et al. 1990). Density estimates varied among regions in relation to temperature and depth, with more frequent observations in deeper, warmer waters. These video encounters of this poorly understood species also provided new information on sex and size distributions throughout the area, as well as swimming speed, and highlighting Scott Inlet as a potentially important area for small sharks <150 cm. Given that a lack of population estimates currently prevents accurate conservation assessment of Greenland shark to direct management of this frequent bycatch species, these results demonstrate the potential of baited cameras as a non-extractive technique for surveying the distribution and abundance of this vulnerable Arctic species. The novelty of this information and the high quality of the video images resulted in presentations of this research as both a scientific paper (Devine et al. 2018) and a popular article (Devine & Fisher 2018). The latter led to worldwide interest in this species and these techniques; video images have been viewed > 140,000 times and individuals and agencies have both sought more information. Furthermore, other components of this survey were incorporated into literature developed during the 2018 Northwest Atlantic Fishery Organization (NAFO) scientific council meeting (Wheeland and Devine 2014).

Remotely-operated vehicle transects covering a distance of 55 km and recording 66 hrs of *in-situ* video documented over 6,900 fish-habitat observations, comprising at least 45 species/taxa across a wide range of sampled depths along the Flemish Cap and Orphan Seamount. As I reported, unique fish assemblages occupied specific depth zones and were not randomly distributed. Additionally, biological habitats appeared to have a greater influence on assemblage structure compared to physical features, and habitat complexity was also important with significant differences between assemblages in more complex physical habitats (e.g. boulder fields and outcrops) and complex biological habitats (e.g. dense corals and sponges) compared to less complex areas. For example, observations of *Macrourus berglax*, *Lepidion eques*, and *Apristurus* spp. suggest these fishes may rely on availability of dense concentrations of deep-water sponges and corals for habitat.

In the absence of physical and biological structures in the pelagos, fish assemblages are largely shaped by changes in hydrography and large-scale oceanographic features such as currents, fronts, and eddies. Examination of > 6,000 fishes collected from mid-water trawls along transects through anti-cyclonic eddies in the North Atlantic eddy field revealed distinct assemblages inside eddy waters, as well as significant differences between upper and mid-mesopelagic depths. Markedly higher biodiversity within warm-core eddies resulted from either entrainment or aggregation of fishes to conditions within, including rare (e.g. *Regalecus glesne* and *Taractes asper*), southern (e.g. *Margrethia obtusirostra* and *Ahliesaurus berryi*), and unique (e.g. *Beryx decadactylus* long-finned specimen and new discovery of *Arctozenus risso* morphotype) taxa for the Northwest Atlantic.

Collectively these dissertation results provide new data on fish distributions and habitat associations in three remote, understudied deep environments. Knowledge of marine distributions and the processes that maintain these patterns form the basis of biogeographical classifications. These frameworks provide new tools for management and conservation planning initiatives worldwide, however, many deep-sea habitats remain poorly known and underrepresented in biogeographic frameworks (Lourie and Vincent 2004; UNESCO 2009). This dissertation therefore directly addresses these knowledge gaps, providing information on spatial distributions and scale of biodiversity within three under-studied frontier areas, and examining how they are maintained across regions and environmental gradients.

Despite the broad distance separating study regions explored in this dissertation, these areas all experience similar anthropogenic pressures. Global climate change now appears inescapable, even in the deep ocean. Rapid climate change in the Arctic has resulted in faster warming than any other region on Earth (Christiansen et al. 2013). In the Northwest Atlantic, modeling predicts warming of shelf waters at a rate nearly three times faster than the global average, resulting from recession of the Labrador Current, a northerly shift in the Gulf Stream, and a weakening of the Atlantic Meridional Overturning Circulation (Saba et al. 2015; Rahmstorf et al. 2015). As already seen in shallow waters (e.g. Devine and Fisher 2014), these changes could potentially shift slope species distributions, and redirection of current trajectories could alter dynamics of the Northwest Atlantic eddy formation field that shape pelagic fish assemblages in the North Atlantic.

Direct human impacts through fisheries exploitation may also affect these frontier deep-sea environments. Loss of Arctic sea ice has increased accessibility in the north, opening shipping corridors and leading to increased interest in fisheries development (Stephenson et al. 2011; Jacobsen et al. 2018) as communities explore local waters for resources to expand subsistence fisheries and potentially join commercial markets. For decades, deep-sea fisheries have increased with advancements in fishing gear technology enabling commercial fishers to move further offshore in search of new markets and fishing grounds (Roberts 2002; Morato et al. 2006), trawling deeper slope waters and along deep-sea seamount features (Clark et al. 2017). Even the mesopelagic environment has been targeted for fisheries development, as global biomass estimates of 10 billion tonnes are viewed as untapped economical potential for use as food, fish meal, and/or nutraceuticals (St. John et al. 2016).

The combination of data limitations and faunal characteristics in the deep ocean add to the vulernability of this environment. Life history traits of many deep species increase risk to overexploitation or habitat disturbance, and the relatively stable conditions throughout the deep ocean evolved highly specialized species that may adapt slowly to changing conditions. But with blithe disregard to these vulnerabilities and the general lack of surveys and sampling in the deep sea, interest in deep-sea fisheries, oil and gas exploration, mining, and even carbon sequestration continue to increase (Ramirez-Llodra et al. 2011). Without adequate knowledge of the relative importance of physical and biological habitats or oceanographic features to deep-sea fishes, we lack the information necessary for effective management and conservation of features that may be essential to the sustainability of deep-sea populations.

Human exploitation of a resource often outpaces our understanding of its sustainability (Haedrich et al. 2001). In Atlantic Canada, deep-water fisheries of Greenland halibut and redfishes (*Sebastes* spp.) represent approximately 25% of the total groundfish landings and a combined value of over $80 million (DFO 2016); however, knowledge gaps exist for both species - even basic biological information regarding age and reproduction. Ageing methods for Greenland halibut have been contentious (Dwyer et al. 2016) and the exact location of spawning areas and seasonal movements remain unknown. Historic declines in redfish populations by upwards of 99% qualify many species as 'endangered' (Devine et al. 2006). Given the harvesting of several similar species (*S. mentella*, *S. fasciatus*, *S. norvegicus*) under the same stock, with known hybridization between some species (Roques et al. 2001), relative catch of each species is unknown and prevents accurate determination of population levels. If knowledge gaps such as these occur in regard to targeted species, often even less is known of bycatch encountered within these deep-sea fisheries, many of which show significant population declines (Baker et al. 2009). Even as new data become available, integration toward management and/or protective measures may lag. For example, experimental fishing in the Canadian Arctic has developed methods for minimizing bycatch of Greenland shark –

a species with potentially high-risk life history traits (Yano et al. 2007; Nielsen et al. 2016) - in longline fisheries (Grant et al. 2014); however, management has been slow to integrate this new information into new handling/protective measures for this frequent bycatch species (Wheeland and Devine 2018).

The Government of Canada has committed to protecting 10% of its oceans by 2020 as part of its commitment to both domestic and global conservation initiatives (Sala et al. 2018). In October 2017, Canada announced the conservation milestone of 5% of domestic marine waters protection, largely through the addition of large areas both offshore and in the Arctic (Fisheries and Oceans Canada 2017). Although these additions undoubtedly protect important habitats, many habitats remain open to human activities such as oil and gas exploration or restricted fishing. Several studies suggest waters not fully protected are less effective and should therefore be excluded from global conservation goals (Lester et al. 2008; Sciberras et al. 2015; Sala et al. 2018). Likewise, some additions have been criticized for not protecting habitats with high exposure to human activities but rather selecting large areas as an expedient display of progress without requiring difficult conservation decisions (Agardy et al. 2016; Hameed et al. 2017). Given the limited examination of habitat relationships in the deep sea, there are few data available to show *how* these refuges will benefit deep-sea fishes. Direction of future placement of conservation areas to maximize effectiveness of conservation efforts will require more robust data on distributions, abundances, and small-scale habitat associations from poorly studied.

The results of this dissertation highlight the need for continued exploration of deep-sea fish distributions and their drivers in Canada's frontier deep environments. I propose the following broad directions for future research:

- Emerging studies should aim to further the collection of baseline data from un-sampled/under-studied regions, preferably utilizing low-impact survey technologies for *in situ* observations and preservation of sensitive benthic habitats.

- Additional research should build upon existing survey data to examine temporal patterns in distributions and abundance, exploring the influence of additional variables not tested here that may drive fish distributions.

Prioritizing *in-situ* sampling whenever possible will help preserve benthic habitat integrity and allow examination of small-scale distributional patterns and fish-habitat relationships. These studies should incorporate additional variables which may drive distributions not examined here, including current velocity, dissolved oxygen, and particle flux/sedimentation rates as they relate to productivity in the surface waters above. Although my dissertation illuminated distributional patterns in abundance and diversity in relation to a variety of habitat factors in each study area, these results do not account for seasonal or interannual variability. Future studies should explore how these patterns may change within a year and across multiple years, and if these habitat relationships vary at different life history stages. Given how little we know about the overall function of biodiversity in deep-sea ecosystems and the relative contribution of species/taxon groups to ecosystem services, future work should continue to resolve data gaps in patterns of diversity and community assemblages across deep-sea habitats. However, most importantly, management and conservation measures must keep pace with new scientific information - and perhaps take more *precautionary* measures when human activities occur in data-poor regions - to ensure adequate protection of deep-sea fishes and their essential habitats.

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Appendix

Table A1 Date and location of CTD (conductivity, temperature, depth) stations.

Location	Date	Station	Latitude N	Longitude W
Arctic Bay	14/08/2015	A	72.958	-85.015
Arctic Bay	14/08/2015	B	73.000	-85.267
Arctic Bay	15/08/2015	C	72.999	-85.552
Arctic Bay	16/08/2015	D	73.000	-85.837
Arctic Bay	17/08/2015	E	73.186	-85.904
Arctic Bay	19/08/2015	F	73.176	-85.078
Arctic Bay	22/08/2015	G	73.247	-85.726
Resolute	24/08/2015	H	74.509	-96.125
Resolute	26/08/2015	I	74.659	-94.925
Resolute	10/09/2015	J	74.647	-94.981
Resolute	10/09/2015	K	74.625	-95.074
Resolute	11/09/2015	L	74.602	-95.176
Resolute	11/09/2015	M	74.583	-95.276
Resolute	12/09/2015	N	74.177	-90.676
Resolute	12/09/2015	O	74.250	-91.100
Resolute	13/09/2015	P	74.286	-91.412
Resolute	14/09/2015	Q	74.363	-91.939
Resolute	15/09/2015	R	74.479	-93.143
Resolute	16/09/2015	S	74.489	-93.935
Resolute	16/09/2015	T	74.555	-94.028
Resolute	16/09/2015	U	74.586	-94.060
Resolute	17/09/2015	V	74.614	-94.092
Jones Sound	29/07/2016	W	76.632	-82.338
Jones Sound	31/07/2016	X	76.552	-82.108
Jones Sound	01/08/2016	Y	76.419	-81.859
Jones Sound	02/08/2016	Z	76.378	-81.258
Jones Sound	03/08/2016	AA	76.111	-82.331
Jones Sound	04/08/2016	BB	76.085	-83.575
Jones Sound	05/08/2016	CC	76.254	-83.326
Jones Sound	06/08/2016	DD	76.377	-83.135

Table A2 Full summary of fish and invertebrate observations from camera deployments at each region. For fishes, values represent n_{max} in each set for all species except *S. microcephalus* where individual counts were possible. Invertebrates are reported as either present (1) or absent (0) for all sets where the seafloor was visible throughout the deployment. Invertebrates were not recorded for sets 11-12, 16-19 as suspended sediments partially obscured the seafloor during set duration, which may prevent observation of small benthic invertebrates.

Region	**Arctic Bay**					**Lancaster Sound**			**Resolute**						**Jones Sound**															**Scott Inlet**	
Set	1	2	3	5	6	4	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
FISHES																															
Somniosus microcephalus	5	15	18	14	1	8	0	5	0	2	0	0	0	1	3	8	3	3	2	11	7	6	1	3	1	4	8	6	0	6	2
Amblyraja hyperborea	0	0	1	0	0	2	2	0	0	0	0	0	0	0	1	1	0	0	0	2	2	1	1	2	2	2	0	0	0	0	0
Boreogadus saida	1	1	1	4	0	0	0	1	1	0	1	2	1	0	1	1	3	5	2	1	1	0	0	0	0	0	1	3	5	1	0
Careproctus reinhardti	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	0	0
Cottidae spp.	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	5	1	1	0	0	0	0	0	0	0	1	3	0	0
Leptagonus decagonus	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	4	1	0	2	2	0	0	0	0	0	0	1	1	0	0
Liparis spp.	0	2	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Lycodes spp.	1	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0
Reinhardtius hippoglossoides	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mallotus villosus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eumicrotremus spinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnelis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Hippoglossoides platessoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Brosme brosme	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Unknown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
INVERTEBRATES																															
Amphipoda	1	1	1	1	1	1	1	1	1	1	-	-	1	1	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1
Actiniaria	1	0	1	1	0	1	0	1	0	0	-	-	0	0	1	-	-	-	-	0	0	1	0	0	0	0	1	0	0	1	1
Chaetognatha	1	1	1	1	1	1	1	1	1	1	-	-	1	1	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1
Asteroidea	1	0	1	1	1	0	1	0	0	1	-	-	0	0	1	-	-	-	-	1	0	1	0	1	0	1	1	1	1	0	0

Ophiurida	1	1	1	1	1	1	1	1	1	1	-	-	1	1	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	1
Bryozoan	1	0	0	0	0	0	0	0	0	1	-	-	0	1	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Heliometra spp.	0	0	0	0	0	0	0	1	0	1	-	-	0	0	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Elpidia spp.	0	1	1	0	0	1	1	0	0	0	-	-	0	0	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Gorgonocephalus spp.	0	0	1	0	0	0	0	0	0	0	-	-	0	1	0	-	-	-	-	0	0	0	0	1	0	0	0	0	0	0	0
Euphausidea	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	-	-	-	-	0	0	0	0	1	1	1	1	1	1	0	0
Nephtheidae	1	1	1	0	1	1	0	1	1	1	-	-	0	1	0	-	-	-	-	0	1	1	1	1	0	1	1	1	0	0	1
Polychaeta	0	1	1	0	1	1	0	0	0	0	-	-	0	0	1	-	-	-	-	1	1	1	0	1	0	1	1	0	1	1	0
Pycnogonidae	0	0	0	0	0	0	0	0	0	1	-	-	0	0	0	-	-	-	-	1	1	0	0	0	0	0	1	0	0	0	0
Caridea	1	0	0	1	1	0	1	1	0	0	-	-	0	0	1	-	-	-	-	1	1	0	1	1	0	0	1	1	1	1	0
Porifera	1	0	0	0	0	0	0	0	0	0	-	-	0	1	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Umbellula ecrinus	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	-	-	-	-	0	0	0	0	1	0	0	0	0	0	0	0
Strongylocentrus spp.	0	0	0	0	0	0	0	0	0	1	-	-	0	0	0	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Buccinidae	1	0	0	1	0	1	0	0	1	0	-	-	1	0	1	-	-	-	-	1	0	1	0	0	0	0	1	1	1	0	1

Table A3 Length (TL in cm) and sex of individuals observed from videos and used in comparison of sex and size between sampling regions. Not included are individuals where only sex but no length were recorded.

Region	Total Length (cm)	Sex
Jones Sound	210	F
Jones Sound	250	F
Jones Sound	206	M
Jones Sound	250	F
Jones Sound	265	M
Jones Sound	248	F
Jones Sound	240	M
Jones Sound	285	F
Jones Sound	275	M
Jones Sound	305	F
Jones Sound	285	M
Jones Sound	205	M
Jones Sound	215	F
Jones Sound	263	F
Jones Sound	270	M
Jones Sound	195	F
Jones Sound	210	M
Jones Sound	230	M
Jones Sound	250	M
Jones Sound	255	F
Jones Sound	238	F
Jones Sound	270	F
Jones Sound	210	M
Jones Sound	205	M
Jones Sound	225	M
Jones Sound	288	M
Jones Sound	290	M
Jones Sound	235	M
Jones Sound	320	F
Jones Sound	256	M
Jones Sound	212	F
Jones Sound	210	F
Jones Sound	306	M
Jones Sound	283	F
Jones Sound	288	F

Jones Sound	233	M
Jones Sound	276	F
Jones Sound	233	F
Jones Sound	259	F
Jones Sound	250	F
Jones Sound	225	M
Jones Sound	196	F
Jones Sound	221	M
Jones Sound	295	F
Jones Sound	220	F
Jones Sound	224	M
Jones Sound	228	F
Jones Sound	240	F
Jones Sound	275	F
Jones Sound	305	F
Jones Sound	252	F
Jones Sound	295	M
Scott Inlet	225	M
Scott Inlet	146	F
Scott Inlet	131	F
Scott Inlet	218	F
Scott Inlet	145	F
Scott Inlet	325	F
Arctic Bay	253	F
Arctic Bay	297	F
Arctic Bay	225	M
Arctic Bay	240	F
Arctic Bay	230	M
Arctic Bay	242	M
Arctic Bay	240	F
Arctic Bay	270	M
Arctic Bay	260	F
Arctic Bay	208	F
Arctic Bay	305	M
Arctic Bay	285	F
Arctic Bay	285	F
Arctic Bay	268	M
Arctic Bay	229	M
Arctic Bay	246	F
Arctic Bay	232	F

Arctic Bay	258	F
Arctic Bay	304	M
Arctic Bay	314	M
Arctic Bay	205	F
Arctic Bay	240	M
Arctic Bay	267	F
Arctic Bay	195	F
Arctic Bay	265	M
Lancaster Sound	157	F
Lancaster Sound	260	F
Lancaster Sound	185	F
Lancaster Sound	266	F
Lancaster Sound	230	M
Lancaster Sound	286	F
Lancaster Sound	265	F
Resolute	266	M
Resolute	314	F
Resolute	264	M

Table A4 Similarity Percentages – Species Contributions (SIMPER) results from two-way analysis between depth class and physical habitat type. Only species which contributed greater than 50% of the cumulative percentage are shown.

SIMPER Similarity Percentages - species contributions

Two-Way Analysis
Resemblance: S17 Bray-Curtis similarity
Cut off for contributions: 50.00%

Depth groups (across all Physical habitats groups)

Group <1500
Average similarity: 49.54

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Macrourus berglax	2.25	14.93	2.48	30.13	30.13
Coryphaenoides rupestris	1.95	10.05	1.02	20.29	50.42

Group 1500-2500
Average similarity: 44.63

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Coryphaenoides carapinus	2.23	15.42	2.12	34.55	34.55
Antimora rostrata	1.97	13.72	1.85	30.74	65.29

Group >2500
Average similarity: 43.22

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Coryphaenoides carapinus	2.28	19.86	1.41	45.94	45.94
Antimora rostrata	1.29	9.26	0.96	21.43	67.38

Groups <1500 & 1500-2500
Average dissimilarity = 64.61

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides carapinus	0.23	2.23	8.67	1.78	13.42	13.42
Coryphaenoides rupestris	1.95	0.68	6.85	1.17	10.60	24.02
Macrourus berglax	2.25	1.06	6.26	1.18	9.69	33.71
Synaphobranchus kaupi	1.00	0.79	3.69	0.98	5.71	39.42
Gaidropsaurus spp.	0.45	0.79	3.37	0.77	5.22	44.64
Antimora rostrata	1.59	1.97	2.99	0.70	4.63	49.28
Myctophidae	0.78	0.29	2.57	0.81	3.98	53.25

Groups <1500 & >2500
Average dissimilarity = 87.76

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib %	Cum.%
Coryphaenoides carapinus	0.23	2.28	10.31	1.16	11.75	11.75
Macrourus berglax	2.25	0.00	10.12	1.89	11.53	23.28
Coryphaenoides rupestris	1.95	0.00	9.93	1.21	11.32	34.60
Coryphaenoides armatus	0.00	1.46	6.58	1.21	7.50	42.10
Halosauropsis macrochir	0.00	0.99	4.24	1.09	4.84	46.93

Macrouridae sp.2	0.07	0.98	4.12	0.93	4.69	51.63

Groups 1500-2500 & >2500
Average dissimilarity = 63.58

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides armatus	0.51	1.46	5.89	1.21	9.26	9.26
Macrourus berglax	1.06	0.00	4.81	0.85	7.57	16.83
Antimora rostrata	1.97	1.29	4.72	0.87	7.43	24.27
Macrouridae sp.2	0.56	0.98	4.49	0.92	7.06	31.32
Gaidropsaurus spp.	0.79	0.00	3.89	0.71	6.11	37.44
Coryphaenoides carapinus	2.23	2.28	3.62	0.68	5.70	43.13
Halosauropsis macrochir	0.36	0.99	3.50	0.90	5.50	48.63
Ophidiidae	0.09	0.82	3.34	0.88	5.25	53.88

Examines Physical habitats groups (across all Depth groups)

Group CS with no/few boulders
Average similarity: 42.87

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	1.89	17.98	2.60	41.95	41.95
Coryphaenoides carapinus	1.33	12.43	1.39	29.00	70.95

Group CS with scattered boulders
Average similarity: 41.59

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.88	16.58	1.81	39.86	39.86
Antimora rostrata	1.62	9.37	1.08	22.53	62.39

Group Boulder field
Average similarity: 36.13

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.80	15.41	1.10	42.64	42.64
Antimora rostrata	1.16	10.21	0.93	28.24	70.88

Group FGS with no/few boulders
Average similarity: 54.40

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	2.13	11.78	7.37	21.66	21.66
Coryphaenoides carapinus	1.71	9.03	1.60	16.60	38.25
Synaphobranchus kaupi	1.15	4.81	1.27	8.84	47.09
Macrourus berglax	1.19	4.15	0.77	7.63	54.71

Group Outcrop
Average similarity: 49.87

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	1.75	13.45	4.53	26.98	26.98
Coryphaenoides carapinus	1.81	13.29	1.71	26.65	53.63

Groups CS with no/few boulders & CS with scattered boulders
Average dissimilarity = 53.95

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides rupestris	0.95	1.11	4.61	0.83	8.54	8.54

Synaphobranchus kaupi	0.75	0.67	4.21	0.99	7.80	16.34
Antimora rostrata	1.89	1.62	4.00	0.83	7.42	23.76
Coryphaenoides armatus	0.48	0.68	3.55	0.86	6.57	30.33
Halosauropsis macrochir	0.57	0.33	3.44	0.82	6.38	36.71
Gaidropsaurus spp.	0.34	0.47	3.31	0.73	6.13	42.84
Macrourus berglax	0.86	0.96	3.06	0.73	5.66	48.51
Coryphaenoides carapinus	1.33	1.88	2.72	0.69	5.04	53.54

Groups CS with no/few boulders & Boulder field
Average dissimilarity = 59.65

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	0.86	0.99	5.61	0.97	9.41	9.41
Coryphaenoides carapinus	1.33	1.80	4.59	0.77	7.69	17.10
Coryphaenoides rupestris	0.95	0.71	4.34	0.83	7.27	24.37
Synaphobranchus kaupi	0.75	0.31	4.26	0.86	7.15	31.52
Gaidropsaurus spp.	0.34	0.54	4.17	0.75	6.98	38.50
Antimora rostrata	1.89	1.16	4.14	0.81	6.94	45.44
Macrouridae sp.2	0.46	0.44	3.91	0.81	6.55	51.99

Groups CS with scattered boulders & Boulder field
Average dissimilarity = 57.42

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.62	1.16	5.60	0.88	9.76	9.76
Macrourus berglax	0.96	0.99	5.25	0.95	9.15	18.91
Gaidropsaurus spp.	0.47	0.54	4.34	0.86	7.55	26.46
Coryphaenoides rupestris	1.11	0.71	4.11	0.77	7.16	33.61
Macrouridae sp.2	0.42	0.44	4.03	0.74	7.02	40.63
Coryphaenoides armatus	0.68	0.56	3.66	0.84	6.38	47.01
Synaphobranchus kaupi	0.67	0.31	3.57	0.92	6.22	53.23

Groups CS with no/few boulders & FGS with no/few boulders
Average dissimilarity = 50.77

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Synaphobranchus kaupi	0.75	1.15	3.40	1.22	6.70	6.70
Coryphaenoides rupestris	0.95	0.85	3.09	0.94	6.08	12.78
Macrouridae sp.1	0.38	0.63	2.67	1.01	5.26	18.04
Gaidropsaurus spp.	0.34	0.47	2.53	0.86	4.97	23.01
Macrourus berglax	0.86	1.19	2.49	0.86	4.90	27.91
Macrouridae sp.2	0.46	0.82	2.42	0.91	4.77	32.68
Myctophidae	0.43	0.78	2.28	1.01	4.49	37.17
Coryphaenoides armatus	0.48	0.66	2.21	0.90	4.35	41.52
Bathysaurus ferox	0.00	0.64	2.12	1.12	4.18	45.70
Halosauropsis macrochir	0.57	0.81	2.06	0.75	4.05	49.76
Coryphaenoides carapinus	1.33	1.71	2.03	0.89	4.00	53.76

Groups CS with scattered boulders & FGS with no/few boulders
Average dissimilarity = 53.88

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides rupestris	1.11	0.85	3.08	0.90	5.72	5.72
Halosauropsis macrochir	0.33	0.81	2.93	0.94	5.43	11.16
Antimora rostrata	1.62	2.13	2.86	0.77	5.31	16.47
Synaphobranchus kaupi	0.67	1.15	2.81	1.04	5.21	21.68

Macrourus berglax	0.96	1.19	2.72	0.93	5.06	26.74
Macrouridae sp.2	0.42	0.82	2.71	1.05	5.02	31.76
Gaidropsaurus spp.	0.47	0.47	2.70	0.92	5.02	36.78
Myctophidae	0.30	0.78	2.40	0.94	4.46	41.24
Macrouridae sp.1	0.14	0.63	2.35	0.98	4.36	45.60
Bathysaurus ferox	0.00	0.64	2.29	1.17	4.25	49.85
Coryphaenoides armatus	0.68	0.66	2.25	0.93	4.18	54.03

Groups Boulder field & FGS with no/few boulders
Average dissimilarity = 59.97

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	0.99	1.19	3.92	1.01	6.53	6.53
Synaphobranchus kaupi	0.31	1.15	3.77	1.28	6.28	12.82
Antimora rostrata	1.16	2.13	3.56	0.91	5.94	18.75
Macrouridae sp.2	0.44	0.82	3.45	1.12	5.74	24.50
Halosauropsis macrochir	0.00	0.81	3.20	0.90	5.33	29.83
Myctophidae	0.00	0.78	2.92	1.02	4.87	34.70
Gaidropsaurus spp.	0.54	0.47	2.89	0.84	4.82	39.52
Macrouridae sp.1	0.00	0.63	2.61	0.95	4.36	43.88
Coryphaenoides carapinus	1.80	1.71	2.61	0.78	4.35	48.23
Alepocephalus spp.	0.46	0.32	2.54	0.74	4.23	52.46

Groups CS with no/few boulders & Outcrop
Average dissimilarity = 52.37

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	0.86	1.76	5.41	1.01	10.33	10.33
Gaidropsaurus spp.	0.34	0.84	4.10	1.23	7.82	18.15
Coryphaenoides rupestris	0.95	0.80	3.91	0.92	7.46	25.61
Synaphobranchus kaupi	0.75	0.51	3.42	0.80	6.53	32.15
Ophidiidae	0.14	0.74	2.65	0.84	5.05	37.20
Coryphaenoides carapinus	1.33	1.81	2.58	0.81	4.92	42.12
Macrouridae sp.2	0.46	0.40	2.36	0.72	4.50	46.63
Coryphaenoides armatus	0.48	0.49	2.29	0.66	4.37	51.00

Groups CS with scattered boulders & Outcrop
Average dissimilarity = 53.41

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	0.96	1.76	4.72	1.02	8.84	8.84
Coryphaenoides rupestris	1.11	0.80	4.22	0.88	7.90	16.74
Gaidropsaurus spp.	0.47	0.84	3.86	1.27	7.23	23.97
Synaphobranchus kaupi	0.67	0.51	3.63	0.98	6.80	30.78
Antimora rostrata	1.62	1.75	3.00	0.90	5.62	36.40
Coryphaenoides armatus	0.68	0.49	2.81	0.89	5.25	41.65
Ophidiidae	0.00	0.74	2.68	0.72	5.02	46.67
Lepidion eques	0.13	0.40	2.28	0.74	4.27	50.94

Groups Boulder field & Outcrop
Average dissimilarity = 56.07

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	0.99	1.76	5.63	1.01	10.03	10.03
Gaidropsaurus spp.	0.54	0.84	4.50	1.23	8.02	18.06
Antimora rostrata	1.16	1.75	4.04	1.02	7.21	25.27

Coryphaenoides carapinus	1.80	1.81	3.88	0.91	6.93	32.20
Macrouridae sp.2	0.44	0.40	3.62	0.81	6.46	38.66
Coryphaenoides rupestris	0.71	0.80	3.41	0.83	6.08	44.74
Alepocephalus spp.	0.46	0.43	3.38	0.83	6.03	50.77

Groups FGS with no/few boulders & Outcrop
Average dissimilarity = 52.59

Species	Av.Abund	Av.Sim	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.19	1.76	3.33	1.01	6.34	6.34
Synaphobranchus kaupi	1.15	0.51	3.25	1.31	6.17	12.51
Gaidropsaurus spp.	0.47	0.84	2.66	1.12	5.05	17.57
Macrouridae sp.2	0.82	0.40	2.54	1.04	4.83	22.40
Coryphaenoides rupestris	0.85	0.80	2.52	0.93	4.79	27.19
Macrouridae sp.1	0.63	0.41	2.49	1.02	4.73	31.91
Myctophidae	0.78	0.25	2.35	1.07	4.47	36.38
Halosauropsis macrochir	0.81	0.20	2.26	0.79	4.30	40.68
Ophidiidae	0.25	0.74	2.09	0.95	3.97	44.66
Bathysaurus ferox	0.64	0.00	2.01	1.13	3.82	48.47
Alepocephalus spp.	0.32	0.43	1.94	0.87	3.68	52.15

Table A5 Similarity Percentages – Species Contributions (SIMPER) results from two-way analysis between depth class and biological habitat type. Only species which contributed greater than 50% of the cumulative percentage are shown.

SIMPER Similarity Percentages - species contributions						
Two-Way Analysis						
Resemblance: S17 Bray-Curtis similarity						
Cut off for contributions: 50.00%						
Examines Depth groups (across all Biological habitats groups)						
Group <1500 Average similarity: 55.80						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Macrourus berglax	2.31	17.06	1.63	30.58	30.58	
Antimora rostrata	1.67	11.37	1.57	20.37	50.95	
Group 1500-2500 Average similarity: 40.98						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Coryphaenoides carapinus	2.07	13.21	1.21	32.23	32.23	
Antimora rostrata	1.88	12.70	1.53	30.99	63.22	
Group >2500 Average similarity: 43.63						
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%	
Coryphaenoides carapinus	2.22	18.53	1.55	42.47	42.47	
Antimora rostrata	1.17	8.92	1.18	20.45	62.92	
Groups <1500 & 1500-2500 Average dissimilarity = 67.81						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides carapinus	0.15	2.07	9.41	1.30	13.87	13.87
Macrourus berglax	2.31	1.08	7.67	0.92	11.31	25.18
Coryphaenoides rupestris	1.63	0.57	7.28	0.96	10.74	35.93
Antimora rostrata	1.67	1.88	5.56	0.78	8.19	44.12
Synaphobranchus kaupi	0.99	0.96	3.76	1.00	5.54	49.66
Myctophidae	0.83	0.41	3.56	0.71	5.26	54.91
Groups <1500 & >2500 Average dissimilarity = 90.93						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	2.31	0.00	11.82	1.78	13.00	13.00
Coryphaenoides carapinus	0.15	2.22	10.78	1.63	11.86	24.86
Coryphaenoides rupestris	1.63	0.00	8.42	1.30	9.26	34.12
Coryphaenoides armatus	0.00	1.48	7.80	0.97	8.58	42.69
Antimora rostrata	1.67	1.17	6.63	0.90	7.29	49.98
Halosauropsis macrochir	0.00	1.36	6.51	0.98	7.16	57.15

Groups 1500-2500 & >2500
Average dissimilarity = 67.20

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides armatus	0.32	1.48	6.72	0.92	10.00	10.00
Antimora rostrata	1.88	1.17	6.06	1.07	9.02	19.02
Halosauropsis macrochir	0.40	1.36	5.43	0.87	8.09	27.11
Coryphaenoides carapinus	2.07	2.22	4.88	0.72	7.26	34.37
Macrourus berglax	1.08	0.00	4.64	0.82	6.90	41.27
Synaphobranchus kaupi	0.96	0.00	4.43	1.11	6.60	47.87
Gaidropsaurus spp.	0.66	0.00	3.72	0.54	5.53	53.40

Examines Biological habitats groups (across all Depth groups)

Group Dense mixed
Average similarity: 43.35

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	1.72	13.22	3.00	30.51	30.51
Coryphaenoides carapinus	1.34	9.88	1.28	22.80	53.30

Group Dense sponges
Average similarity: 49.33

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.62	14.84	1.09	30.08	30.08
Macrourus berglax	1.50	8.85	1.14	17.94	48.02
Antimora rostrata	1.70	7.38	0.93	14.96	62.99

Group Sparse mixed
Average similarity: 49.77

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	1.59	20.11	2.30	40.41	40.41
Coryphaenoides carapinus	1.78	14.99	1.07	30.11	70.52

Group Sparse sponges
Average similarity: 53.03

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	2.13	12.68	3.52	23.92	23.92
Coryphaenoides carapinus	1.76	9.51	1.58	17.93	41.85
Synaphobranchus kaupi	1.03	5.12	1.80	9.66	51.51

Group Absent
Average similarity: 48.31

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	2.07	14.82	4.54	30.68	30.68
Coryphaenoides carapinus	1.94	13.33	2.63	27.59	58.27

Group Sparse corals
Average similarity: 23.07

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Antimora rostrata	1.26	9.16	0.93	39.73	39.73
Coryphaenoides carapinus	1.22	6.40	0.59	27.73	67.47

Group Dense corals Average similarity: 33.09					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Macrourus berglax	2.10	14.89	1.06	44.99	44.99
Coryphaenoides carapinus	1.23	13.38	0.62	40.44	85.42

Groups Dense mixed & Dense sponges Average dissimilarity = 51.51						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.72	1.70	6.01	0.97	11.67	11.67
Synaphobranchus kaupi	0.94	0.82	3.49	0.94	6.78	18.45
Coryphaenoides carapinus	1.34	1.62	3.33	0.61	6.47	24.91
Gaidropsaurus spp.	0.59	0.83	3.31	0.96	6.43	31.35
Macrourus berglax	1.41	1.50	3.31	0.69	6.43	37.78
Coryphaenoides rupestris	0.89	0.92	3.08	0.82	5.98	43.76
Coryphaenoides armatus	0.43	0.36	2.57	0.44	5.00	48.75
Myctophidae	0.57	0.68	2.40	0.92	4.65	53.41

Groups Dense mixed & Sparse mixed Average dissimilarity = 58.45						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.41	1.01	5.56	0.92	9.52	9.52
Antimora rostrata	1.72	1.59	5.06	0.93	8.66	18.18
Coryphaenoides carapinus	1.34	1.78	4.67	0.82	7.99	26.18
Synaphobranchus kaupi	0.94	0.25	4.31	1.10	7.37	33.55
Coryphaenoides rupestris	0.89	0.85	4.06	0.88	6.95	40.50
Halosauropsis macrochir	0.15	0.79	3.77	0.73	6.46	46.96
Gaidropsaurus spp.	0.59	0.00	3.28	0.93	5.61	52.57

Groups Dense sponges & Sparse mixed Average dissimilarity = 58.12						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.70	1.59	8.07	1.07	13.88	13.88
Macrourus berglax	1.50	1.01	5.93	0.79	10.21	24.09
Gaidropsaurus spp.	0.83	0.00	4.85	1.03	8.34	32.43
Coryphaenoides carapinus	1.62	1.78	4.07	0.56	7.01	39.44
Synaphobranchus kaupi	0.82	0.25	3.59	0.99	6.18	45.61
Coryphaenoides rupestris	0.92	0.85	3.30	0.80	5.68	51.30

Groups Dense mixed & Sparse sponges Average dissimilarity = 52.11						
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides rupestris	0.89	0.80	3.02	0.98	5.80	5.80
Macrouridae sp.2	0.07	0.72	3.00	0.98	5.76	11.57
Macrourus berglax	1.41	1.22	2.86	0.95	5.48	17.05
Coryphaenoides armatus	0.43	0.81	2.68	0.90	5.15	22.19
Halosauropsis macrochir	0.15	0.66	2.57	0.75	4.93	27.12
Coryphaenoides carapinus	1.34	1.76	2.52	0.81	4.83	31.95
Bathysaurus ferox	0.00	0.62	2.34	1.07	4.48	36.43
Synaphobranchus kaupi	0.94	1.03	2.32	1.03	4.44	40.88
Myctophidae	0.57	0.55	2.28	0.96	4.37	45.25
Gaidropsaurus spp.	0.59	0.43	2.20	1.04	4.23	49.48

Antimora rostrata	1.72	2.13	2.12	0.81	4.08	53.55

Groups Dense sponges & Sparse sponges
Average dissimilarity = 51.56

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.70	2.13	3.59	0.81	6.97	6.97
Synaphobranchus kaupi	0.82	1.03	3.00	1.03	5.81	12.78
Coryphaenoides rupestris	0.92	0.80	2.99	0.85	5.81	18.59
Macrourus berglax	1.50	1.22	2.97	0.88	5.76	24.35
Gaidropsaurus spp.	0.83	0.43	2.94	1.05	5.71	30.05
Macrouridae sp.2	0.00	0.72	2.81	0.88	5.45	35.50
Coryphaenoides armatus	0.36	0.81	2.50	0.88	4.86	40.36
Bathysaurus ferox	0.00	0.62	2.29	1.08	4.44	44.80
Myctophidae	0.68	0.55	2.21	0.90	4.29	49.09
Halosauropsis macrochir	0.25	0.66	2.09	0.68	4.05	53.14

Groups Sparse mixed & Sparse sponges
Average dissimilarity = 56.38

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.01	1.22	4.86	0.84	8.62	8.62
Coryphaenoides rupestris	0.85	0.80	4.09	0.61	7.26	15.88
Synaphobranchus kaupi	0.25	1.03	3.47	1.19	6.16	22.04
Antimora rostrata	1.59	2.13	3.28	0.57	5.81	27.85
Macrouridae sp.2	0.22	0.72	3.25	1.07	5.77	33.61
Coryphaenoides armatus	0.39	0.81	2.85	1.10	5.05	38.67
Coryphaenoides carapinus	1.78	1.76	2.80	0.76	4.97	43.64
Bathysaurus ferox	0.13	0.62	2.46	1.20	4.36	48.00
Myctophidae	0.00	0.55	2.35	0.96	4.17	52.17

Groups Dense mixed & Absent
Average dissimilarity = 54.22

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.41	0.60	3.78	1.00	6.96	6.96
Halosauropsis macrochir	0.15	0.89	3.27	0.94	6.02	12.99
Coryphaenoides rupestris	0.89	0.57	3.23	0.99	5.96	18.95
Synaphobranchus kaupi	0.94	1.26	3.06	0.96	5.64	24.59
Coryphaenoides carapinus	1.34	1.94	2.96	1.08	5.46	30.06
Macrouridae sp.2	0.07	0.76	2.66	0.77	4.91	34.97
Gaidropsaurus spp.	0.59	0.44	2.66	1.05	4.91	39.87
Macrouridae sp.1	0.00	0.69	2.59	1.09	4.77	44.64
Antimora rostrata	1.72	2.07	2.55	1.01	4.71	49.36
Alepocephalus spp.	0.32	0.42	2.49	0.82	4.59	53.95

Groups Dense sponges & Absent
Average dissimilarity = 54.73

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.70	2.07	4.76	0.79	8.70	8.70
Macrourus berglax	1.50	0.60	4.39	1.08	8.03	16.73
Synaphobranchus kaupi	0.82	1.26	3.51	0.97	6.42	23.15
Gaidropsaurus spp.	0.83	0.44	3.47	0.96	6.34	29.49
Coryphaenoides rupestris	0.92	0.57	3.21	0.87	5.87	35.36
Halosauropsis macrochir	0.25	0.89	2.82	0.84	5.15	40.51

Macrouridae sp.1	0.24	0.69	2.65	1.02	4.84	45.35
Rajella spp.	0.19	0.52	2.54	0.78	4.64	49.98
Macrouridae sp.2	0.00	0.76	2.50	0.73	4.57	54.55

Groups Sparse mixed & Absent
Average dissimilarity = 55.96

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.01	0.60	5.90	0.88	10.55	10.55
Synaphobranchus kaupi	0.25	1.26	5.62	1.09	10.04	20.59
Coryphaenoides rupestris	0.85	0.57	3.83	0.57	6.84	27.43
Coryphaenoides carapinus	1.78	1.94	3.72	0.84	6.65	34.07
Macrouridae sp.1	0.37	0.69	3.20	1.12	5.73	39.80
Halosauropsis macrochir	0.79	0.89	2.95	0.89	5.27	45.07
Gaidropsaurus spp.	0.00	0.44	2.88	0.74	5.14	50.21

Groups Sparse sponges & Absent
Average dissimilarity = 47.82

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides rupestris	0.80	0.57	2.68	0.89	5.59	5.59
Macrourus berglax	1.22	0.60	2.57	0.95	5.38	10.98
Macrouridae sp.2	0.72	0.76	2.48	1.02	5.19	16.17
Synaphobranchus kaupi	1.03	1.26	2.48	0.84	5.18	21.35
Macrouridae sp.1	0.47	0.69	2.20	1.16	4.61	25.96
Coryphaenoides armatus	0.81	0.58	2.12	1.11	4.43	30.38
Halosauropsis macrochir	0.66	0.89	2.11	0.87	4.40	34.79
Gaidropsaurus spp.	0.43	0.44	1.98	0.89	4.14	38.93
Myctophidae	0.55	0.24	1.88	0.94	3.94	42.86
Bathysaurus ferox	0.62	0.34	1.87	1.22	3.91	46.77
Rajella spp.	0.00	0.52	1.87	0.83	3.90	50.68

Groups Dense mixed & Sparse corals
Average dissimilarity = 61.68

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.34	1.22	6.23	0.80	10.10	10.10
Gaidropsaurus spp.	0.59	0.35	4.61	0.85	7.47	17.58
Macrourus berglax	1.41	0.89	4.42	0.90	7.16	24.74
Synaphobranchus kaupi	0.94	0.57	4.19	1.03	6.80	31.53
Antimora rostrata	1.72	1.26	3.99	0.80	6.46	38.00
Coryphaenoides rupestris	0.89	0.46	3.88	0.89	6.29	44.28
Myctophidae	0.57	0.39	3.45	0.90	5.59	49.87
Coryphaenoides armatus	0.43	0.44	2.96	0.44	4.79	54.67

Groups Dense sponges & Sparse corals
Average dissimilarity = 65.54

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.70	1.26	7.53	1.17	11.50	11.50
Coryphaenoides carapinus	1.62	1.22	6.34	0.60	9.67	21.17
Gaidropsaurus spp.	0.83	0.35	6.15	0.67	9.38	30.55
Macrourus berglax	1.50	0.89	5.27	0.94	8.04	38.60
Synaphobranchus kaupi	0.82	0.57	4.79	1.01	7.31	45.91
Myctophidae	0.68	0.39	4.00	0.96	6.10	52.01

Groups Sparse mixed & Sparse corals
Average dissimilarity = 63.23

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.01	0.89	8.17	0.83	12.93	12.93
Coryphaenoides carapinus	1.78	1.22	6.95	0.86	10.98	23.91
Antimora rostrata	1.59	1.26	6.50	0.71	10.28	34.19
Coryphaenoides rupestris	0.85	0.46	5.20	0.60	8.22	42.41
Gaidropsaurus spp.	0.00	0.35	4.13	0.40	6.53	48.94
Synaphobranchus kaupi	0.25	0.57	3.78	0.79	5.98	54.92

Groups Sparse sponges & Sparse corals
Average dissimilarity = 60.04

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	2.13	1.26	4.20	0.84	7.00	7.00
Coryphaenoides carapinus	1.76	1.22	4.10	0.93	6.83	13.83
Macrouridae sp.2	0.72	0.47	3.39	1.03	5.65	19.48
Synaphobranchus kaupi	1.03	0.57	3.32	1.19	5.54	25.02
Gaidropsaurus spp.	0.43	0.35	3.27	0.71	5.44	30.46
Coryphaenoides rupestris	0.80	0.46	3.26	0.84	5.44	35.90
Macrourus berglax	1.22	0.89	3.23	0.96	5.38	41.27
Coryphaenoides armatus	0.81	0.44	3.04	1.06	5.06	46.33
Myctophidae	0.55	0.39	2.75	1.03	4.59	50.92

Groups Absent & Sparse corals
Average dissimilarity = 61.30

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.94	1.22	5.20	0.99	8.49	8.49
Synaphobranchus kaupi	1.26	0.57	5.08	1.04	8.28	16.77
Antimora rostrata	2.07	1.26	4.64	0.83	7.56	24.33
Gaidropsaurus spp.	0.44	0.35	4.14	0.77	6.75	31.08
Macrouridae sp.1	0.69	0.28	3.71	1.07	6.06	37.14
Halosauropsis macrochir	0.89	0.46	3.43	0.99	5.59	42.73
Coryphaenoides rupestris	0.57	0.46	3.26	0.81	5.32	48.05
Macrouridae sp.2	0.76	0.47	3.09	0.78	5.04	53.09

Groups Dense mixed & Dense corals
Average dissimilarity = 56.69

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.72	1.07	7.10	1.32	12.53	12.53
Synaphobranchus kaupi	0.94	0.41	5.08	1.28	8.97	21.50
Macrourus berglax	1.41	2.10	4.93	0.85	8.70	30.20
Coryphaenoides rupestris	0.89	0.78	4.79	1.03	8.46	38.65
Coryphaenoides carapinus	1.34	1.23	4.57	0.98	8.07	46.72
Gaidropsaurus spp.	0.59	0.47	4.05	1.04	7.15	53.87

Groups Dense sponges & Dense corals
Average dissimilarity = 52.90

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	1.70	1.07	6.76	1.02	12.77	12.77
Macrourus berglax	1.50	2.10	5.60	0.73	10.58	23.35
Gaidropsaurus spp.	0.83	0.47	5.51	1.00	10.41	33.76
Coryphaenoides carapinus	1.62	1.23	5.09	0.80	9.62	43.38

Coryphaenoides rupestris	0.92	0.78	4.63	0.85	8.76	52.13

Groups Sparse mixed & Dense corals
Average dissimilarity = 58.98

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Macrourus berglax	1.01	2.10	9.03	0.95	15.30	15.30
Antimora rostrata	1.59	1.07	8.27	0.99	14.02	29.32
Coryphaenoides carapinus	1.78	1.23	7.22	0.78	12.24	41.56
Coryphaenoides rupestris	0.85	0.78	6.18	0.65	10.48	52.04

Groups Sparse sponges & Dense corals
Average dissimilarity = 63.22

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	2.13	1.07	6.09	1.09	9.64	9.64
Macrourus berglax	1.22	2.10	4.40	1.12	6.95	16.59
Synaphobranchus kaupi	1.03	0.41	4.37	1.99	6.91	23.51
Coryphaenoides carapinus	1.76	1.23	3.91	1.15	6.18	29.69
Coryphaenoides rupestris	0.80	0.78	3.90	0.96	6.18	35.86
Myctophidae	0.55	0.77	3.50	0.84	5.54	41.41
Macrouridae sp.2	0.72	0.00	3.20	1.03	5.07	46.47
Coryphaenoides armatus	0.81	0.00	2.99	1.16	4.73	51.20

Groups Absent & Dense corals
Average dissimilarity = 65.53

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Antimora rostrata	2.07	1.07	7.00	1.04	10.68	10.68
Macrourus berglax	0.60	2.10	6.81	1.37	10.39	21.07
Synaphobranchus kaupi	1.26	0.41	6.18	1.39	9.43	30.50
Coryphaenoides carapinus	1.94	1.23	5.05	1.26	7.71	38.21
Gaidropsaurus spp.	0.44	0.47	4.01	0.95	6.12	44.33
Coryphaenoides rupestris	0.57	0.78	3.96	0.91	6.04	50.37

Groups Sparse corals & Dense corals
Average dissimilarity = 70.02

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Coryphaenoides carapinus	1.22	1.23	08.95	0.76	12.79	12.79
Antimora rostrata	1.26	1.07	8.18	1.02	11.69	24.48
Macrourus berglax	0.89	2.10	8.06	1.07	11.51	35.98
Gaidropsaurus spp.	0.35	0.47	6.79	0.55	9.69	45.67
Myctophidae	0.39	0.77	5.93	0.88	8.48	54.15

Table A6 Results of two-way Analysis of Similarities (ANOSIM) of fish assemblages based on physical habitats observed during *in situ* surveys off Newfoundland Canada in 2010. Bottom left half of the table shows *R*-statistics and the top right half of the table shows significance values for pair-wise comparisons.

Physical Habitat Types	CS with no/few boulders	CS with scattered boulders	Boulder field	FGS with no/few boulders	Outcrop
CS with no/few boulders	-	0.875	0.714	0.163	0.442
CS with scattered boulders	-0.1549	-	0.828	0.16	0.433
Boulder field	-0.0749	-0.1207	-	0.047*	0.619
FGS with no/few boulders	0.146	0.1253	0.231	-	0.046*
Outcrop	0.013	0.0055	-0.0459	0.293	-

Table A7 Results of two-way Analysis of Similarities (ANOSIM) of fish assemblages based on biological habitats observed during *in situ* surveys off Newfoundland Canada in 2010. Bottom left half of the table shows *R*-statistics and the top right half of the table shows significance values for pair-wise comparisons.

Biological Habitat Types	Dense mixed	Dense sponges	Sparse mixed	Sparse sponges	Absent	Sparse corals	Dense corals
Dense mixed	-	0.604	0.176	0.525	0.916	0.674	0.432
Dense sponges	-0.044	-	0.091	0.126	0.062	0.335	0.731
Sparse mixed	0.112	0.221	-	0.055	0.121	0.459	0.381
Sparse sponges	-0.024	0.156	0.2748	-	0.381	0.378	0.023*
Absent	-0.190	0.212	0.1897	0.0345	-	0.385	0.008*
Sparse corals	-0.045	0.042	$-2.68e^{-17}$	0.0191	0.0241	-	0.794
Dense corals	0.0102	-0.136	0.0202	0.367	0.4596	0.1226	-

Table A8 Similarity Percentages – Species Contributions (SIMPER) results from one-way analysis of SIMPROF groups based on fishing sets. Only species which contributed greater than 70% of the cumulative percentage are shown.

SIMPER Similarity Percentages - species contributions

Resemblance: S17 Bray-Curtis similarity
Cut off for low contributions: 70.00%

SIMPROF Factor Groups

d: 1,2,14,17
g: 3,4
f: 5,6
b: 7,9
j: 8,23
c: 10,11,15,16,18
a: 12
h: 13
e: 19,21
i: 20,22

Group d
Average similarity: 52.55

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Benthosema glaciale	2.23	12.11	3.20	23.05	23.05
Maurolicus muelleri	1.84	9.27	2.75	17.64	40.69
Notoscopelus kroyeri	1.46	7.96	4.20	15.14	55.83
Chauliodus sloani	1.57	7.61	3.77	14.48	70.32

Group g
Average similarity: 64.29

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Myctophum punctatum	2.11	8.19	-	12.74	12.74
Notoscopelus bolini	1.84	6.99	-	10.87	23.61
Notoscopelus kroyeri	1.77	6.60	-	10.27	33.88
Diaphus rafinesquii	1.60	6.03	-	9.38	43.27
Argyropelecus aculateus	1.64	5.05	-	7.86	51.13
Argyropelecus hemigymnus	1.74	4.70	-	7.31	58.44
Ceratoscopelus maderensis	1.12	4.25	-	6.61	65.05
Chauliodus sloani	1.38	4.03	-	6.27	71.33

Group f
Average similarity: 74.51

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Benthosema glaciale	2.06	7.43	-	9.97	9.97
Notoscopelus kroyeri	2.06	7.32	-	9.83	19.80
Myctophum punctatum	2.06	7.30	-	9.80	29.60
Chauliodus sloani	1.51	4.83	-	6.48	36.09
Diaphus rafinesquii	1.41	4.61	-	6.19	42.27
Lobianchia gemellari	1.12	4.10	-	5.50	47.77

Notoscopelus bolini	1.25	4.10	-	5.50	53.27
Arctozenus risso	1.38	3.99	-	5.36	58.63
Argyropelecus hemigymnus	1.32	3.88	-	5.20	63.83
Stomias boa ferox	1.41	3.67	-	4.93	68.76
Argyropelecus aculateus	0.95	3.47	-	4.66	73.42

Group b
Average similarity: 51.67

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Nemichthys scolopaceus	2.00	13.68	-	26.48	26.48
Notoscopelus kroyeri	2.00	13.68	-	26.48	52.97
Myctophum punctatum	1.83	12.80	-	24.76	77.73

Group j
Average similarity: 64.65

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Serrivomer beani	2.06	5.39	-	8.34	8.34
Sigmops elongatum	1.57	4.13	-	6.39	14.73
Chauliodus sloani	1.93	3.88	-	6.00	20.73
Notoscopelus bolini	1.28	3.61	-	5.58	26.31
Benthosema glaciale	1.67	3.18	-	4.92	31.23
Myctophum punctatum	1.19	3.18	-	4.92	36.15
Arctozenus risso	1.16	2.94	-	4.56	40.71
Diaphus effulgens	1.24	2.94	-	4.56	45.26
Nemichthys scolopaceus	1.17	2.88	-	4.45	49.71
Stomias boa ferox	1.52	2.68	-	4.14	53.85
Melanostomias bartonbeani	0.90	2.48	-	3.83	57.69
Lobianchia gemellari	1.10	2.42	-	3.74	61.43
Malacosteus niger	0.99	2.42	-	3.74	65.17
Notoscopelus kroyeri	1.13	2.08	-	3.22	68.39
Benthodesmus elongatus	0.83	2.08	-	3.22	71.61

Group c
Average similarity: 49.18

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Nemichthys scolopaceus	1.82	9.72	4.51	19.76	19.76
Chauliodus sloani	1.95	9.39	2.70	19.08	38.84
Serrivomer beani	1.67	9.08	4.85	18.46	57.30
Stomias boa ferox	1.68	6.81	1.11	13.85	71.15

Group a
Less than 2 samples in group

Group h
Less than 2 samples in group

Group e
Average similarity: 56.99

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Sigmops elongatum	2.36	8.50	-	14.91	14.91
Chauliodus sloani	1.78	6.67	-	11.71	26.62
Ceratoscopelus maderensis	1.58	6.14	-	10.76	37.39

Diplospinosus multistriata	1.63	5.92	-	10.39	47.77
Arctozenus risso	1.54	5.80	-	10.18	57.95
Benthodesmus elongatus	1.57	5.80	-	10.18	68.13
Lobianchia gemellari	1.35	4.98	-	8.73	76.87

Group i
Average similarity: 76.79

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Lobianchia gemellari	1.95	5.10	-	6.64	6.64
Sigmops elongatum	1.88	4.93	-	6.42	13.06
Notoscopelus kroyeri	1.77	4.60	-	5.99	19.05
Diaphus effulgens	1.67	4.40	-	5.73	24.78
Arctozenus risso	1.74	4.31	-	5.62	30.40
Chauliodus sloani	1.54	3.77	-	4.90	35.30
Lampadena atlantica	1.50	3.36	-	4.38	39.68
Howella sherborni	1.26	3.28	-	4.27	43.95
Nannobrachium atrum	1.13	2.92	-	3.81	47.75
Bathylagus euryops	1.10	2.83	-	3.68	51.44
Benthosema glaciale	1.26	2.83	-	3.68	55.12
Benthodesmus elongatus	1.07	2.68	-	3.48	58.61
Scopelosaurus lepidus	1.05	2.60	-	3.39	61.99
Stomias boa ferox	1.31	2.60	-	3.39	65.38
Notoscopelus bolini	1.00	2.49	-	3.24	68.62
Argyropelecus hemigymnus	0.97	2.29	-	2.98	71.60

Groups d & g
Average dissimilarity = 58.56

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Argyropelecus aculateus	0.00	1.64	4.19	3.13	7.16	7.16
Diaphus rafinesquii	0.00	1.60	4.02	9.24	6.87	14.02
Benthosema glaciale	2.23	0.79	3.89	1.27	6.64	20.66
Maurolicus muelleri	1.84	0.51	3.30	2.08	5.63	26.29
Lobianchia gemellari	0.27	1.38	2.90	1.89	4.95	31.25
Myctophum punctatum	1.02	2.11	2.86	1.46	4.88	36.12
Ceratoscopelus maderensis	0.00	1.12	2.83	6.52	4.83	40.95
Argyropelecus hemigymnus	0.72	1.74	2.81	1.33	4.80	45.75
Arctozenus risso	1.08	0.00	2.75	1.30	4.69	50.44
Notoscopelus bolini	0.91	1.84	2.35	1.43	4.01	54.45
Bathophilus vaillanti	0.00	0.90	2.25	7.52	3.85	58.30
Diaphus effulgens	0.21	0.84	2.01	1.05	3.44	61.74
Benthodesmus elongatus	0.67	0.87	1.93	2.28	3.30	65.04
Hygophum benoiti	0.00	0.65	1.75	0.93	2.99	68.03
Chauliodus sloani	1.57	1.38	1.55	1.11	2.64	70.67

Groups d & f
Average dissimilarity = 51.35

Species	Av.Abund	Av.Abund	Av.Dis	Diss/SD	Contrib%	Cum.%
Diaphus rafinesquii	0.00	1.41	3.50	4.30	6.82	6.82
Stomias boa ferox	0.00	1.41	3.43	3.20	6.68	13.50
Maurolicus muelleri	1.84	0.42	3.34	1.98	6.50	20.00
Myctophum punctatum	1.02	2.06	2.70	1.37	5.25	25.25
Argyropelecus aculateus	0.00	0.95	2.32	9.59	4.53	29.77

Lobianchia gemellari	0.27	1.12	2.18	1.65	4.24	34.01
Serrivomer beani	0.21	0.91	2.15	1.05	4.19	38.21
Ceratoscopelus maderensis	0.00	0.86	2.14	3.94	4.17	42.37
Gonostoma atlanticum	0.00	0.84	2.08	4.30	4.06	46.43
Nemichthys scolopaceus	0.57	1.20	1.99	1.35	3.87	50.29
Arctozenus risso	1.08	1.38	1.83	1.54	3.57	53.86
Sigmops elongatum	0.00	0.75	1.83	7.03	3.56	57.43
Diaphus effulgens	0.21	0.91	1.78	1.77	3.46	60.89
Argyropelecus hemigymnus	0.72	1.32	1.75	1.24	3.41	64.30
Benthodesmus elongatus	0.67	0.74	1.71	1.70	3.34	67.64
Notoscopelus kroyeri	1.46	2.06	1.66	1.78	3.24	70.88

Groups g & f
Average dissimilarity = 37.28

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Stomias boa ferox	0.00	1.41	2.73	2.99	7.31	7.31
Arctozenus risso	0.00	1.38	2.67	4.07	7.16	14.47
Benthosema glaciale	0.79	2.06	2.57	1.31	6.88	21.36
Bathophilus vaillanti	0.90	0.00	1.75	8.76	4.68	26.04
Serrivomer beani	0.00	0.91	1.71	0.86	4.58	30.62
Sternoptyx diaphana	0.85	0.00	1.68	3.52	4.51	35.13
Diaphus effulgens	0.84	0.91	1.65	6.55	4.42	39.54
Gonostoma atlanticum	0.00	0.84	1.65	4.56	4.42	43.96
Argyropelecus aculateus	1.64	0.95	1.39	1.54	3.72	47.68
Hygophum benoiti	0.65	0.48	1.28	1.13	3.45	51.12
Argyropelecus hemigymnus	1.74	1.32	1.26	1.35	3.38	54.50
Sigmops elongatum	0.58	0.75	1.14	2.32	3.06	57.56
Notoscopelus bolini	1.84	1.25	1.13	3.00	3.02	60.58
Lampanyctus macdonaldi	0.00	0.59	1.11	0.86	2.99	63.57
Maurolicus muelleri	0.51	0.42	1.00	1.04	2.68	66.25
Macroparalepis affinis	0.51	0.00	0.95	0.86	2.55	68.80
Melanostomias bartonbeani	0.51	0.00	0.95	0.86	2.55	71.36

Groups d & b
Average dissimilarity = 66.64

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Benthosema glaciale	2.23	0.00	8.57	2.44	12.86	12.86
Chauliodus sloani	1.57	0.00	5.99	2.00	8.98	21.84
Nemichthys scolopaceus	0.57	2.00	5.73	1.62	8.61	30.45
Argyropelecus aculateus	0.00	1.25	4.59	0.92	6.89	37.33
Maurolicus muelleri	1.84	1.05	4.40	1.33	6.60	43.93
Stomias boa ferox	0.00	1.10	4.26	0.92	6.40	50.33
Arctozenus risso	1.08	0.00	4.13	1.31	6.19	56.52
Notoscopelus bolini	0.91	0.00	3.43	1.41	5.14	61.66
Myctophum punctatum	1.02	1.83	3.43	1.17	5.14	66.81
Sigmops elongatum	0.00	0.78	3.01	0.92	4.52	71.33

Groups g & b
Average dissimilarity = 60.86

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Notoscopelus bolini	1.84	0.00	4.93	27.42	8.10	8.10
Diaphus rafinesquii	1.60	0.00	4.27	30.62	7.02	15.12

Chauliodus sloani	1.38	0.00	3.65	4.34	5.99	21.11
Lobianchia gemellari	1.38	0.00	3.63	3.18	5.96	27.07
Nemichthys scolopaceus	0.73	2.00	3.40	3.08	5.59	32.67
Argyropelecus aculateus	1.64	1.25	3.36	1.83	5.52	38.19
Stomias boa ferox	0.00	1.10	3.01	0.86	4.94	43.13
Ceratoscopelus maderensis	1.12	0.00	3.00	8.12	4.94	48.06
Maurolicus muelleri	0.51	1.05	2.79	1.32	4.58	52.64
Bathophilus vaillanti	0.90	0.00	2.39	11.60	3.93	56.57
Benthodesmus elongatus	0.87	0.00	2.34	6.72	3.85	60.42
Electrona risso	0.87	0.00	2.32	18.02	3.82	64.24
Sternoptyx diaphana	0.85	0.00	2.32	3.33	3.81	68.05
Diaphus effulgens	0.84	0.70	2.23	1.01	3.66	71.71

Groups f & b
Average dissimilarity = 56.59

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Benthosema glaciale	2.06	0.00	5.41	7.89	9.56	9.56
Chauliodus sloani	1.51	0.00	3.91	7.77	6.91	16.47
Diaphus rafinesquii	1.41	0.00	3.72	4.41	6.57	23.04
Arctozenus risso	1.38	0.00	3.57	4.44	6.31	29.35
Notoscopelus bolini	1.25	0.00	3.31	4.41	5.84	35.19
Argyropelecus aculateus	0.95	1.25	3.24	3.67	5.73	40.92
Lobianchia gemellari	1.12	0.00	2.94	8.94	5.20	46.12
Stomias boa ferox	1.41	1.10	2.87	1.83	5.07	51.19
Maurolicus muelleri	0.42	1.05	2.71	1.27	4.79	55.98
Ceratoscopelus maderensis	0.86	0.00	2.27	3.97	4.02	60.00
Serrivomer beani	0.91	0.00	2.26	0.87	3.99	63.99
Gonostoma atlanticum	0.84	0.00	2.21	4.41	3.91	67.90
Nemichthys scolopaceus	1.20	2.00	2.15	1.35	3.80	71.69

Groups d & j
Average dissimilarity = 62.05

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	0.21	2.06	3.80	3.41	6.13	6.13
Sigmops elongatum	0.00	1.57	3.16	10.73	5.09	11.22
Stomias boa ferox	0.00	1.52	3.02	2.63	4.87	16.09
Maurolicus muelleri	1.84	0.72	2.18	1.76	3.52	19.60
Diaphus effulgens	0.21	1.24	2.14	2.11	3.45	23.06
Malacosteus niger	0.00	0.99	2.00	7.05	3.22	26.27
Lampadena speculigera	0.00	0.97	1.94	3.91	3.12	29.39
Argyropelecus aculateus	0.00	0.95	1.90	4.17	3.06	32.45
Lobianchia gemellari	0.27	1.10	1.82	1.95	2.93	35.38
Benthosema glaciale	2.23	1.67	1.81	1.35	2.91	38.29
Astronectes gemmifer	0.00	0.87	1.77	4.31	2.85	41.14
Evermannella balbo	0.00	0.79	1.59	9.64	2.56	43.70
Benthodesmus elongatus	0.67	0.83	1.52	2.02	2.45	46.15
Chauliodus sloani	1.57	1.93	1.52	1.19	2.44	48.59
Arctozenus risso	1.08	1.16	1.51	2.96	2.43	51.02
Melanostomias bartonbeani	0.17	0.90	1.51	2.11	2.43	53.45
Nemichthys scolopaceus	0.57	1.17	1.48	1.27	2.38	55.83
Synaphobranchus kaupi	0.00	0.72	1.46	10.95	2.35	58.18
Dolicholagus longirostris	0.00	0.72	1.46	10.95	2.35	60.52
Astronectes niger	0.00	0.72	1.46	10.95	2.35	62.87

Gonostoma denudatum	0.00	0.62	1.30	0.93	2.09	64.96
Diretmus argenteus	0.27	0.72	1.29	3.22	2.08	67.04
Vinciguerria attenuata	0.44	0.36	1.22	1.07	1.97	69.01
Notoscopelus kroyeri	1.46	1.13	1.17	1.35	1.89	70.90

Groups g & j
Average dissimilarity = 53.67

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	0.00	2.06	3.44	6.88	6.41	6.41
Stomias boa ferox	0.00	1.52	2.49	2.43	4.65	11.06
Argyropelecus hemigymnus	1.74	0.36	2.34	1.66	4.36	15.41
Arctozenus risso	0.00	1.16	1.94	5.61	3.62	19.04
Benthosema glaciale	0.79	1.67	1.88	1.39	3.50	22.53
Diaphus rafinesquii	1.60	0.55	1.78	1.59	3.31	25.84
Sigmops elongatum	0.58	1.57	1.68	1.40	3.14	28.98
Malacosteus niger	0.00	0.99	1.65	7.13	3.07	32.04
Lampadena speculigera	0.00	0.97	1.60	3.66	2.98	35.02
Myctophum punctatum	2.11	1.19	1.53	7.50	2.85	37.87
Astronectes gemmifer	0.00	0.87	1.45	4.36	2.71	40.57
Electrona risso	0.87	0.00	1.44	11.04	2.69	43.27
Diaphus effulgens	0.84	1.24	1.43	1.50	2.66	45.93
Evermannella balbo	0.00	0.79	1.31	11.36	2.44	48.36
Chauliodus sloani	1.38	1.93	1.27	1.29	2.36	50.72
Synaphobranchus kaupi	0.00	0.72	1.20	18.07	2.23	52.96
Dolicholagus longirostris	0.00	0.72	1.20	18.07	2.23	55.19
Astronectes niger	0.00	0.72	1.20	18.07	2.23	57.42
Argyropelecus aculateus	1.64	0.95	1.18	1.31	2.20	59.63
Hygophum benoiti	0.65	0.00	1.13	0.86	2.10	61.73
Gonostoma denudatum	0.00	0.62	1.06	0.86	1.98	63.71
Notoscopelus kroyeri	1.77	1.13	1.05	1.39	1.96	65.67
Ceratoscopelus maderensis	1.12	0.47	1.05	1.21	1.96	67.63
Lampanyctus macdonaldi	0.00	0.59	0.95	0.86	1.77	69.41
Howella sherborni	0.00	0.59	0.95	0.86	1.77	71.18

Groups f & j
Average dissimilarity = 42.60

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	0.91	2.06	1.95	1.06	4.57	4.57
Malacosteus niger	0.00	0.99	1.62	7.28	3.80	8.37
Argyropelecus hemigymnus	1.32	0.36	1.59	1.62	3.74	12.11
Lampadena speculigera	0.00	0.97	1.57	3.68	3.69	15.80
Notoscopelus kroyeri	2.06	1.13	1.51	1.98	3.54	19.35
Melanostomias bartonbeani	0.00	0.90	1.48	10.83	3.47	22.82
Diaphus rafinesquii	1.41	0.55	1.46	1.24	3.43	26.25
Myctophum punctatum	2.06	1.19	1.44	3.69	3.38	29.63
Astronectes gemmifer	0.00	0.87	1.43	4.42	3.36	32.98
Gonostoma atlanticum	0.84	0.00	1.38	4.80	3.24	36.22
Sigmops elongatum	0.75	1.57	1.34	4.38	3.16	39.38
Evermannella balbo	0.00	0.79	1.29	12.03	3.03	42.41
Diretmus argenteus	0.00	0.72	1.18	21.87	2.77	45.18
Dolicholagus longirostris	0.00	0.72	1.18	21.87	2.77	47.95
Electrona risso	0.68	0.00	1.11	21.25	2.61	50.56
Gonostoma denudatum	0.00	0.62	1.04	0.87	2.45	53.01

Chauliodus sloani	1.51	1.93	1.04	1.19	2.43	55.44
Lampanyctus macdonaldi	0.59	0.59	0.97	0.87	2.28	57.72
Howella sherborni	0.36	0.59	0.96	1.18	2.25	59.97
Stomias boa ferox	1.41	1.52	0.95	1.07	2.22	62.19
Benthosema glaciale	2.06	1.67	0.94	1.15	2.20	64.39
Diplospinosus multistriata	0.00	0.50	0.85	0.87	2.00	66.39
Hygophum benoiti	0.48	0.00	0.81	0.86	1.91	68.30
Ceratoscopelus maderensis	0.86	0.47	0.80	1.16	1.89	70.19

Groups b & j
Average dissimilarity = 71.21

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	0.00	2.06	4.40	6.74	6.17	6.17
Chauliodus sloani	0.00	1.93	4.15	2.57	5.83	12.00
Benthosema glaciale	0.00	1.67	3.50	2.94	4.92	16.92
Notoscopelus bolini	0.00	1.28	2.72	14.67	3.82	20.74
Argyropelecus aculateus	1.25	0.95	2.63	2.79	3.70	24.44
Arctozenus risso	0.00	1.16	2.49	5.48	3.49	27.93
Argyropelecus hemigymnus	1.48	0.36	2.40	2.31	3.37	31.30
Stomias boa ferox	1.10	1.52	2.33	1.39	3.27	34.57
Lobianchia gemellari	0.00	1.10	2.32	4.56	3.25	37.82
Maurolicus muelleri	1.05	0.72	2.21	2.86	3.11	40.93
Malacosteus niger	0.00	0.99	2.10	8.22	2.95	43.88
Lampadena speculigera	0.00	0.97	2.03	3.86	2.86	46.73
Melanostomias bartonbeani	0.00	0.90	1.92	10.30	2.70	49.43
Astronectes gemmifer	0.00	0.87	1.86	4.26	2.61	52.04
Notoscopelus kroyeri	2.00	1.13	1.82	1.49	2.55	54.59
Nemichthys scolopaceus	2.00	1.17	1.78	1.84	2.51	57.10
Benthodesmus elongatus	0.00	0.83	1.78	5.13	2.50	59.60
Sigmops elongatum	0.78	1.57	1.77	1.02	2.49	62.08
Evermannella balbo	0.00	0.79	1.67	15.51	2.35	64.43
Diaphus effulgens	0.70	1.24	1.55	1.10	2.18	66.61
Synaphobranchus kaupi	0.00	0.72	1.53	24.63	2.15	68.76
Diretmus argenteus	0.00	0.72	1.53	24.63	2.15	70.91

Groups d & c
Average dissimilarity = 64.33

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Maurolicus muelleri	1.84	0.00	5.87	3.31	9.12	9.12
Stomias boa ferox	0.00	1.68	5.55	1.71	8.62	17.75
Serrivomer beani	0.21	1.67	5.00	2.21	7.77	25.52
Benthosema glaciale	2.23	0.99	4.81	1.25	7.48	33.00
Nemichthys scolopaceus	0.57	1.82	4.50	1.37	6.99	39.99
Notoscopelus kroyeri	1.46	0.72	2.90	1.01	4.51	44.50
Arctozenus risso	1.08	1.09	2.78	1.25	4.32	48.81
Chauliodus sloani	1.57	1.95	2.69	1.25	4.18	52.99
Notoscopelus bolini	0.91	0.47	2.54	1.37	3.95	56.94
Myctophum punctatum	1.02	1.21	2.52	1.08	3.92	60.86
Benthodesmus elongatus	0.67	0.22	2.25	0.97	3.50	64.36
Argyropelecus hemigymnus	0.72	0.15	2.09	1.32	3.25	67.62
Nessorhamphus ingolfianus	0.00	0.54	1.89	0.77	2.94	70.56

Groups g & c
Average dissimilarity = 72.17

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	0.00	1.67	4.10	3.72	5.67	5.67
Stomias boa ferox	0.00	1.68	4.08	1.73	5.65	11.33
Argyropelecus aculateus	1.64	0.00	4.04	3.26	5.60	16.92
Argyropelecus hemigymnus	1.74	0.15	3.97	2.05	5.50	22.43
Diaphus rafinesquii	1.60	0.00	3.88	11.25	5.37	27.80
Notoscopelus bolini	1.84	0.47	3.31	2.20	4.59	32.39
Lobianchia gemellari	1.38	0.00	3.30	3.28	4.57	36.95
Nemichthys scolopaceus	0.73	1.82	2.71	2.08	3.75	40.70
Notoscopelus kroyeri	1.77	0.72	2.68	1.48	3.71	44.41
Arctozenus risso	0.00	1.09	2.60	1.46	3.61	48.02
Myctophum punctatum	2.11	1.21	2.24	1.11	3.11	51.13
Benthosema glaciale	0.79	0.99	2.21	1.11	3.07	54.20
Ceratoscopelus maderensis	1.12	0.22	2.20	1.90	3.05	57.25
Electrona risso	0.87	0.00	2.11	9.83	2.92	60.17
Sternoptyx diaphana	0.85	0.00	2.10	3.53	2.91	63.09
Diaphus effulgens	0.84	0.00	1.92	0.94	2.66	65.75
Chauliodus sloani	1.38	1.95	1.89	1.23	2.62	68.37
Benthodesmus elongatus	0.87	0.22	1.81	2.46	2.51	70.87

Groups f & c
Average dissimilarity = 54.85

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Diaphus rafinesquii	1.41	0.00	3.38	4.54	6.16	6.16
Notoscopelus kroyeri	2.06	0.72	3.30	1.80	6.01	12.17
Argyropelecus hemigymnus	1.32	0.15	2.84	2.25	5.17	17.34
Benthosema glaciale	2.06	0.99	2.82	1.28	5.14	22.49
Lobianchia gemellari	1.12	0.00	2.67	7.76	4.87	27.36
Serrivomer beani	0.91	1.67	2.48	1.25	4.52	31.88
Argyropelecus aculateus	0.95	0.00	2.24	11.69	4.09	35.97
Stomias boa ferox	1.41	1.68	2.17	1.63	3.95	39.92
Diaphus effulgens	0.91	0.00	2.15	9.89	3.93	43.85
Myctophum punctatum	2.06	1.21	2.13	1.07	3.88	47.73
Notoscopelus bolini	1.25	0.47	1.96	1.38	3.58	51.31
Gonostoma atlanticum	0.84	0.23	1.76	2.46	3.22	54.53
Ceratoscopelus maderensis	0.86	0.22	1.76	2.20	3.21	57.74
Sigmops elongatum	0.75	0.57	1.72	2.40	3.14	60.88
Nemichthys scolopaceus	1.20	1.82	1.67	1.17	3.05	63.93
Electrona risso	0.68	0.00	1.61	11.74	2.94	66.87
Lampanyctus macdonaldi	0.59	0.35	1.60	1.05	2.93	69.79
Chauliodus sloani	1.51	1.95	1.60	1.20	2.91	72.70

Groups b & c
Average dissimilarity = 66.83

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chauliodus sloani	0.00	1.95	6.98	2.61	10.45	10.45
Serrivomer beani	0.00	1.67	6.03	3.36	9.03	19.47
Argyropelecus hemigymnus	1.48	0.15	4.83	3.12	7.22	26.70
Notoscopelus kroyeri	2.00	0.72	4.81	1.52	7.20	33.89
Argyropelecus aculateus	1.25	0.00	4.35	0.94	6.50	40.40
Stomias boa ferox	1.10	1.68	4.18	1.14	6.25	46.65

Arctozenus risso	0.00	1.09	3.78	1.44	5.66	52.31
Maurolicus muelleri	1.05	0.00	3.65	0.94	5.47	57.77
Benthosema glaciale	0.00	0.99	3.29	1.08	4.93	62.70
Sigmops elongatum	0.78	0.57	3.01	1.07	4.50	67.20
Myctophum punctatum	1.83	1.21	2.76	0.97	4.12	71.32

Groups j & c
Average dissimilarity = 57.66

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Diaphus effulgens	1.24	0.00	2.45	4.35	4.25	4.25
Sigmops elongatum	1.57	0.57	2.24	1.75	3.88	8.12
Lobianchia gemellari	1.10	0.00	2.14	4.66	3.72	11.84
Benthosema glaciale	1.67	0.99	2.00	1.30	3.47	15.31
Lampadena speculigera	0.97	0.00	1.88	4.02	3.26	18.58
Argyropelecus aculateus	0.95	0.00	1.84	4.29	3.20	21.78
Melanostomias bartonbeani	0.90	0.00	1.77	9.12	3.08	24.85
Stomias boa ferox	1.52	1.68	1.77	1.38	3.07	27.92
Malacosteus niger	0.99	0.25	1.67	2.39	2.90	30.82
Notoscopelus bolini	1.28	0.47	1.58	1.31	2.74	33.56
Astronectes gemmifer	0.87	0.24	1.51	2.45	2.63	36.18
Benthodesmus elongatus	0.83	0.22	1.42	2.52	2.46	38.64
Synaphobranchus kaupi	0.72	0.00	1.41	13.08	2.45	41.09
Diretmus argenteus	0.72	0.00	1.41	13.08	2.45	43.55
Dolicholagus longirostris	0.72	0.00	1.41	13.08	2.45	46.00
Maurolicus muelleri	0.72	0.00	1.41	13.08	2.45	48.45
Astronectes niger	0.72	0.00	1.41	13.08	2.45	50.90
Notoscopelus kroyeri	1.13	0.72	1.40	1.31	2.43	53.34
Chauliodus sloani	1.93	1.95	1.38	1.26	2.40	55.73
Evermannella balbo	0.79	0.22	1.36	3.18	2.35	58.09
Lampanyctus macdonaldi	0.59	0.35	1.33	1.05	2.31	60.40
Nemichthys scolopaceus	1.17	1.82	1.33	1.28	2.31	62.71
Gonostoma denudatum	0.62	0.00	1.26	0.94	2.19	64.90
Arctozenus risso	1.16	1.09	1.19	1.38	2.06	66.96
Howella sherborni	0.59	0.00	1.12	0.94	1.94	68.90
Nessorhamphus ingolfianus	0.00	0.54	1.10	0.77	1.90	70.80

Groups d & a
Average dissimilarity = 78.36

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.00	2.86	9.86	6.45	12.58	12.58
Maurolicus muelleri	1.84	0.00	6.12	3.21	7.80	20.39
Chauliodus sloani	1.57	0.00	5.47	1.88	6.98	27.36
Macroparalepis affinis	0.00	1.46	5.04	6.45	6.43	33.79
Nemichthys scolopaceus	0.57	1.87	4.73	1.57	6.04	39.83
Malacosteus niger	0.00	1.32	4.55	6.45	5.81	45.64
Ceratoscopelus maderensis	0.00	1.11	3.83	6.45	4.89	50.53
Bathylagus euryops	0.00	1.11	3.83	6.45	4.89	55.42
Dolicholagus longirostris	0.00	1.11	3.83	6.45	4.89	60.30
Diplospinosus multistriata	0.00	1.11	3.83	6.45	4.89	65.19
Arctozenus risso	1.08	0.00	3.77	1.22	4.81	69.99
Myctophum punctatum	1.02	0.00	3.31	1.45	4.22	74.22

Groups g & a
Average dissimilarity = 76.39

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.58	2.86	5.83	2.27	7.63	7.63
Myctophum punctatum	2.11	0.00	5.30	15.25	6.93	14.57
Notoscopelus bolini	1.84	0.00	4.62	31.77	6.05	20.62
Argyropelecus hemigymnus	1.74	0.00	4.45	1.91	5.83	26.45
Argyropelecus aculateus	1.64	0.00	4.18	2.53	5.47	31.92
Diaphus rafinesquii	1.60	0.00	4.01	38.79	5.25	37.16
Chauliodus sloani	1.38	0.00	3.42	3.49	4.48	41.65
Lobianchia gemellari	1.38	0.00	3.41	2.56	4.46	46.11
Malacosteus niger	0.00	1.32	3.32	11.15	4.35	50.45
Nemichthys scolopaceus	0.73	1.87	2.85	28.91	3.73	54.18
Bathylagus euryops	0.00	1.11	2.79	11.15	3.65	57.83
Dolicholagus longirostris	0.00	1.11	2.79	11.15	3.65	61.49
Diplospinosus multistriata	0.00	1.11	2.79	11.15	3.65	65.14
Macroparalepis affinis	0.51	1.46	2.46	1.21	3.23	68.37
Bathophilus vaillanti	0.90	0.00	2.25	9.20	2.94	71.31

Groups f & a
Average dissimilarity = 73.11

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.75	2.86	5.20	7.18	7.11	7.11
Myctophum punctatum	2.06	0.00	5.08	5.85	6.95	14.06
Chauliodus sloani	1.51	0.00	3.68	6.24	5.03	19.09
Macroparalepis affinis	0.00	1.46	3.59	14.47	4.91	23.99
Diaphus rafinesquii	1.41	0.00	3.49	3.67	4.78	28.77
Stomias boa ferox	1.41	0.00	3.42	2.56	4.68	33.45
Arctozenus risso	1.38	0.00	3.36	3.58	4.59	38.04
Argyropelecus hemigymnus	1.32	0.00	3.27	2.58	4.47	42.51
Malacosteus niger	0.00	1.32	3.24	14.47	4.43	46.94
Notoscopelus bolini	1.25	0.00	3.11	3.67	4.25	51.19
Lobianchia gemellari	1.12	0.00	2.76	7.67	3.78	54.97
Bathylagus euryops	0.00	1.11	2.73	14.47	3.73	58.70
Dolicholagus longirostris	0.00	1.11	2.73	14.47	3.73	62.42
Diplospinosus multistriata	0.00	1.11	2.73	14.47	3.73	66.15
Notoscopelus kroyeri	2.06	1.11	2.35	3.61	3.21	69.36
Argyropelecus aculateus	0.95	0.00	2.32	66.52	3.17	72.53

Groups b & a
Average dissimilarity = 72.55

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.78	2.86	7.69	2.00	10.61	10.61
Myctophum punctatum	1.83	0.00	6.79	5.72	9.37	19.97
Benthosema glaciale	0.00	1.57	5.86	29.64	8.08	28.05
Argyropelecus hemigymnus	1.48	0.00	5.53	9.21	7.62	35.67
Macroparalepis affinis	0.00	1.46	5.45	29.64	7.52	43.19
Malacosteus niger	0.00	1.32	4.93	29.64	6.79	49.98
Argyropelecus aculateus	1.25	0.00	4.54	0.71	6.26	56.24
Stomias boa ferox	1.10	0.00	4.21	0.71	5.80	62.04
Ceratoscopelus maderensis	0.00	1.11	4.14	29.64	5.71	67.75
Bathylagus euryops	0.00	1.11	4.14	29.64	5.71	73.46

Groups j & a
Average dissimilarity = 68.89

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	2.06	0.00	4.18	5.63	6.06	6.06
Chauliodus sloani	1.93	0.00	3.94	2.12	5.72	11.78
Stomias boa ferox	1.52	0.00	3.02	2.04	4.38	16.16
Macroparalepis affinis	0.00	1.46	2.95	16.83	4.28	20.44
Sigmops elongatum	1.57	2.86	2.61	5.16	3.79	24.23
Notoscopelus bolini	1.28	0.00	2.59	12.80	3.75	27.98
Diaphus effulgens	1.24	0.00	2.52	3.40	3.65	31.63
Myctophum punctatum	1.19	0.00	2.39	34.58	3.47	35.11
Arctozenus risso	1.16	0.00	2.36	4.55	3.43	38.53
Bathylagus euryops	0.00	1.11	2.24	16.83	3.25	41.78
Lobianchia gemellari	1.10	0.00	2.20	3.70	3.20	44.98
Lampadena speculigera	0.97	0.00	1.93	3.13	2.81	47.79
Argyropelecus aculateus	0.95	0.00	1.90	3.37	2.75	50.54
Melanostomias bartonbeani	0.90	0.00	1.82	8.76	2.65	53.19
Astronectes gemmifer	0.87	0.00	1.76	3.52	2.56	55.75
Benthodesmus elongatus	0.83	0.00	1.69	4.26	2.45	58.20
Evermannella balbo	0.79	0.00	1.59	12.55	2.30	60.51
Synaphobranchus kaupi	0.72	0.00	1.45	23.40	2.11	62.62
Diretmus argenteus	0.72	0.00	1.45	23.40	2.11	64.73
Maurolicus muelleri	0.72	0.00	1.45	23.40	2.11	66.84
Astronectes niger	0.72	0.00	1.45	23.40	2.11	68.95
Nemichthys scolopaceus	1.17	1.87	1.42	2.62	2.06	71.01

Groups c & a
Average dissimilarity = 70.61

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.57	2.86	7.69	2.26	10.90	10.90
Chauliodus sloani	1.95	0.00	6.41	2.47	9.08	19.97
Serrivomer beani	1.67	0.00	5.53	3.29	7.84	27.81
Stomias boa ferox	1.68	0.00	5.50	1.63	7.79	35.60
Macroparalepis affinis	0.41	1.46	4.26	2.78	6.03	41.63
Myctophum punctatum	1.21	0.00	3.85	1.50	5.45	47.08
Dolicholagus longirostris	0.00	1.11	3.64	7.99	5.15	52.23
Diplospinosus multistriata	0.00	1.11	3.64	7.99	5.15	57.38
Malacosteus niger	0.25	1.32	3.63	1.87	5.14	62.52
Arctozenus risso	1.09	0.00	3.48	1.37	4.93	67.45
Bathylagus euryops	0.20	1.11	3.07	1.94	4.35	71.80

Groups d & h
Average dissimilarity = 67.69

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Stomias boa ferox	0.00	2.06	4.37	10.36	6.46	6.46
Chiasmodon niger	0.00	1.85	3.93	10.36	5.81	12.28
Maurolicus muelleri	1.84	0.00	3.83	2.98	5.65	17.93
Scopelosaurus lepidus	0.00	1.49	3.17	10.36	4.68	22.61
Synaphobranchus kaupi	0.00	1.39	2.95	10.36	4.36	26.97
Melanonus zugmayeri	0.00	1.25	2.67	10.36	3.94	30.91
Sigmops elongatum	0.00	1.25	2.67	10.36	3.94	34.85

Malacosteus niger	0.00	1.17	2.48	10.36	3.66	38.51
Serrivomer beani	0.21	1.33	2.42	2.45	3.58	42.09
Macroparalepis affinis	0.00	1.05	2.24	10.36	3.31	45.40
Ceratoscopelus maderensis	0.00	1.05	2.24	10.36	3.31	48.71
Lampadena speculigera	0.00	1.05	2.24	10.36	3.31	52.02
Pseudoscopelus astronesthidens	0.00	1.05	2.24	10.36	3.31	55.33
Benthosema glaciale	2.23	1.25	2.12	1.22	3.14	58.47
Benthodesmus elongatus	0.67	1.17	1.97	3.23	2.92	61.38
Notoscopelus bolini	0.91	0.00	1.93	1.28	2.85	64.23
Melanostomias bartonbeani	0.17	1.05	1.91	2.32	2.82	67.05
Nessorhamphus ingolfianus	0.00	0.89	1.88	10.36	2.78	69.83
Evermannella balbo	0.00	0.89	1.88	10.36	2.78	72.62

Groups g & h
Average dissimilarity = 66.45

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Stomias boa ferox	0.00	2.06	3.57	16.14	5.37	5.37
Chiasmodon niger	0.00	1.85	3.21	16.14	4.83	10.20
Notoscopelus bolini	1.84	0.00	3.19	270.92	4.80	15.00
Arctozenus risso	0.00	1.68	2.92	16.14	4.39	19.40
Argyropelecus aculateus	1.64	0.00	2.87	2.71	4.32	23.71
Diaphus rafinesquii	1.60	0.00	2.77	497.06	4.16	27.88
Scopelosaurus lepidus	0.00	1.49	2.59	16.14	3.89	31.77
Synaphobranchus kaupi	0.00	1.39	2.41	16.14	3.62	35.39
Lobianchia gemellari	1.38	0.00	2.36	2.41	3.56	38.95
Serrivomer beani	0.00	1.33	2.30	16.14	3.46	42.41
Melanonus zugmayeri	0.00	1.25	2.17	16.14	3.27	45.68
Myctophum punctatum	2.11	0.89	2.12	49.41	3.18	48.86
Malacosteus niger	0.00	1.17	2.02	16.14	3.05	51.91
Lampadena speculigera	0.00	1.05	1.83	16.14	2.75	54.66
Pseudoscopelus astronesthidens	0.00	1.05	1.83	16.14	2.75	57.41
Bathophilus vaillanti	0.90	0.00	1.55	7.34	2.34	59.75
Nessorhamphus ingolfianus	0.00	0.89	1.54	16.14	2.31	62.06
Evermannella balbo	0.00	0.89	1.54	16.14	2.31	64.38
Howella sherborni	0.00	0.89	1.54	16.14	2.31	66.69
Eustomias filifer	0.00	0.89	1.54	16.14	2.31	69.00
Photonectes margarita	0.00	0.89	1.54	16.14	2.31	71.32

Groups f & h
Average dissimilarity = 52.93

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chiasmodon niger	0.00	1.85	3.16	20.80	5.97	5.97
Scopelosaurus lepidus	0.00	1.49	2.54	20.80	4.81	10.77
Diaphus rafinesquii	1.41	0.00	2.42	3.97	4.57	15.35
Notoscopelus bolini	1.25	0.00	2.15	3.97	4.07	19.42
Melanonus zugmayeri	0.00	1.25	2.14	20.80	4.04	23.46
Myctophum punctatum	2.06	0.89	2.01	4.41	3.81	27.26
Malacosteus niger	0.00	1.17	1.99	20.80	3.76	31.03
Lobianchia gemellari	1.12	0.00	1.92	9.13	3.62	34.65
Synaphobranchus kaupi	0.30	1.39	1.87	2.29	3.53	38.18
Macroparalepis affinis	0.00	1.05	1.80	20.80	3.40	41.58

Lampadena speculigera	0.00	1.05	1.80	20.80	3.40	44.98
Pseudoscopelus astronesthidens	0.00	1.05	1.80	20.80	3.40	48.38
Melanostomias bartonbeani	0.00	1.05	1.80	20.80	3.40	51.78
Argyropelecus aculateus	0.95	0.00	1.61	165.63	3.04	54.82
Serrivomer beani	0.91	1.33	1.58	1.47	2.98	57.80
Diaphus effulgens	0.91	0.00	1.55	18.72	2.92	60.72
Nessorhamphus ingolfianus	0.00	0.89	1.51	20.80	2.86	63.58
Evermannella balbo	0.00	0.89	1.51	20.80	2.86	66.44
Eustomias filifer	0.00	0.89	1.51	20.80	2.86	69.30
Photonectes margarita	0.00	0.89	1.51	20.80	2.86	72.16

Groups b & h
Average dissimilarity = 70.82

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chauliodus sloani	0.00	1.98	4.44	49.40	6.27	6.27
Chiasmodon niger	0.00	1.85	4.15	49.40	5.85	12.12
Arctozenus risso	0.00	1.68	3.77	49.40	5.32	17.45
Scopelosaurus lepidus	0.00	1.49	3.34	49.40	4.72	22.16
Synaphobranchus kaupi	0.00	1.39	3.11	49.40	4.39	26.55
Serrivomer beani	0.00	1.33	2.97	49.40	4.19	30.75
Melanonus zugmayeri	0.00	1.25	2.81	49.40	3.97	34.71
Benthosema glaciale	0.00	1.25	2.81	49.40	3.97	38.68
Argyropelecus aculateus	1.25	0.00	2.75	0.71	3.88	42.56
Benthodesmus elongatus	0.00	1.17	2.61	49.40	3.69	46.25
Malacosteus niger	0.00	1.17	2.61	49.40	3.69	49.94
Stomias boa ferox	1.10	2.06	2.44	0.82	3.44	53.38
Macroparalepis affinis	0.00	1.05	2.36	49.40	3.33	56.72
Ceratoscopelus maderensis	0.00	1.05	2.36	49.40	3.33	60.05
Lampadena speculigera	0.00	1.05	2.36	49.40	3.33	63.38
Pseudoscopelus astronesthidens	0.00	1.05	2.36	49.40	3.33	66.72
Melanostomias bartonbeani	0.00	1.05	2.36	49.40	3.33	70.05

Groups j & h
Average dissimilarity = 46.58

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chiasmodon niger	0.00	1.85	2.74	22.88	5.89	5.89
Scopelosaurus lepidus	0.00	1.49	2.21	22.88	4.75	10.64
Notoscopelus bolini	1.28	0.00	1.90	16.01	4.08	14.72
Melanonus zugmayeri	0.00	1.25	1.86	22.88	3.99	18.71
Diaphus effulgens	1.24	0.00	1.85	3.58	3.97	22.67
Lobianchia gemellari	1.10	0.00	1.62	3.50	3.49	26.16
Macroparalepis affinis	0.00	1.05	1.56	22.88	3.36	29.51
Pseudoscopelus astronesthidens	0.00	1.05	1.56	22.88	3.36	32.87
Argyropelecus aculateus	0.95	0.00	1.40	3.21	3.00	35.87
Nessorhamphus ingolfianus	0.00	0.89	1.31	22.88	2.82	38.69
Photonectes margarita	0.00	0.89	1.31	22.88	2.82	41.51
Astronectes gemmifer	0.87	0.00	1.29	3.72	2.78	44.29
Serrivomer beani	2.06	1.33	1.10	2.68	2.36	46.66
Diretmus argenteus	0.72	0.00	1.07	37.02	2.29	48.95
Dolicholagus longirostris	0.72	0.00	1.07	37.02	2.29	51.25

Maurolicus muelleri	0.72	0.00	1.07	37.02	2.29	53.54
Astronectes niger	0.72	0.00	1.07	37.02	2.29	55.83
Synaphobranchus kaupi	0.72	1.39	0.99	16.19	2.12	57.96
Notoscopelus kroyeri	1.13	1.80	0.98	1.24	2.10	60.06
Gonostoma denudatum	0.62	0.00	0.94	0.71	2.03	62.08
Howella sherborni	0.59	0.89	0.89	1.37	1.92	64.00
Stomias boa ferox	1.52	2.06	0.89	0.76	1.91	65.91
Lampanyctus macdonaldi	0.59	0.00	0.85	0.71	1.83	67.74
Ceratoscopelus maderensis	0.47	1.05	0.85	0.90	1.82	69.56
Chauliodus sloani	1.93	1.98	0.85	11.69	1.82	71.37

Groups c & h
Average dissimilarity = 53.87

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chiasmodon niger	0.27	1.85	3.19	2.73	5.92	5.92
Scopelosaurus lepidus	0.00	1.49	3.08	12.86	5.71	11.63
Synaphobranchus kaupi	0.00	1.39	2.86	12.86	5.31	16.95
Melanonus zugmayeri	0.00	1.25	2.59	12.86	4.80	21.75
Notoscopelus kroyeri	0.72	1.80	2.30	1.50	4.28	26.02
Lampadena speculigera	0.00	1.05	2.17	12.86	4.04	30.06
Pseudoscopelus astronesthidens	0.00	1.05	2.17	12.86	4.04	34.10
Melanostomias bartonbeani	0.00	1.05	2.17	12.86	4.04	38.13
Macroparalepis affinis	0.41	1.05	2.14	10.41	3.98	42.11
Malacosteus niger	0.25	1.17	1.99	1.89	3.70	45.81
Sigmops elongatum	0.57	1.25	1.96	1.84	3.63	49.44
Benthodesmus elongatus	0.22	1.17	1.96	1.90	3.63	53.07
Howella sherborni	0.00	0.89	1.83	12.86	3.39	56.46
Eustomias filifer	0.00	0.89	1.83	12.86	3.39	59.86
Photonectes margarita	0.00	0.89	1.83	12.86	3.39	63.25
Ceratoscopelus maderensis	0.22	1.05	1.76	1.85	3.27	66.52
Benthosema glaciale	0.99	1.25	1.65	1.42	3.06	69.58
Evermannella balbo	0.22	0.89	1.55	2.42	2.88	72.46

Groups a & h
Average dissimilarity = 65.10

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Stomias boa ferox	0.00	2.06	4.37	-	6.71	6.71
Chauliodus sloani	0.00	1.98	4.21	-	6.47	13.18
Chiasmodon niger	0.00	1.85	3.93	-	6.04	19.21
Arctozenus risso	0.00	1.68	3.57	-	5.49	24.70
Sigmops elongatum	2.86	1.25	3.41	-	5.23	29.93
Scopelosaurus lepidus	0.00	1.49	3.17	-	4.86	34.80
Synaphobranchus kaupi	0.00	1.39	2.95	-	4.53	39.32
Serrivomer beani	0.00	1.33	2.81	-	4.32	43.65
Melanonus zugmayeri	0.00	1.25	2.66	-	4.09	47.73
Benthodesmus elongatus	0.00	1.17	2.48	-	3.81	51.54
Bathylagus euryops	1.11	0.00	2.36	-	3.62	55.16
Dolicholagus longirostris	1.11	0.00	2.36	-	3.62	58.78
Diplospinosus multistriata	1.11	0.00	2.36	-	3.62	62.40
Lampadena speculigera	0.00	1.05	2.24	-	3.44	65.84
Pseudoscopelus astronesthidens	0.00	1.05	2.24	-	3.44	69.27

Melanostomias bartonbeani	0.00	1.05	2.24	-	3.44	72.71

Groups d & e
Average dissimilarity = 73.09

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.00	2.36	6.01	5.79	8.22	8.22
Maurolicus muelleri	1.84	0.00	4.54	3.29	6.21	14.44
Diplospinosus multistriata	0.00	1.63	4.13	6.13	5.65	20.09
Ceratoscopelus maderensis	0.00	1.58	4.01	9.37	5.49	25.58
Benthosema glaciale	2.23	0.82	3.79	1.29	5.19	30.76
Notoscopelus kroyeri	1.46	0.00	3.76	2.46	5.15	35.91
Squaliolus laticaudus	0.00	1.29	3.29	7.86	4.50	40.41
Benthodesmus elongatus	0.67	1.57	2.91	2.21	3.98	44.38
Lampanyctus alatus	0.00	1.13	2.87	7.60	3.92	48.30
Lobianchia gemellari	0.27	1.35	2.81	1.96	3.84	52.14
Myctophum punctatum	1.02	0.00	2.47	1.55	3.38	55.52
Argyropelecus aculateus	0.00	0.85	2.10	0.93	2.88	58.40
Arctozenus risso	1.08	1.54	1.89	1.46	2.58	60.98
Nemichthys scolopaceus	0.57	0.67	1.73	1.02	2.37	63.35
Diaphus rafinesquii	0.00	0.69	1.70	0.93	2.33	65.68
Notoscopelus bolini	0.91	1.29	1.61	1.43	2.20	67.88
Malacosteus niger	0.00	0.61	1.58	0.93	2.16	70.04

Groups g & e
Average dissimilarity = 62.20

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Myctophum punctatum	2.11	0.00	4.20	22.67	6.76	6.76
Sigmops elongatum	0.58	2.36	3.63	2.18	5.84	12.60
Notoscopelus kroyeri	1.77	0.00	3.55	7.97	5.70	18.30
Diplospinosus multistriata	0.00	1.63	3.25	7.17	5.23	23.52
Arctozenus risso	0.00	1.54	3.07	13.20	4.94	28.46
Squaliolus laticaudus	0.00	1.29	2.59	11.12	4.16	32.62
Argyropelecus hemigymnus	1.74	0.52	2.50	1.32	4.01	36.64
Lampanyctus alatus	0.00	1.13	2.26	9.34	3.63	40.27
Argyropelecus aculateus	1.64	0.85	2.03	1.19	3.27	43.53
Diaphus rafinesquii	1.60	0.69	1.84	1.13	2.95	46.48
Bathophilus vaillanti	0.90	0.00	1.79	9.44	2.87	49.35
Electrona risso	0.87	0.00	1.73	13.36	2.79	52.14
Sternoptyx diaphana	0.85	0.00	1.72	3.55	2.77	54.91
Diaphus effulgens	0.84	0.62	1.65	1.10	2.66	57.57
Benthosema glaciale	0.79	0.82	1.63	0.89	2.62	60.18
Benthodesmus elongatus	0.87	1.57	1.40	5.31	2.24	62.43
Hygophum benoiti	0.65	0.00	1.37	0.87	2.20	64.62
Nemichthys scolopaceus	0.73	0.67	1.34	7.94	2.16	66.78
Malacosteus niger	0.00	0.61	1.24	0.86	1.99	68.77
Notoscopelus bolini	1.84	1.29	1.10	1.68	1.77	70.54

Groups f & e
Average dissimilarity = 55.83

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Myctophum punctatum	2.06	0.00	4.05	7.69	7.26	7.26
Notoscopelus kroyeri	2.06	0.00	4.04	7.96	7.24	14.50

Diplospinosus multistriata	0.00	1.63	3.19	7.46	5.71	20.21
Sigmops elongatum	0.75	2.36	3.18	4.39	5.70	25.91
Squaliolus laticaudus	0.00	1.29	2.54	12.25	4.55	30.46
Benthosema glaciale	2.06	0.82	2.48	1.28	4.44	34.89
Lampanyctus alatus	0.00	1.13	2.22	9.91	3.97	38.86
Stomias boa ferox	1.41	0.52	1.82	1.29	3.25	42.12
Serrivomer beani	0.91	0.00	1.71	0.87	3.07	45.19
Argyropelecus aculateus	0.95	0.85	1.67	6.21	2.99	48.17
Gonostoma atlanticum	0.84	0.00	1.65	4.70	2.96	51.14
Benthodesmus elongatus	0.74	1.57	1.62	6.48	2.91	54.05
Argyropelecus hemigymnus	1.32	0.52	1.62	1.17	2.91	56.95
Diaphus rafinesquii	1.41	0.69	1.61	1.10	2.89	59.85
Nemichthys scolopaceus	1.20	0.67	1.50	1.42	2.69	62.53
Ceratoscopelus maderensis	0.86	1.58	1.40	5.05	2.51	65.04
Electrona risso	0.68	0.00	1.33	35.76	2.38	67.42
Diaphus effulgens	0.91	0.62	1.23	1.82	2.20	69.62
Malacosteus niger	0.00	0.61	1.21	0.86	2.18	71.80

Groups b & e
Average dissimilarity = 84.06

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Notoscopelus kroyeri	2.00	0.00	5.40	4.69	6.42	6.42
Myctophum punctatum	1.83	0.00	4.91	6.54	5.84	12.26
Chauliodus sloani	0.00	1.78	4.80	19.33	5.71	17.98
Diplospinosus multistriata	0.00	1.63	4.39	7.39	5.22	23.20
Ceratoscopelus maderensis	0.00	1.58	4.26	45.92	5.07	28.27
Sigmops elongatum	0.78	2.36	4.25	1.70	5.06	33.33
Benthodesmus elongatus	0.00	1.57	4.23	15.08	5.04	38.37
Arctozenus risso	0.00	1.54	4.15	21.92	4.94	43.30
Lobianchia gemellari	0.00	1.35	3.63	8.42	4.32	47.63
Nemichthys scolopaceus	2.00	0.67	3.54	1.55	4.21	51.83
Squaliolus laticaudus	0.00	1.29	3.49	12.75	4.16	55.99
Notoscopelus bolini	0.00	1.29	3.47	4.69	4.12	60.12
Argyropelecus aculateus	1.25	0.85	3.34	1.13	3.97	64.09
Lampanyctus alatus	0.00	1.13	3.05	11.79	3.62	67.71
Stomias boa ferox	1.10	0.52	3.00	1.18	3.57	71.28

Groups j & e
Average dissimilarity = 56.05

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	2.06	0.00	3.45	7.25	6.16	6.16
Myctophum punctatum	1.19	0.00	1.98	27.28	3.53	9.70
Notoscopelus kroyeri	1.13	0.00	1.91	2.26	3.40	13.10
Lampanyctus alatus	0.00	1.13	1.89	9.83	3.37	16.46
Benthosema glaciale	1.67	0.82	1.86	1.44	3.32	19.79
Diplospinosus multistriata	0.50	1.63	1.85	1.94	3.29	23.08
Ceratoscopelus maderensis	0.47	1.58	1.83	2.20	3.27	26.35
Stomias boa ferox	1.52	0.52	1.74	1.30	3.10	29.45
Lampadena speculigera	0.97	0.00	1.60	3.71	2.86	32.31
Squaliolus laticaudus	0.36	1.29	1.55	2.43	2.76	35.07
Melanostomias bartonbeani	0.90	0.00	1.51	11.52	2.69	37.76
Astronectes gemmifer	0.87	0.00	1.46	4.45	2.60	40.36
Argyropelecus aculateus	0.95	0.85	1.42	2.87	2.53	42.90

Sigmops elongatum	1.57	2.36	1.34	2.34	2.39	45.28
Evermannella balbo	0.79	0.00	1.31	13.24	2.34	47.63
Diaphus effulgens	1.24	0.62	1.23	1.14	2.19	49.82
Benthodesmus elongatus	0.83	1.57	1.23	4.59	2.19	52.01
Synaphobranchus kaupi	0.72	0.00	1.20	31.18	2.15	54.15
Diretmus argenteus	0.72	0.00	1.20	31.18	2.15	56.30
Dolicholagus longirostris	0.72	0.00	1.20	31.18	2.15	58.45
Maurolicus muelleri	0.72	0.00	1.20	31.18	2.15	60.59
Astronectes niger	0.72	0.00	1.20	31.18	2.15	62.74
Diaphus rafinesquii	0.55	0.69	1.14	1.04	2.04	64.78
Nemichthys scolopaceus	1.17	0.67	1.11	1.15	1.98	66.76
Gonostoma denudatum	0.62	0.00	1.07	0.87	1.90	68.66
Malacosteus niger	0.99	0.61	1.01	1.32	1.80	70.46

Groups c & e
Average dissimilarity = 71.97

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.57	2.36	4.51	1.95	6.26	6.26
Serrivomer beani	1.67	0.00	4.12	3.83	5.72	11.98
Diplospinosus multistriata	0.00	1.63	3.98	6.71	5.53	17.51
Stomias boa ferox	1.68	0.52	3.35	1.67	4.65	22.17
Ceratoscopelus maderensis	0.22	1.58	3.33	2.81	4.63	26.80
Benthodesmus elongatus	0.22	1.57	3.31	2.73	4.59	31.39
Lobianchia gemellari	0.00	1.35	3.29	7.31	4.58	35.97
Squaliolus laticaudus	0.00	1.29	3.17	9.06	4.40	40.38
Myctophum punctatum	1.21	0.00	2.90	1.61	4.02	44.40
Nemichthys scolopaceus	1.82	0.67	2.83	1.33	3.93	48.33
Lampanyctus alatus	0.00	1.13	2.76	8.57	3.84	52.17
Benthosema glaciale	0.99	0.82	2.27	1.14	3.15	55.32
Notoscopelus bolini	0.47	1.29	2.13	1.53	2.97	58.28
Argyropelecus aculateus	0.00	0.85	2.03	0.94	2.82	61.10
Notoscopelus kroyeri	0.72	0.00	1.66	1.14	2.30	63.40
Diaphus rafinesquii	0.00	0.69	1.64	0.94	2.28	65.69
Arctozenus risso	1.09	1.54	1.62	1.08	2.24	67.93
Malacosteus niger	0.25	0.61	1.52	0.95	2.11	70.04

Groups a & e
Average dissimilarity = 66.29

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chauliodus sloani	0.00	1.78	4.50	16.47	6.79	6.79
Benthodesmus elongatus	0.00	1.57	3.97	12.55	5.99	12.78
Arctozenus risso	0.00	1.54	3.89	19.05	5.87	18.65
Macroparalepis affinis	1.46	0.00	3.69	30.04	5.57	24.22
Lobianchia gemellari	0.00	1.35	3.41	7.08	5.14	29.36
Squaliolus laticaudus	0.00	1.29	3.28	11.03	4.94	34.31
Notoscopelus bolini	0.00	1.29	3.25	3.81	4.91	39.21
Nemichthys scolopaceus	1.87	0.67	2.97	1.29	4.49	43.70
Lampanyctus alatus	0.00	1.13	2.86	9.69	4.31	48.01
Notoscopelus kroyeri	1.11	0.00	2.81	30.04	4.23	52.24
Bathylagus euryops	1.11	0.00	2.81	30.04	4.23	56.48
Dolicholagus longirostris	1.11	0.00	2.81	30.04	4.23	60.71
Benthosema glaciale	1.57	0.82	2.11	0.77	3.19	63.89
Argyropelecus aculateus	0.00	0.85	2.10	0.71	3.16	67.06

Malacosteus niger	1.32	0.61	1.76	0.83	2.66	69.71
Diaphus rafinesquii	0.00	0.69	1.70	0.71	2.56	72.27

Groups h & e
Average dissimilarity = 59.74

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chiasmodon niger	1.85	0.00	3.22	43.59	5.40	5.40
Notoscopelus kroyeri	1.80	0.00	3.14	43.59	5.25	10.64
Diplospinosus multistriata	0.00	1.63	2.84	6.60	4.75	15.39
Stomias boa ferox	2.06	0.52	2.69	1.99	4.50	19.89
Synaphobranchus kaupi	1.39	0.00	2.42	43.59	4.04	23.93
Lobianchia gemellari	0.00	1.35	2.35	7.64	3.93	27.86
Serrivomer beani	1.33	0.00	2.31	43.59	3.86	31.72
Squaliolus laticaudus	0.00	1.29	2.26	12.44	3.78	35.50
Notoscopelus bolini	0.00	1.29	2.24	3.67	3.76	39.26
Lampanyctus alatus	0.00	1.13	1.97	8.81	3.30	42.56
Sigmops elongatum	1.25	2.36	1.94	3.02	3.25	45.80
Macroparalepis affinis	1.05	0.00	1.84	43.59	3.07	48.88
Lampadena speculigera	1.05	0.00	1.84	43.59	3.07	51.95
Pseudoscopelus astronesthidens	1.05	0.00	1.84	43.59	3.07	55.02
Melanostomias bartonbeani	1.05	0.00	1.84	43.59	3.07	58.10
Scopelosaurus lepidus	1.49	0.51	1.69	1.38	2.83	60.93
Nessorhamphus ingolfianus	0.89	0.00	1.54	43.59	2.58	63.51
Evermannella balbo	0.89	0.00	1.54	43.59	2.58	66.09
Myctophum punctatum	0.89	0.00	1.54	43.59	2.58	68.68
Howella sherborni	0.89	0.00	1.54	43.59	2.58	71.26

Groups d & i
Average dissimilarity = 68.22

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Sigmops elongatum	0.00	1.88	3.60	12.29	5.27	5.27
Maurolicus muelleri	1.84	0.00	3.45	3.17	5.05	10.32
Lobianchia gemellari	0.27	1.95	3.25	2.98	4.77	15.10
Lampadena atlantica	0.00	1.50	2.87	5.39	4.21	19.30
Diaphus effulgens	0.21	1.67	2.82	3.31	4.14	23.44
Stomias boa ferox	0.00	1.31	2.51	3.54	3.67	27.12
Howella sherborni	0.00	1.26	2.42	11.97	3.54	30.66
Nannobrachium atrum	0.00	1.13	2.16	11.74	3.17	33.83
Bathylagus euryops	0.00	1.10	2.11	11.51	3.09	36.92
Gonostoma denudatum	0.00	1.10	2.10	3.89	3.08	40.00
Scopelosaurus lepidus	0.00	1.05	2.01	9.36	2.94	42.94
Diaphus rafinesquii	0.00	1.05	2.00	4.59	2.93	45.87
Benthosema glaciale	2.23	1.26	1.89	1.28	2.78	48.65
Argyropelecus aculateus	0.00	0.96	1.83	6.87	2.68	51.33
Pseudoscopelus astronesthidens	0.00	0.92	1.77	5.39	2.59	53.92
Nansenia oblita	0.00	0.89	1.70	10.74	2.49	56.41
Astronectes gemmifer	0.00	0.89	1.69	3.44	2.48	58.89
Benthodesmus elongatus	0.67	1.07	1.68	3.27	2.46	61.35
Myctophum punctatum	1.02	0.87	1.66	1.26	2.44	63.79
Synaphobranchus kaupi	0.00	0.85	1.62	5.36	2.37	66.17
Malacosteus niger	0.00	0.85	1.62	5.36	2.37	68.54

Arctozenus risso	1.08	1.74	1.49	1.12	2.18	70.72

Groups g & i
Average dissimilarity = 55.33

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Arctozenus risso	0.00	1.74	2.77	11.32	5.00	5.00
Sigmops elongatum	0.58	1.88	2.11	1.82	3.81	8.82
Stomias boa ferox	0.00	1.31	2.08	3.38	3.77	12.58
Howella sherborni	0.00	1.26	2.01	19.09	3.63	16.22
Myctophum punctatum	2.11	0.87	1.97	1.23	3.56	19.77
Nannobrachium atrum	0.00	1.13	1.80	18.09	3.25	23.03
Bathylagus euryops	0.00	1.10	1.75	17.13	3.17	26.19
Gonostoma denudatum	0.00	1.10	1.75	3.74	3.16	29.35
Lampadena atlantica	0.45	1.50	1.70	1.69	3.07	32.42
Scopelosaurus lepidus	0.00	1.05	1.67	11.27	3.01	35.44
Pseudoscopelus astronesthidens	0.00	0.92	1.47	5.37	2.65	38.09
Bathophilus vaillanti	0.90	0.00	1.42	8.66	2.57	40.67
Nansenia oblita	0.00	0.89	1.41	14.56	2.55	43.22
Astronectes gemmifer	0.00	0.89	1.41	3.28	2.55	45.77
Diaphus effulgens	0.84	1.67	1.39	0.88	2.51	48.28
Sternoptyx diaphana	0.85	0.00	1.37	3.70	2.47	50.75
Synaphobranchus kaupi	0.00	0.85	1.35	5.34	2.43	53.18
Malacosteus niger	0.00	0.85	1.35	5.34	2.43	55.62
Notoscopelus bolini	1.84	1.00	1.33	9.43	2.40	58.02
Benthosema glaciale	0.79	1.26	1.29	1.31	2.32	60.34
Argyropelecus hemigymnus	1.74	0.97	1.26	1.17	2.27	62.62
Ceratoscopelus maderensis	1.12	0.36	1.21	1.81	2.19	64.80
Chiasmodon niger	0.00	0.75	1.20	6.42	2.16	66.97
Argyropelecus aculateus	1.64	0.96	1.10	1.50	1.99	68.96
Serrivomer beani	0.00	0.68	1.09	14.77	1.97	70.93

Groups f & i
Average dissimilarity = 45.92

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lampadena atlantica	0.00	1.50	2.35	5.44	5.13	5.13
Myctophum punctatum	2.06	0.87	1.88	1.17	4.09	9.22
Sigmops elongatum	0.75	1.88	1.78	6.92	3.88	13.09
Nannobrachium atrum	0.00	1.13	1.77	21.31	3.86	16.96
Bathylagus euryops	0.00	1.10	1.73	19.77	3.76	20.71
Gonostoma denudatum	0.00	1.10	1.72	3.76	3.75	24.47
Scopelosaurus lepidus	0.00	1.05	1.64	11.94	3.58	28.04
Pseudoscopelus astronesthidens	0.00	0.92	1.45	5.44	3.15	31.20
Howella sherborni	0.36	1.26	1.43	2.05	3.13	34.32
Serrivomer beani	0.91	0.68	1.41	3.93	3.08	37.40
Nansenia oblita	0.00	0.89	1.39	16.08	3.03	40.43
Astronectes gemmifer	0.00	0.89	1.39	3.30	3.02	43.46
Malacosteus niger	0.00	0.85	1.33	5.40	2.89	46.35
Gonostoma atlanticum	0.84	0.00	1.32	4.93	2.88	49.22
Lobianchia gemellari	1.12	1.95	1.30	19.95	2.82	52.05
Benthosema glaciale	2.06	1.26	1.26	2.94	2.75	54.80
Nemichthys scolopaceus	1.20	0.42	1.20	1.24	2.61	57.41

Diaphus effulgens	0.91	1.67	1.19	31.22	2.59	60.00
Chiasmodon niger	0.00	0.75	1.18	6.54	2.57	62.57
Regelecus glesne	0.00	0.68	1.07	16.37	2.34	64.91
Lampanyctus alatus	0.00	0.66	1.03	0.87	2.24	67.14
Lampanyctus macdonaldi	0.59	0.00	0.90	0.87	1.96	69.10
Synaphobranchus kaupi	0.30	0.85	0.87	1.39	1.89	71.00

Groups b & i
Average dissimilarity = 73.76

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lobianchia gemellari	0.00	1.95	3.91	44.69	5.30	5.30
Arctozenus risso	0.00	1.74	3.49	13.09	4.73	10.03
Nemichthys scolopaceus	2.00	0.42	3.16	2.48	4.28	14.32
Chauliodus sloani	0.00	1.54	3.08	11.06	4.18	18.50
Lampadena atlantica	0.00	1.50	3.01	5.53	4.08	22.58
Howella sherborni	0.00	1.26	2.53	35.22	3.43	26.02
Benthosema glaciale	0.00	1.26	2.52	5.66	3.42	29.43
Argyropelecus aculateus	1.25	0.96	2.49	3.68	3.37	32.81
Nannobrachium atrum	0.00	1.13	2.27	29.73	3.08	35.88
Bathylagus euryops	0.00	1.10	2.21	26.10	2.99	38.88
Gonostoma denudatum	0.00	1.10	2.20	3.80	2.99	41.87
Stomias boa ferox	1.10	1.31	2.20	2.47	2.98	44.85
Sigmops elongatum	0.78	1.88	2.19	1.24	2.97	47.82
Benthodesmus elongatus	0.00	1.07	2.15	14.47	2.92	50.74
Scopelosaurus lepidus	0.00	1.05	2.10	12.96	2.85	53.59
Diaphus rafinesquii	0.00	1.05	2.10	4.58	2.85	56.43
Myctophum punctatum	1.83	0.87	2.09	1.13	2.84	59.27
Maurolicus muelleri	1.05	0.00	2.07	0.87	2.81	62.08
Notoscopelus bolini	0.00	1.00	2.01	13.48	2.73	64.81
Diaphus effulgens	0.70	1.67	1.95	1.18	2.65	67.45
Pseudoscopelus astronesthidens	0.00	0.92	1.85	5.53	2.51	69.96
Nansenia oblita	0.00	0.89	1.78	18.99	2.41	72.38

Groups j & i
Average dissimilarity = 43.78

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Serrivomer beani	2.06	0.68	1.90	5.58	4.34	4.34
Lampadena atlantica	0.36	1.50	1.58	2.16	3.61	7.95
Nannobrachium atrum	0.00	1.13	1.56	22.37	3.56	11.51
Bathylagus euryops	0.00	1.10	1.52	20.58	3.46	14.97
Scopelosaurus lepidus	0.00	1.05	1.44	12.13	3.30	18.27
Lampadena speculigera	0.97	0.00	1.32	3.63	3.02	21.29
Pseudoscopelus astronesthidens	0.00	0.92	1.27	5.46	2.90	24.20
Nansenia oblita	0.00	0.89	1.22	16.50	2.79	26.99
Myctophum punctatum	1.19	0.87	1.19	2.30	2.73	29.71
Lobianchia gemellari	1.10	1.95	1.18	2.64	2.69	32.40
Evermannella balbo	0.79	0.00	1.08	12.43	2.48	34.88
Chiasmodon niger	0.00	0.75	1.04	6.57	2.36	37.24
Nemichthys scolopaceus	1.17	0.42	1.02	1.43	2.32	39.56
Diretmus argenteus	0.72	0.00	0.99	51.34	2.26	41.83
Maurolicus muelleri	0.72	0.00	0.99	51.34	2.26	44.09

Astronectes niger	0.72	0.00	0.99	51.34	2.26	46.36
Howella sherborni	0.59	1.26	0.95	0.97	2.16	48.52
Regelecus glesne	0.00	0.68	0.94	16.84	2.15	50.67
Gonostoma denudatum	0.62	1.10	0.91	1.27	2.08	52.75
Lampanyctus alatus	0.00	0.66	0.90	0.87	2.06	54.81
Diaphus rafinesquii	0.55	1.05	0.87	1.18	1.99	56.81
Notoscopelus kroyeri	1.13	1.77	0.86	1.43	1.97	58.78
Argyropelecus hemigymnus	0.36	0.97	0.84	1.34	1.92	60.70
Chauliodus sloani	1.93	1.54	0.80	1.19	1.83	62.53
Stomias boa ferox	1.52	1.31	0.79	1.31	1.81	64.34
Lampanyctus macdonaldi	0.59	0.00	0.79	0.87	1.81	66.15
Arctozenus risso	1.16	1.74	0.79	3.05	1.80	67.95
Benthosema glaciale	1.67	1.26	0.79	1.21	1.80	69.75
Electrona risso	0.00	0.53	0.73	0.87	1.68	71.43

Groups c & i
Average dissimilarity = 67.20

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lobianchia gemellari	0.00	1.95	3.63	14.76	5.40	5.40
Diaphus effulgens	0.00	1.67	3.10	15.12	4.61	10.01
Lampadena atlantica	0.00	1.50	2.80	5.63	4.16	14.17
Nemichthys scolopaceus	1.82	0.42	2.63	2.05	3.92	18.09
Sigmops elongatum	0.57	1.88	2.50	1.60	3.72	21.81
Howella sherborni	0.00	1.26	2.35	14.36	3.50	25.31
Nannobrachium atrum	0.00	1.13	2.11	13.98	3.13	28.44
Gonostoma denudatum	0.00	1.10	2.05	4.01	3.04	31.49
Notoscopelus kroyeri	0.72	1.77	2.01	1.56	2.99	34.47
Scopelosaurus lepidus	0.00	1.05	1.95	10.46	2.90	37.38
Diaphus rafinesquii	0.00	1.05	1.95	4.76	2.90	40.28
Serrivomer beani	1.67	0.68	1.85	2.58	2.76	43.03
Argyropelecus aculateus	0.00	0.96	1.78	7.32	2.65	45.68
Pseudoscopelus astronesthidens	0.00	0.92	1.72	5.63	2.56	48.24
Stomias boa ferox	1.68	1.31	1.71	1.89	2.54	50.78
Bathylagus euryops	0.20	1.10	1.71	2.09	2.54	53.33
Myctophum punctatum	1.21	0.87	1.70	1.19	2.53	55.86
Nansenia oblita	0.00	0.89	1.65	12.41	2.46	58.32
Benthodesmus elongatus	0.22	1.07	1.62	2.00	2.41	60.73
Synaphobranchus kaupi	0.00	0.85	1.58	5.60	2.35	63.08
Argyropelecus hemigymnus	0.15	0.97	1.54	2.32	2.29	65.36
Benthosema glaciale	0.99	1.26	1.51	1.50	2.25	67.61
Astronectes gemmifer	0.24	0.89	1.45	2.15	2.16	69.77
Malacosteus niger	0.25	0.85	1.42	2.93	2.11	71.88

Groups a & i
Average dissimilarity = 71.76

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lobianchia gemellari	0.00	1.95	3.73	48.71	5.19	5.19
Arctozenus risso	0.00	1.74	3.33	10.89	4.64	9.83
Diaphus effulgens	0.00	1.67	3.18	186.68	4.43	14.26
Chauliodus sloani	0.00	1.54	2.94	9.16	4.10	18.36
Lampadena atlantica	0.00	1.50	2.87	4.53	4.00	22.36
Macroparalepis affinis	1.46	0.00	2.79	1300.03	3.89	26.25

Nemichthys scolopaceus	1.87	0.42	2.75	2.41	3.84	30.08
Stomias boa ferox	0.00	1.31	2.51	2.80	3.49	33.57
Howella sherborni	0.00	1.26	2.41	33.65	3.36	36.94
Nannobrachium atrum	0.00	1.13	2.16	27.05	3.01	39.95
Diplospinosus multistriata	1.11	0.00	2.12	1300.03	2.95	42.91
Gonostoma denudatum	0.00	1.10	2.10	3.10	2.93	45.83
Benthodesmus elongatus	0.00	1.07	2.05	12.09	2.86	48.69
Scopelosaurus lepidus	0.00	1.05	2.00	10.79	2.79	51.48
Diaphus rafinesquii	0.00	1.05	2.00	3.74	2.79	54.27
Notoscopelus bolini	0.00	1.00	1.92	11.22	2.67	56.94
Sigmops elongatum	2.86	1.88	1.86	29.94	2.60	59.54
Argyropelecus hemigymnus	0.00	0.97	1.84	6.65	2.57	62.11
Argyropelecus aculateus	0.00	0.96	1.83	6.24	2.55	64.66
Pseudoscopelus astronesthidens	0.00	0.92	1.76	4.53	2.46	67.12
Nansenia oblita	0.00	0.89	1.70	16.15	2.36	69.48
Astronectes gemmifer	0.00	0.89	1.69	2.71	2.36	71.84

Groups h & i
Average dissimilarity = 45.74

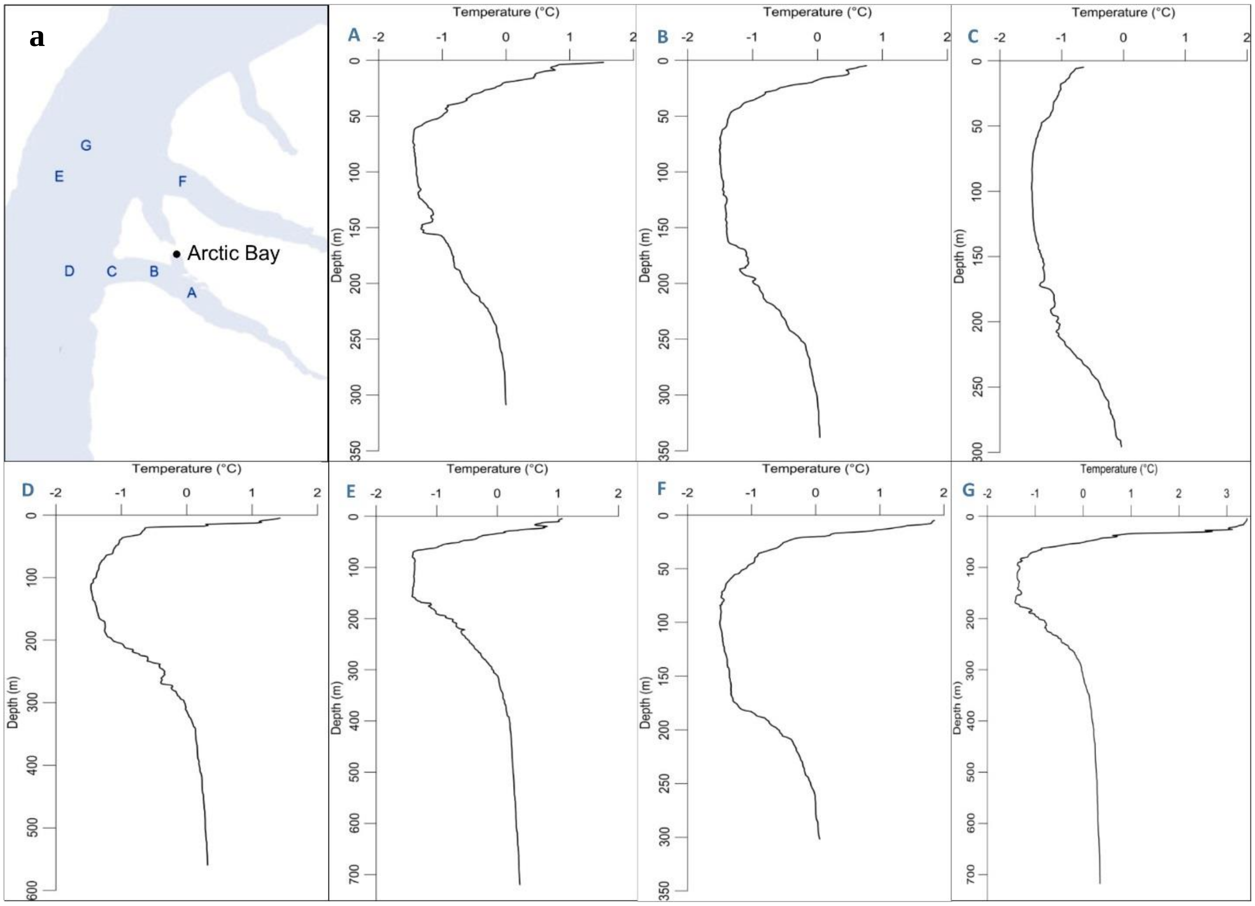
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lobianchia gemellari	0.00	1.95	2.78	49.18	6.08	6.08
Diaphus effulgens	0.00	1.67	2.37	193.76	5.19	11.26
Lampadena atlantica	0.00	1.50	2.14	4.53	4.68	15.94
Nannobrachium atrum	0.00	1.13	1.61	27.20	3.53	19.47
Bathylagus euryops	0.00	1.10	1.57	22.98	3.43	22.90
Gonostoma denudatum	0.00	1.10	1.57	3.10	3.43	26.33
Chiasmodon niger	1.85	0.75	1.56	8.08	3.42	29.75
Macroparalepis affinis	1.05	0.00	1.50	1743.33	3.28	33.03
Lampadena speculigera	1.05	0.00	1.50	1743.33	3.28	36.31
Diaphus rafinesquii	0.00	1.05	1.49	3.74	3.26	39.58
Notoscopelus bolini	0.00	1.00	1.43	11.20	3.12	42.70
Argyropelecus aculateus	0.00	0.96	1.36	6.24	2.98	45.68
Nemichthys scolopaceus	1.33	0.42	1.28	1.50	2.81	48.49
Melanonus zugmayeri	1.25	0.36	1.28	1.78	2.79	51.28
Nansenia oblita	0.00	0.89	1.27	16.10	2.77	54.05
Astronectes gemmifer	0.00	0.89	1.26	2.71	2.76	56.81
Evermannella balbo	0.89	0.00	1.26	1743.33	2.76	59.57
Eustomias filifer	0.89	0.00	1.26	1743.33	2.76	62.33
Photonectes margarita	0.89	0.00	1.26	1743.33	2.76	65.09
Myctophum punctatum	0.89	0.87	1.24	32.41	2.70	67.79
Stomias boa ferox	2.06	1.31	1.06	1.60	2.32	70.12

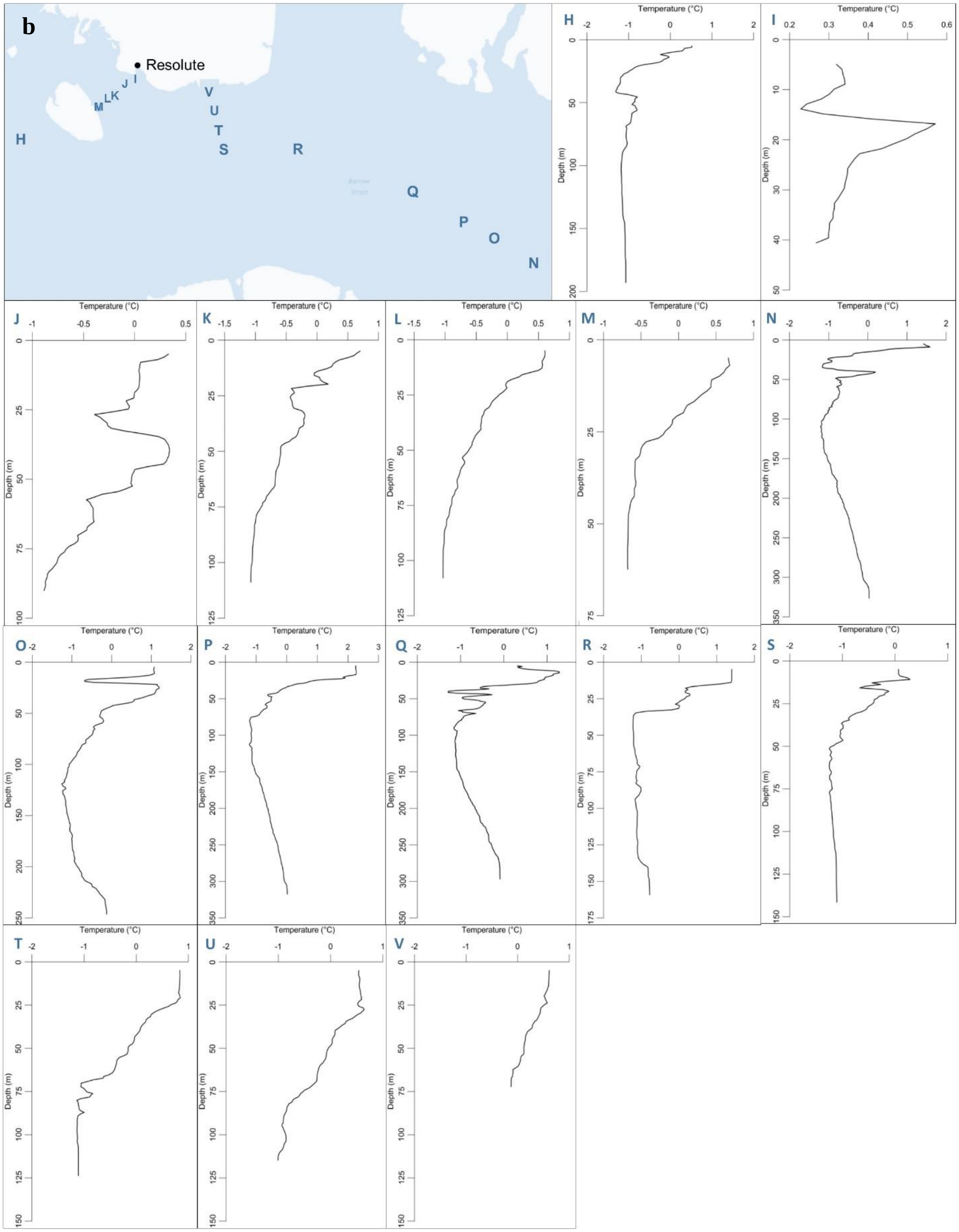
Groups e & i
Average dissimilarity = 52.05

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Notoscopelus kroyeri	0.00	1.77	2.82	37.87	5.41	5.41
Diplospinosus multistriata	1.63	0.00	2.60	8.18	4.99	10.40
Howella sherborni	0.00	1.26	2.02	33.55	3.87	14.28
Ceratoscopelus maderensis	1.58	0.36	1.95	2.96	3.76	18.03
Nannobrachium atrum	0.00	1.13	1.81	28.88	3.47	21.50
Bathylagus euryops	0.00	1.10	1.76	25.38	3.38	24.88
Gonostoma denudatum	0.00	1.10	1.76	3.79	3.37	28.25

Diaphus effulgens	0.62	1.67	1.68	1.43	3.23	31.48
Lampadena atlantica	0.51	1.50	1.57	1.55	3.01	34.49
Squaliolus laticaudus	1.29	0.36	1.50	2.24	2.88	37.37
Pseudoscopelus astronesthidens	0.00	0.92	1.47	5.53	2.83	40.20
Nansenia oblita	0.00	0.89	1.42	18.70	2.72	42.93
Astronectes gemmifer	0.00	0.89	1.41	3.32	2.72	45.65
Myctophum punctatum	0.00	0.87	1.38	0.87	2.66	48.30
Argyropelecus aculateus	0.85	0.96	1.36	4.53	2.61	50.91
Synaphobranchus kaupi	0.00	0.85	1.35	5.49	2.60	53.51
Stomias boa ferox	0.52	1.31	1.32	1.22	2.54	56.05
Benthosema glaciale	0.82	1.26	1.31	1.45	2.53	58.58
Chiasmodon niger	0.00	0.75	1.20	6.69	2.31	60.88
Diaphus rafinesquii	0.69	1.05	1.11	1.43	2.12	63.01
Serrivomer beani	0.00	0.68	1.09	19.15	2.10	65.11
Regelecus glesne	0.00	0.68	1.09	19.15	2.10	67.21
Nemichthys scolopaceus	0.67	0.42	1.08	1.18	2.08	69.28
Lampanyctus alatus	1.13	0.66	1.05	1.17	2.01	71.29

Figure A1 Maps of CTD sampling stations (see Table A1) and temperature profiles from each station within the study regions of a) Arctic Bay; b) Resolute; and c) Jones Sound.




b
Resolute
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
Barrow Strait
Temperature (°C)
Depth (m)
H -2 -1 0 1 2
I 0.2 0.3 0.4 0.5 0.6
J -1 -0.5 0 0.5
K -1.5 -1 -0.5 0 0.5 1
L -1.5 -1 -0.5 0 0.5 1
M -1 -0.5 0 0.5 1
N -2 -1 0 1 2
O -2 -1 0 1 2
P -2 -1 0 1 2 3
Q -2 -1 0 1
R -2 -1 0 1 2
S -2 -1 0 1
T -2 -1 0 1
U -2 -1 0 1
V -2 -1 0 1
0
25
50
75
100
125
150
175
200
250
300
350

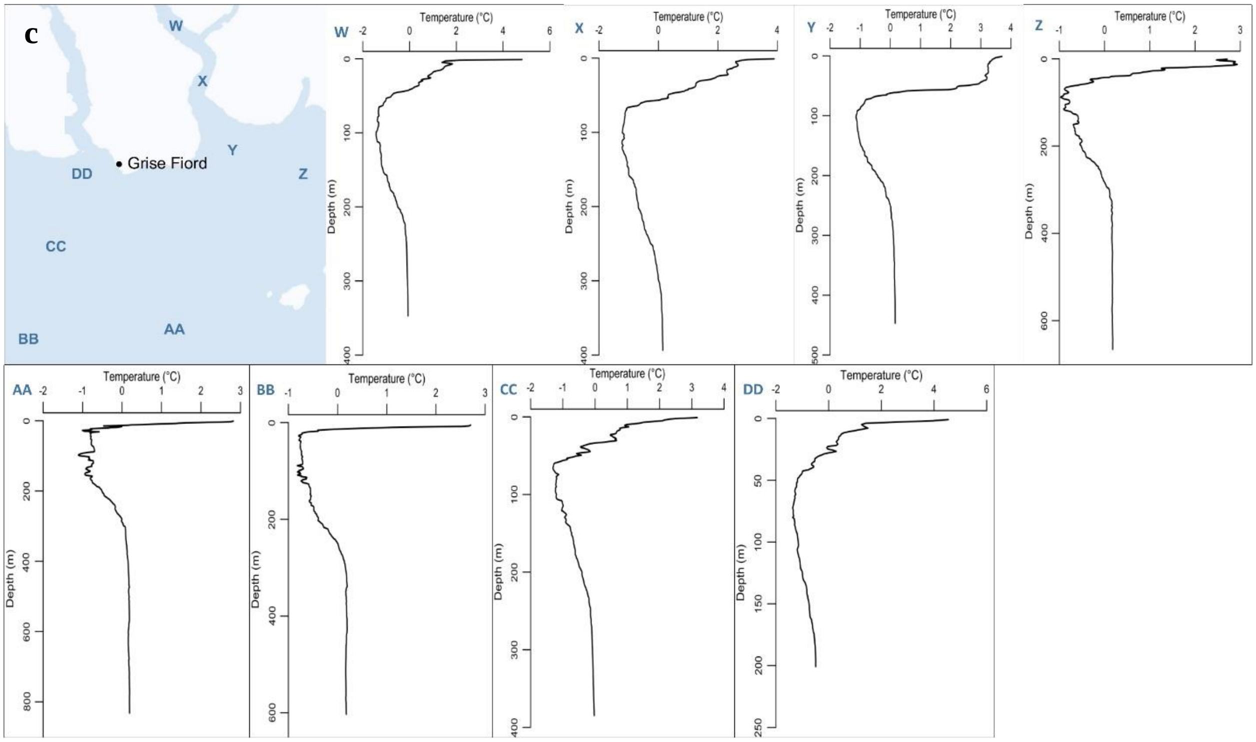

c
W
X
Y
Z
DD
CC
BB
AA
Grise Fiord
Temperature (°C)
Depth (m)
W -2 0 2 4 6
0 100 200 300 400
X -2 0 2 4
0 100 200 300 400
Y -2 -1 0 1 2 3 4
0 100 200 300 400 500
Z -1 0 1 2 3
0 200 400 600
AA -2 -1 0 1 2 3
0 200 400 600 800
BB -1 0 1 2 3
0 200 400 600
CC -2 -1 0 1 2 3 4
0 100 200 300 400
DD -2 0 2 4 6
0 50 100 150 200 250

Figure A2 Spatial distribution of physical and biological habitat types observed at each fish record for Dive R1335 on the southern Flemish Cap.

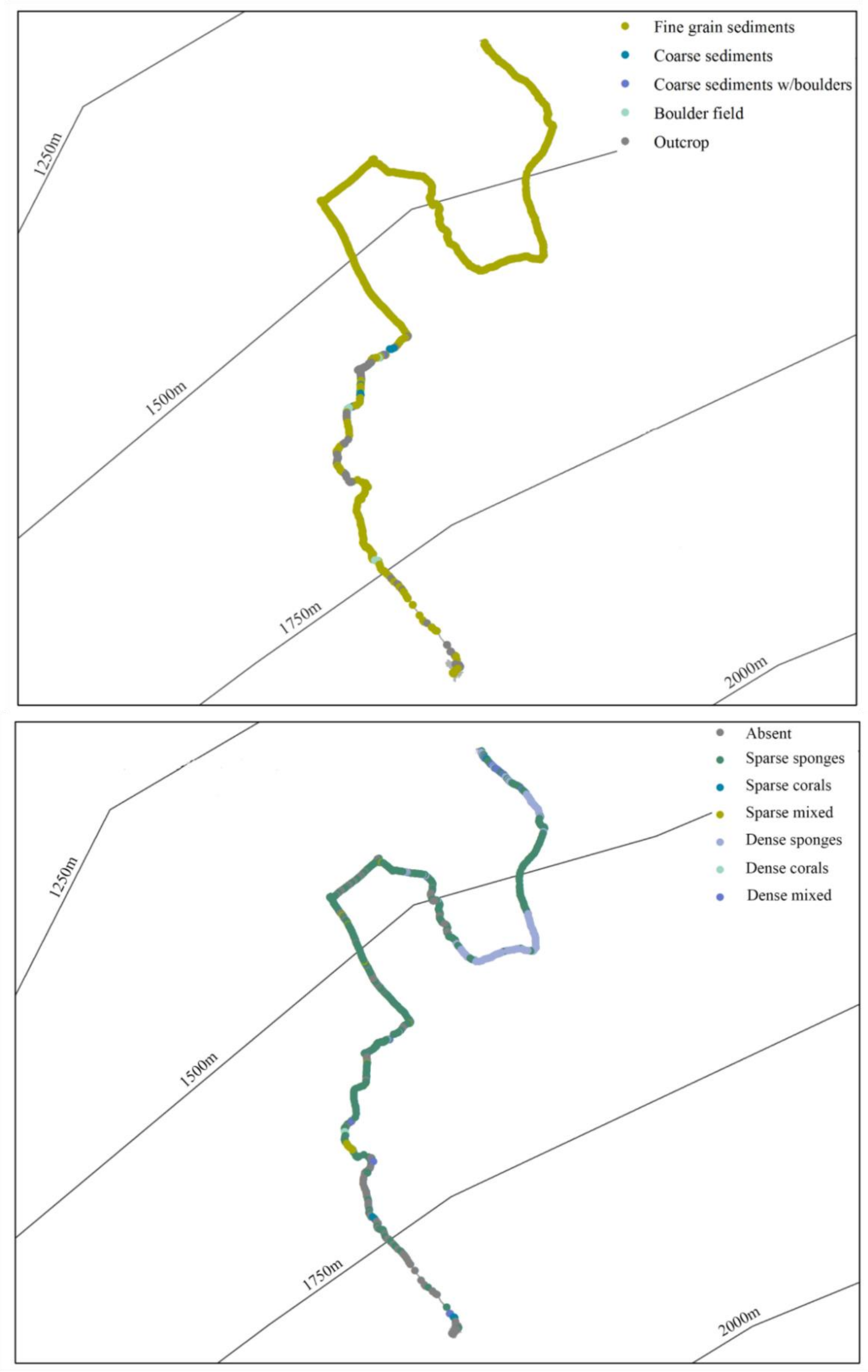


Figure A3 Spatial distribution of physical and biological habitat types observed at each fish record for Dive R1336 on the southern Flemish Cap.

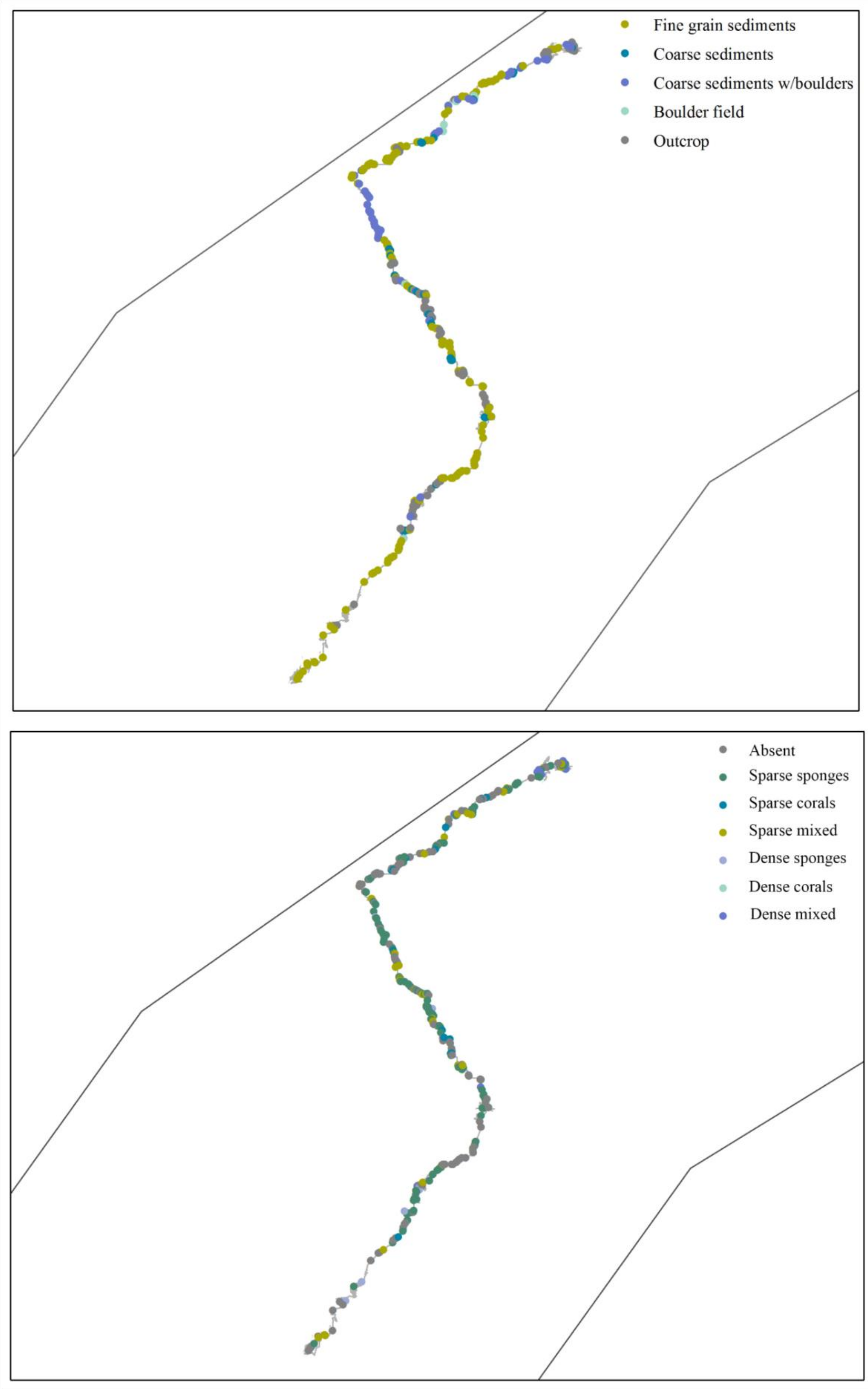


Figure A4 Spatial distribution of physical and biological habitat types observed at each fish record for Dive R1337 on the southern Flemish Cap.

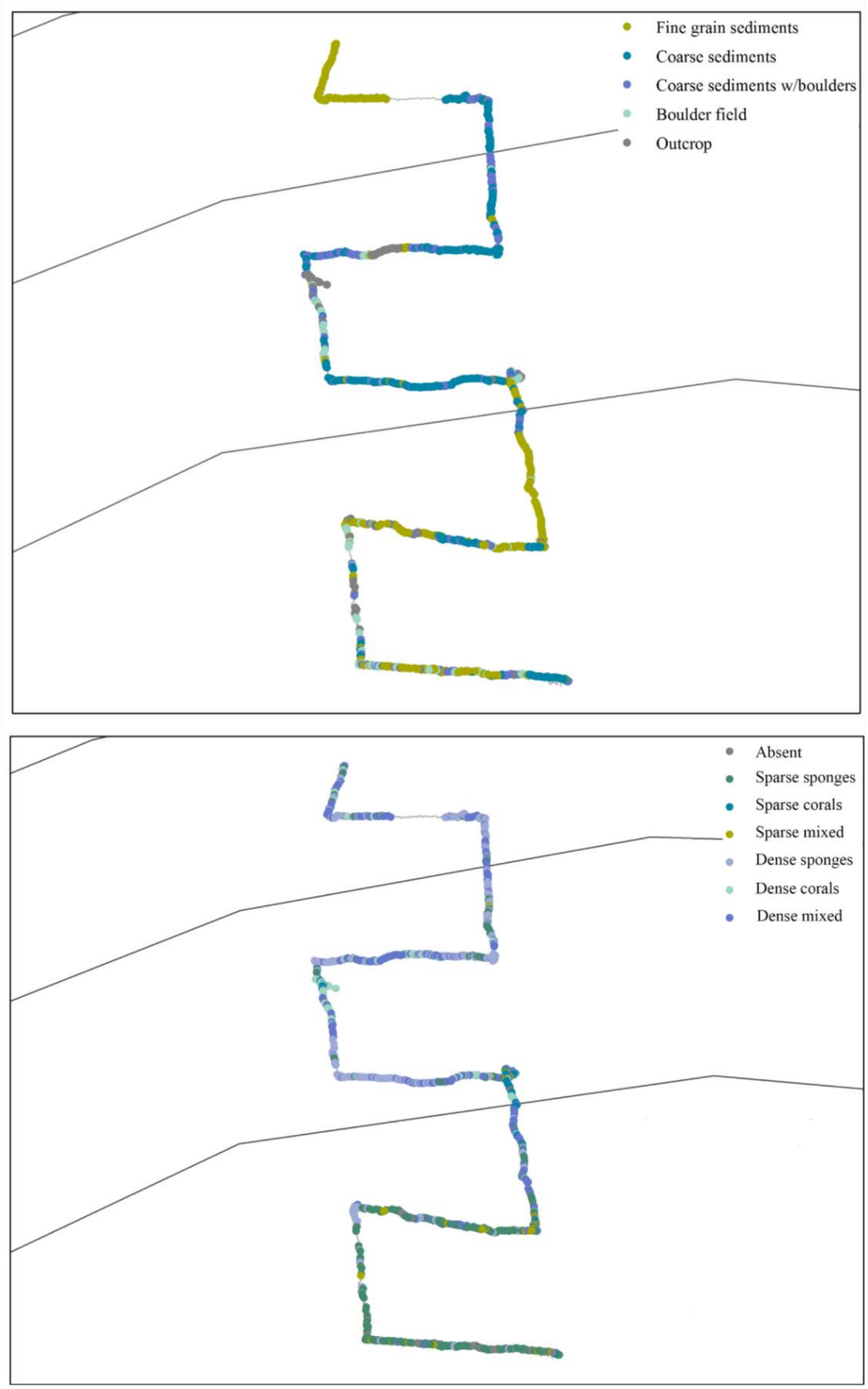


Figure A5 Spatial distribution of physical and biological habitat types observed at each fish record for Dive R1339 on the northeastern Flemish Cap.

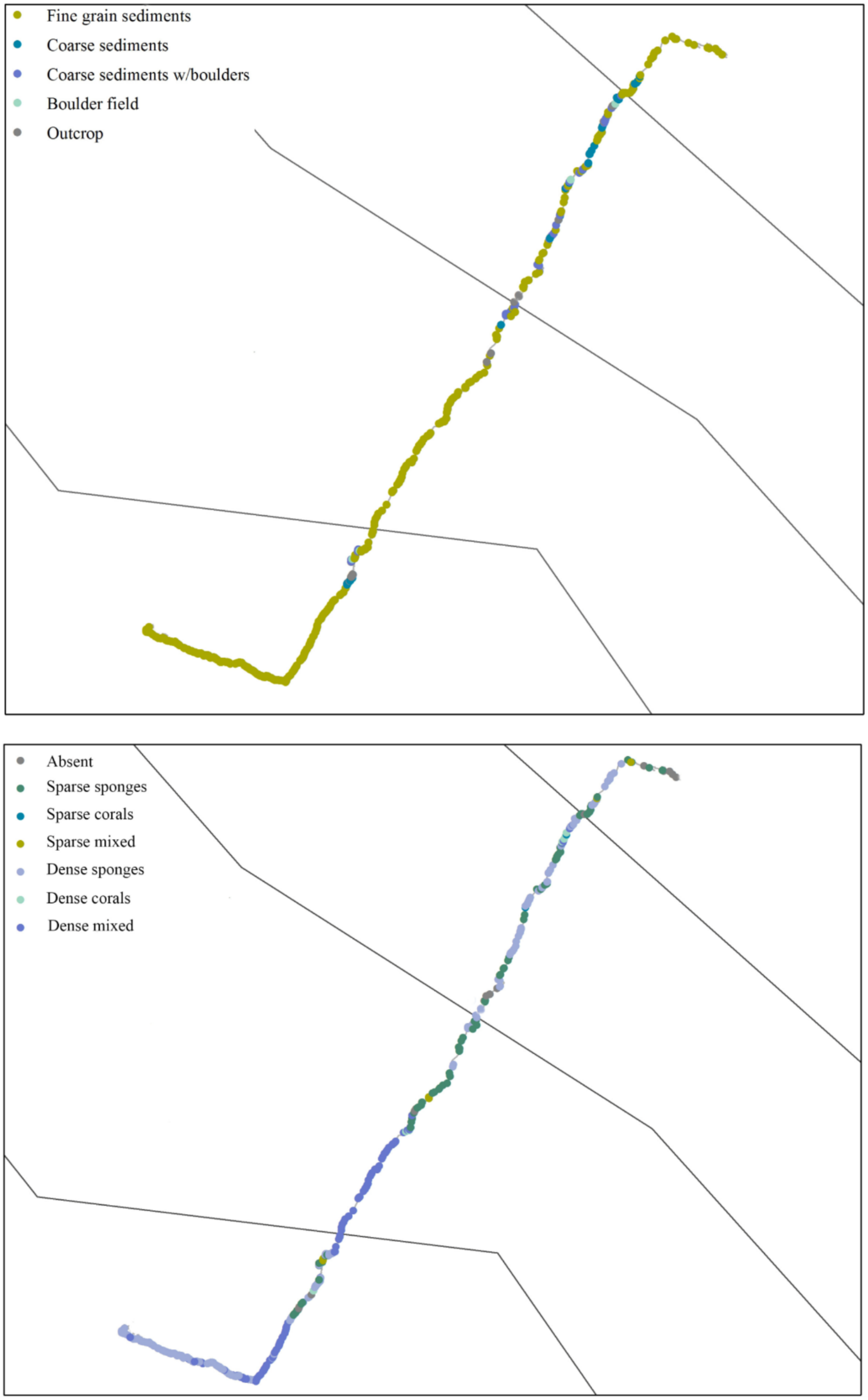
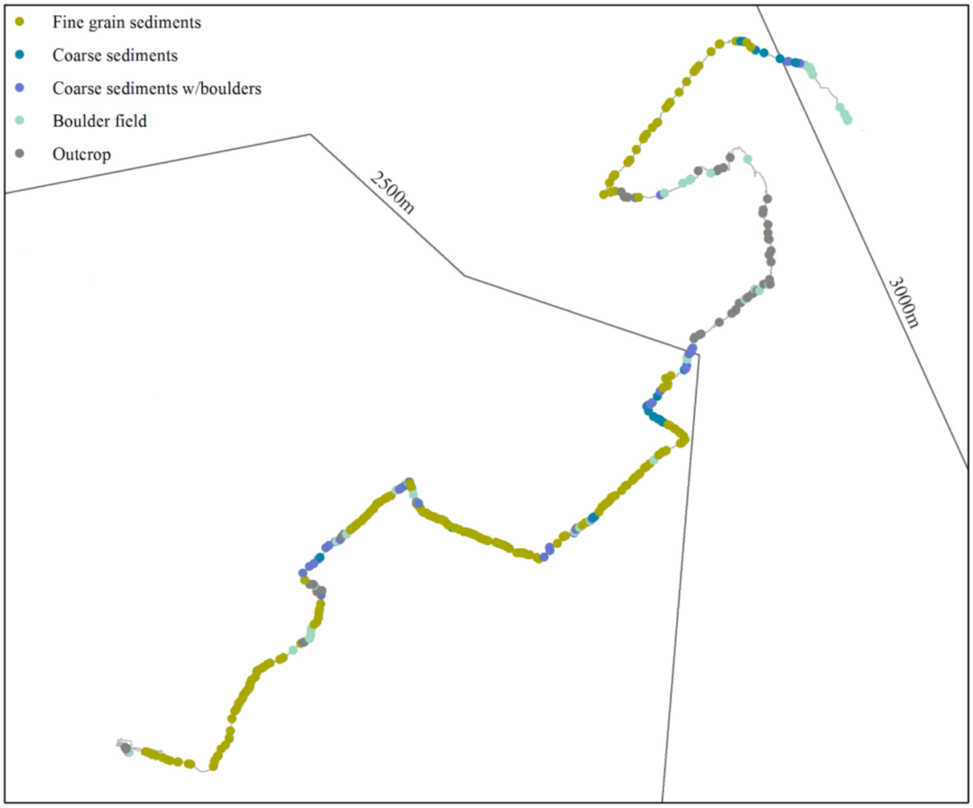


Figure A6 Spatial distribution of physical and biological habitat types observed at each fish record for Dive R1340 on the north side of the Orphan Seamount.



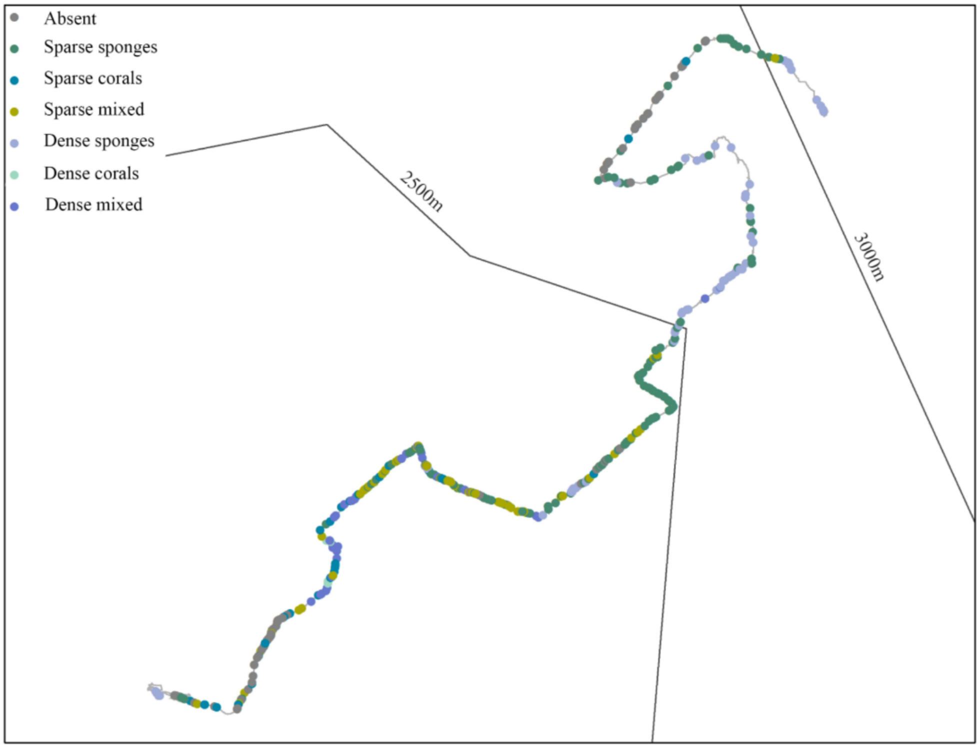


Figure A7 Representation of each biological habitat type within each physical habitat type observed throughout the ROV survey. FGS signifies ‘fine grain sediment’ and CS represents ‘coarse sediment’.

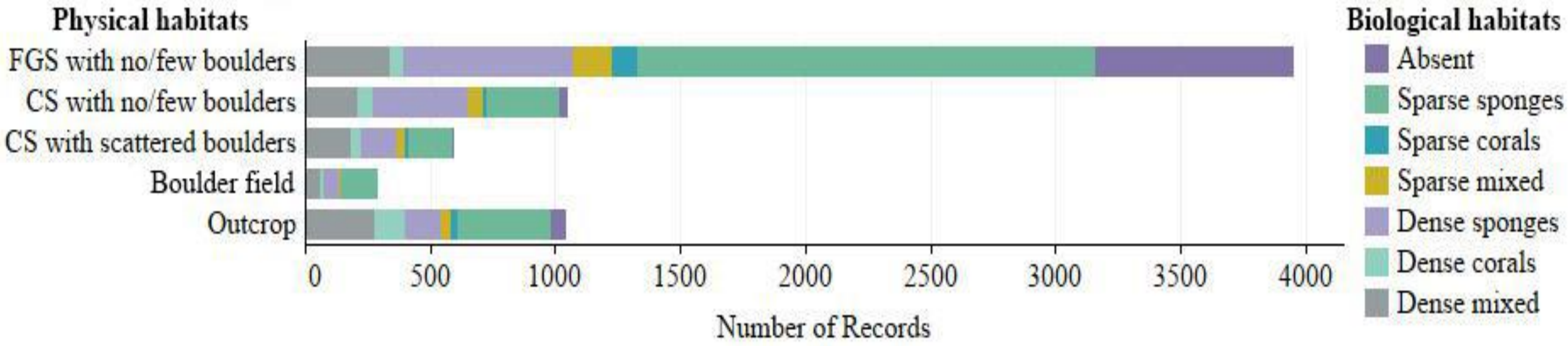


Figure A8 Photograph of the atypical long-finned morphotype of the alfonsino *Beryx decadactylus* captured in Set 19 of the 2016 survey aboard the *RV Celtic Explorer*. Specimen was 17.5 cm in total length.