SPATIAL ECOLOGY AND CONSERVATION OF DEEP-SEA FISHES AND CORALS OFF NEWFOUNDLAND AND LABRADOR, CANADA

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Spatial Ecology and Conservation of Deep-Sea Fishes and Corals off Newfoundland and Labrador, Canada

by

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Abstract

Ongoing deep-sea fisheries off Newfoundland and Labrador, Canada since the late 1960s have resulted in large population declines of both targeted and non-targeted species. The lack of *in situ* observations from deep waters in this region limit our understanding of the factors influencing distributions of vulnerable taxa such as corals and fish, and the links between them. I analyzed data from a research cruise that used a remotely operated vehicle to explore 105 km of seafloor, spanning a depth range of 351 – 2245 m, in three canyons off Newfoundland and Labrador in 2007. I observed over 160,000 coral colonies, comprising 28 species, and over 18,000 individual fishes, comprising at least 74 species. Distinct assemblages of deep-sea corals and fishes were found based on habitat type (or bottom type) and depth. *Keratoisis grayi* was more likely to be broken, dead or partially dead, and less abundant in trawled areas. Multiple factors predicted grenadier abundance and/or presence, but these varied in importance with sampling resolution. Using life table analyses, I predict prolonged recovery rates for two deep-sea fishes: *Coryphaenoides rupestris* and *Macrourus berglax*. These findings illustrate that deep-sea corals influence the distribution and abundance of fishes, that trawling negatively affects long-lived deep-sea corals in this region, that deep-sea fishes will recover slowly (if at all) from documented declines, and that many unknowns remain regarding the sustainability of this ecosystem. Nonetheless, these findings can help to support deep-sea conservation efforts off Newfoundland and Labrador.

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Abbreviations

ANOSIM – analysis of similarities

CCAMLR – Convention on the Conservation of Antarctic Marine Living Resources

COSEWIC – Committee on the Status of Endangered Wildlife in Canada

ECNASAP – East Coast North American Strategic Assessment Project

EEZ – exclusive economic zone

GLM – generalised linear model

IUCN – International Union for Conservation of Nature

MDS – multidimensional scaling

NAFO – Northwest Atlantic Fisheries Organization

RFMO – Regional Fisheries Management Organization

ROPOS – Remotely Operated Platform for Ocean Sciences

ROV – remotely operated vehicle

SARA – Species at Risk Act

SIMPER – similarity percentage

UNGA – United Nations General Assembly

VME – vulnerable marine ecosystem

Co-authorship Statement

The student's contribution to the thesis manuscripts are as follows:

- Led the initial development of research ideas
- Participant in the 2007 cruise planning
- Participant in the 2007 cruise off Nova Scotia and Newfoundland
- Led the finalization of research questions
- Led all analysis of video from the Newfoundland portion of the 2007 ROPOS cruise
- Led all planning and implementation of data analyses in all chapters
- Lead author on all papers and manuscripts

Dr. Paul Snelgrove (Memorial University) co-authored Chapters 2, 3, and 4, provided financial support and advice regarding survey design, and reviewed drafts of manuscripts. Dr. Evan Edinger (Memorial University) co-authored Chapters 2, 3, and 4, reviewed drafts of manuscripts, provided financial support and advised on survey design. Dr. Richard Haedrich (Memorial University) co-authored Chapters 2, 3, 4, 5, and 6 and provided advice regarding survey designs and data analyses. He also helped identify deep-sea fishes and reviewed drafts of the manuscripts. Dr. Kent Gilkinson (Fisheries and Oceans Canada) co-authored Chapters 2, 3, 4, and 5, reviewed drafts of manuscripts, provided advice regarding survey design, and provided financial support. All 4 of these authors were co-investigators on the 2007 cruise. David Fifield co-authored Chapters 2, 3, and 5, provided help with programming within R and Microsoft Access, reviewed manuscripts, and provided advice regarding data analyses. Vonda Wareham (Fisheries and Oceans Canada) co-authored Chapters 2, 3, and 4, provided training on deep-sea coral identification, and reviewed drafts of manuscripts. Dr. Jennifer Devine co-authored

Chapter 6 and reviewed drafts of the manuscript, participated in initial discussions about the research idea, and conducted an analysis that was added to the publication from this chapter (this analysis is not included in this thesis).

Publications Arising

This thesis is based on the following published articles and manuscripts:

Chapter 2:

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Chapter 3:

Baker KD, Snelgrove PVR, Fifield DA, Edinger EN, Wareham V, Haedrich RL, Gilkinson K (*in prep*) Small-scale patterns and the effects of trawling on the status of bamboo coral, *Keratoisis grayi,* in canyons on the Grand Banks, Newfoundland.

Chapter 4:

Baker KD, Haedrich RL, Snelgrove P, Wareham V, Edinger EN, Gilkinson K (2012) Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. Deep Sea Research I 65: 171-188.

Chapter 5:

Baker KD, Haedrich RL, Fifield DA, Gilkinson, K (2012) Grenadier abundance examined at varying spatial scales in deep waters off Newfoundland, Canada, with special focus on the influence of corals. Journal of Ichthyology 52: 678-689.

Chapter 6 [1]:

Baker KD, Devine JA, Haedrich RL (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. Environmental Biology of Fishes 85: 79-88.

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[1] This chapter was published as part of a larger article that included an additional analysis regarding population trends of deep-sea fishes in Canada's Atlantic Ocean.

1 Introduction

Once considered a vast space void of life and coined the "azoic zone" by Edward Forbes in 1843, the deep sea continues to astonish researchers and the public alike with its impressive diversity, strange new species, and remote connectedness. Although previously thought to be pristine and even untouchable, deep-sea ecosystems, like many other ecosystems on Earth, face an assortment of anthropogenic threats. But unlike most ecosystems, understanding the occurrences, ecology, and vulnerability of deep-sea fauna presents unique challenges, and as a result deep-sea science often lags far behind what is needed to adequately inform decision makers. Moreover, available scientific results are often disregarded or ignored in response to political pressures.

1.1 Deep-sea corals

Only recently have deep-sea corals received worldwide attention. The First International Symposium on Deep-sea Corals was held in Halifax, NS in 2000, and since then there have been four additional symposia hosted by institutions around the world. A search on *Web of Science* using the keyword 'deep-sea coral' identified 669 publications, with the vast majority published from 2000 onwards (Figure 1-1). This growing body of research has created a better understanding of deep-sea coral distributions, biology, ecology, and vulnerability to anthropogenic disturbances, leading Santi Roberts and Michael Hirshfield to title a 2004 paper "Deep-sea corals: out of sight, but no longer out of mind" (Roberts & Hirshfield 2004). Nevertheless, new species are regularly being discovered; it is estimated that 800 species of scleractinian species alone are still to be discovered (Cairns 1999).

Although deep-sea corals were long known to exist off Atlantic Canada, the first targeted research examining their distributions was published in 1997. Breeze et al. (1997) used ecological knowledge collected from fishers, fisheries observers, and researchers to map the approximate distribution of corals off Nova Scotia. Fisheries and Oceans Canada documented only four species off Newfoundland and Labrador between 1993 and 2000 (MacIsaac et al. 2001). Later work by Mortensen et al. (2006) identified the presence of 10 species, and Wareham and Edinger (2007) documented the occurrence of 30 species. We now know that at least 60 species of deep-sea corals occur off Newfoundland and Labrador (Fisheries and Oceans Canada, unpublished data), some extending to depths greater than 3000 m (K.D. Baker, unpublished data).

Deep-sea corals have been linked to a variety of environmental predictors, but given the large diversity of corals, sweeping generalizations regarding their distributional patterns and habitats are difficult to make (Bryan & Metaxas 2006). Many deep-sea corals require a hard substrate to attach their basal holdfast (Roberts et al. 2009). For example, large *Paragorgia arborea* colonies were found almost exclusively on boulders in the Northeast Channel off Nova Scotia (Mortensen & Buhl-Mortensen 2004). Conversely, many sea pens inhabit areas where their peduncles can anchor in soft substrate (Williams 2011).

Deep-sea corals obtain their nutrition by capturing food particles from the surrounding water. As a result, they frequently occur in areas of strong currents, and are often more abundant in areas of topographic relief, such as shelf breaks, ridges, seamounts, and rocky outcrops (Mortensen & Buhl-Mortensen 2004; Bryan & Metaxas 2007; Roberts et al. 2009). For example, *Desmophyllum dianthus* is often reported on outcrops, vertical walls, and the undersides of rock ledges (Forsterra et al. 2005; Packer et al. 2007). In a submarine canyon off Nova Scotia, *Keratoisis grayi* and *Duva florida* were associated with steep topography and semi-consolidated mudstone (Mortensen & Buhl-Mortensen 2005). *Paragorgia* spp. along the Pacific and Atlantic Continental Margins occurred in areas with steep slopes, linking their distribution to areas with low sediment deposition, hard substrate, and strong currents (Bryan & Metaxas 2006). However, Etnoyer and Morgan (2007) note that less than 1 m of relief can be sufficient to provide suitable habitat for suspension feeders such as gorgonians.

Temperature is thought to control the distribution of many deep-sea coral species (Mortensen et al. 2006; Bryan & Metaxas 2007; Roberts et al. 2009; Davies & Guinotte 2011; Waller et al. 2011), and was identified as one of the most important ecological factors influencing distributions by Roberts et al. (2009). For example, high temperatures (>10 °C) may restrict the upper depth limit of *Paragorgia arborea* off Atlantic Canada (Mortensen et al. 2006). However, the large depth range inhabited by many deep-sea corals (Etnoyer & Morgan 2005; Roberts et al. 2009), indicates that many species likely tolerate a relatively wide range of temperatures.

Previous studies link deep-sea coral distributions to a variety of other environmental characteristics including the aragonite saturation state, salinity, dissolved oxygen, and chlorophyll *a*. For example, scleractinian corals require aragonite to build their skeletons (Guinotte et al. 2006). In a global habitat suitability model for five framework-forming corals (*Enallopsammia rostrata*, *Goniocorella dumosa*, *Lophelia pertusa*, *Madrepora oculata*, and *Solenosemillia variabilis*), most distribution records coincided with waters supersaturated with aragonite (Davies & Guinotte 2011). Bryan and Metaxas (2007) modelled Paragorgiidae occurrences on the Pacific Continental Margin of North America using a combination of temperature, slope, current, and chlorophyll *a* concentration.

In general, deep-sea corals are long-lived and slow growing, and some taxonomic groups have hard and somewhat delicate skeletons. *Lophelia pertusa* reef complexes in the North Atlantic were dated to at least 4550 years old (Hall-Spencer et al. 2002), predating Stonehenge! Off Newfoundland, *Paramuricea* sp. was dated to 205 years old, *Keratoisis grayi* to 200 years old, an undescribed antipatharian to 82 years old, and *Acanella arbuscula* to 30 years old (Sherwood & Edinger 2009). Relatively slow radial and axial growth rates characterized all these species (Sherwood & Edinger 2009). Whereas some deep-sea corals have soft, flexible skeletons (Henry et al. 2003), others are relatively fragile and fracture easily. These biological characteristics of deep-sea corals make them particularly vulnerable to (and slow to recover from) anthropogenic disturbances, such as oil and gas extraction and fisheries. Here, I focus on the documented impacts of fisheries, likely the most significant current threat to coral communities off the coast of Newfoundland and Labrador.

Multiple studies document negative influences of trawling on the abundance, diversity, and health of deep-sea corals. Active trawling of seamounts off Australia reduced cover of *Solenosmilia* spp. thickets by 2 orders of magnitude and significantly increased the density of large gorgonians and black corals with broken stems, compared to seamounts that had never been trawled (Althaus et al. 2009). A study in Norwegian waters estimated that 30 - 50 % of the total area covered by *Lophelia pertusa* was damaged by fishing activities (Fossa et al. 2002). In the Gulf of Alaska, only 31 *Primnoa* spp. colonies remained in a trawl path revisited seven years after the removal of 1 ton of corals; of those remaining, five large colonies were missing 95-99 % of their branches and 80% of the polyps were missing from two smaller colonies (Krieger 2001). Although trawling is prevalent on the slopes off Newfoundland (Kulka & Pitcher 2001), no previous *in situ* research examined the impacts of this trawling on deep-sea corals.

With my collaborators, I used Fisheries and Oceans Canada scientific survey data, as well as Fisheries Observer Program data to examine the distribution and source of coral bycatch off Newfoundland and Labrador in relation to fisheries bottom gear. We found that although trawling produced significant levels of coral bycatch, all gear types (regardless of directed species) reported coral bycatch (Edinger et al. 2007). This gear included crab pots, longlines, and/or gillnets. Trawling activity was much more widespread, but longline fisheries contained the highest frequency of sets with corals (Edinger et al. 2007). Early studies documented coral bycatch and damage related to longlines off Alaska; *Primnoa* and other corals were caught on sablefish hooks in 1998 and submersible dives in the Gulf of Alaska in 1997 documented *Primnoa* colonies that had been tipped and dragged (Krieger 2001).

The significance of fishing impacts becomes increasingly apparent when examining the potential ecological importance of deep-sea corals for other taxa. Multiple studies suggest deep-sea corals create shelter, feeding habitats, surfaces for attachment, and simple structural complexity for a variety of organisms (Husebo et al. 2002; Ross & Quattrini 2007; Buhl-Mortensen et al. 2010), including fish (Baillon et al. 2012), echinoderms (Krieger & Wing 2002), polychaetes (Schembri et al. 2007; Fiege & Barnich 2009), crustaceans (Krieger & Wing 2002), and other invertebrates (Krieger & Wing 2002; Roberts & Hirshfield 2004).

Most research on species interactions with deep-sea corals has focussed on deep reefs, in particular *Lophelia pertusa* reefs (Roberts et al. 2009). The size and architectural complexity of organisms has been positively linked to the associated species diversity (Buhl-Mortensen et al. 2010). Deep reefs can provide a variety of complex microhabitats beneficial to an assortment of taxa (Mortensen et al. 1995) and thus create pockets of high diversity (Buhl-Mortensen et al. 2010). Species-specific interactions have also been noted. For example, *Eunice norvegica* (a polychaete) uses the calcium carbonate deposits of *Lophelia pertusa* to coat its tube, search for food close to the coral's polyps, and clean sediments from the coral polyps (Mortensen 2001). *Munna boecki* (an isopod) associates with *Lophelia pertusa* for shelter and attachable substrate (Fossa and Mortensen 1998, referenced within Buhl-Mortensen & Mortensen 2005).

Much less research has focussed on the importance of non-reef forming coral habitats (including those found off Newfoundland and Labrador) for other taxa. However, non-reef forming corals also create habitat for deep-dwelling species: *Primnoa* *resedaeformis* and *P. arborea* host various taxa off Atlantic Canada (Buhl-Mortensen & Mortensen 2005), *Gersemia* is a host for young, newly metamorphosed basket stars, whereas adult basket stars are often found clinging to gorgonians (Mortensen 1927) and *Funiculina quadrangularis* and other sea pens enhance access to food (mainly copepods) for *Asteronyx loveni* (an ophiuroid) in the Northeast Atlantic (Mortensen 1927; Buhl-Mortensen et al. 2010).

1.2 Deep-sea fishes

We know next to nothing regarding the small-scale habitat requirements or preferences of deep-sea fishes, particularly in Newfoundland waters, but several studies have attempted to examine deep-sea fish distributions in relation to coldwater corals. Most examined the importance of corals in relation to adult fishes and inferred a facultative, fairly loose relationship. Two recent studies provide evidence of functional and possibly even obligate relationships between fishes and deep-sea corals: (1) Off the southern United States, prime reef and transition reef habitats support distinct fish assemblages compared to off-reef habitats, suggesting that these deep reefs host unique fish communities (Ross & Quattrini 2007). (2) Baillon et al. (2012) found evidence that coldwater corals in Newfoundland waters provide shelter for fish larvae (predominately *Sebastes* spp.). Before this work, most evidence of relationships between early life history stages of fish and deepwater corals was anecdotal. For example, swollen, gravid *Sebastes* and ray egg cases were reported on *Lophelia pertusa* reefs in the Northeast Atlantic (Fossa et al. 2002; Husebo et al. 2002; Costello et al. 2005) and catshark egg cases were found attached to gorgonians in the Gulf of Mexico (Etnoyer & Warrenchuk 2007).

Much previous work related to patterns in deep-sea fish distributions focussed on depth relationships throughout many of the world's oceans. Early studies documented zonation within the deep sea (Carney et al. 1983), evidence of fish assemblages at the upper (500 m) and mid-slope (800-1200 m) depths off southeast Australia (Koslow et al. 1994) and the possibility of 'bigger-deeper' relationships between fish size and depth off New England (Haedrich & Rowe 1977). Most often depth-related patterns are associated with individual species or species richness. For example, although Marlin-spike (*Nezumia bairdii*) has been documented in waters from 16 to 2295 m, it most commonly occur between 90 and 700 m (Cohen et al. 1990). Species richness patterns of fishes commonly peak near 1500 m (Priede et al. 2010; Campbell et al. 2011), although exceptions have been noted (Kendall & Haedrich 2006).

In general, deep-sea fishes live long, mature late, and produce few offspring compared to shelf-dwelling fishes (Merrett & Haedrich 1997). For example, orange roughy (*Hoplostethus atlanticus*) has been aged to 149 years (Fenton et al. 1991), giant grenadier (*Albatrossia pectoralis*) to 58 years (Clausen & Rodgveller 2008), and blue ling (*Molva dypterygia*) to 30 years (Large et al. 2003). These species are thought to mature at 22-40, 23, and 7 years of age, respectively. These k-selected life-history characteristics of deep-sea fishes alone make them vulnerable to mismanagement and overexploitation (Norse et al. 2012). Their vulnerability to fishing would be amplified if any of their life-history stages depend on deep-sea corals.

As continental shelf fisheries began to collapse in the 1960s and 1970s, fishers moved offshore into deeper waters in search of new fish stocks (Koslow et al. 2000; Morato et al. 2006). In the North Atlantic, mean fishing depth increased at a rate of 5.5 m per decade from 1950 to 1989, and 32.1 m per decade since 1990 (Morato et al. 2006). In the high seas, fishing depth increased approximately 250 m. Currently, 40 % of the world's trawling grounds lie deeper than the continental shelves (Roberts 2002).

Deep-sea trawl fisheries around the world exhibit boom and bust trends (Koslow et al. 2000). This is characterized by an unfished population being exploited quickly at high rates until the population is depleted and the point of commercial extinction is reached (often within 5-10 years) (Koslow et al. 2000). In the Northwest Atlantic, a *Coryphaenoides rupestris* fishery was initiated in 1967, landings peaked in 1971 at over 75,000 tonnes, then declined rapidly (Atkinson 1995; Koslow et al. 2000). By 1997 reported landings were only a few hundred tonnes and only 4 tonnes were reportedly landed between 2000 and 2006 within Canadian waters (Koslow et al. 2000; COSEWIC 2008). These trends of boom and bust often coincide with serial depletions of populations (Norse et al. 2012). Therefore, large portions of the population have already been removed before the 'bust' is detected. The *C. rupestris* fishery began in northern Labrador and moved south until it concluded in southern New England (Norse et al. 2012). The rapid decline of deep-sea fish landings is not surprising considering that in almost all deep-sea fisheries, the science lags so far behind the technological advancements and exploitation capabilities of fisheries that they are managed using little or no biological data of the target (as well as non-target) species (Haedrich et al. 2001).

Past studies identify population declines of both target and non-target deep-sea fishes. An analysis of 15 abundant deep-sea fishes in the Porcupine Seabight and Abyssal Plain area (where a mixed-species fishery began in 1989) found that nine species exhibited significant declines in abundance between 1977 and 2002 (Bailey et al. 2009; Priede et al. 2011). Although most fisheries are still restricted to depths shallower than 1600 m, fishing impacts may extend beyond depths reached by fishing gear (Bailey et al. 2009). Bailey et al. (2009) found that even *Halosauropsis macrochir*, which has been documented in waters greater than 4000 m, exhibited a significant decline in abundance. The effect of these declines on the overall deep-sea community remains unclear.

Large population declines have also been documented in deep-sea fishes off Newfoundland and Labrador. Five species exhibited such dramatic population declines that they could be considered Endangered using The World Conservation Union (IUCN) criteria (Devine et al. 2006). Roughhead grenadier (*Macrourus berglax*) declined by 93 % and Roundnose grenadier (*C. rupestris*) declined by 99.6 % between 1978 and 2003 (Devine et al. 2006). Despite federal resistance (Devine 2006), these dramatic declines led the Committee on the Status of Wildlife in Canada (COSEWIC) to assess Roundnose Grenadier as Endangered, and Roughhead Grenadier as Special Concern (Environment Canada 2013). Other relatively deep-dwelling fish off Newfoundland have also been assessed by COSEWIC as species at risk: Northern Wolffish (Threatened), Spotted Wolffish (Threatened), Atlantic Wolffish (Special Concern), Acadian Redfish (Threatened/Special Concern), and Deepwater Redfish (Threatened/Endangered)

(Environment Canada 2013). It is unknown how long these populations may take to recover from such declines.

1.3 Deep-sea field work off Newfoundland conducted for dissertation

Past deep-sea research off Newfoundland and Labrador relied heavily on destructive survey methodologies (mainly trawls) that damage the very taxa being surveyed and studied, but this reliance is slowly decreasing. During my PhD studies, I participated in two research cruises focussed on deep-sea ecosystems off Newfoundland using a Remotely Operated Vehicle (ROV). The Newfoundland portion of the 2007 cruise concentrated on dedicated surveys of various coral habitats within three submarine canyons off the Grand Banks (more details are provided throughout my dissertation). In July 2010, the cruise focussed on the geology, biogeography, and genetic connectivity of deep-sea corals in the Orphan Knoll, Orphan Basin, and Flemish Cap. Partnering with oil companies (such as Chevron Canada Ltd.) also provided glimpses of deep-sea ecosystems within the Orphan Basin and Laurentian Channel using ROVs. Although these opportunities created a wealth of exciting data to analyze, this dissertation only analyzed the extensive video footage collected during the 2007 research cruise.

The 2007 research cruise used the ROV, Remotely Operated Platform for Ocean Sciences (ROPOS) (see Table 1-1 and Figure 1-2 for details). The cruise's scientific team consisted of representatives from two universities and two Fisheries and Oceans Canada regions. The cruise formed part of a much larger 3-year, collaborative project concentrated on eight major themes: (1) coral distribution, abundance, and diversity (2) inter-relationships between corals and fish, (3) trophic relationships, (4) condition of corals, (5) coral growth rates/longevity, (6) oceanographic conditions, (7) taphonomy, and (8) reproduction and recruitment (Gilkinson & Edinger 2009). My research ties into themes 1, 2, and 4.

1.4 Thesis outline

My dissertation consists of seven chapters. My introduction illustrates how a variety of factors can influence the distribution of deep-sea taxa and highlights the vulnerability of both deep-sea corals and fishes to anthropogenic disturbances (particularly fishing).

In Chapter 2, I identify the species and abundance of deep-sea corals observed during the 2007 ROPOS cruise. I also determine if patterns of deep-sea coral assemblages occur in the survey area. A general understanding of which deep-sea corals occur off Newfoundland, knowledge of their abundances, and identifying factors that influence their assemblage patterns will allow better informed decisions about future conservation actions. For example, with a better understanding of depth distributions, it may be possible to determine whether protecting an area of restricted depth will protect a wide range of corals. While recognizing the importance of understanding the distributional patterns of coral assemblages, there are also compelling reasons to understand factors influencing the distribution, size, and health of fragile, long-lived species.

In Chapter 3, I explore how environment and fishing affect the abundance, size, and state of *Keratoisis grayi*, one of the most abundant, large/fragile corals off Newfoundland. Although other studies document fishing impacts elsewhere around the world, the novelty of this chapter is in determining quantitatively how fishing influences a specific coral in a part of the world lacking previous studies.

Deep-sea corals merit protection in their own right, but increasing attention focusses on their importance for other fauna, including fish. If fishing impacts *K. grayi*, potential knock-on effects on coral-associated species such as fish add additional concern and need for understanding how these and other corals influence fishes. In Chapter 4, I identify the factors influencing deep-sea fish distributions and assemblages.

Fish assemblage patterns in relation to corals may be difficult to decipher using large, coral-related habitat categories because such analysis may mask distributional patterns of individual species. In Chapter 5, I conduct species-specific analyses on the four most abundant grenadiers (Macrouridae) to identify potential factors influencing their distributional patterns, with a special focus on the influence of corals.

In Chapter 6, I collate current knowledge (and gaps) on the biology of deep-sea fishes off Newfoundland and Labrador. I then use available biological information to estimate potential recovery times for two species of grenadier using life table analyses. I use these results to illustrate the need for more dedicated deep-sea research and (more importantly) to emphasize the minimal timeframes fisheries managers and scientists must consider when developing conservation objectives and plans for deep-sea recovery.

I conclude my dissertation with a summary of what I have learned from the research described above and identify progress made in deep-sea conservation nationally and internationally off Newfoundland and Labrador.

1.5 Literature cited

Althaus F., Williams A., Schlacher T.A., Kloser R.J., Green M.A., Barker B.A., Bax N.J., Brodie P., Schlacher-Hoenlinger M.A. (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series 397: 279-294.

Atkinson D.B. (1995) The biology and fishery of Roundnose Grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the North West Atlantic. In: A.G. Hopper (Ed). Deep-water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, Netherlands. 51-111 pp.

Bailey D.M., Collins M.A., Gordon J.D.M., Zuur A.F., Priede I.G. (2009) Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? Proceedings of the Royal Society B-Biological Sciences 276(1664): 1965-1969.

Baillon S., Hamel J.-F., Wareham V.E., Mercier A. (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10(7): 351-356.

Breeze H., Davis D.S., Butler M., Kostylev V. (1997) Distribution and Status of Deep Sea Corals off Nova Scotia. Ecology Action Centre, Halifax, NS: 58 pp.

Bryan T.L., Metaxas A. (2006) Distribution of deep-water corals along the North American continental margins: Relationships with environmental factors. Deep Sea Research Part I: Oceanographic Research Papers 53(12): 1865-1879.

Bryan T.L., Metaxas A. (2007) Predicting suitable habitat for deep-water gorgonian corals on the Atlantic and Pacific Continental Margins of North America. Marine Ecology Progress Series 330: 113-126.

Buhl-Mortensen L., Mortensen P.B. (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: A. Freiwald & J.M. Roberts (Eds). Cold-water Corals and Ecosystems. Springer-Verlag, Berlin Heidelberg. 849-879 pp.

Buhl-Mortensen L., Vanreusel A., Gooday A.J., Levin L.A., Priede I.G., Buhl-Mortensen P., Gheerardyn H., King N.J., Raes M. (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31(1): 21-50.

Cairns S. (1999) Species richness of recent Scleractina. Atoll Research Bulletin 459: 1-46.

Campbell N., Neat F., Burns F., Kunzlik P. (2011) Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). ICES Journal of Marine Science 68(2): 365-376.

Carney R.S., Haedrich R.L., Rowe G.T. (1983) Zonation of fauna in the deep sea. In: G.T. Rowe (Ed). Deep-sea Biology. John Wiley & Sons, New York. 371-398 pp.

Clausen D.M., Rodgveller C.J. (2008) Assessment of grenadiers in the Gulf of Alaska, Eastern Bering Sea, and Aleutian Islands. NPFMC: 613-656 pp.

Cohen D.M., Inada T., Iwamoto T., Scialabba N. (1990) Gadiform Fishes of the World (Order Gadiformes). Food and Agriculture Organization of the United Nations, Rome: 442 pp.

COSEWIC (2008) COSEWIC assessment and status report on the Roundnose Grenadier *Coryphaenoides rupestris* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa: 42 pp.

Costello M.J., McCrea M., Freiwald A., Lundalv T., Jonsson L., Bett B.J., van Weering T.C.E., de Haas H., Roberts J.M., Allen D. (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: A. Freiwald & J.M. Roberts (Eds). Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin. 771-805 pp.

Davies A.J., Guinotte J.M. (2011) Global habitat suitability for framework-forming cold-water corals. PLoS ONE 6(4): e18483.

Devine J.A. (2006) Temporal Trends in a Large Marine Ecosystem. Department of Biology. Memorial University of Newfoundland, St. John's, NL.

Devine J.A., Baker K.D., Haedrich R.L. (2006) Fisheries: Deep-sea fishes qualify as endangered. Nature 439(7072): 29.

Edinger E.N., Baker K.D., Devillers R., Wareham V. (2007) Coldwater corals off Newfoundland and Labrador: distribution and fisheries impacts. World Wildlife Fund, Toronto, Canada: 41 pp.

Environment Canada (2013) Species at Risk Public Registry. www.sararegistry.gc.ca, Accessed 11 March.

Etnoyer P., Morgan L. (2007) Predictive habitat model for deep gorganians needs better resolution: Comment on Bryan & Metaxas (2007). Marine Ecology Progress Series 339: 311-312.

Etnoyer P., Morgan L.E. (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: A. Freiwald & J.M. Roberts (Eds). Cold-water corals and ecosystems. Springer-Verlag, Berlin. 331-343 pp.

Etnoyer P., Warrenchuk J. (2007) A catshark nursery in a deep gorgonian field in the Mississippi Canyon, Gulf of Mexico. Bulletin of Marine Science 81(3): 553-559.

Fenton G.E., Short S.A., Ritz D.A. (1991) Age determination of Orange Roughy, *Hoplostethus atlanticus* (Pisces, Trachichthyidae) using 210 Pb / 266 Ra disequilibria. Marine Biology 109(2): 197-202.

Fiege D., Barnich R. (2009) Polynoidae (Annelida: Polychaeta) associated with cold-water coral reefs of the northeast Atlantic and the Mediterranean Sea. In: N.J. Maciolek & J.A. Blake (Eds). Proceedings of the 9th International Polychaete Conference 149-164 pp.

Forsterra G., Beuck L., Haussermann V., Freiwald A. (2005) Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: A. Freiwald & J.M. Roberts (Eds). Cold-water corals and ecosystems. Springer-Verlag, Berlin. 937-977 pp.

Fossa J.H., Mortensen P.B., Furevik D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471: 1-12.

Gilkinson K., Edinger E.N. (2009) The ecology of deep-sea corals of Newfoundland and Labrador waters: biogeography, life history, biogeochemistry and relation to fishes: 136 pp.

Guinotte J.M., Orr J., Cairns S., Freiwald A., Morgan L., George R. (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Frontiers in Ecology and the Environment 4(3): 141-146.

Haedrich R.L., Merrett N.R., O'Dea N.R. (2001) Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. Fisheries Research 51(2-3): 113-122.

Haedrich R.L., Rowe G.T. (1977) Megafaunal biomass in the deep sea. Nature 269(5624): 141-142.

Hall-Spencer J., Allain V., Fossa J.H. (2002) Trawling damage to Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1490): 507-511.

Henry L.A., Kenchington E.L.R., Silvaggio A. (2003) Effects of mechanical experimental disturbance on aspects of colony responses, reproduction, and regeneration in the cold-water octocoral *Gersemia rubiformis*. Canadian Journal of Zoology 81(10): 1691-1701.

Husebo A., Nottestad L., Fossa J.H., Furevik D.M., Jorgensen S.B. (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91-99.

Kendall V.J., Haedrich R.L. (2006) Species richness in Atlantic deep-sea fishes assessed in terms of the mid-domain effect and Rapoport's rule. Deep Sea Research Part I: Oceanographic Research Papers 53(3): 506-515.

Koslow J.A., Boehlert G.W., Gordon J.D.M., Haedrich R.L., Lorance P., Parin N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57(3): 548-557.

Koslow J.A., Bulman C.M., Lyle J.M. (1994) The mid-slope demersal fish community off southeastern Australia. Deep-Sea Research Part I: Oceanographic Research Papers 41(1): 113-141.

Krieger K.J. (2001) Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. In: J.H.M. Willison, J. Hall, S.E. Gasset al (Eds). First International Symposium on Deep Sea Corals. Ecology Action Centre, Halifax, Nova Scotia: 156-165.

Krieger K.J., Wing B.L. (2002) Megafauna associations with deepwater corals (*Primnoa spp.*) in the Gulf of Alaska. Hydrobiologia 471: 83-90.

Kulka D.W., Pitcher D.A. (2001) Spatial and temporal patterns in trawling activity in the Canadian and Pacific. ICES CM R:02: 1-55.

Large P.A., Hammer C., Bergstad O.A., Gordon J.D.M., Lorance P. (2003) Deep-water Fisheries of the Northeast Atlantic: II. Assessment and Management Approaches. Journal of Northwest Atlantic Fishery Science 31: 151-164.

MacIsaac K., Bourbonnais C., Kenchington E., Gordon D., Gass S.E. (2001) Observations on the occurence and habitat preference of corals in Atlantic Canada. In: J.H.M. Willison, J. Hall, S.E. Gasset al (Eds). Proceedings of the First International Symposium on Deep-sea Corals, Halifax, NS. 58-75 pp.

Merrett N.R., Haedrich R.L. (1997) Deep-sea Demersal Fish and Fisheries. Chapman and Hall, London: 282 pp.

Morato T., Watson R., Pitcher T.J., Pauly D. (2006) Fishing down the deep. Fish and Fisheries 7(1): 24-34.

Mortensen T. (1927) Handbook of Echinoderms of the British Isles. Humphrey Milford, Oxford University Press, Toronto, Ontario. 471 pp.

Mortensen P.B. (2001) Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (Scleractina) and selected associated invertebrates. Ophelia 54(2): 83-104.

Mortensen P.B., Buhl-Mortensen L. (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Marine Biology 144(6): 1223-1238.

Mortensen P.B., Buhl-Mortensen L. (2005) Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada In: A. Freiwald & J.M. Roberts (Eds). Cold-water corals and ecosystems. Springer-Verlag, Berlin. 247-277 pp.

Mortensen P.B., Buhl-Mortensen L., Gass S.E., Gordon D.C., Kenchington E., Bourbonnais C., Macsaac K.G. (2006) Deep-water corals in Atlantic Canada: A summary of ESRF-funded Research (2001-2003): 83 pp.

Mortensen P.B., Buhl-Mortensen L., Gordon D.C. (2006) Distribution of deep-water corals in Atlantic Canada. Proceedings of the 10th International Coral Reef Symposium: 1832-1848.

Mortensen P.B., Hovland M., Brattegard T., Farestveit R. (1995) Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64° N on the Norwegian shelf: Structure and associated megafauna. Sarsia 80(2): 145-158.

Norse E.A., Brooke S., Cheung W.W.L., Clark M.R., Ekeland L., Froese R., Gjerde K.M., Haedrich R.L., Heppell S.S., Morato T., et al. (2012) Sustainability of deep-sea fisheries. Marine Policy 36(2): 307-320.

Packer D., Boelke D., Guida V., McGee L. (2007) State of deep coral ecosystems in the Northeastern US region: Maine to Cape Hatteras. In: S.E. Lumsden, T.F. Hourigan, A. Bruckner & G. Dorr (Eds). The State of Deep Coral Ecosystems of the United States. NOAA, Silver Spring, MD. 195-231 pp.

Priede I.G., Godbold J.A., King N.J., Collins M.A., Bailey D.M., Gordon J.D.M. (2010) Deep-sea demersal fish species richness in the Porcupine Seabight, NE Atlantic Ocean: global and regional patterns. Marine Ecology 31(1): 247-260.

Priede I.G., Godbold J.A., Niedzielski T., Collins M.A., Bailey D.M., Gordon J.D.M., Zuur A.F. (2011) A review of the spatial extent of fishery effects and species vulnerability of the deep-sea demersal fish assemblage of the Porcupine Seabight, Northeast Atlantic Ocean (ICES Subarea VII). ICES Journal of Marine Science: Journal du Conseil 68(2): 281-289.

Roberts C.M. (2002) Deep impact: the rising toll of fishing in the deep sea. Trends in Ecology & Evolution 17(5): 242-245.

Roberts J.M., Wheeler A.J., Freiwald A., Cairns S. (2009) Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats. Cambridge University Press, New York: 334 pp.

Roberts S., Hirshfield M. (2004) Deep-sea corals: out of sight, but no longer out of mind. Frontiers in Ecology and the Environment 2(3): 123-130.

Ross S.W., Quattrini A.M. (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Research Part I: Oceanographic Research Papers 54(6): 975-1007.

Schembri P.J., Dimech M., Camilleri M., Page R. (2007) Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cahiers de Biologie Marine 48(1): 77-83.

Sherwood O.A., Edinger E.N. (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 66(1): 142-152.

Waller R.G., Scanlon K.M., Robinson L.F. (2011) Cold-water coral distributions in the Drake Passage area from towed camera observations - initial interpretations. PLoS ONE 6(1).

Wareham V.E., Edinger E.N. (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. Bulletin of Marine Science 81(1): 289-313.

Williams G.C. (2011) The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). PLoS ONE 6(7): 1-11.

Table 1-1. Details of an *in situ* research cruise conducted on the slope of the southwest Grand Banks, Newfoundland in 2007.

Cruise Title	Biogeography, biodiversity, and reproductive ecology of deep-sea corals (NSERC Discovery Ship Time Cruise)
Vessel	*CCGS Hudson*
Submersible	*ROPOS*
Dates of embarkation / disembarkation	6 - 27 July 2007
Port of embarkation and disembarkation	Bedford Institute of Oceanography (Dartmouth, Nova Scotia)

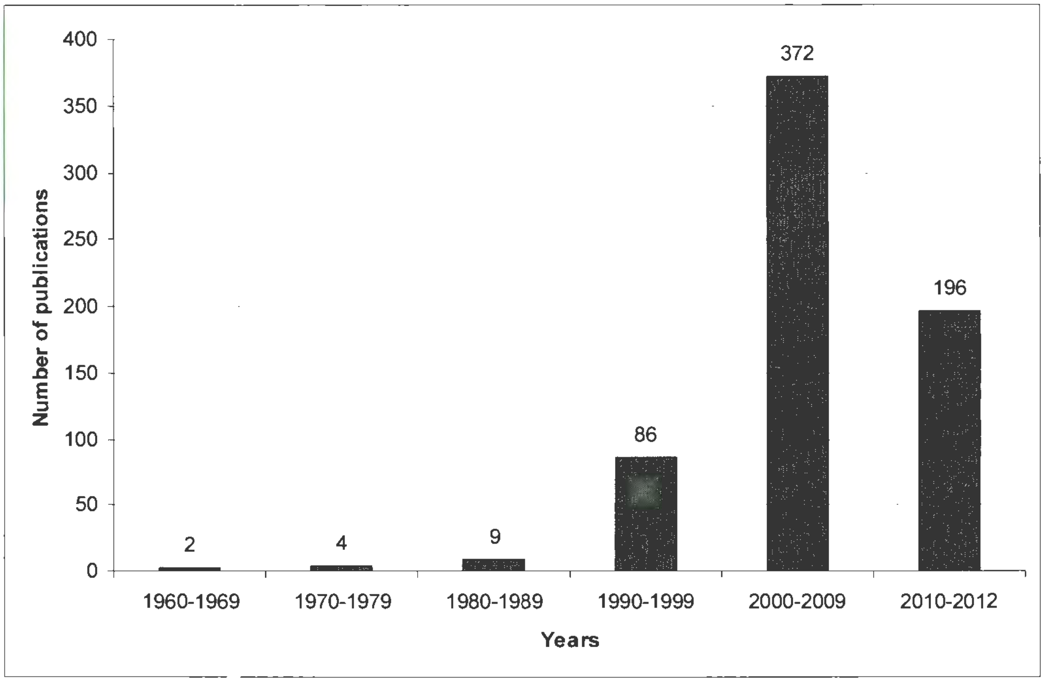

Figure 1-1. The number of publications in each decade listed in *Web of Science*, searched using the keyword "deep-sea coral" on 13 May 2012.

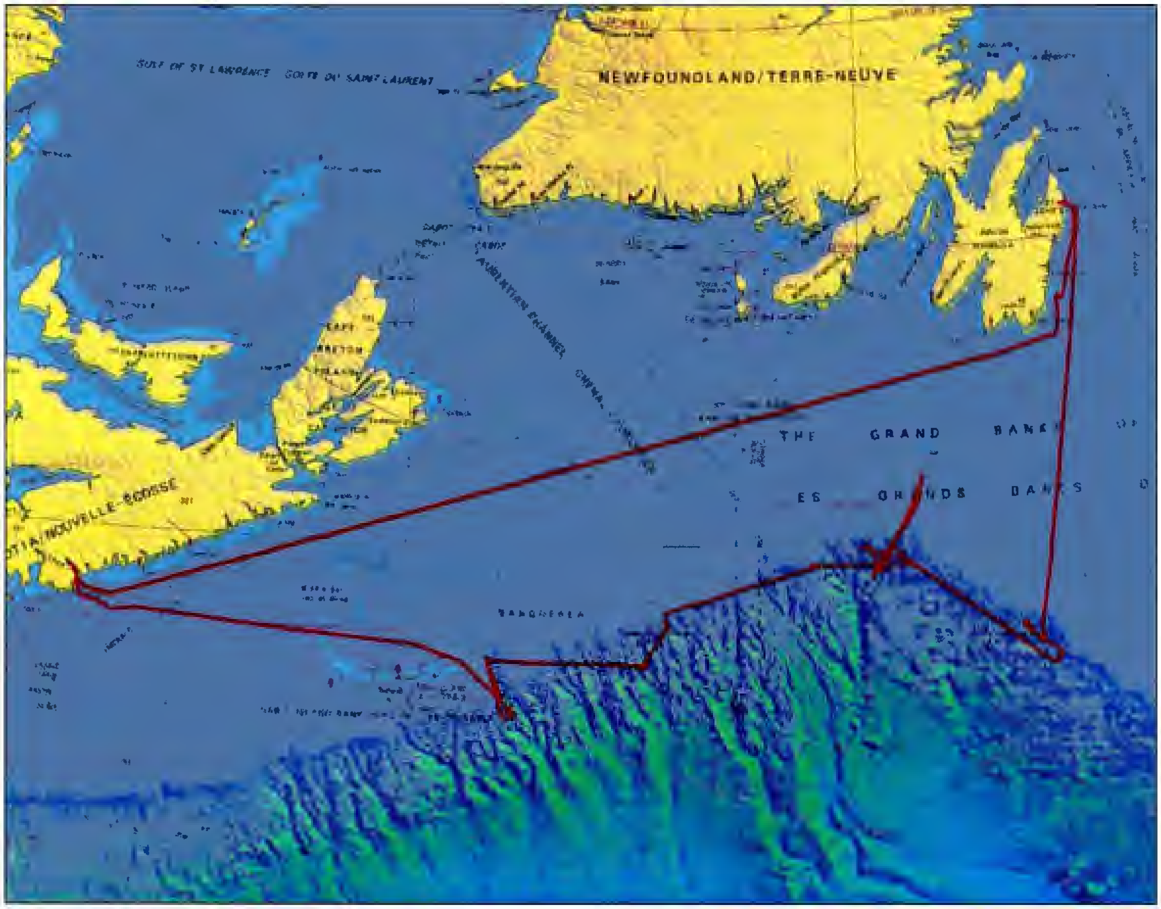

Figure 1-2. Cruise track of research cruise conducted on the slope of southwest Grand Banks, Newfoundland in 2007 (from Gilkinson & Edinger 2009).

2 Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada

Abstract

Deep-sea corals are fragile and long-lived species that provide important habitat for a variety of taxa. The rarity of *in situ* observations in deep waters off Newfoundland, Canada motivated the first extensive deep-sea research cruise to that region in 2007. We conducted seven dives in three canyons (Haddock Channel, Halibut Channel, and Desbarres Canyon) with ROPOS (Remotely Operated Platform for Ocean Science). Over 160,000 solitary and colonial corals were enumerated and, of the 28 species found, *Acanella arbuscula*, *Pennatula* spp., and *Flabellum* spp. were most frequently observed. The largest coral observed was *Keratoisis grayi* at over 2 m in height. Corals spanned the entire depth range sampled (351 – 2245 m) and inhabited all bottom types surveyed, but boulder and cobble habitats were most species-rich. Assemblages differed significantly with depth and bottom type. The unique assemblage at outcrops was strongly driven by the presence of *Desmophyllum dianthus*. *Keratoisis grayi*, *D. dianthus,* and *Anthomastus* spp. were largely absent in mud-sand habitats. Sea pen meadows covered large tracts of muddy seafloor spanning over 1 km. *Acanella arbuscula* and *Flabellum* spp. characterised large coral fields with abundant corals but relatively low species richness. These results highlight not only the importance of bottom type in determining patterns of coral distributions, abundances, and assemblages, but also

the need to focus conservation efforts on a variety of habitats to ensure protection for the full suite of deep-sea coral species.

2.1 Introduction

Deep-sea corals are long-lived, slow growing, and highly vulnerable to fishing gear damage (Roberts et al. 2006; Edinger et al. 2007; Althaus et al. 2009; Roark et al. 2009; Roberts et al. 2009; Sherwood & Edinger 2009), climate change, and ocean acidification (Turley et al. 2007; Guinotte & Fabry 2008; Hall-Spencer et al. 2008). Corals create feeding habitats, shelter, surfaces for attachment, and simple structural complexity for other organisms including fish (Husebo et al. 2002; Ross & Quattrini 2007; Buhl-Mortensen et al. 2010), echinoderms (Krieger & Wing 2002), polychaetes (Schembri et al. 2007; Fiege & Barnich 2009), crustaceans (Krieger & Wing 2002), and other invertebrates (Krieger & Wing 2002; Roberts & Hirshfield 2004). Deep-sea coral habitats often have greater species diversity than surrounding areas and host unique species assemblages (Henry & Roberts 2007; Ross & Quattrini 2007). These characteristics underscore the importance of understanding distribution patterns of deep-sea corals for planning appropriate ocean conservation measures.

The rapid growth of knowledge on deep-sea coral distributions has focussed largely on specific regions or sites (Roberts et al. 2005) and associated research tends to concentrate on scleractinian coral reefs (Fossa et al. 2002; Cordes et al. 2008). Coral research in the deep waters off Newfoundland and Labrador is still in its infancy, but substantial knowledge and data began to accumulate from the previously unknown deep waters of this region when dedicated deep-sea coral research began in 2003 (e.g. Edinger et al. 2007; Wareham & Edinger 2007; Gilkinson & Edinger 2009; Murillo et al. 2010). These biogeographic and ecological studies concentrated on results from broad-scale trawl surveys and/or bycatch from fisheries observer programs. Video studies in 2002 examined deep-sea corals on the slope of the Southwest Grand Banks, but covered only a few kilometres of bottom to a maximum depth of 500 m (Mortensen et al. 2006a; Mortensen et al. 2006b). Therefore, little information is available on deep-sea coral distributions and patterns on small spatial scales for this region and *in situ* observations of deep-sea corals are rare. Fine-scale, *in situ* observations allow better understanding of local patterns of distribution, changes in abundance, assemblages, associations with other taxa, and impacts of deep-sea fishing.

Like most marine organisms, deep-sea corals have preferred depth distributions and habitat characteristics. Temperature, salinity, substrate, currents, and slope all contribute to distributional trends and levels of abundance (Roberts et al. 2009). For example, in Atlantic Canada, Mortensen et al. (2006a) found *Flabellum* spp. on primarily muddy substratum and most coral species occurred between 4.5 and 6.0 °C. In a submarine canyon off Nova Scotia, *Keratoisis grayi* and *Duva florida* were associated with steep topography and semi-consolidated mudstone (Mortensen & Buhl-Mortensen 2005).

Most previous deep-sea coral studies focussed on individual distributions of species and few examined patterns in composition among and between coral communities and species' co-occurrences. Understanding these facets of coral ecology will allow development of more appropriate conservation actions that recognize the importance of unique and/or diverse assemblages above and beyond individual species.

We present here the results of the first extensive, *in situ* study of deep-sea corals on the slope of the southwest Grand Banks of Newfoundland, and describe the distributions and abundances of the observed species, assemblages, and species diversity with respect to bottom type, depth, and study area. We increase the known distribution, depth range, and abundance concentrations for multiple species and genera, and conclude by describing how this new knowledge may facilitate deep-sea conservation planning.

2.2 Methods

2.2.1 Video surveys

We focussed on three submarine canyons on the slopes of the Grand Banks south of Newfoundland: Halibut Channel, Haddock Channel, and Desbarres Canyon (Figure 2-1). A small bank separates Halibut Channel and Haddock Channel, which are situated approximately 110 km and 175 km east of Laurentian Channel, and approximately 150 km and 200 km northwest of Desbarres Canyon, respectively. The cold Labrador Current from the north and the warm Gulf Stream from the south both influence the study area. Similar temperature regimes in the three canyons averaged *ca.* 5 °C bottom temperature during relatively shallow dives (<1100 m) and *ca.* 4.4 °C during relatively deep dives (>1100 m). Bottom current measurements taken in Haddock Channel (*ca.* 700 m) indicated relatively slow current speeds (5-10 cm s^{-1}), compared to previously studied coral habitats on the slope of the Scotian Shelf (e.g. Northeast Channel, The Gully, Stone

Fence) (Zedel & Fowler 2009). Data from Fisheries and Oceans Canada surveys and bycatch records suggested species rich and abundant corals at these three locations (Edinger et al. 2007).

The remotely operated vehicle (ROV), ROPOS (Remotely Operated Platform for Ocean Science) (CSSF 2010) performed video surveys from *CCGS Hudson* during seven dives between 16 - 24 July 2007 (Table 2-1). Lasers on the ROV placed 10 cm apart indicated scale. Depth, date, time, altitude (distance above bottom), temperature, and position were logged at 1-second intervals, though sporadic problems with the logger resulted in several long periods with no temperature data.

Based on known distributions of corals and bathymetry from previous work, we planned 1-km transects every 200 m of depth along depth contours between 2200 and 600 m and along contours every 100 m in waters shallower than 500 m (Figure 2-1). We standardized transects by keeping the ROV as close to the bottom as possible, maintaining a constant slow speed (*ca.* 0.2 – 0.5 m s^{-1}) while tilting the camera down slightly on a wide-angle view in order to image the seafloor and water column directly above. Between pre-selected transects, we explored the area with ROPOS, capturing still images and video of interesting features, and collecting physical specimens to validate visual identification.

2.2.2 Video processing

Using the program ClassAct Mapper (Benjamin 2007), we continuously recorded geo-referenced data describing bottom type, ROV behaviour, and corals. All corals were identified to the lowest possible taxonomic level and the colony height and diameter of relatively large corals (antipatharians, Isididae, *Paramuricea* spp., and other gorgonians) were measured to the nearest 5 cm using the lasers for scale.

We characterized bottom type every second by primary (most abundant) substrate and secondary (next most abundant) substrate, with optional additional comments. We categorized bottom type as (1) outcrop (vertically exposed bedrock and consolidated Quaternary sediment), (2) boulder (> 25 cm), (3) cobble (5 - 25 cm), (4) gravel (0.2 – 5 cm), or (5) mud-sand (fine-grain) sediments (Thrush et al. 2001). For example, a bottom type description might consist of mud-sand as the primary bottom type and gravel as the secondary bottom type, with 'scattered boulders' as an additional comment.

ROV behaviour was categorized at 1-second intervals as transect-mode, benthic-mode, sampling, too high, stationary viewing, panning, or view obstruction. 'Transect-mode' was defined as any portion of the video when the ROV followed the prescribed methodology for transects (described above), regardless of whether the transect was planned. 'Benthic-mode' described periods when the ROV moved forward with a clear view of the seafloor and the camera pointed directly toward the sediment. 'Sampling' denoted any sections of the video during which sampling occurred and 'stationary-viewing' denoted periods when we stopped the ROV to view a feature of interest. 'Panning' described situations when the ROV moved forward, but with the camera at an inconsistent angle or position. 'View obstruction' occurred when other sampling gear (e.g. pushcore handles) obstructed part of the camera view.

2.2.3 Data analysis

We characterized survey sites according to depth, duration, and distance surveyed and used transect segments to describe bottom type. We illustrated the overall characteristics of the habitats surveyed by plotting bottom type versus depth for each second of data when the ROV moved forward with a clear view of the seafloor (i.e. transect-mode, benthic-mode, and panning). All dead corals in the video were noted, but because live coral communities were the focus of this study, we removed dead corals from the analyses.

2.2.3.1 Species composition and occurrence

We described the overall distribution and composition of corals by calculating the number of colonies and their sizes for each species (or species group) and by examining occurrence of each species in relation to depth.

For more detailed analyses of patterns, we focussed on those species identified to the lowest possible taxonomic level. For example, we excluded gorgonians that could not be identified to a unique genus from further analysis. We could easily distinguish one species of *Pennatula* (*Pennatula* sp. 1) during video processing, but combined all other *Pennatula* into *Pennatula* spp., so that the abundant 'Unidentified *Pennatula'* could be included in analyses. For the same reason, we combined all *Flabellum* into the single category *Flabellum* spp.

We assigned a single bottom type to each 1-second observation based on the premise that hard substrate can influence the coral assemblage regardless of its prevalence. Therefore, bottom type was categorized as the largest sediment structure for each 1-second observation. For example, if a given observation included the bottom type categories of cobble (Primary), boulders (Secondary), and scattered gravel (comments), we assigned it the bottom type "Boulders". We found one large fishing net in an otherwise muddy habitat that created attachment structure for several coral species, so we removed this portion of the data from analyses involving bottom type. We then examined coral occurrence in relation to bottom type and depth.

We split video data collected in transect mode into a series of 10-m segments (= samples). For each sample, we defined bottom type as the largest structure encountered during the 10-m segment and depth as the mean depth recorded within the segment. Coral abundance was calculated as the number of colonies per sample and this value was used to investigate maximum abundance for each species (or species group).

We used the 10-m segments to examine patterns in coral richness by calculating species richness for each sample and comparing among dive locations, depth categories, and bottom types. We defined depth categories based on the distribution of corals and the number of samples in each category: (1) 300-800 m, (2) 800-1300 m, and (3) 1300-2300 m. Patterns in richness among bottom types were compared graphically using box-plots.

2.2.3.2 Assemblages

We determined patterns in assemblages within the samples using Primer 6.0 (Clarke & Gorley 2006) analyses of square-root transformed data to reduce the influence of abundant species. A Bray-Curtis similarity matrix was used to conduct a two-way analysis of similarities (ANOSIM) test for differences in assemblages between and within samples. We examined species similarities (and dissimilarities) within and between depth classes and bottom types in SIMPER (similarity percentages).

We examined similarities between species by creating a Bray-Curtis species similarity matrix of standardized samples and species that contributed at least 50 % to a sample. We then produced a multi-dimensional scaling (MDS) plot and dendrogram (using group average clustering) based on these similarities.

2.3 Results

In total, we recorded 90 h of bottom video footage over the seven dives, covering a distance of approximately 105 km (Table 2-1) and a depth range of 351 – 2245 m. We recorded 5031 samples (10-m transect segments) over a variety of habitats and depths (Table 2-2). Most transect segments were over mud-sand habitats (Figure 2-2) within the 300 – 800 m depth category. Boulders were rare in deep waters and outcrops were rare over the entire depth range sampled. Dive R1070 produced the most samples (n = 901).

2.3.1 Species composition and occurrence

We recorded over 160,000 coral colonies, comprising at least 28 distinct species (Table 2-3). Although we identified *Flabellum macandrewi*, *F. alabastrum*, and *F. angulare* from specimens collected during the cruise, these species were usually grouped as *Flabellum* spp. in the video analysis. The most abundant species were *Pennatula* sp. 2

(possibly *Pennatula aculeata), Acanella arbuscula*, *Flabellum* spp. and *Acanthogorgia armata*. The maximum number of a single species observed in a 10-m segment was *Pennatula* spp. (622 colonies), followed by *Flabellum* spp. (300 individuals), and *Heteropolypus* cf. *insolitus* (123 colonies) (Table 2-4). Rare species included antipatharians, *Lepidisis* sp., and *Paragorgia arborea.*

The tallest coral observed was a *Keratoisis grayi* colony measuring 215 cm in height. Although rare, antipatharians were fairly large, one exceeding 60 cm in height. Two of the three *Paragorgia arborea* observed were only ~5 cm in height, whereas the largest colony was only approximately 20 cm. The abundant corals *Acanella arbuscula* and *Acanthogorgia armata* both averaged almost 10 cm in height.

Many species spanned a wide depth range and appeared unrestricted by depth (Figure 2-3). This pattern was especially true for many of the sea pens (e.g. *Protoptilum carpenteri*, *Anthoptilum grandiflorum*, and *Halipteris finmarchica*). The distribution of *Flabellum alabastrum* spanned nearly 1900 m (355 – 2244 m), resulting in the widest depth range of all coral species observed, however *Halipteris finmarchica* also spanned a considerable depth range (353 - 2217 m). Very few species were restricted to deep water, although *Chrysogorgia agassizii* was limited to depths greater than 1997 m and the single colony of *Bathypathes patula* was found at 2242 m. In comparision, many more species were limited to the upper and middle slope, including all *Pennatula* spp. (< 1204 m), *Keratoisis grayi* (< 967 m), *Duva florida* (< 906 m), and *Paragorgia arborea* (< 800 m).

Most corals occurred in a variety of bottom types, but several appeared to be restricted in relation to bottom type (Figure 2-4). *Javania cailleti*, *Desmophyllum* *dianthus*, *Paragorgia arborea*, and Schizopathidae n. gen. et n. sp. occurred only in areas with large, hard substratum. *Paramuricea* spp., *Keratoisis grayi*, and *Anthomastus* spp. were mostly limited to areas with hard substratum, but that bottom type ranged in size and included small substrate, such as gravel. In comparison, *Distichoptilum gracile*, *Umbellula* spp., *Bathypathes patula*, and *Kophobelemnon stelliferum* occurred primarily in soft sediments. Species that spanned a wide variety of bottom types included *Flabellum alabastrum*, *Acanella arbuscula*, *Acanthogorgia armata* and others.

Although many species spanned a variety of bottom types and depths, when we plotted their abundances within 10-m transect segments against bottom type and depth, several patterns emerged (Figure 2-5). For example, *Flabellum* spp. colonies spanned a large depth range, but were most dense in waters less than 500 m. Although *Heteropolypus* cf. *insolitus* and *Pennatula* spp. spanned a variety of bottom types, they were much more abundant in mud-sand sediments than in bottom types categorized by hard substratum.

In general, species richness was highest in boulder areas (Figure 2-6). The maximum species richness within any sample (7 species) occurred twice in boulders (489 m and 470 m, Halibut Channel) and once in cobble (600 m, Haddock Channel) (Table 2-5). The maximum number of coral colonies was associated with mud-sand sediments (835 m) in Desbarres Canyon (Table 2-5), but only three of these were colonies other than *Pennatula* spp.

2.3.2 Assemblages

The global ANOSIM showed assemblages differed significantly among depth classes ($p < 0.001$) and pairwise comparisons showed significant differences between each depth class ($p < 0.001$) (Table 2-6). However, the R-statistic indicated that assemblage composition differed most between depth ranges 300 - 800 m and 1300 - 2300 m ($R = 0.471$). This dissimilarity (average dissimilarity = 92.6 %) was largely driven by higher abundances of *Acanella arbuscula* and *Pennatula* spp. in shallower waters. *Pennatula* spp. and *A. arbuscula* also drove differences between the 300 - 800 m and 800 - 1300 m assemblages (average dissimilarity = 85 %); *Pennatula* spp. was most abundant in the 800 - 1300 m depth class, whereas *A. arbuscula* was more abundant in the 300 - 800 m depth class. The assemblage differences between the 800 - 1300 m and 1300 - 2300 m depth classes (average dissimilarity = 88 %) were largely driven by *Pennatula* spp. and *Protoptilum carpenteri*. *Pennatula* spp. occurred in the shallower depth range but not in deeper waters and *P. carpenteri* was more abundant in the deeper depth class compared to the shallower depth range.

The ANOSIM analysis showed significant differences in composition among bottom types ($p < 0.001$) (Table 2-6). Mud-sand sediment assemblages differed from those associated with boulders ($R = 0.316$, $p < 0.001$) and outcrops ($R = 0.552$, $p < 0.001$). Assemblages in boulder habitats also differed from those in gravel ($R = 0.440$, $p < 0.001$) and outcrops ($R = 0.56$, $p = 0.069$), but not from assemblages associated with cobble ($R = 0.073$). Coral assemblages on outcrops also differed from those in cobble ($R = 0.585$, $p = 0.02$) and gravel ($R = 0.466$, $p < 0.001$) habitats.

Generally, the paucity of species in mud-sand habitats had the greatest influence on assemblage dissimilarities. For example, fine sediments generally lacked *Keratoisis grayi*, *Desmophyllum dianthus*, and *Anthomastus* spp. and abundances of *Flabellum* spp. and *Acanella arbusula* were lower than in areas with hard substrate like boulders (average dissimilarity = 86.9 %) and outcrops (average dissimilarity = 99.31 %). The high dissimilarity of coral assemblages between boulders and outcrops (87.3 %) was largely driven by low abundances of *Keratoisis grayi* colonies on outcrops and the absence of *Desmophyllum dianthus* from boulder habitats. The higher abundance of *Flabellum* spp. in gravel contributed most to the dissimilarities between boulders and gravel (84.2 %). The low abundance of *A. arbusula* and high abundance of *D. dianthus* associated with outcrops drove dissimilarities with cobble (95.0 %). Unlike outcrops, gravel had abundant *Flabellum* spp., but lacked *D. dianthus* (average dissimilarity = 99.2 %).

Species similarity analyses grouped *Keratoisis grayi*, *Acanthogorgia armata*, and *Anthomastus* spp. in the dendrogram (Figure 2-7) and MDS plot (Figure 2-8), indicating regular co-occurrence. *Acanella arbuscula* and *Flabellum* spp. also grouped closely in the MDS plot. *Desmophyllum dianthus*, *Chrysogorgia agassizi*, *Pennatula* sp. 1, *Umbellula* spp., and *Radicipes gracilis* were generally not associated with other species in the plot. The dendrogram showed the same species as outliers and illustrated groupings (albeit with relatively weak similarity of ~ 20 %) of *Kophobelemnon stelliferum* and *Protoptilum carpenteri*, and *Funiculina quadrangularis* and *Pennatula* spp.

2.4 Discussion

2.4.1 Patterns in species occurrences and abundances

Bottom type and depth clearly influenced species occurrences and abundance. Physical characteristics of some species explain how bottom type influences their distributions. Peduncles anchor sea pens in sediments, thus largely restricting them to muddy habitats (Williams 2011). Some species can retract into the sediment when disturbed (Packer et al. 2007), elevating their requirement for muddy substrate. We often observed rapid retraction of entire colonies of *Protoptilum carpenteri* into the sediment, complicating sampling of this species. Although we found sea pens occupied a variety of bottom types, they were almost always anchored in the mud/sand portions of these substrata. The one exception was *Halipteris finmarchica*, which sometimes anchored in gravelly habitat with little mud or sand. As reported by Mortensen et al. (2006a) and Hecker & Blechschmidt (1980), holdfast structures anchored *Radicipes gracilis* and *Acanella arbuscula* in the soft substratum. Other species, such as *Keratoisis grayi, Anthomastus* spp., Schizopathidae n. gen. et n. sp. and *Duva florida,* require hard substrate for attachment (Roberts et al. 2009), and their distributions are therefore limited by hard structure availability.

As reported elsewhere (Packer et al. 2007), *Desmophyllum dianthus* typically occurred in high abundances on outcrops (Figure 2-5). A strong base attaches this cup coral to hard substrate where it can benefit from high currents associated with local topographic features (Dolan et al. 2008). Försterra et al. (2005) also recorded *D. dianthus* on vertical walls and the undersides of rock ledges, and they hypothesized the coral's downward facing polyps were caused by sensitivity to sedimentation. Laboratory experiments demonstrate physiological thresholds in corals beyond which they cannot compensate for sedimentation (Brooke et al. 2009). *Desmophyllum dianthus* strongly influenced the unique assemblage associated with outcrops and thus could be considered an indicator species for vertical cliff-like structures in the study region (i.e. large quantities of *D. dianthus* likely indicate outcrop-type substrate).

Many species spanned wide depth ranges, including *Flabellum alabastrum*, *Protoptilum carpenteri*, and *Halipteris finmarchica*. This pattern parallels findings of exceptionally wide depth ranges in corals from the Northeast Pacific Ocean; Antipathidae, Primnoidae, and Paragorgiidae spanned minimum depths shallower than 30 m to depths greater than 1900 m (Etnoyer & Morgan 2005). The especially wide depth ranges of Pennatulaceans are thought, in part, to reflect their ability to inhabit soft sediments (such as those found in the abyssal plains) (Williams 2011). In contrast to the wide depth ranges of some species, several species in our study, such as *Duva florida* and *Paragorgia arborea* were restricted to relatively shallow depths (< 906 m). The influence of depth on coral distributions likely reflects associated changes in environmental characteristics, such as temperature (Roberts et al. 2009), available bottom type (Figure 2-2), and currents.

Temperature is thought to restrict deep-sea coral distributions (Mortensen et al. 2006a; Roberts et al. 2009). For example, high temperatures (>10 °C) may restrict the upper depth limit of *Paragorgia arborea* off Atlantic Canada (Mortensen et al. 2006a). Given that our study focussed on relatively deep waters, the maximum temperatures for each species were well within the temperature ranges recorded by Mortensen et al. (2006a). In comparison to other surveys off Canada that recorded temperature (Mortensen et al. 2006a; Beazley 2011), we extended the known *in situ* minimum temperature in this region for *Radicipes gracilis* (4.4 °C), *Anthomastus* spp. (4.3 °C), *Acanella arbuscula* (3.5 °C), and *Flabellum alabastrum* (3.7 °C). Nevertheless, because these species are known to occur in higher latitudes and in deeper waters off Atlantic Canada (DFO and K Baker, unpub. data), these values likely do not represent their lower temperature limit.

2.4.2 Patterns in community composition and diversity

Keratoisis grayi, Anthomastus spp., and *Acanthogorgia armata* co-occurred (Figure 2-9a) at relatively shallow depths (< 1000 m) with boulders and cobbles throughout Halibut and Haddock Channels. The most species-rich and diverse transects were similar in species composition, comprised of *A. armata, Anthomastus* spp., *K. grayi, Acanella arbuscula,* and *Halipteris finmarchica* among others. The associated bottom types were boulders or cobble, but closer examination of the bottom classification indicated that these assemblages occurred in specific segments of transects with mixed substrate. For example, we recorded sand (primary), boulders (secondary), and scattered cobble/gravel (comments) for one of the most species rich segments. These features created a small-scale habitat mosaic in which a variety of species could co-occur.

The most numerous species occurred within a variety of bottom types and with a variety of other species, but these dominant corals also created unique assemblages in relatively uniform sediments. *Pennatula* spp. sometimes occurred in large sea pen meadows more than 1 km in length (Figure 2-9b), and reached maximum numbers of 622 colonies per 10-m segment. Many colonies oriented in a similar direction (presumably to maximize use of currents) (Roberts et al. 2009). *Halipteris finmarchica, Protoptilum carpenteri*, *Kophobelemnon stelliferum*, and other sea pens were scattered throughout these meadows. Although it is unclear what role these meadows play in the wider ecosystem context, their large extent, large number of colonies, and added structure in an otherwise low-structure habitat suggest their presence may be important for other taxa (Tissot et al. 2006; Baillon et al. 2012). Tissot et al. (2006) hypothesized that aggregations of sea pens may create important refugia for small invertebrates, alter current regimes, and influence prey availability. The sea pen meadows did not appear to host noticeably more abundant or diverse megafauna, but this does not preclude their potential importance for macrofauna or small life stages of mobile megafauna.

Acanella arbuscula (Figure 2-9c) or *Flabellum* spp. (Figure 2-9d) also dominated large tracts of seafloor. We observed both types of coral fields in fine sediments, sometimes with scattered gravel. In general, species richness in *A. arbuscula* fields was low with only a few species in any 10-m segment. Sea pens and *Flabellum* spp. (Figure 2-8) were also present in *A. arbuscula* fields. Low coral species richness (≤ 2 species) also characterized fields with an abundance of *Flabellum* spp. Although few species were present in these fields, numbers of corals were considerable and appeared to represent unique ecosystems in this area.

2.4.3 Large scale patterns in species distributions and diversity

We observed at least 28 coral species during the seven dives. Murillo et al. (2010) found only 17 species on the Grand Banks during their bottom trawl surveys, Mortensen et al. (2006a) identified 12 species on the Grand Banks using a variety of techniques, and Wareham & Edinger (2007) recorded 30 species throughout all Newfoundland and Labrador waters. In a towed camera survey of more southerly canyons, Hecker et al. (1980) found at least 12 species of corals in Baltimore Canyon, 13 species in Lydonia Canyon, and 16 species in Oceanographer Canyon.

Our study represents the first observations for many deep-sea coral species in Newfoundland waters: *Heteropolypus* cf. *insolitu, Lepidisis* sp., *Bathypathes patula*, Schizopathidae n. gen. et n. sp., *Protoptilum carpenteri*, *Umbellula* sp. (likely *encrinus*), *Flabellum macandrewi*, and *Javania cailleti*. Other species found in this study confirm those recorded in extensive fishery and trawl surveys of the Grand Banks and surrounding areas, though several studies did not report *Chrysogorgia agassizi* (Gass & Willison 2005; Wareham & Edinger 2007; Murillo et al. 2010). Our cruise identified at least three species of *Flabellum*, compared to the one (*Flabellum alabastrum*) recorded by the other survey methods (Wareham & Edinger 2007; Murillo et al. 2010). Mortensen et al. (2006a) found *Flabellum macandrewi* along the Scotian Shelf and within The Gully off Nova Scotia, but not off Newfoundland and Labrador. *Pennatula aculeata* and *Pennatula grandis* were commonly found in surveys by Murillo et al. (2010), but at least three species of *Pennatula* could be distinguished from our video and require additional taxonomic and genetic work.

2.4.4 Coral size

Although the tallest *Keratoisis grayi* was 215 cm in height, many colonies were greater in width than height (e.g., 160 x 250 cm and 200 x 230 cm). The ages and growth rates of corals sampled suggest that the 215 cm tall *K. grayi* is likely over 200 years old (Sherwood and Edinger 2009). The tallest Schizopathidae n. gen. et n. sp. (incorrectly identified as *Stauropathes arctica* in Sherwood and Edinger (2009)) was over 50 years old, and the tallest *Acanella arbuscula* (30 cm) was approximately 30 years old. These large sizes and slow growth rates highlight the slow recovery times for disturbed coral assemblages and the need for strong conservation measures in the deep sea.

2.4.5 Conservation implications

Scientists recognize the importance of protecting deep-sea corals (Roberts & Hirshfield 2004), which is often achieved through protected areas (Brock et al. 2009). But despite the growing international push for coral protection, no official marine protected areas currently exist off Newfoundland and Labrador to protect deep-sea corals within Canadian waters. Conservation objectives should guide selection of which areas to protect. Many conservation efforts prioritize protection of high concentrations / abundances of corals, high species richness, or unique corals. Our high-resolution video surveys provide *in situ* observations and highlight patterns that can be used to help guide future conservation initiatives.

If the objective is to protect rare, unique assemblages of corals, our results indicate that known deep-sea outcrops off Newfoundland would be an appropriate starting point, given the relatively rare species for this region present at outcrops, such as *Paragorgia arborea*, antipatharians, and several species of cup corals. Protection of high coral species richness should concentrate on upper to middle slope areas with a variety of substratum including boulders, cobble, and fine sediments. Selection of areas to protect high abundances of corals varies with species. The middle to upper slope with large areas of relatively hard substrate should be targeted if the goal is to protect large, fragile corals (such as gorgonians and antipatharians). Although conservation priorities should not shift from rarer species, conservation efforts should at least consider common species as well (Gaston 2010). More common species (such as sea pens and *Flabellum* spp.) tend to be overlooked in conservation initiatives (for example Edinger et al. 2007; Brock et al. 2009), *in lieu* of large, spectacular corals or deep-water coral reefs. The fine sediment habitats where these common species occur contain unique coral assemblages and often have abundant corals.

Nevertheless, we believe the most successful conservation initiative for deep-sea corals off Atlantic Canada would take a holistic approach to conservation planning and use a representative network of protected areas to help conserve a variety of species and assemblages.

In 2008, the Northwest Atlantic Fisheries Organization (NAFO) created a closed area for corals off the slope of the Grand Banks to protect corals from bottom fishing (NAFO 2011). The protection zone runs roughly along the 800 – 1000 m isobath crossing into Canada's exclusive economic zone (Rogers & Gianni 2010). In general, our results show the highest abundance of fragile corals and highest species richness occur on the upper to middle slope, adding to the growing research that indicates this zone is too deep for its intended purpose (Rogers & Gianni 2010). Therefore, this zone should be extended into shallower waters where corals currently remain at risk to fishing activities.

2.4.6 Future work

Although this study illuminates general patterns of deep-sea coral occurrence off Newfoundland, the unique sampling problems associated with deep-sea corals necessitates much more *in situ* research in this region. Studies should aim to collect detailed multibeam bathymetry data (Dolan et al. 2008), geological samples, sedimentation rates, current speed and direction (Mortensen & Buhl-Mortensen 2004), and temporal and spatial trends in primary productivity to understand better the processes driving coral distributions. Many sites thought to be important for corals based on fishing or trawl survey data (Edinger et al. 2007) remain unexplored with other methods, constraining any comprehensive understanding of coral abundances, assemblages, and diversity. Meanwhile, deep-water fishing (especially bottom trawling) activities continue to threaten corals, and as long these activities remain our primary data source, destruction will outpace our understanding of coral distributions and assemblage patterns.

2.5 Literature cited

Althaus F., Williams A., Schlacher T.A., Kloser R.J., Green M.A., Barker B.A., Bax N.J., Brodie P., Schlacher-Hoenlinger M.A. (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series 397: 279-294.

Baillon S., Hamel J.-F., Wareham V.E., Mercier A. (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10(7): 351-356.

Beazley L. (2011) Reproductive biology of the deep-water gorgonian coral *Acanella arbuscula* from the Northwest Atlantic. Department of Biology. Dalhousie University, Halifax, NS: 144.

Benjamin R. (2007) ClassAct Mapper. Fisheries and Oceans Canada, Dartmouth, NS.

Brock R., English E., Kenchington E., Tasker M. (2009) The alphabet soup that protects cold-water corals in the North Atlantic. Marine Ecology Progress Series 397: 355-360.

Brooke S.D., Holmes M.W., Young C.M. (2009) Sediment tolerance of two different morphotypes of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico. Marine Ecology Progress Series 390: 137-144.

Buhl-Mortensen L., Vanreusel A., Gooday A.J., Levin L.A., Priede I.G., Buhl-Mortensen P., Gheerardyn H., King N.J., Raes M. (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31(1): 21-50.

Clarke K.R., Gorley R.N. (2006) PRIMER v6: user manual / tutorial. PRIMER-E, Plymouth.

Cordes E.E., McGinley M.P., Podowski E.L., Becker E.L., Lessard-Pilon S., Viada S.T., Fisher C.R. (2008) Coral communities of the deep Gulf of Mexico. Deep-Sea Research Part I: Oceanographic Research Papers 55(6): 777-787.

CSSF (2010). Canadian Scientific Submersible Facility. www.ropos.com, Accessed November.

Dolan M.F.J., Grehan A.J., Guinan J.C., Brown C. (2008) Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data. Deep-Sea Research Part I: Oceanographic Research Papers 55(11): 1564-1579.

Edinger E.N., Baker K.D., Devillers R., Wareham V. (2007) Coldwater corals off Newfoundland and Labrador: distribution and fisheries impacts. World Wildlife Fund, Toronto, Canada: 41 pp.

Etnoyer P., Morgan L.E. (2005) Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: A. Freiwald & J.M. Roberts (Eds). Cold-water corals and ecosystems. Springer-Verlag, Berlin. 331-343 pp.

Fiege D., Barnich R. (2009) Polynoidae (Annelida: Polychaeta) associated with cold-water coral reefs of the northeast Atlantic and the Mediterranean Sea. In: N.J. Maciolek & J.A. Blake (Eds). Proceedings of the 9th International Polychaete Conference 149-164 pp.

Forsterra G., Beuck L., Haussermann V., Freiwald A. (2005) Shallow-water *Desmophyllum dianthus* (Scleractinia) from Chile: characteristics of the biocoenoses, the bioeroding community, heterotrophic interactions and (paleo)-bathymetric implications. In: A. Freiwald & J.M. Roberts (Eds). Cold-water corals and ecosystems. Springer-Verlag, Berlin. 937-977 pp.

Fossa J.H., Mortensen P.B., Furevik D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471: 1-12.

Gass S.E., Willison J.H.M. (2005) An assessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge. In: A. Freiwald & J.M. Roberts (Eds). Cold-Water corals and ecosystems 223-245 pp.

Gaston K.J. (2010) Valuing common species. Science 327(5962): 154-155.

Guinotte J.M., Fabry V.J. (2008) Ocean acidification and its potential effects on marine ecosystems. Annals of the New York Academy of Sciences 1134: 320-342.

Hall-Spencer J.M., Rodolfo-Metalpa R., Martin S., Ransome E., Fine M., Turner S.M., Rowley S.J., Tedesco D., Buia M.C. (2008) Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454(7200): 96-99.

Hecker B., Blechschmidt G. (1980) Appendix A: Epifauna of the Northeastern US Continental Margin, Final historical coral report for the Canyon Assessment Study in the Mid- and North Atlantic areas of the US outer continental shelf. In: B. Hecker, G. Blechschmidt & P. Gibson (Eds). Canyon Assessment Study. US Department of Interior Bureau of Land Management, Washington, DC.

Hecker B., Blechschmidt G., Gibson P. (1980) Epifaunal zonation and community structure in three Mid- and North Atlantic canyons. US Department of Interior Bureau of Land Management, Washington, DC.

Henry L.A., Roberts J.M. (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Research Part I: Oceanographic Research Papers 54(4): 654-672.

Husebo A., Nottestad L., Fossa J.H., Furevik D.M., Jorgensen S.B. (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91-99.

Krieger K.J., Wing B.L. (2002) Megafauna associations with deepwater corals (*Primnoa spp.*) in the Gulf of Alaska. Hydrobiologia 471: 83-90.

Mortensen P.B., Buhl-Mortensen L. (2004) Distribution of deep-water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). Marine Biology 144(6): 1223-1238.

Mortensen P.B., Buhl-Mortensen L. (2005) Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada In: A. Freiwald & J.M. Roberts (Eds). Cold-water Corals and Ecosystems. Springer-Verlag, Berlin. 247-277 pp.

Mortensen P.B., Buhl-Mortensen L., Gass S.E., Gordon D.C., Kenchington E., Bourbonnais C., Macsaac K.G. (2006a) Deep-water corals in Atlantic Canada: A summary of ESRF-funded Research (2001-2003): 83 pp.

Mortensen P.B., Buhl-Mortensen L., Gordon D.C. (2006b) Distribution of deep-water corals in Atlantic Canada. Proceedings of the 10th International Coral Reef Symposium: 1832-1848.

Murillo F.J., Durán Muñoz P., Altuna A., Serrano A. (2010) Distribution of deep-water corals of the Flemish Cap, Flemish Pass, and the Grand Banks of Newfoundland (Northwest Atlantic Ocean): interaction with fishing activities. ICES Journal of Marine Science 68(2): 319.

NAFO (2011) Northwest Atlantic Fisheries Organization. www.nafo.int, Accessed 30 Sept.

Packer D., Boelke D., Guida V., McGee L. (2007) State of deep coral ecosystems in the Northeastern US region: Maine to Cape Hatteras. In: S.E. Lumsden, T.F.

Hourigan, A. Bruckner & G. Dorr (Eds). The State of Deep Coral Ecosystems of the United States. NOAA, Silver Spring, MD. 195-231 pp.

Roark E.B., Guilderson T.P., Dunbar R.B., Fallon S.J., Mucciarone D.A. (2009) Extreme longevity in proteinaceous deep-sea corals. Proceedings of the National Academy of Sciences of the United States of America 106(13): 5204-5208.

Roberts J.M., Brown C.J., Long D., Bates C.R. (2005) Acoustic mapping using a multibeam echosounder reveals cold-water coral reefs and surrounding habitats. Coral Reefs 24(4): 654-669.

Roberts J.M., Wheeler A.J., Freiwald A. (2006) Reefs of the deep: The biology and geology of cold-water coral ecosystems. Science 312(5773): 543-547.

Roberts J.M., Wheeler A.J., Freiwald A., Cairns S. (2009) Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats. Cambridge University Press, New York: 334 pp.

Roberts S., Hirshfield M. (2004) Deep-sea corals: out of sight, but no longer out of mind. Frontiers in Ecology and the Environment 2(3): 123-130.

Rogers A., Gianni M. (2010) The implementation of UNGA Resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas. International Programme of the State of the Ocean, London, UK: 97 pp.

Ross S.W., Quattrini A.M. (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Research Part I: Oceanographic Research Papers 54(6): 975-1007.

Schembri P.J., Dimech M., Camilleri M., Page R. (2007) Living deep-water *Lophelia* and *Madrepora* corals in Maltese waters (Strait of Sicily, Mediterranean Sea). Cahiers de Biologie Marine 48(1): 77-83.

Sherwood O.A., Edinger E.N. (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 66(1): 142-152.

Thrush S.F., Hewitt J.E., Funnell G.A., Cummings V.J., Ellis J., Schultz D., Talley D., Norkko A. (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. Marine Ecology Progress Series 223: 277-286.

Tissot B.N., Yoklavich M.M., Love M.S., York K., Amend M. (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fishery Bulletin 104(2): 167-181.

Turley C.M., Roberts J.M., Guinotte J.M. (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26(3): 445-448.

Wareham V.E., Edinger E.N. (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. Bulletin of Marine Science 81(1): 289-313.

Williams G.C. (2011) The global diversity of sea pens (Cnidaria: Octocorallia: Pennatulacea). PLoS ONE 6(7): 1-11.

Zedel L., Fowler W.A. (2009) Comparison of boundary layer current profiles in locations with and without corals in Haddock Channel, southwest Grand Banks. In: K. Gilkinson & E.N. Edinger (Eds). The ecology of deep-sea corals of Newfoundland and Labrador waters: biogeography, life history, biogeochemistry, and relation to fish. Canadian Technical Report of Fisheries and Aquatic Sciences 97-104 pp.

Table 2-1. Dives from an ROV cruise on the slope of the southwest Grand Banks of Newfoundland in 2007, and their associated depths, time on bottom, and distance covered.

Dive	Date	Depth range	Time on bottom (h)	Distance (km)
R1065	16 – 17 July	606 – 1015 m	12.6	10.7
R1066	17 – 18 July	493 – 1020 m	16.0	15.8
R1067	18 – 19 July	395 – 996 m	10.2	13.4
R1068	19 July	1990 – 2245 m	4.5	5.9
R1070	21 July	351 – 940 m	15.5	23.6
R1071	22 – 23 July	353 – 1174 m	12.8	16.9
R1072	23 – 24 July	1116 – 1900 m	18.8	19.0
Total			90.4	105.3

Table 2-2. Number of 10-m transect segments in each dive, in relation to depth categories and bottom types from an *in situ* survey off the southwest Grand Banks of Newfoundland in 2007.

Depth (m)	Bottom type	ROPOS dive number R1065	R1066	R1067	R1068	R1070	R1071	R1072	Total
300-800	Mud-sand	159	192	14		490	371		1226
	Gravel		35	8		56	9		108
	Cobble	98	345	320		223	54		1040
	Boulders	30	75	124		7	17		253
	Outcrop			1					1
800-1300	Mud-sand	200	203	103		507	289	246	1548
	Gravel	2							2
	Cobble	14		1					15
	Boulders	4						3	7
	Outcrop			2					2
1300-2300	Mud-sand				101			640	741
	Gravel				69			6	75
	Cobble				7				7
	Outcrop							6	6
Total		507	850	573	177	1283	740	901	5031

Table 2-3. Taxonomic composition, abundance, and heights of coral colonies found off the southwest Grand Banks of Newfoundland during the 2007 *in situ* survey.

Coral group	Species	Number observed	Maximum height (cm)	Average height (cm)
Antipatharians	*Bathypathes patula*	1	15	
	Schizopathidae n. gen. et n. sp.	2	> 60	58
	Antipatharian (unidentified)	1	50	
Scleractinians	*Vaughanella* sp.	7		
	Desmophyllum dianthus	143		
	Flabellum alabastrum	6965		
	Flabellum macandrewi	320		
	Flabellum spp.	7894		
	Javania cailleti	4		
	Scleractinian (unidentified)	5		
Gorgonians	*Keratoisis grayi*	5116	215	37
	Lepidisis sp.	1	30	
	Acanella arbuscula	24334	30	9
	Isididae (unidentified)	3	30	30
	Paramuricea spp.	32	45	15
	Paragorgia arborea	3	20	12
	Radicipes gracilis	212		
	Chrysogorgia agassizii	80	30	13
	Acanthogorgia armata	7688	51	8
	Gorgonian (unidentified)	2	50	38
Alcyonaceans	*Anthomastus* spp.	3239		
	Heteropolypus cf. *insolitus*	4869		
	Duva florida	232		
	Neptheidae (unidentified)	417		
Pennatulaceans	*Anthoptilum grandiflorum*	355		
	Funiculina quadrangularis	4694		
	Halipteris finmarchica	1681		
	Kophobelemnon stelliferum	1812		
	Pennatula grandis	6032		
	Pennatula sp. 1	152		
	Pennatula sp. 2	67752		
	Pennatula (unidentified)	11350		
	Protoptilum carpenteri	3086		
	Distichoptilum gracile	665		
	Umbellula spp.	20		
	Pennatulacea (unidentified)	2220		
Unknown	Coral – Unidentified	11		

Table 2-4. Maximum abundance of corals in 10-m transect segments. Depth and dive of maximum abundance are noted. Coral abundance with a maximum of 1 are not included.

Coral group	Species	Maximum abundance	Depth (m)	Dive
Scleractinians	*Desmophyllum dianthus*	61	1506	R1072
	Flabellum spp.	300	380	R1070
Gorgonians	*Keratoisis grayi*	43	573	R1067
	Acanella arbuscula	77	639	R1065
	Paramuricea spp.	3	664	R1065
	Radicipes gracilis	31	1427	R1072
	Chrysogorgia agassizii	3	2243	R1068
	Acanthogorgia armata	36	540	R1066
Alcyonaceans	*Anthomastus* spp.	54	573	R1067
	Heteropolypus cf. *insolitus*	123	611	R1070
	Duva florida	35	406	R1070
Pennatulaceans	*Anthoptilum grandiflorum*	3	843	R1070
	Funiculina quadrangularis	17	930	R1070
	Halipteris finmarchica	12	437	R1071
	Kophobelemnon stelliferum	13	585	R1071
	Pennatula sp. 1	7	912	R1071
	Pennatula spp.	622	835	R1071
	Protoptilum carpenteri	9	993	R1071
	Distichoptilum gracile	4	1323	R1072
	Distichoptilum gracile	4	1294	R1072

Table 2-5. Maximum species richness and number of coral colonies in 10-m transect segments in a variety of habitat categories.

	Habitat category	Maximum species richness	Maximum number of colonies
Sediment type	Outcrop	3	61
	Boulders	7	99
	Cobble	7	82
	Gravel	5	200
	Mud-sand	6	625
Depth category	300 – 800 m	7	301
	800 – 1300 m	6	625
	1300 – 2300 m	4	61
Dive	R1065	6	79
	R1066	7	183
	R1067	7	99
	R1068	2	4
	R1070	6	301
	R1071	6	625
	R1072	5	61

Table 2-6. Results from two-way Analysis of Similarity (ANOSIM) to compare coral assemblages between depths and sediment types from a ROV survey off the southwest Grand Banks of Newfoundland in 2007.

Comparison group	R statistic	Level of significance (p)	Permutations > R
Depth – global test	0.302	0.001	0
300 – 800, 800 – 1300 m	0.239	0.001	0
300 – 800, 1300 – 2300 m	0.471	0.001	0
800 – 1300, 1300 – 2300 m	0.292	0.001	0
Sediment type – global test	0.224	0.001	0
Mud-sand, Boulders	0.316	0.001	0
Mud-sand, Cobble	0.171	0.001	0
Mud-sand, Gravel	0.222	0.001	0
Mud-sand, Outcrop	0.552	0.001	0
Boulders, Cobble	0.073	0.001	0
Boulders, Gravel	0.440	0.001	0
Boulders, Outcrop	0.560	0.069	68
Cobble, Gravel	0.191	0.001	0
Cobble, Outcrop	0.585	0.020	19
Gravel, Outcrop	0.466	0.001	0

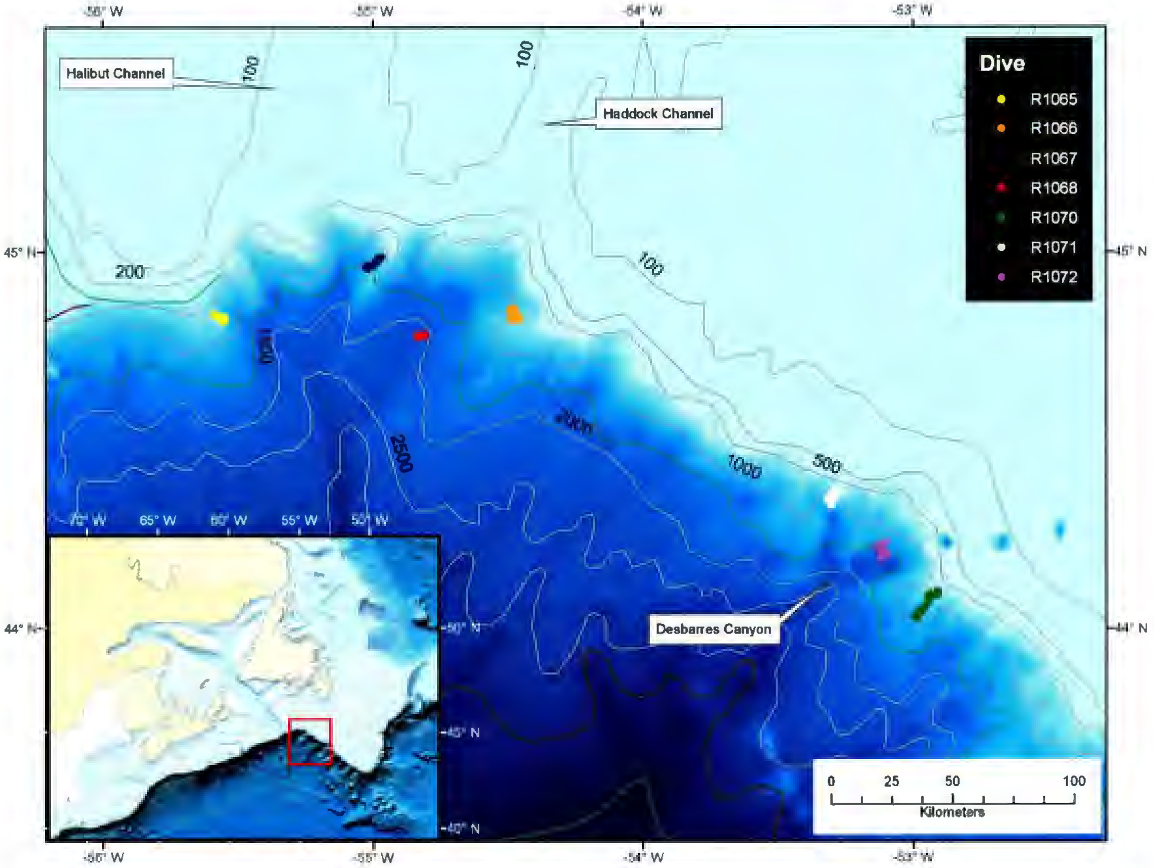

Figure 2-1. Map illustrating location of ROV dive sites during a 2007 cruise off the southwest Grand Banks of Newfoundland, Canada.

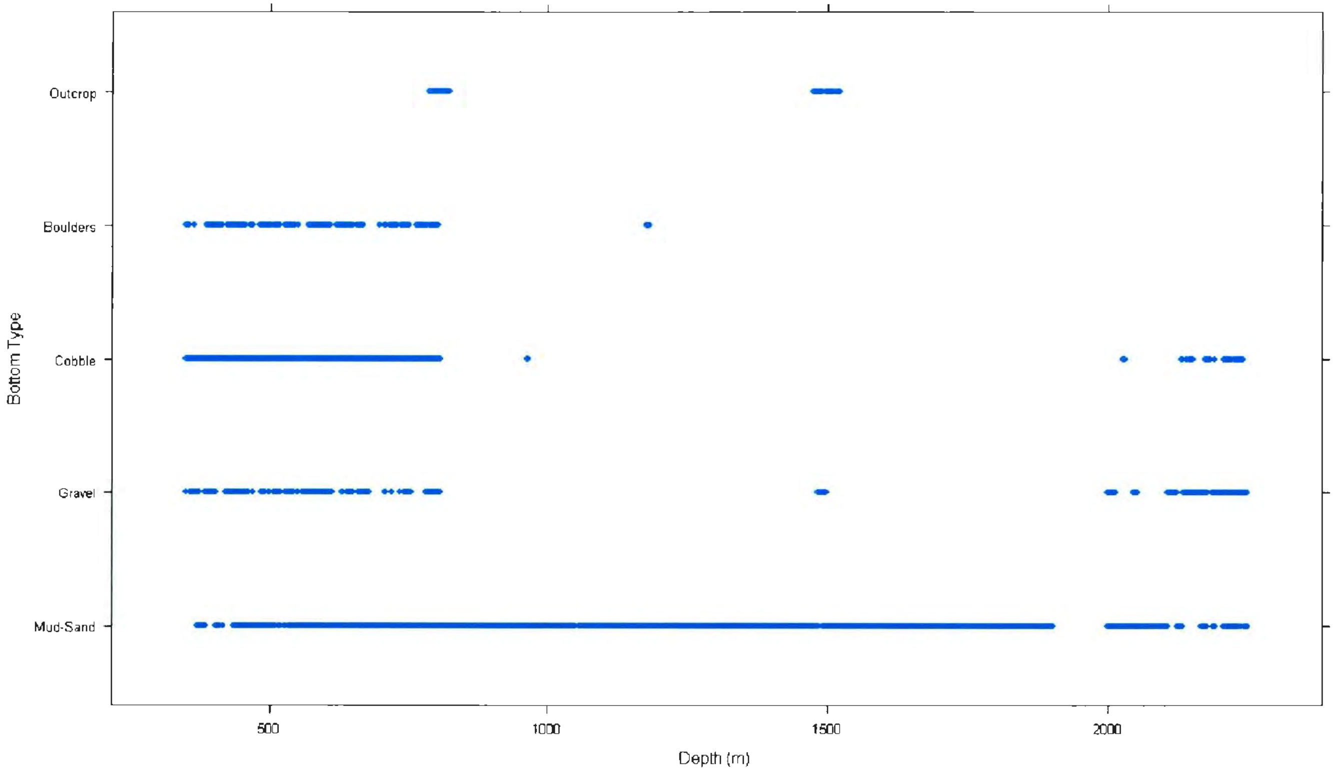

Figure 2-2. Depth and sediment type surveyed off the southwest Grand Banks of Newfoundland during the 2007 *in situ* survey. Each point represents one second of video footage while the remotely operated vehicle was moving forward with an unobstructed view of the seafloor.

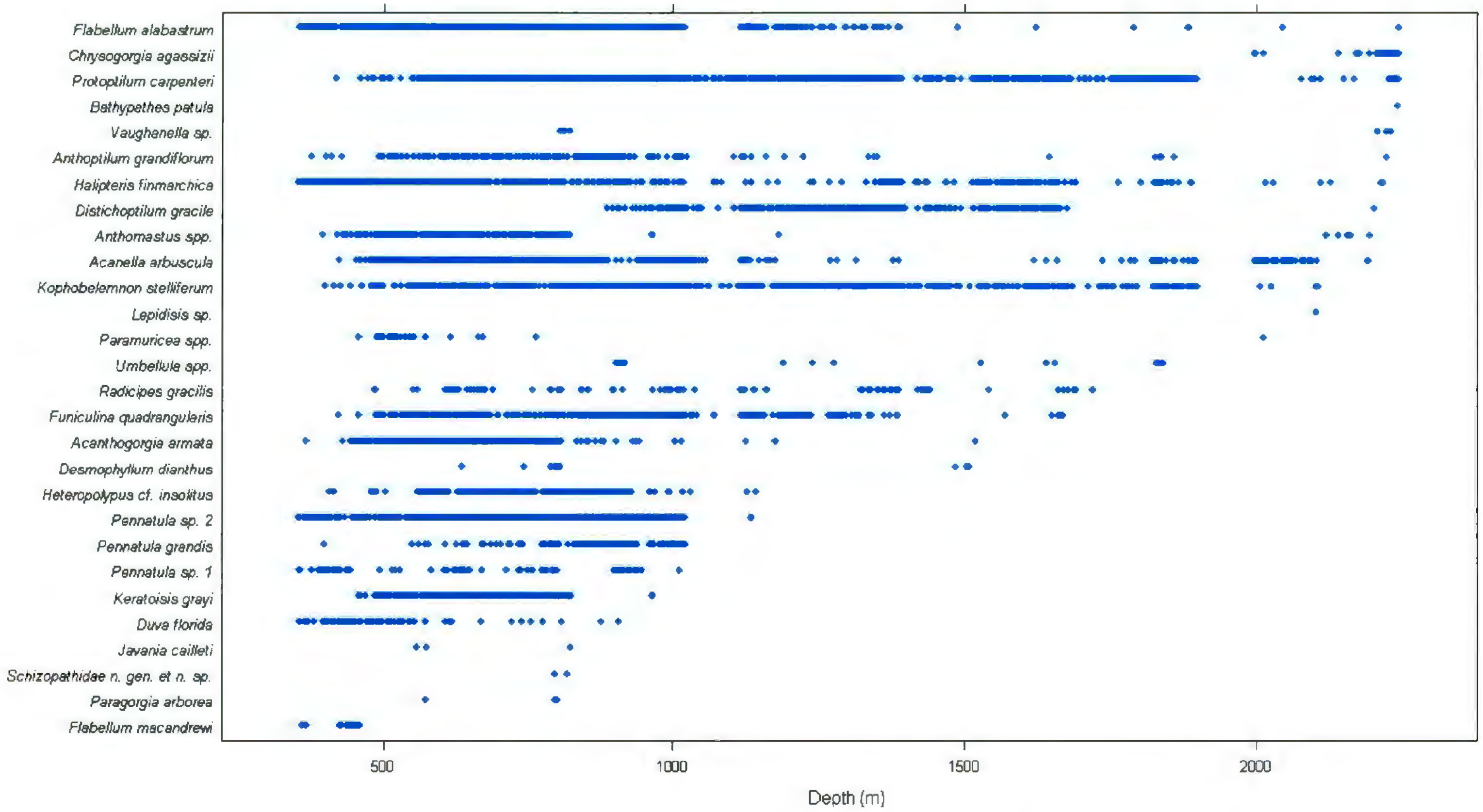

Figure 2-3. Depth distributions of coral species observed off the southwest Grand Banks of Newfoundland during the 2007 *in situ* survey. Each point represents a single coral observation.

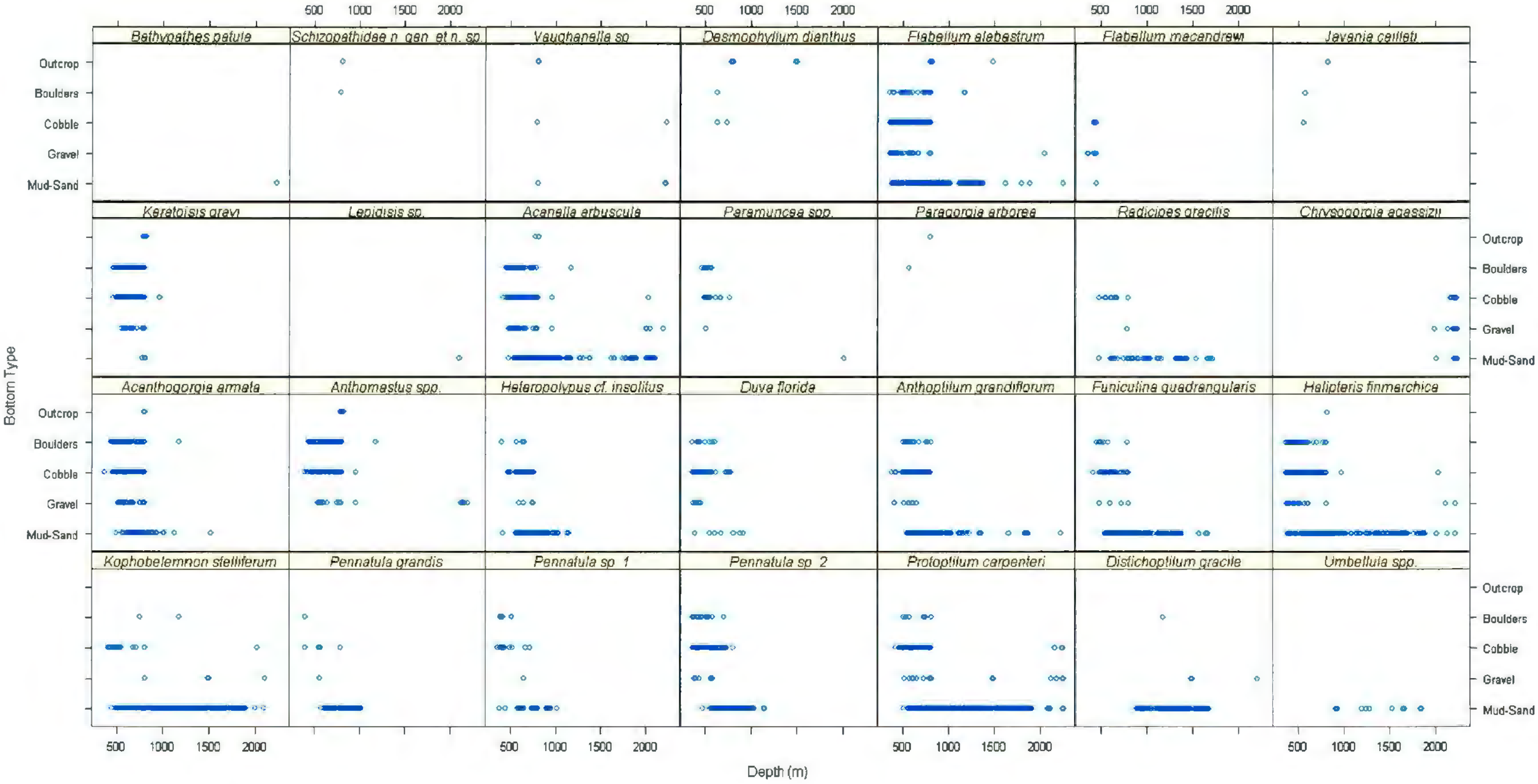

Figure 2-4. Depth and sediment type of habitats where corals were observed off the southwest Grand Banks of Newfoundland during the 2007 *in situ* survey. Each point represents a single coral observation.

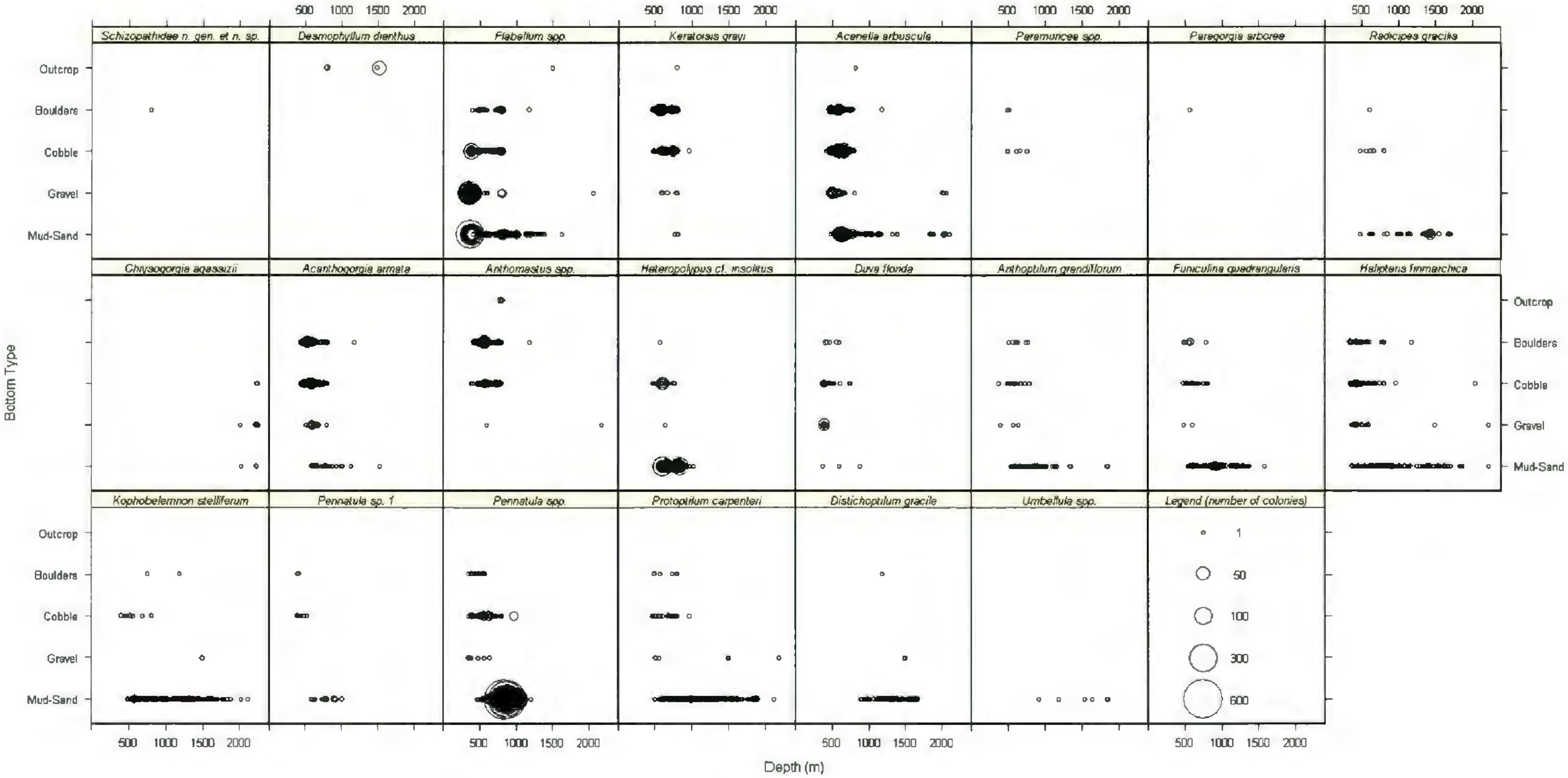
Schizopathidae n. gen. et n. sp.
Desmophyllum dianthus
Flabellum spp.
Keratoisis grayi
Acanella arbuscula
Paramuricea spp.
Paragorgia arborea
Radicipes gracilis
Chrysogorgia agassizii
Acanthogorgia armata
Anthomastus spp.
Heteropolypus cf. insolitus
Duva florida
Anthoptilum grandiflorum
Funiculina quadrangularis
Halipteris finmarchica
Kophobelemnon stelliferum
Pennatula sp. 1
Pennatula spp.
Protoptilum carpenteri
Distichoptilum gracile
Umbellula spp.
Legend (number of colonies)
1
50
100
300
600
Outcrop
Boulders
Cobble
Gravel
Mud-Sand
Bottom Type
500
1000
1500
2000
Depth (m)

Figure 2-5. The number of coral colonies found in 10-m transect segments plotted in relation to depth and sediment type (from *in situ* surveys off the southwest Grand Banks of Newfoundland in 2007). The sizes of the circles are directly proportional to the square root of the number of colonies.

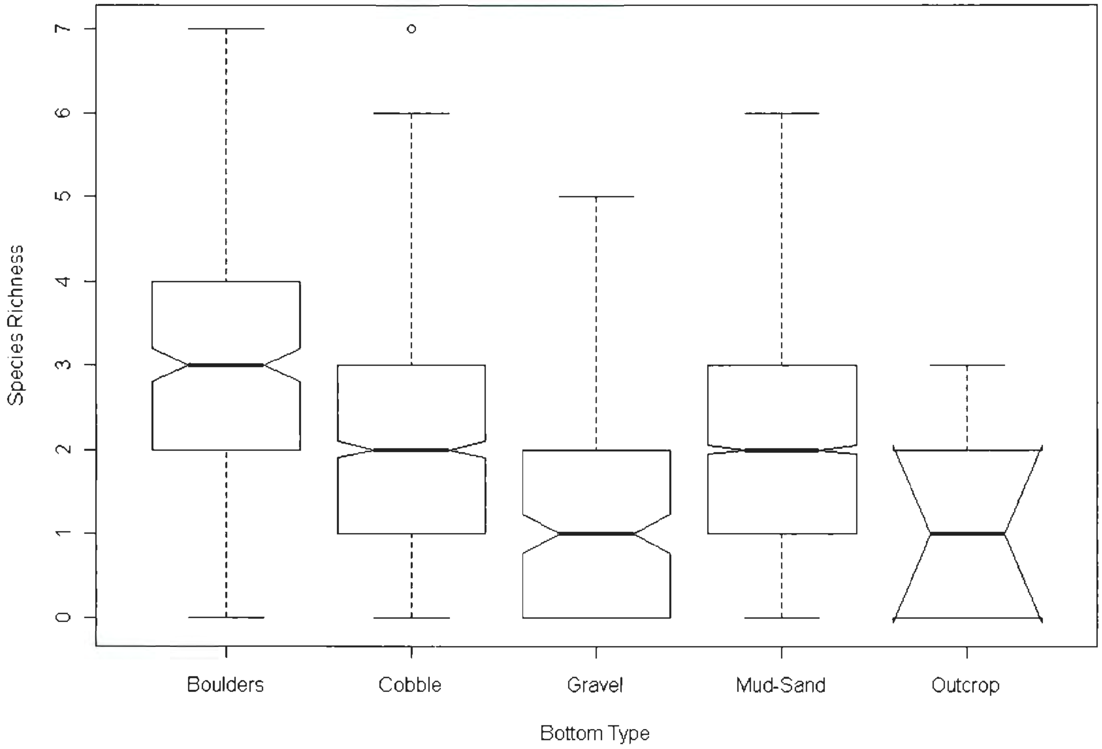

Figure 2-6. Box and whisker plot of species richness in relation to sediment type from 10-m transect segments recorded by an ROV off the southwest Grand Banks of Newfoundland, Canada in 2007. The median, upper and lower quartiles, minimum and maximum values, and an outlier of species richness are illustrated.

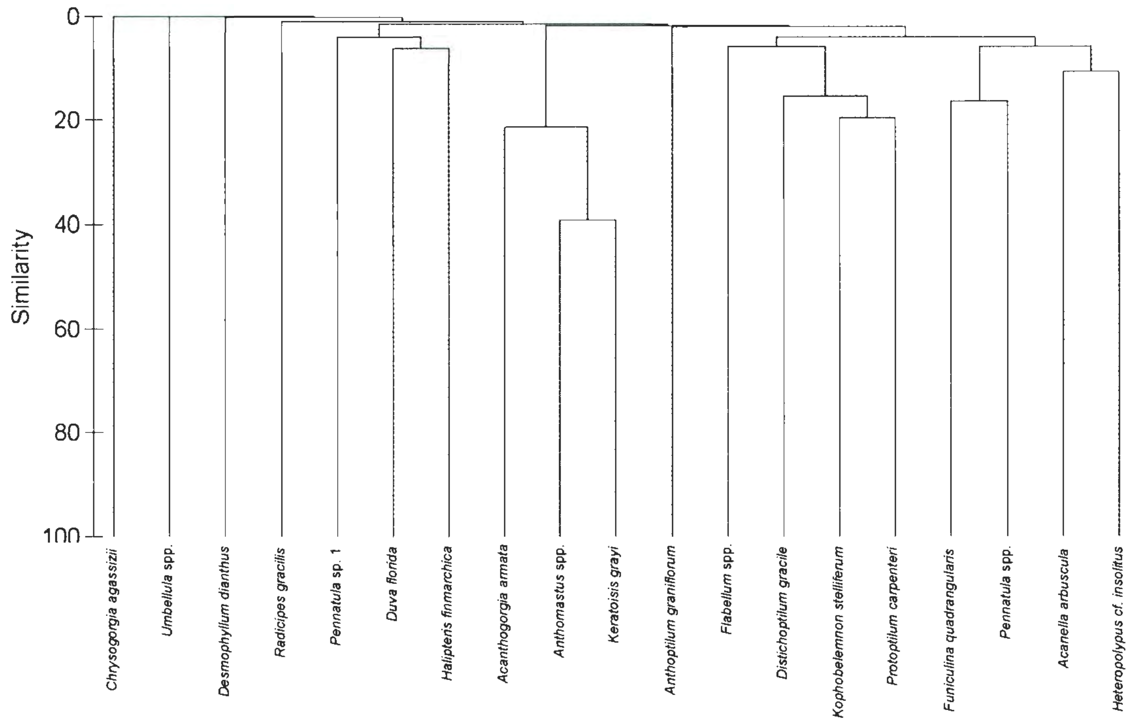

Figure 2-7. Dendrogram of species, using group-average clustering from Bray-Curtis similarities on standardized samples (data collected using an ROV off the southwest Grand Banks of Newfoundland in 2007).

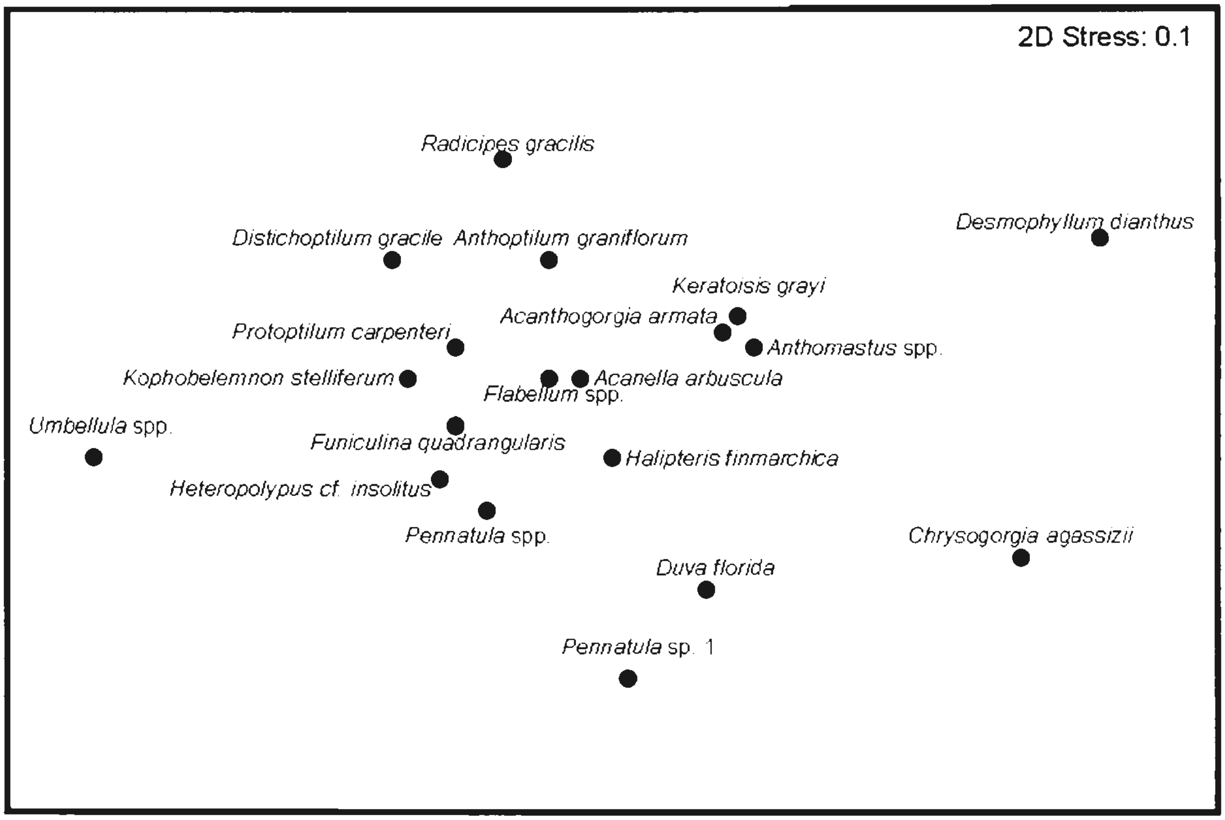

Figure 2-8. MDS plot of Bray-Curtis similarity matrix based on standardized samples and species that contribute at least 50 % to a sample (data collected using an ROV off the southwest Grand Banks of Newfoundland in 2007).

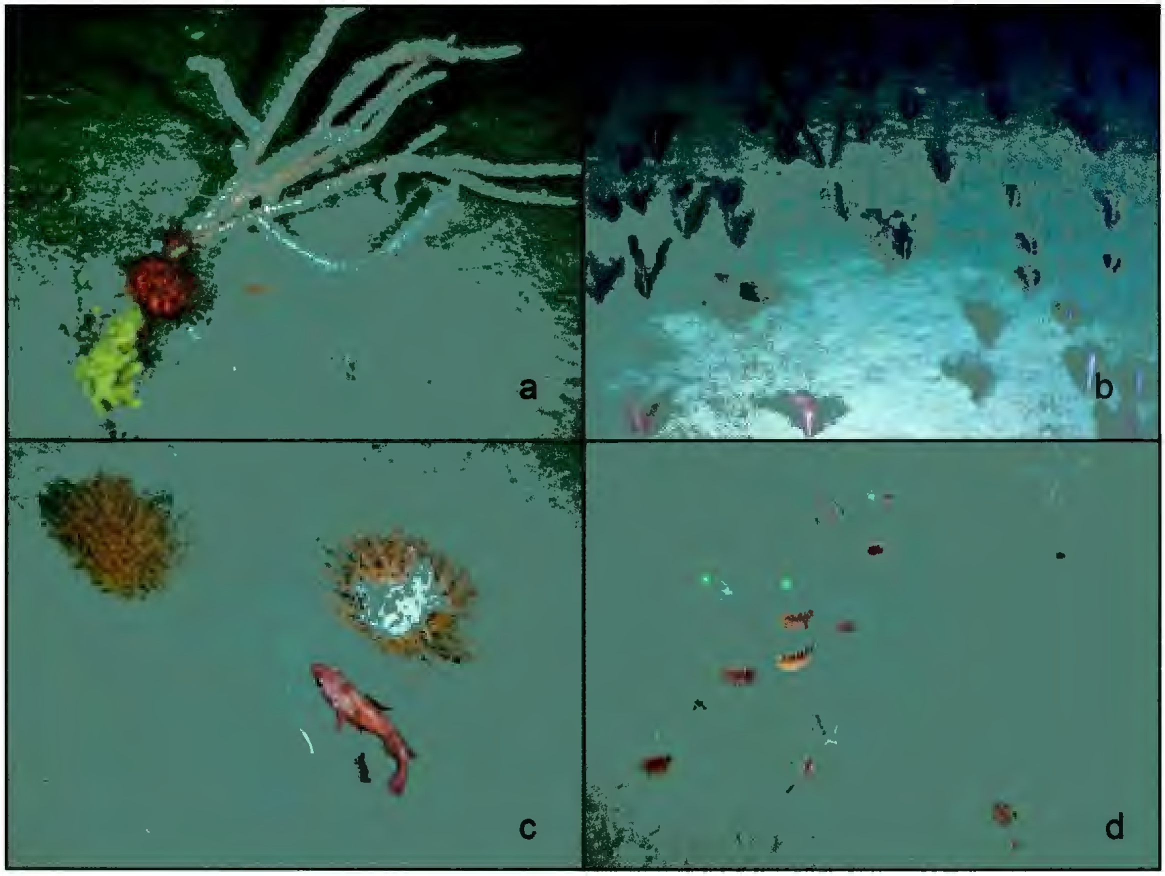

Figure 2-9. Photos of coral in ROPOS transects off the southwest Grand Banks of Newfoundland in 2007; (a) assemblage of *Keratoisis grayi*, *Anthomastus* sp., and *Acanthogorgia armata* on a small boulder during dive R1065 at 671 m (*Flabellum* sp. can also be seen), (b) sea pen field (mostly *Pennatula* spp.) in fine-sediment habitat (R1071, 835 m), (c) close up view of two *Acanella arbuscula* in fine sediments with *Sebastes* sp. (R1071, 594 m), (d) view of *Flabellum* spp. in fine sediments during dive R1065 at 946 m.

3 Small-scale patterns and the effects of trawling on the condition of bamboo coral, *Keratoisis grayi,* in canyons on the Grand Banks, Newfoundland

Abstract

We employed *in situ* data collected in three canyons off the Grand Banks, Newfoundland to quantitatively examine the influence of depth, bottom type, canyon, and trawling intensity on the distribution, abundance, height, and status of *Keratoisis grayi*, a large and abundant gorgonian coral in this region. While surveying 105 km of seafloor with a remotely operated vehicle, we observed 5770 *K. grayi* colonies and 167 trawl marks. We found that *K. grayi* were significantly more likely to occur in boulder areas than in cobble or gravel. We found a significant positive relationship between bottom depth and colony height and the largest colonies were found in boulder areas in Halibut Channel, and in boulder and cobble areas in Haddock Channel. The majority of colonies observed were undamaged, but we also recorded overturned, broken, dead and partially dead colonies. *Keratoisis grayi* colonies were more likely to occur in trawled areas, but these colonies were more likely to be broken, smaller in size, and less abundant than colonies outside trawled areas. These results indicate that trawling has negatively impacted *K. grayi* colonies off Newfoundland and that fishers may disproportionately target areas where these corals occur.

3.1 Introduction

Deep-sea corals have garnered world-wide attention in recent years because of their potential longevity (Roark et al. 2009; Sherwood & Edinger 2009), importance for other taxa (Buhl-Mortensen et al. 2010), susceptibility to fishing damage (Dayton et al. 1995; Edinger et al. 2007; Althaus et al. 2009), and vulnerability to other anthropogenic disturbances such as oil and gas extraction and ocean acidification (Rogers 1999; Roberts & Hirshfield 2004; Guinotte et al. 2006; Hoegh-Guldberg et al. 2007). Deep-sea coral conservation concerns underscore the growing need to increase our understanding of factors influencing coral ecology and distributions at a range of spatial scales.

Previous studies related deep-sea coral distributional patterns to the aragonite saturation horizon (Guinotte et al. 2006; Davies & Guinotte 2011), temperature (Bryan & Metaxas 2006; Mortensen et al. 2006; Roberts et al. 2009), substrate (Roberts et al. 2009; Baker et al. 2012b), salinity (Mortensen et al. 2006; Davies & Guinotte 2011), and other environmental factors. For example, Paragorgiidae along the Atlantic continental margin occurred mainly between 300 - 500 m, in areas with slopes between 1.1° and 1.4°, temperatures 5 - 11 °C, currents between 10 – 30 cm s^{-1}, and low chlorophyll *a* concentrations (Bryan & Metaxas 2006). Watanabe et al. (2009) found that *Primnoa resedaeformis* abundance in the Northeast Channel, Canada correlated negatively with depth and positively with cobble and/or boulders.

Given the known vulnerability of coldwater corals to trawling damage, current distributional patterns could be related to current and past fishing intensity (Roberts et al. 2009). Cover of *Solenosmilia* spp. thickets was reduced by 2 orders of magnitude on actively trawled seamounts off Australia, compared to untrawled seamounts (Althaus et al. 2009). Fishing activities damaged an estimated 30 - 50 % of the total area covered by *Lophelia pertusa* in Norwegian waters (Fossa et al. 2002), and illegal trawling activity was blamed for destruction of all but 10 % of *Oculina* spp. in a Florida reserve (Koenig et al. 2005).

The coral colonies that remain in previously trawled areas may be heavily damaged. Only 31 *Primnoa* spp. colonies remained in a trawl path seven years after the removal of 1 ton of corals in 1990 in the Gulf of Alaska. Of these, five large colonies were missing 95 - 99 % of their branches and 80 % of the polyps were missing from two smaller colonies (Krieger 2001). On actively trawled seamounts off Australia, the densities of *Solenosmilia variabilis* with broken bases were significantly higher compared to seamounts not currently trawled (Althaus et al. 2009).

Keratoisis grayi (synonym: *K. ornata*), a long-living bamboo coral found throughout the North Atlantic and Mediterranean Sea (Appeltans et al. 2012), is among the most common large gorgonians off Newfoundland and Labrador, Canada (Wareham & Edinger 2007; Baker et al. 2012b). Using Fisheries and Oceans Canada fisheries observer and survey data from that region, Wareham and Edinger (2007) documented *K. grayi* at depths from 195 to 1,262 m. Baker et al. (2012b) found *K. grayi* often co-occurred with *Acanthogorgia armata* and *Anthomastus* spp. at relatively shallow depths (< 1000 m) with boulders and cobbles. *Keratoisis grayi* was associated with steep topography and semi-consolidated mudstone in a submarine canyon off Nova Scotia (Mortensen & Buhl-Mortensen 2005). Large gorgonians (including *K. grayi*) were recorded as bycatch in multiple fisheries including trawl sets (*Pandalus borealis*, *Reinhardtius hippoglossoides*, and *Sebastes* spp. fisheries), crab pots, longlines (*Reinhardtius hippoglossoides* and *Hippoglossus hippoglossus* fisheries), and gillnets (*Reinhardtius hippoglossoides* and *Sebastes* spp. fisheries) off Newfoundland between 2004 and 2005 (Edinger et al. 2007), illustrating the vulnerability of *K. grayi* to fishing disturbances.

We employed *in situ* data collected in three canyons off the Grand Banks to quantitatively examine the influence of depth, bottom type, canyon, and trawling intensity on *Keratoisis grayi* abundance, height, and status at small spatial scales.

3.2 Methods

3.2.1 Video surveys

We used the remotely operated vehicle (ROV), ROPOS (Remotely Operated Platform for Ocean Sciences) (CSSF 2010) to explore three submarine canyons on the slopes of the Grand Banks south of Newfoundland: Halibut Channel, Haddock Channel, and Desbarres Canyon (Figure 2-1). We completed video surveys from *CCGS Hudson* during seven ROPOS dives between 16 - 24 July 2007 (see Baker et al. 2012a; Baker et al. 2012b for details). The ROV was equipped with lasers placed 10 cm apart to indicate scale. Depth, date, time, altitude (distance above bottom), temperature, and position were logged at 1-second intervals (though sporadic problems with the logger resulted in several long periods with no temperature data).

Based on known distributions of corals in relation to bathymetry, we planned 1-km long transects every 200 m of depth along depth contours between 2200 and 600 m and along contours every 100 m in waters shallower than 500 m (Baker et al. 2012b). We standardized transects by maintaining the ROV as close to the bottom as possible, at a constant slow speed (approx. 0.2 – 0.5 m s^{-1}) while tilting the camera down slightly on a wide-angle view in order to image the seafloor and water column directly above. Between pre-selected transects, we explored the area with ROPOS, capturing still images and video of interesting features, and collecting voucher specimens to validate visual identification.

3.2.2 Video processing

Using the program ClassAct Mapper (Benjamin 2007), we recorded continuous geo-referenced data describing bottom type, ROV mode, trawl marks, and corals. We identified all corals to the lowest possible taxonomic level (typically species) and measured colony height and diameter of *K. grayi* to the nearest 5 cm using the lasers for scale. Whenever possible, we quantified the general status of colonies using two descriptors: proportion of colony dead and overall status. We estimated the proportion of each colony that appeared to be dead (no living polyps or tissue) to the nearest 5 %, again using the lasers for scale. The overall status of each *K. grayi* colony (regardless of proportion dead) was scored as 'normal' (the colony appeared upright and intact), 'broken' (the colony or pieces of the colony appeared to be detached), or 'overturned' (the colony was tilted and laying against another object, such as the substrate). We classified colonies that were both broken and overturned as broken.

We characterized bottom type every second by primary (most abundant) substrate and secondary (next most abundant) substrate, with optional additional comments. Bottom types included (1) outcrop (vertically exposed bedrock and consolidated Quaternary sediment), (2) boulder (> 25 cm), (3) cobble (5 - 25 cm), (4) gravel (0.2 – 5 cm), or (5) mud-sand (fine-grain) sediments (Thrush et al. 2001).

'Transect-mode' defined any portion of the video when the ROV followed the prescribed methodology for transects (described above), regardless of whether the transect was planned. We combined all other ROV bottom activities as 'Other' (Baker et al. 2012b).

3.2.3 Data analysis

Commercial trawl-doors off Newfoundland spread approximately 116 m for flatfish trawlers (P. Winger, pers comm.) and 95 m for *Sebastes* spp. trawlers (W. Savoury, pers comm.). We therefore created circular 100-m buffers around each location (i.e. second) where a trawl mark was observed using ArcGIS 9.3 (ESRI 2008). We then calculated the frequency that each second of video coincided with a buffer to determine the potential trawling intensity at each location.

Our analysis considered the effect of average temperature, bottom type, depth, canyon, trawl intensity (Trawl), and their interactions on the abundance, height, and status of *K. grayi*. However, because average temperature and depth exhibited strong collinearity and 72 % of the colonies had no associated temperature records, we removed average temperature from consideration. When necessary, we used a $\log_{10}$-transformation of Trawl in our models (logTrawl). We used empirical variograms to ensure there were no significant spatial autocorrelations at multiple scales. All final models were chosen through backward selection using likelihood ratio tests to remove non-significant terms.

3.2.3.1 Abundance

We examined patterns in *K. grayi* colony abundance observed when the ROV was in transect-mode by splitting transects into 10-m segments (= sample unit) and summing the number of live *K. grayi* colonies (< 100 % dead) in each segment. Large, hard substrates influence *K. grayi* distribution (Baker et al. 2012b). Therefore, we used the largest sediment size in each 10-m segment to classify bottom type in that segment. We used mean depth of each 10-m segment as 'depth' and maximum number of trawl mark buffers coinciding with any point in the segment as the Trawl value for that segment. The 10-m segments in mud-sand, outcrops, or depths > 1000 m were removed from the analysis because of low sample size. Because the data were zero-inflated we chose a hurdle (zero-altered) model. A hurdle model consists of two parts: a binomial generalised linear model (GLM) to model presence/absence, combined with a count model for values greater than zero (Zuur et al. 2009). Our count data were overdispersed, so we implemented a truncated negative binomial GLM count model using the *Pscl* package (Jackman et al. 2011) in *R* (RDevCoreTeam 2012).

3.2.3.2 Height

We used all video (regardless of ROV mode) to examine patterns in *K. grayi* colony height, treating each *K. grayi* colony as a sample unit. Desbarres Canyon and mud-sand data were removed because of low sample size. A gamma GLM with identity link produced the best model for examining patterns in height of *K. grayi*.

3.2.3.3 Status

We examined all video for patterns in *K. grayi* status, again removing Desbarres Canyon and mud-sand data because of low sample size. Status was assessed using two approaches: proportion dead and overall status (normal, broken, or overturned).

Values of zero (n = 5037) and 1 (n = 317) strongly skewed the proportion dead (i.e. very few partially dead colonies were observed; n = 75), and common transformations related to proportional data (e.g. arcsine and logit) did not improve our ability to meet model assumptions. As a result, we categorized all colonies with any dead portions as 'dead/partially dead', thereby creating a binary response variable: dead/partially dead (1) or alive (0). We used a binomial GLM to examine patterns in live versus dead/partially dead colonies, and a multinomial logit model to examine overall status (normal, broken, or overturned).

3.3 Results

We surveyed approximately105 km (90 hours) of seafloor, and recorded a total of 5031 10-m segments using all dives and depth categories. We observed 5770 *K. grayi* colonies. Most *K. grayi* occurred in Halibut Channel (n = 4341) and Haddock Channel (n = 1427), whereas only two colonies were observed in Desbarres Canyon (Table 3-1).

We recorded 167 trawl marks (Table 3-2), spanning all canyons and depths from 377 m to 821 m. A total of 1086 *K. grayi* colonies occurred within at least one 100-m trawl buffer zone, and the greatest number of buffers overlapping with a *K. grayi* colony was 13 (n = 8).

3.3.1 Abundance

We enumerated a total of 3765 live *K. grayi* colonies while the ROV was in transect-mode, 2820 of which occurred in 10-m segments. Of the 10-m segments used in the model (n = 1422), a total of 440 segments contained *K. grayi*. The median of counts greater than zero in a 10-m segment was 3 and the maximum of 43 occurred at 573 m with boulders in Halibut Channel (Dive R1067).

Bottom type ($p < 0.0001$), Trawl ($p = 0.018$), and the interaction of Depth and Canyon ($p < 0.0001$) were significant predicators of live *K. grayi* presence within a 10-m segment (Table 3-3). Live *K. grayi* colonies were significantly more likely to be present as Trawl increased (Figure 3-1). The probability of *K. grayi* presence in boulders was significantly greater than in cobble ($p < 0.0001$) and gravel ($p < 0.0001$), but cobble and gravel did not differ significantly ($p = 0.053$).

The interaction of Depth and Bottom type was a significant predictor of *K. grayi* counts greater than zero ($p = 0.004$) (Table 3-3), and as trawl intensity (logTrawl) increased, counts of *K. grayi* decreased ($p < 0.0001$). Trawling intensity appeared to have the greatest negative influence on *K. grayi* counts during the first trawl (Figure 3-2). In cobble, counts were greatly influenced by depth, which was less obvious in boulders and gravel (Figure 3-2).

3.3.2 Height

Height (median = 30 cm) could be determined confidently for 4654 *K. grayi* colonies. The tallest colony (215 cm) occurred in cobble in the absence of trawling at 776 m in Halibut Channel.

Depth ($p < 0.0001$), logTrawl ($p < 0.0001$), and the interaction of Canyon and Bottom type ($p < 0.0001$) were significant predictors of *K. grayi* height (Table 3-3). We found a significant negative relationship between *K. grayi* colony height and logTrawl, and a significant positive relationship between height and depth. The predicted height of *K. grayi* increased by 7 cm for each 1-m increase in depth. In Halibut Channel, the largest colonies occurred in boulders, in contrast with Haddock Channel where the largest colonies occurred in cobble and boulders (Figure 3-3).

3.3.3 Status

The great majority of *K. grayi* colonies we recorded appeared to be undamaged (Table 3-1). LogTrawl ($p = 0.0001$) and the interaction of Canyon and Depth ($p < 0.0001$) were significant predictors of a *K. grayi* colony having dead portions ($n = 5428$) (Table 3-3). As logTrawl increased, so did the probability of recording a colony with dead portions (Figure 3-4). Depth strongly influenced the probability of *K. grayi* having dead portions in Haddock Channel, but not Halibut Channel. The probability of a *K. grayi* having dead portions in Haddock Channel was highest in the shallowest depths (Figure 3-4).

Canyon ($p < 0.0001$), Depth ($p = 0.004$) and logTrawl ($p < 0.0001$) were significant predictors of *K. grayi* overall status ($n = 5513$) (Table 3-3). As trawl intensity increased, the probability of a normal *K. grayi* colony decreased (Figure 3-5) and the probability of a broken colony increased ($p < 0.0001$) (Figure 3-5). There was no significant relationship between logTrawl and probability of a colony being overturned ($p = 0.848$). Normal *K. grayi* were more likely and broken colonies less likely in Halibut Channel ($p < 0.0001$) compared to Haddock Channel. There was no significant difference between canyons when comparing the probability of a colony being overturned ($p = 0.313$). As depth increased, the probability of a *K. grayi* colony being overturned decreased ($p = 0.003$) (Figure 3-5). There was no significant relationship between the probability of a colony being broken and depth ($p = 0.155$).

3.4 Discussion

3.4.1 Abundance

Keratoisis grayi colonies were significantly more likely to occur in boulder areas than cobble or gravel. This species requires hard substrate for attachment, therefore, we can expect that boulders create more available stable habitat for attachment than smaller substrate, such as gravel or cobble. Off Nova Scotia, *K. grayi* also associate with large, hard substrate (consolidated mudstone) (Mortensen & Buhl-Mortensen 2005).

We found significant interactions when modelling both presence and counts of *K. grayi*. The significant Depth*Canyon interaction when predicting *K. grayi* presence indicated that the probablity of finding *K. grayi* at a given depth differs between canyons. This contrast implies that although depth is important, other environmental factors that differ between canyons likely also influence *K. grayi* presence. The Depth*Bottom type interaction significantly predicted *K. grayi* counts. Other factors that co-vary with depth may account for the difference in *K. grayi* counts between bottom types. For example, current regime may change with depth and vary in effect among bottom types. Multiple environmental factors that we did not measure, such as current velocity, temperature, sedimentation rates, slope, and food availability that likely influence presence and abundance may differ among depths and/or canyons and therefore help to explain these interactions (Roberts et al. 2009; Watanabe et al. 2009).

3.4.2 Height

We found a significant positive relationship between bottom depth and colony height. Bubble gum coral, *Paragorgia arborea,* exhibited a similar positive relationship between colony size and depth in the Northeast Channel off Nova Scotia (Watanabe et al. 2009). Thresher (2009) found slower radial growth rates in bamboo corals collected at lower temperatures. The conjunction between greater colony size and slower colony growth rate implies that the deeper, taller corals have been growing for much longer periods of time without disturbance effects, compared to the shallower, faster growing colonies.

Our results predict that the largest bamboo coral colonies will occur on boulders in Halibut Channel and boulders and cobble in Haddock Channel (although we did find a significant positive interaction between canyon and bottom type). We suspect that the larger surface area of boulders represents a more stable surface as a colony grows in size, therefore allowing a colony to grow larger before tipping and overturning the stone (Tunnicliffe & Syvitski 1983).

Similar to coral abundance patterns, size and growth rates may link to a variety of environmental factors that vary with depth and differ between canyons. These factors include, but are not limited to, currents, and surface productivity (Thresher 2009).

3.4.3 Status

The great majority of *K. grayi* colonies observed in both Halibut and Haddock Channels were normal and completely alive. Dead/partially dead colonies of *K. grayi* were more prevalent at shallower depths in Haddock Channel than Halibut Channel, and colonies in Haddock Channel were broken more often and less likely to be normal compared to those in Halibut Channel. Many of the variables that likely differ between canyons and affect size and abundance (e.g. current velocity, sedimentation rates, and temperature), may also impact overall *K. grayi* status and contribute to canyon-related patterns.

Numerous mechanisms can overturn and break colonies (Tunnicliffe & Syvitski 1983). For example, large fish may come into contact with the colony, disease, predation or infection may cause death of portions of the colony, and longlines or gillnets may hook corals (Krieger 2001). Therefore, we cannot identify the direct mechanism responsible for the colonies that were overturned and/or broken in our video.

3.4.4 Trawling impacts

Our results clearly illustrate the negative influence of trawling on the size, status, and number of *K. grayi* colonies off Newfoundland. However, *K. grayi* colonies were also more likely to occur in trawled areas, perhaps because fishers target areas with high densities of fish, which could coincide with coral presence (Husebo et al. 2002; Costello et al. 2005; Stone 2006). Remaining corals in trawled areas were more likely to be dead, broken, smaller in size, and less abundant. These findings confirm other studies on trawling effects. For example, Freese (2001) found an immediate 16 % reduction in sponge density post-trawling, a 21 % reduction 11 months post trawling, and almost half of the sponges (46.8 %) that remained in three trawl paths were damaged. Cover of *Solenosmilia* thickets was significantly reduced on trawled seamounts, compared to seamounts that were never trawled and the density of large gorgonians and black corals with broken stems was significantly higher on seamounts with active trawling (Althaus et al. 2009). In the Gulf of Mexico, an estimated 27 % of the corals in a trawl net path were detached and 50 - 90 % of these corals were missing their polyps (Krieger 2001). Damaged corals may be more susceptible to predation (Malecha & Stone 2009), infection and disease, and ultimately mortality (Krieger 2001), with reduced reproductive capabilities (Henry et al. 2003), reduced feeding abilities (Krieger 2001), and slower growth rates (Meesters et al. 1994). For example, Malecha and Stone (2009) found

Tritonia diomedea actively feeding on sea whips lying on the seafloor after simulated trawl disturbance.

Our data corroborate previous research illustrating that the first pass of a trawl can cause significant damage. We found the largest incremental effect of trawling with the smallest number of trawls (illustrated by initial slopes in Figures 3.2 to 3.5), and found only very modest incremental effects as trawling intensity increased. On the continental shelf of Australia, a single pass of a trawl damaged 90 % of the large epibenthic organisms in the trawl path (Sainsbury et al. 1992). A single trawl pass in the Gulf of Alaska removed or damaged a significant number of emergent epifauna (Freese et al. 1999). Van Dolah et al. (1987) found significantly reduced barrel sponge abundances, and octocorals and stony corals broken at the base after only a single trawl pass.

Although trawling significantly influenced the status, height, and number of *K. grayi*, the overall impacts observed as trawling intensity increased past a single trawl were modest. For example, the probablity of a *K. grayi* colony being normal as trawl intensity increased from 2 to 12 was still nearly 0.8 and the probablity of being dead or partially dead as trawl intensity increased from 2 to 12 remained relatively stable in Halibut Channel (*ca.* 0.1). The reasons for observing only relatively modest impacts are unclear.

Longlines and gillnets are also regularly used in deep waters off Newfoundland. Relatively high levels of gorgonian bycatch from these gears have been recorded in all three canyons (Edinger et al. 2007). These gears leave behind no direct evidence on the seafloor and therefore could not be accounted for in our analyses. Nevertheless, they may account for some of the observed differences in *K. grayi* conditions related to canyons and depths. Fisheries and Oceans observer data collected in 2004 and 2005 indicate that Haddock Channel is targeted by gillnets more heavily than Halibut Channel, while both longlines and gillnets are used heavily in Desbarres Canyon. In general, longlines were used in deeper waters than both gillnets and trawls (Edinger et al. 2007).

Our findings add to the growing research demonstrating clear impacts of trawling on deep-sea ecosystems (e.g. Watling & Norse 1998; Freese 2001; Althaus et al. 2009; Norse et al. 2012). Corals, such as *K. grayi* are slow-growing and long-lived and recover slowly, if ever, from disturbances (Roberts et al. 2009). Corals may play important roles for other taxa in the deep sea (Buhl-Mortensen et al. 2010; Baillon et al. 2012). Collectively, these findings raise significant concerns regarding trawling and sustainability of deep-sea ecosystems. Therefore, we believe closing large areas of the seafloor to bottom fishing is necessary to protect corals, associated taxa, and their ecosystems. Furthermore, in areas that remain open to trawling (and other fishing practices), accountability and transparency are essential for ensuring appropriate fisheries management in an ecosystem context (Weaver et al. 2011).

3.5 Conclusions

Our results clearly illustrate the negative influence of trawling on *K. grayi* counts, size, and status. As trawling intensity increased, counts of live *K. grayi* colonies decreased, the probability of recording a colony broken or with dead portions increased, and the height of the colonies decreased. Our findings also suggest fishers may preferentially target areas with *K. grayi* (even if unintentionally), underscoring the urgency of addressing this conservation threat. Therefore, our research adds to growing evidence for the need to protect large seabed areas from bottom fishing gear. Such protected areas will help to reduce the overall footprint of fishing and initiate recovery efforts for deep-sea corals and associated marine fauna.

3.6 Literature cited

Althaus F., Williams A., Schlacher T.A., Kloser R.J., Green M.A., Barker B.A., Bax N.J., Brodie P., Schlacher-Hoenlinger M.A. (2009) Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Marine Ecology Progress Series 397: 279-294.

Appeltans W., Bouchet P., Boxshell G.A., De Broyer C., de Voodg N.J., Gordon D.P., Hoeksema B.W., Horton T., Kennedy M., Mees J., et al. (2012) World Register of Marine Species. www.marinespecies.org, Accessed 4 April.

Baillon S., Hamel J.-F., Wareham V.E., Mercier A. (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10(7): 351-356.

Baker K.D., Haedrich R.L., Snelgrove P., Wareham V., Edinger E.N., Gilkinson K. (2012a) Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. Deep Sea Research Part I: Oceanographic Research Papers 65: 171-188.

Baker K.D., Wareham V., Snelgrove P.V.R., Haedrich R.L., Fifield D.A., Edinger E.N., Gilkinson K. (2012b) Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. Marine Ecology Progress Series 445: 235-249.

Benjamin R. (2007) ClassAct Mapper. Fisheries and Oceans Canada, Dartmouth, NS.

Bryan T.L., Metaxas A. (2006) Distribution of deep-water corals along the North American continental margins: Relationships with environmental factors. Deep Sea Research Part I: Oceanographic Research Papers 53(12): 1865-1879.

Buhl-Mortensen L., Vanreusel A., Gooday A.J., Levin L.A., Priede I.G., Buhl-Mortensen P., Gheerardyn H., King N.J., Raes M. (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31(1): 21-50.

Costello M.J., McCrea M., Freiwald A., Lundalv T., Jonsson L., Bett B.J., van Weering T.C.E., de Haas H., Roberts J.M., Allen D. (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: A. Freiwald & J.M. Roberts (Eds). Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin. 771-805 pp.

CSSF (2010) Canadian Scientific Submersible Facility. www.ropos.com, Accessed November.

Davies A.J., Guinotte J.M. (2011) Global habitat suitability for framework-forming cold-water corals. PLoS ONE 6(4): e18483.

Dayton P.K., Thrush S.F., Agardy M.T., Hofman R.J. (1995) Environmental effects of marine fishing. Aquatic Conservation-Marine and Freshwater Ecosystems 5(3): 205-232.

Edinger E.N., Baker K.D., Devillers R., Wareham V. (2007) Coldwater corals off Newfoundland and Labrador: distribution and fisheries impacts. World Wildlife Fund, Toronto, Canada: 41 pp.

ESRI (2008) ArcGIS 9.3. Environmental Systems Research Institute, Redlands, CA.

Fossa J.H., Mortensen P.B., Furevik D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471: 1-12.

Freese J.L. (2001) Trawl-induced damage to sponges observed from a research submersible. Marine Fisheries Review 63(3): 7-13.

Freese L., Auster P.J., Heifetz J., Wing B.L. (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Marine Ecology Progress Series 182: 119-126.

Guinotte J.M., Orr J., Cairns S., Freiwald A., Morgan L., George R. (2006) Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? Frontiers in Ecology and the Environment 4(3): 141-146.

Henry L.A., Kenchington E.L.R., Silvaggio A. (2003) Effects of mechanical experimental disturbance on aspects of colony responses, reproduction, and regeneration in the cold-water octocoral *Gersemia rubiformis*. Canadian Journal of Zoology 81(10): 1691-1701.

Hoegh-Guldberg O., Mumby P.J., Hooten A.J., Steneck R.S., Greenfield P., Gomez E., Harvell C.D., Sale P.F., Edwards A.J., Caldeira K., et al. (2007) Coral reefs under rapid climate change and ocean acidification. Science 318(5857): 1737-1742.

Husebo A., Nottestad L., Fossa J.H., Furevik D.M., Jorgensen S.B. (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91-99.

Jackman S., Tahk A., Zeileis A., Maimone C., Fearon J. (2011) Package 'pscl'. Standford University California.

Koenig C.C., Shepard A.N., Reed J.K., Coleman F.C., Brooke S.D., Brusher J., Scanlon K. (2005) Habitat and fish populations in the deep-sea *Oculina* coral ecosystem of the western Atlantic. American Fisheries Society Symposium 41: 795-805.

Krieger K.J. (2001) Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. In: J.H.M. Willison, J. Hall, S.E. Gasset al (Eds). First International Symposium on Deep Sea Corals. Ecology Action Centre, Halifax, Nova Scotia: 156-165.

Malecha P.W., Stone R.P. (2009) Response of the sea whip *Halipteris willemoesi* to simulated trawl disturbance and its vulnerability to subsequent predation. Marine Ecology Progress Series 388: 197-206.

Meesters E.H., Noordeloos M., Bak R.P.M. (1994) Damage and regeneration - links to growth in the reef-building coral *Montastrea annularis*. Marine Ecology Progress Series 112(1-2): 119-128.

Mortensen P.B., Buhl-Mortensen L. (2005) Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada In: A. Freiwald & J.M. Roberts (Eds). Cold-water Corals and Ecosystems. Springer-Verlag, Berlin. 247-277 pp.

Mortensen P.B., Buhl-Mortensen L., Gordon D.C. (2006) Distribution of deep-water corals in Atlantic Canada. Proceedings of the 10th International Coral Reef Symposium: 1832-1848.

Norse E.A., Brooke S., Cheung W.W.L., Clark M.R., Ekeland L., Froese R., Gjerde K.M., Haedrich R.L., Heppell S.S., Morato T., et al. (2012) Sustainability of deep-sea fisheries. Marine Policy 36(2): 307-320.

RDevCoreTeam (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roark E.B., Guilderson T.P., Dunbar R.B., Fallon S.J., Mucciarone D.A. (2009) Extreme longevity in proteinaceous deep-sea corals. Proceedings of the National Academy of Sciences of the United States of America 106(13): 5204-5208.

Roberts J.M., Wheeler A.J., Freiwald A., Cairns S. (2009) Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats. Cambridge University Press, New York: 334 pp.

Roberts S., Hirshfield M. (2004) Deep-sea corals: out of sight, but no longer out of mind. Frontiers in Ecology and the Environment 2(3): 123-130.

Rogers A.D. (1999) The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. International Review of Hydrobiology 84(4): 315-406.

Sainsbury K.J., Campbell D.E., Whitelaw A.W. (1992) Effects of trawling on the marine habitat on the North West shelf of Australia and implications for sustainable fisheries management. In: D.A. Hancock (Ed). Sustainable Fisheries through Sustaining Fish Habitat. Australian Society for Fish Biology Workshop. Australian Government Publishing Service, Canberra. 137-145 pp.

Sherwood O.A., Edinger E.N. (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 66(1): 142-152.

Stone R. (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25(2): 229-238.

Thresher R.E. (2009) Environmental and compositional correlates of growth rate in deep-water bamboo corals (Gorgonacea; Isididae). Marine Ecology Progress Series 397: 187-196.

Thrush S.F., Hewitt J.E., Funnell G.A., Cummings V.J., Ellis J., Schultz D., Talley D., Norkko A. (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. Marine Ecology Progress Series 223: 277-286.

Tunnicliffe V., Syvitski J.P.M. (1983) Corals move boulders - an unusual mechanism of sediment transport. Limnology and Oceanography 28(3): 564-568.

Van Dolah R.F., Wendt P.H., Nicholson N. (1987) Effects of a research trawl on a hard-bottom assemblage of sponges and corals. Fisheries Research 5(1): 39-54.

Wareham V.E., Edinger E.N. (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. Bulletin of Marine Science 81(1): 289-313.

Watanabe S., Metaxas A., Sameoto J., Lawton P. (2009) Patterns in abundance and size of two deep-water gorgonian octocorals, in relation to depth and substrate features off Nova Scotia. Deep Sea Research Part I: Oceanographic Research Papers 56(12): 2235-2248.

Watling L., Norse E.A. (1998) Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. Conservation Biology 12(6): 1180-1197.

Weaver P.P.E., Benn A., Arana P., Ardron J., Bailey D.M., Baker K.D., Billett D.S.M., Clark M., Davies A.J., Durán Muñoz P., et al. (2011) The impact of deep-sea fisheries and implementation of the UNGA Resolutions 61/105 and 64/72. Report of an international scientific workshop. National Oceanography Centre, Southampton, UK: 45 pp.

Weinbauer M.G., Brandstatter F., Velimirov B. (2000) On the potential use of magnesium and strontium concentrations as ecological indicators in the calcite skeleton of the red coral (*Corallium rubrum*). Marine Biology 137(5-6): 801-809.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York: 574 pp.

Table 3-1. Number of *Keratoisis grayi* colonies and condition observed during ROV surveys off the southwest Grand Banks of Newfoundland in 2007.

Canyon	Dive	# Observed	# Normal[1]	# Broken[2]	# Over-turned	# Dead / Partially Dead	# Alive
Halibut Channel	R1065	192	154	19	9	19	150
Haddock Channel	R1066	1427	1090	184	57	213	1117
Halibut Channel	R1067	4149	3738	140	131	164	3773
Haddock Channel	R1068	0	0	0	0	0	0
Desbarres Canyon	R1070	2	1	1	0	1	1
Desbarres Canyon	R1071	0	0	0	0	0	0
Desbarres Canyon	R1072	0	0	0	0	0	0
	Total	5770[3]	4983	344	197	397	5041

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[1] Colony was upright and intact

[2] Includes colonies that were both broken (pieces detached) and overturned.

[3] Sum of columns representing colony status and proportion dead do not add up to 5770 because these characteristics could not be determined for all colonies observed.

Table 3-2. Number of trawl marks observed by depth and dive during ROV surveys (all ROV modes) off the southwest Grand Banks of Newfoundland in 2007.

Dive	Depth (m)						
	300-400	400-500	500-600	600-700	700-800	800-900	900-1000
R1065	-	-	-	5	4	1	0
R1066	-	1	26	52	0	1	0
R1067	0	2	0	0	0	0	0
R1068	-	-	-	-	-	-	-
R1070	3	6	33	18	0	0	0
R1071	1	2	11	1	0	0	0
R1072	-	-	-	-	-	-	-
Total	4	11	70	76	4	2	

Table 3-3. Significant terms in models examining abundance, height, and status of *Keratoisis grayi* colonies from ROV surveys off the southwest Grand Banks of Newfoundland in 2007.

Response	Model terms	Relationship	p-value
Abundance: presence/absence of live colonies	Bottom type		<0.0001
	Trawl	Positive	0.0178
	Depth*Canyon		<0.0001
Abundance: counts of live colonies	$\log_{10}$Trawl	Negative	<0.0001
	Depth*Bottom type		0.0036
Height	$\log_{10}$Trawl	Negative	<0.0001
	Depth	Positive	<0.0001
	Canyon*Bottom type		<0.0001
Probability of having dead portions	Canyon*Depth		<0.0001
	$\log_{10}$Trawl	Positive	0.0001
Overall status	Canyon		<0.0001
	Depth		0.0037
	$\log_{10}$Trawl		<0.0001

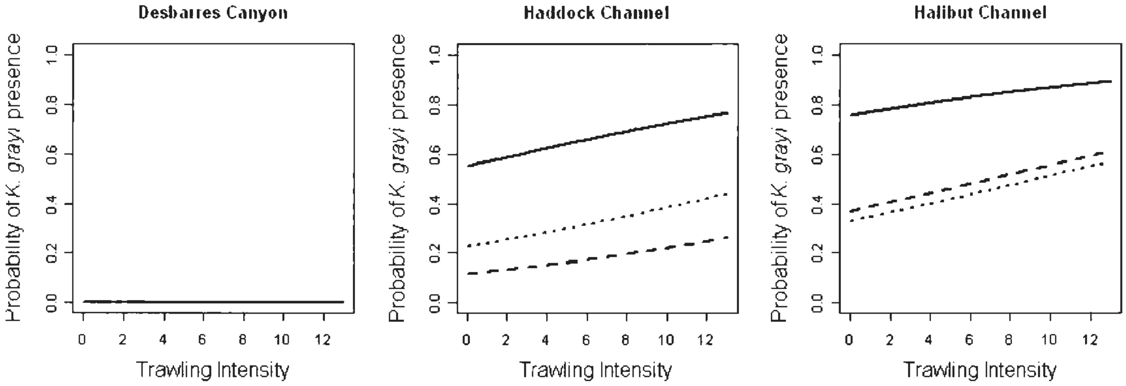

Figure 3-1. Model predictions of the influence of trawl intensity on the probability of live *K. grayi* presence in boulders (solid), cobble (dotted), and gravel (dashed) within each canyon. Depth was held constant at the mean depth in each canyon in all models.

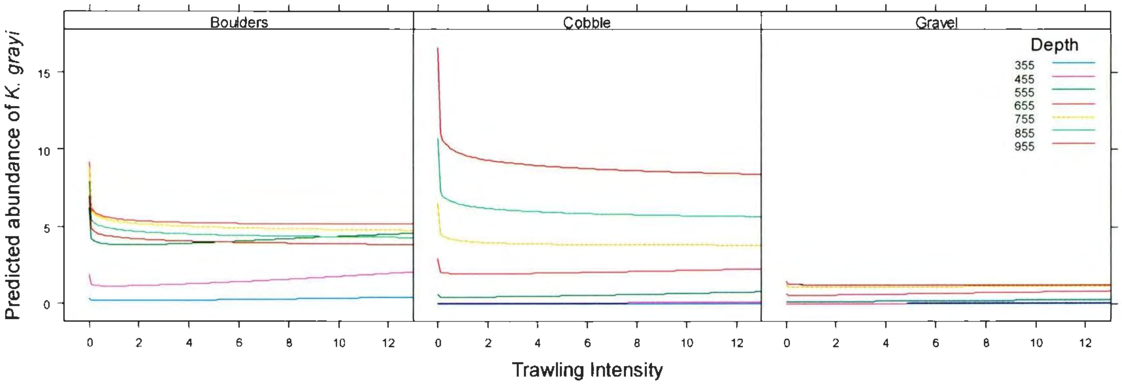

Figure 3-2. Model predictions of the influence of trawling intensity on *Keratoisis grayi* counts in boulders, cobble, and gravel at various depths.

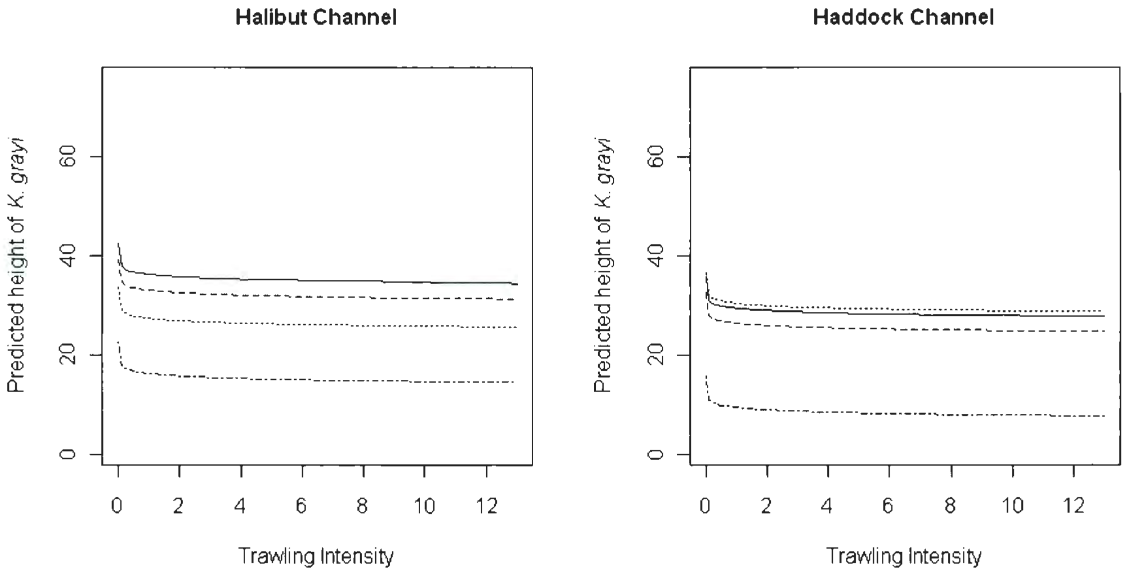

Figure 3-3. Model predictions of the influence of trawling intensity on *Keratoisis grayi* height in Halibut and Haddock Channels in boulders (solid), cobble (dotted), gravel (dashed), and outcrops (dot/dash) at mean depth (650 m).

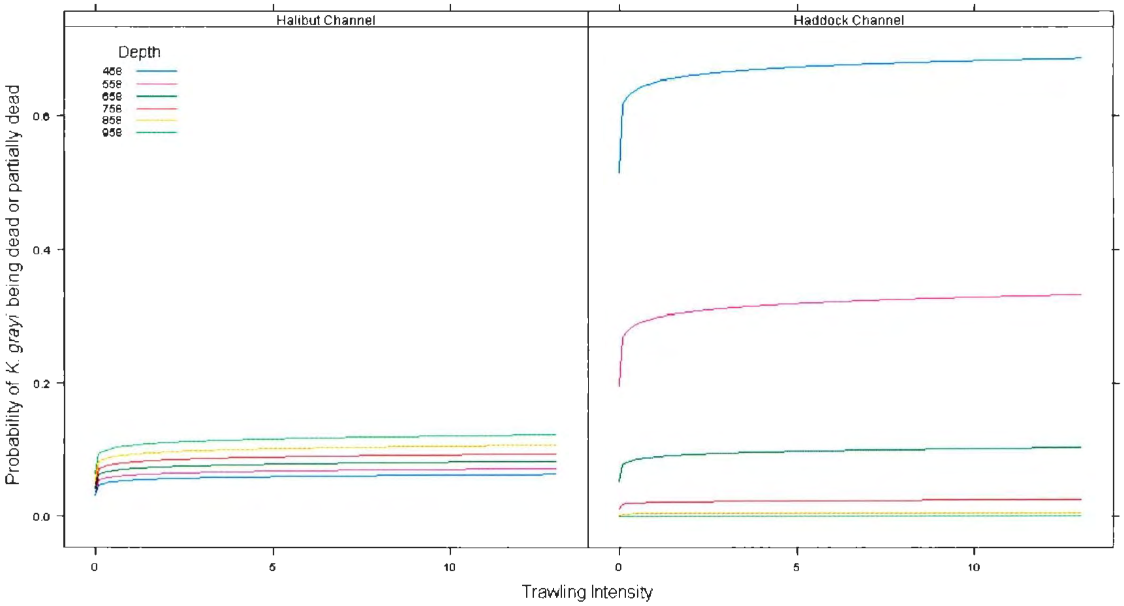

Figure 3-4. Model predictions of the influence of trawling intensity and depth on the probability of dead / partially dead versus live *Keratoisis grayi* in Halibut Channel and Haddock Channel.

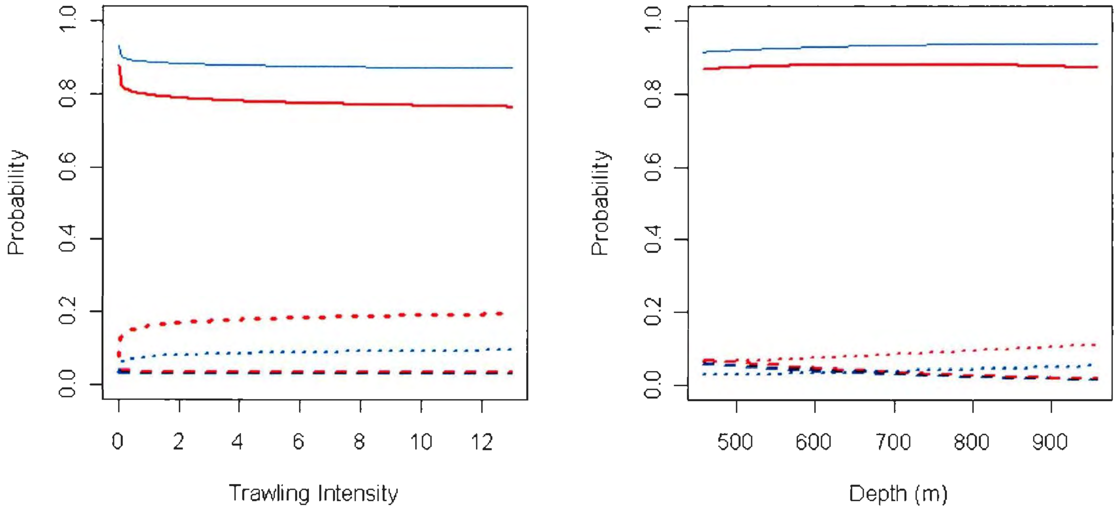

Figure 3-5. Model predictions of the probability of *Keratoisis grayi* being normal (solid), overturned (dashed), or broken (dotted) in Halibut Channel (blue) and Haddock Channel (red) in relation to trawl intensity (depth = 650 m) and depth (trawl intensity = 0).

4 Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope

Abstract

Deep-sea fishes are the target of directed fisheries and are considered a conservation concern. Yet, we still know little about the factors that affect deep-sea fish distributions and assemblage patterns on relatively small spatial scales. We used results from remotely operated vehicle surveys that observed 105 km (~ 346 960 m^2) of seafloor over a depth range of 351 – 2245 m in three canyons off Newfoundland to examine the occurrence, behaviour, habitat specificity, and assemblage patterns of deep-sea fishes in this region. We found distinct assemblages based on both depth and habitat classifications. The most obvious unique assemblage was that associated with outcrops, which served as habitat for relatively rare species such as *Neocyttus helgae*, *Hoplostethus atlanticus*, and *Lepidion eques*. Several coral habitats hosted distinct assemblages when compared to habitats with low or medium structural complexity. Our results illustrate that any program targeted at protecting deep-sea ecosystems must protect a wide-range of habitats and depths to conserve a variety of fish species and assemblages.

4.1 Introduction

In general, we know little about the biology of deep-sea fishes (Bailey et al. 2009; Baker et al. 2009), and even less about their community dynamics, the factors that influence small-scale distributions, and the functional role of deep-sea fish habitats. Ecologists widely accept the importance of shallow-water corals as habitat for fishes, but debate parallel functions for deep-water corals. The role and importance of deep-water corals as habitat for fishes remain unclear (Roberts et al. 2009; Buhl-Mortensen et al. 2010). Some studies suggest that deep-water corals provide refuge (Krieger & Wing 2002; Costello et al. 2005), enhance prey capture (Husebo et al. 2002; Costello et al. 2005), and serve as nursery or spawning grounds (Costello et al. 2005; Koenig et al. 2005; Baillon et al. 2012) for deep-sea fishes. In the latter case, supporting evidence includes records of swollen, gravid *Sebastes* spp. on *Lophelia* reefs (Fossa et al. 2002; Husebo et al. 2002; Costello et al. 2005), ray egg cases on reefs (Costello et al. 2005) and fish larvae in the polyps of seapens (Baillon et al. 2012). In general, deep-sea corals are thought to create structure in an environment where structurally complex habitats are often scarce (Buhl-Mortensen et al. 2010).

Higher abundances of several fishes have been recorded in areas with coldwater corals compared to areas without corals. Costello et al. (2005) found greater fish species richness and abundance in *Lophelia*-associated habitats than in surrounding areas and argued that reefs may play an important functional role as fish habitat in deep-water ecosystems. Higher catches and larger individuals of redfish (*Sebastes marinus*), ling

(*Molva molva*), and cusk (*Brosme brosme*) inside *Lophelia* reefs off Norway compared to those outside (Husebo et al. 2002) further support this hypothesis. Off Alaska, 85 % of the economically important fish were associated with corals or other emergent fauna (Stone 2006) and off Ireland, *Guttigadus latifrons* was only observed in areas with live corals (Soffker et al. 2011).

Other research suggests that fish only use deep-coral and sponge habitats opportunistically (Auster 2005; Tissot et al. 2006). Auster (2005) argued that high local densities of fishes do not mean that corals enhance fish populations. Dense corals and epifauna hosted equivalent fish communities in the Gulf of Maine compared to less complex habitats. These results indicate that coral habitats may not be functionally unique and provide similar levels of shelter and prey compared to other complex habitats (such as boulder fields) (Auster 2005). Another study further hypothesized that the physical structure of reefs attracted redfish, and not the coral itself (Husebo et al. 2002). This perspective was defended using observations of redfish associated with shipwrecks, or found hiding in the vicinity of large boulders or sponges (Husebo et al. 2002). Tissot et al. (2006) found six species of fishes more abundant adjacent to coral colonies than predicted, but concluded that corals and fishes simply co-occurred in the same habitats.

One of the only quantitative studies that showed convincing evidence of obligate relationships examined fish assemblages in deep-reef habitats off the southern United States (Ross & Quattrini 2007). These researchers found distinct fish assemblages in prime reef and transition reef habitats compared to off-reef habitats (Ross & Quattrini 2007), suggesting that deep reefs host unique fish communities. Baillon et al. (2012)

found evidence of a functional relationship between corals and fish off Newfoundland and Labrador: they found fish larvae (predominately *Sebastes* spp.) within polyps of sea pen, thereby hinting that corals may provide shelter for fish larvae.

Until recently, trawl data were the only means to study fish-coral relationships off Newfoundland. Edinger et al. (2007) found highest species richness of fishes in fishing sets that contained small gorgonian corals, but found no strong relationships between corals and abundances of the 10 groundfish species examined. Nonetheless, trawls are not ideal for studying such patterns at small scales because they sample large areas of the seafloor in a region with relatively small, patchy coral distributions (KD Baker, unpublished data).

The vulnerability of deep-sea fishes to overexploitation has been demonstrated by the boom-and-bust of many deep-sea fisheries (Koslow et al. 2000), dramatic population declines of fishes over relatively short time scales (Devine et al. 2006), the indiscriminate impact of fisheries on non-target species (Bailey et al. 2009), and the potential for lengthy recovery times (Baker et al. 2009). The idea that corals may influence fish distributions underscores the urgency of understanding these relationships. As destruction and threats to deep-sea corals continue to mount (Fossa et al. 2002; Hall-Spencer et al. 2002; Turley et al. 2007), availability of aggregating sites, survival probability, and population resilience of deep-sea fishes could be in precipitous decline.

We present the results from an *in situ* camera-based survey of deep-sea fishes conducted through a variety of coral and non-coral habitats on the Newfoundland continental slope. Specifically, we examine patterns in fish assemblages in relation to both depth and habitat classifications, and discuss the conservation implications of these findings. We also describe fish occurrence, behaviour, and reaction to the ROV, and examine habitat specificity in relation to the complexity of habitats.

4.2 Methods

4.2.1 Survey design

We used the remotely operated vehicle (ROV) ROPOS (Remotely Operated Platform for Ocean Science) (CSSF 2010) to examine the fauna of three submarine canyons on the slope of the Grand Banks south of Newfoundland: Halibut Channel, Haddock Channel, and Desbarres Canyon (Figure 2-1). A small bank separates Halibut Channel and Haddock Channel, which are situated approximately 110 km and 175 km east of Laurentian Channel respectively, and approximately 150 km and 200 km northwest of Desbarres Canyon respectively. The temperature regimes in the three canyons were similar, averaging ~ 5.0 °C during relatively shallow dives (<1100 m) and ~ 4.4 °C during relatively deep dives (>1100 m). ROPOS performed video surveys from *CCGS Hudson* in July 2007, and was equipped with lasers placed 10 cm apart to indicate scale. Depth, temperature (during most dives), date, time, altitude, and position were logged at 1-second intervals.

We planned 1-km transects along depth contours every 200 m between 2200 and 600 m and along contours every 100 m in waters shallower than 500 m. We standardized transects by keeping the ROV as close to the bottom as possible (< 1 m), maintaining a constant slow speed (approx. 0.2 – 0.5 m s^{-1}) while tilting the color camera down slightly on a wide-angle view in order to image the seafloor and water column directly above. Whenever possible, the camera was angled so the 'horizon' was in the center of view and the farthest field of view was approximately 5-6 m wide (estimated using lasers). The camera was positioned approximately 0.8 m high on ROPOS. ROPOS was also equipped with a monochrome camera positioned approximately 1.5 m from the bottom of the ROV and oriented slightly downward so the seafloor was in view. Between the pre-selected transects, we explored the area, capturing still images and video of features of interest, and collecting voucher specimens of invertebrates where possible.

4.2.2 Video processing

We used ClassAct Mapper (Benjamin 2007) to analyze the video footage from the color video camera and to collect geo-referenced data on fish, habitat, and ROV operation mode. We identified each fish to the lowest possible taxonomic level, which was often to species except for some groups such as myctophids or redfish (*Sebastes*) where voucher specimens are usually necessary to differentiate among morphologically similar species. When fish orientation made identification difficult, the monochrome camera images aided identification by providing a different viewing angle of the individual. Video clips and frame grabs of individuals that could not be identified with certainty were sent to taxonomic experts for confirmation. Behavioral responses of fishes are a significant concern when analyzing ROV observations (Stoner et al. 2008). We categorized fish behaviour and reaction to the ROV based on first sighting. We grouped fish behaviour as actively swimming, hovering, hiding, feeding, or resting and categorized reaction to the ROV as no reaction, avoidance, or attraction (Costello et al. 2005).

To reduce double-counting individual fish, we did not count fish that approached the field of view from behind the ROV. *Sebastes* spp. (redfish) followed and often circled the ROV, so only individuals that were resting on the seafloor where the sediment was undisturbed were counted. If we could identify each individual, they were also counted. We noted all other redfish, but coded them as 'suspicious' and did not include them in analyses. *Centroscyllium fabricii* (black dogfish) appeared to follow the ROV, so we measured and described unique characteristics (size, obvious parasites, scars, etc.) for each individual to avoid double-counting individuals.

We categorized habitat associated with each fish observation as (1) outcrop, (2) dense large coral cover, (3) boulder field, (4) sparse large coral cover, (5) dense small coral cover, (6) sparse small coral cover, (7) sea pen field, (8) sponge field, (9) cup coral field, (10) *Heteropolypus* cf. *insolitus* field, or (11) fine sediments with sparse epifauna (Figure 4-1) (Baker et al. 2012). Outcrop described cliff-like, vertical structures with exposed bedrock or consolidated Quaternary sediment and encrusting sponges, *Desmophyllum dianthus*, and sometimes antipatharians: Schizopathidae n. gen. et n. sp. Dense, large coral cover consisted of dense assemblages (average = 1.6 large coral colonies m^{-1})[1] of *Keratoisis grayi* colonies of any size (or on rare occasions *Acanthogorgia armata* colonies ≥ 30 cm in height or dense *Radicipes gracilis* > 60 cm in height) with boulders (> 25 cm) and cobble, often mixed with gravel and fine-sediments.

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[1] Average abundances were calculated after video analysis was complete.

Boulder fields consisted of rocks greater than 25 cm mixed with cobble, gravel, and fine sediments and contained few large corals, sponges, or epifauna. Sparse, large coral cover included habitats with sparse colonies of *K. grayi* (or on rare occasions *R. gracilis* > 60 cm in height) (average = 0.35 large coral colonies m^{-1}), sometimes with small coral colonies and sparse boulders and/or cobble. Dense, small coral cover habitats contained assemblages of abundant (average = 1.75 small coral colonies m^{-1}), relatively small coral species (< 30 cm in height), such as *Acanella arbuscula,* small *A. armata,* and *Radicipes gracilis,* with occasional cobble and small boulders (usually < 30 cm). Sparse, small coral habitats were similar to dense, small coral habitats, but with fewer corals (average = 0.43 small coral colonies m^{-1}) and occurred in relatively fine-sediments. Sea pen fields occurred in fine-sediment with numerous *Pennatula* spp. often interspersed with *Halipteris finmarchica, Protoptilum carpenteri*, and *Kophobelemnon stelliferum* (average = 8.4 sea pens m^{-1}). Sponge fields occurred in relatively fine-sediments (sometimes with gravel or sparse cobble) and consisted of unidentified small, white sponges (< 10 cm). Cup coral fields consisted of *Flabellum* spp. in fine sediment habitats with few other megafauna present (average = 8.0 cup corals m^{-1}). *Heteropolypus* cf. *insolitus* fields occurred in relatively fine sediments with primarily *Heteropolypus* cf. *insolitus* and sometimes *K. stelliferum* (average = 3.0 *H. insolitus* colonies m^{-1}). Fine sediment with sparse epifauna habitat was composed of mud-sand sediments with very few corals, sponges, or large epifauna. Common invertebrates in these habitats included relatively small cerianthids, ophiurids, sabellids, and occasional corals (mostly sparse sea pens).

One person completed all video processing to reduce subjectivity in habitat classifications.

We characterized ROV operation mode at 1-second intervals. ‘Dead time’ was when the view was obstructed, the ROV was travelling too high for an adequate view of the benthic fauna, or physical sample collection was underway. All other ROV operation modes (e.g. panning, transect-mode) were grouped into a single category for our analyses (Baker et al. 2012).

4.2.3 Data analysis

We recorded the presence of all fish taxa in all portions of the video, regardless of ROV operation mode, and plotted these in relation to depth. We examined fish behaviour and reaction to the ROV. The presence or absence of unique fish taxa was recorded for each habitat type (using all data) and we then calculated relative abundances within each habitat (based on percent of total fish observed) using a subset of the data that excluded dead time.

4.2.3.1 Habitat specificity

We examined habitat specificity (or preference) by grouping habitat types into categories that likely represented low, medium, and high habitat complexity (as determined by their assumed profiles and sizes relative to fishes) (Buhl-Mortensen et al. 2010). We defined outcrops, dense large corals, boulder fields, sparse large corals, and dense small corals as high complexity habitats. Sparse, small coral habitats, sea pen fields, and sponge fields were classified as medium complexity habitats, and cup coral fields, *Heteropolypus* cf. *insolitus* fields, and fine sediment with sparse epifauna were categorized as low complexity (simple) habitats. We examined the relative abundances of unique fish taxa (represented by three or more individuals) within each category (Ross & Quattrini 2007).

4.2.3.2 Assemblage analysis

We identified the following depth classes: (1) 300-800 m (shelf edge and upper slope), (2) 800-1300 m (middle slope), and (3) 1300-2300 m (lower slope) (Baker et al. 2012). These were chosen to ensure balanced survey coverage of each depth category and to reflect fish distributions in previous studies throughout the world (Haedrich & Merrett 1988; Koslow et al. 1994; Francis et al. 2002; D'Onghia et al. 2004). We conducted multivariate analyses in Primer 6.0 (Clarke & Gorley 2006) to evaluate differences in fish assemblages between and within habitats. Following Ross and Quanttrini (2007), we considered each unique combination of dive, depth class, and habitat type as a sample unit and calculated the number of individuals belonging to each unique taxon for each sample unit. Dead time was excluded from this analysis. We standardized samples to account for varying survey effort in each sample unit, and fourth-root transformed counts to reduce overemphasis on abundant species. We used a Bray-Curtis similarity matrix to create a non-metric multidimensional scaling (MDS) plot, and an associated dendrogram using a group average link function.

We used a two-way analysis of similarities (ANOSIM) based on depth and habitat to test for differences in fish assemblages. We then used SIMPER (similarity percentages) to identify the species that contributed most to the observed similarities and dissimilarities between samples in relation to depth and habitat type.

We examined similarities between species by creating a Bray-Curtis species similarity matrix of standardized samples and species that contributed at least 10 % to a sample. We then produced an MDS plot and dendrogram (using group-average clustering) based on these similarities to examine species groupings.

4.3 Results

Seven dives captured 90 h of bottom video footage and covered a distance of approximately 105 km (Table 4-1) over a depth range of 351 – 2245 m. Based on the average viewing width during each ROV operation mode, we surveyed an area of approximately 346 960 m^2. Fine sediment with sparse epifauna was the most surveyed habitat (43,765 m), followed by dense small coral habitat (12,954 m) (Table 4-2). *Heteropolypus* cf. *insolitus* fields were the least surveyed habitat (302 m). Most survey coverage occurred in the shallowest depth range (300-800 m) (43,845 m).

4.3.1 Species composition and occurrence

We recorded over 18,000 individual fishes, comprising at least 74 species or unique taxa (Table 4-3); 9901 of these could be identified to 45 species. Most other individuals (n = 7249) could only be identified to a unique genus, family, or unknown group (29 unique taxa). The most common taxon was *Synaphobranchus kaupii* (Kaup's arrowtooth eel) (n = 6586), followed by *Sebastes* spp. (n = 4767), Myctophidae (n = 1663), and *Nezumia bairdii* (marlin-spike grenadier) (n = 876). Rare species in our surveys included *Apristurus profundorum* (deepwater catshark) (n = 2), *Harriotta haeckeli* (smallspine spookfish) (n = 1), and *Coryphaenoides armatus* (abyssal grenadier) (n = 1). While some fish taxa were observed as solitary individuals, other taxa (e.g. *Sebastes* spp.) were often observed in aggregations.

Synaphobranchus kaupii and *Sebastes* spp. consistently represented large percentages of the fish taxa within most habitat types (Table 4-4). *Synaphobranchus kaupii* represented over 20 % of the total fish in every habitat, except outcrops. *Sebastes* spp. accounted for over 25 % of the total abundance in every habitat type, except outcrops, sea pen fields, and *Heteropolypus* cf. *insolitus* fields. Only 10 taxa occurred at outcrops including high relative abundances of myctophids (27 % of total), *Coryphaenoides carapinus* (carapine grenadier), and *Neocyttus helgae* (false boarfish) (both 15 % of total) within these habitats. Myctophids, *Nezumia bairdii*, and *Coryphaenoides rupestris* (roundnose grenadier) also represented relatively large proportions of the fishes (> 5 %) in five or more habitat categories.

4.3.2 Species behaviour

Most fish were actively swimming (n = 9690), resting (n = 5004), or hovering (n = 3631) (Table 4-5). *Centroscyllium fabricii* was always actively swimming and was often attracted to the ROV. Macrouridae (e.g., *Coryphaenoides carapinus* and *C.*

rupestris) mostly hovered just above the seafloor, but also actively swam, hid in coral cover, and rested on the sediments. We observed only two incidents of feeding; a *Synaphobranchus kaupii* and a *Sebastes* sp. were observed feeding on unknown fishes.

Most fish (n = 9346) exhibited no obvious or consistent reaction to the ROV (Table 4-5), but there were several exceptions. Myctophids often swam quickly toward the seafloor or ROV, crashed into the sediments, and then rapidly swam away. *Centroscyllium fabricii* often circled the ROV, and also swam directly toward it. *Synaphobranchus kaupii* was sometimes attracted to the ROV (~25 % encountered) and even changed direction to swim directly toward it. Individuals of some species, such as *Simenchelys parasitica* (snubnosed eel), *Reinhardtius hippogolossoides*, and *Rajella fyllae* (round skate), exhibited avoidance behaviour, but other individuals of the same species were attracted to the ROV and/or did not react. No species where more than two individuals were observed exclusively avoided the ROV.

4.3.3 Depth range

Many species spanned a wide depth range, but several were observed only in deep waters (< 1200 m) including *Coryphaenoides armatus* (2202 m), *Hydrolagus affinis* (> 2008 m), *Apristurus profundorum* (deep-water catshark) (> 1348 m), and *Serrivomer beanii* (Bean's sawtooth eel) (1304 m) (Figure 4-2). The deepest species observed were *Aldrovandia* sp. (2244 m), *Antimora rostrata* (blue hake) (2243 m), and *Halosauropsis macrochir* (abyssal halosaur) (2242 m). Many more species, including primarily shelf species, were restricted to shallower waters (< 600 m) including *Gadus morhua* (Atlantic cod) (355 m), *Anarhichas lupus* (Atlantic wolffish) (358 m), *Myxine glutinosa* (Atlantic hagfish) (< 363 m), and *Argentina silus* (Atlantic argentine) (< 612 m). *Alepocephalus* spp. (slickhead) (511 – 2220 m), *Antimora rostrata* (626 – 2243 m), *Aldrovandia* sp.1, (659 – 2244 m) and *Harriota raleighana* (642 – 2218 m) spanned the greatest depth ranges.

4.3.4 Habitat specificity

Some species, including *Anarhichas minor* (n = 5) and *Neocyttus helgae* (n = 4), occurred exclusively in habitats that we defined as complex, based on size and assumed profiles relative to fishes (Figure 4-3). Others, such as *Hydrolagus affinis* (n = 3), *Bathysaurus ferox* (n = 17), and *Simenchelys parasitica* (snubnosed eel) (n = 6) occurred only in relatively simple habitats. Many species spanned high, medium, and low complexity habitats, including more abundant species such as *Nezumia bairdii* (n = 876), *Harriotta raleighana* (n = 19), and *Synaphobranchus kaupii* (n = 6586).

4.3.5 Fish assemblage analysis

The MDS plot and dendrogram clearly illustrate the influence of depth on fish assemblages (Figure 4-4, Figure 4-5), but the effect of habitat varied. Boulders, sea pen fields, and sediment with sparse epifauna appeared to support somewhat distinct fish assemblages. Within the shallowest depth range (300-800 m), dense large corals and dense small corals showed evidence of distinct fish assemblages, but in deeper waters (> 800 m) there was no evidence of distinct assemblages within these habitats. No other clear assemblage patterns based on habitats could be distinguished from the MDS plot or dendrogram.

The global ANOSIM showed significant differences in assemblages with depth (R = 0.684, p = 0.001). Pairwise comparisons between each depth category showed that assemblages within each category also differed significantly from each other ($R \geq 0.556$, p = 0.001). Abundant *Sebastes* spp. in the shallow depth category (300 – 800 m) contributed most to significant dissimilarity in assemblages between both the shallowest and mid-depth class (800 – 1300 m) (58.5 %) and shallowest and deepest depth classes (1300 – 2300 m) (86.9 %) (see Appendix A). The high relative abundance of *Synaphobranchus kaupii* in shallower waters, but not deeper waters, also differentiated the shallowest (300 – 800 m) and deepest (1300 – 2300 m) depth classes. The low relative abundance of *S. kaupii* and *Coryphaenoides rupestris* and the high proportion of *Halosauropsis macrochir* at greater depths (1300 – 2300 m) contributed most to the significant dissimilarities (77.3 %) in assemblages between the deepest and the mid-depth range (800 – 1300 m) groupings.

The global ANOSIM also showed significant differences in assemblages with habitat (R = 0.391, p = 0.001). Based on the R-statistics from the ANOSIM (Table 4-6), species assemblages associated with outcrops and boulder fields differed consistently from almost every other habitat type. The high relative abundance of *Sebastes* spp. (contribution = 51.9 %) greatly influenced similarity within boulder fields. The absence of *Coryphaenoides rupestris*, and *Glyptocephalus cynoglossus* (witch flounder), the low relative abundances of myctophids and *Nezumia bairdii*, and the numerous *Sebastes* spp.

in boulder fields all contributed to the dissimilarities between boulders and other habitat types (see Appendix A). Fish were only observed at three outcrops, each in a different depth zone, so similarities within outcrops could not be examined. The absence of *Nezumia bairdii*, *G. cynoglossus*, and *Sebastes* spp., the presence of *Neocyttus helgae* and *Hoplostethus atlanticus* (orange roughy), the great abundance of myctophids, and the low relative abundance of *Synaphobranchus kaupii* all contributed to dissimilarities between outcrops and other habitats.

Fish assemblages associated with sea pen fields differed from all habitats considered highly complex, sparse small corals, and cup coral fields, but we observed no differences between sea pen fields and sponge fields, fine sediments with epifauna, and *Heteropolypus* cf. *insolitus* fields. *Synaphobranchus kaupii*, Myctophidae, *Nezumia bairdii*, and *Glyptocephalus cynoglossus* contributed most to the similarity within sea pen fields. Dissimilarities with other habitats were largely driven by numerous *Coryphaenoides rupestris*, *G. cynoglossus*, and myctophids and lower relative abundance of *Sebastes* spp. in sea pen fields (see Appendix A).

Fish assemblages differed between dense small corals and sponge fields, as well as cup coral fields and *H. insolitus* fields. A variety of species drove dissimilarities in fish assemblages associated with dense small coral habitats and sponge fields, including the absence of *Glyptocephalus cynoglossus*, *Rajella fyllae*, and Macrouridae sp. 3 and the lower relative abundance of *Centroscyllium fabricii, Macrourus berglax*, and Zoarcidae sp. 1 in sponge fields. The higher relative abundance of myctophids and *Nezumia bairdii*, the absence of *Sebastes* spp., and the lower relative abundance of *Coryphaenoides* *rupestris* in *H. insolitus* fields were largely responsible for the dissimilarities between dense small corals and *H. insolitus* fields. The lower relative abundance of *C. rupestris* and the high relative abundance of *G. cynoglossus* in cup corals fields contributed most to the dissimilarity observed with dense small corals.

Fish assemblages also differed between fine sediments with sparse epifauna and *H. insolitus* fields, sparse large corals, and cup coral fields. The higher relative abundances of *Sebastes* spp., *Glyptocephalus cynoglossus*, *Antimora rostrata*, *Coryphaenoides rupestris*, and myctophids in fine sediment habitat contributed most to the observed differences. Fish assemblages in cup coral fields also differed from those in sparse small coral habitats, largely because of low relative abundances of *C. rupestris* and myctophids and higher abundance of *G. cynoglossus* in cup coral fields. We detected no differences in fish assemblages between other habitat types.

The species-related MDS plot and dendrogram illustrate the co-occurrence of relatively deep species (*Aldrovandia* sp. 1, *Coryphaenoides carapinus*, and *Halosauropsis macrochir*) (Figure 4-6). *Sebastes* spp. and *Phycis chesteri* also grouped together in the MDS plot and dendrogram. Outliers in the plot and dendrogram included *Neocyttus helgae*, *Hoplostethus atlanticus*, *Lepidion eques* (North Atlantic codling), *Aldrovandia* sp. 2, and *Anarhichas minor*.

4.4 Discussion

4.4.1 Assemblages patterns

We found distinct fish assemblages based on pre-defined depth categories, corresponding to the upper slope and shelf edge (300-800 m), the middle slope (800-1300 m), and the lower slope (1300-2300 m). The idea that fish assemblages occur across depth gradients is not new; similar findings have been found throughout the world's oceans. For example, D'Onghia et al. (2004) found distinct assemblages in the Mediterranean Sea at ~ 600 m, on the middle slope between 800 and 1300 m, and on the lower slope below 1300 m. Francis et al. (2002) identified four fish assemblages associated with the inner continental shelf, mid-outer continental shelf and shelf edge, upper continental slope, and mid continental slope off New Zealand. Koslow et al. (1994) found assemblages off southeast Australia based on similar depth categories. Lorance et al. (2002) found three major carnivorous fish fauna assemblages in the Northeast Atlantic associated with the shelf, upper slope, and mid-slope. Theories to explain such depth-related ichthyofaunal assemblages include differences related to food availability, changes in topography with depth, and transitions between water masses (Haedrich et al. 1980; Hecker 1990; Koslow et al. 1994; D'Onghia et al. 2004).

We also found distinct assemblages based on habitat types. Outcrops and boulder fields both differed consistently when compared to most other habitat categories. Outcrops supported relatively rare species in this region, such as *Hoplostethus atlanticus, Neocyttus helgae*, and *Lepidion eques*. The distinct assemblages associated with boulder fields contradict observations from the Gulf of Maine that showed dense corals were equivalent to other fairly complex habitats, such as boulders with sparse coral cover (Auster 2005). The contractary findings could be related to distinct differences in overall habitat types (and species that define these), the dissimilarities between fish species present in each study area, and the timing of the surveys (August versus July).

Contrary to Ross and Quattrini (2007), we did not find clear relationships between fish assemblages and corals. Most other studies around the world focussed on coldwater coral reef structures, where reefs are thought to provide shelter, and possibly increased food availability for fishes (Costello et al. 2005; Sulak et al. 2007; Roberts et al. 2009). It is possible that the importance of non-reef-forming corals in influencing fish assemblages and distributions is less than that of reef-forming corals given the former's reduced complexity (in terms of size and profile) and therefore available shelter (Buhl-Mortensen et al. 2010). Alternatively, patterns associated with non-reef habitats may also be more difficult to decipher due to the less distinct transition between habitat types.

Few studies have documented the importance of sea pen fields for fishes, though surveys observed hundreds of *Sebastes alutus* (Pacific Ocean perch) in Pribilof Canyon (Bering Sea) inside dense aggregations of sea pens (*Halipteris willemoesi*) (Brodeur 2001) and fish larvae were documented in sea pen polyps off Newfoundland and Labrador (Baillon et al. 2012). Tissot et al. (2006) hypothesized that sea pen fields may create important refugia for small invertebrates and influence prey availability by adding structure in an otherwise low-structured environment. In our study, fish assemblages associated with sea pen fields differed from those categorized as highly complex habitats and cup coral fields but not from those in sponge fields or sediment with sparse epifauna.

Perhaps other stationary megafauna (in addition to sea pens) play equivalent roles for some fish species.

Even though we found distinct assemblages based on both habitat and depth, we cannot infer a direct mechanism for the patterns or functional roles of the habitats. Indeed, it is possible that current regimes, temperature, topography, and other environmental factors separately influence the relative proportion of fishes and the invertebrates used in our habitat classification scheme. Because so little is known about the influence of small-scale variables on corals and sponges, we cannot eliminate the possibility that similar explanatory variables independently drive fish and invertebrate distribution patterns.

Assemblages consist of loosely co-occurring groups of species in a given location at a given time, whereas communities are fauna that interact, co-exist, and/or co-adapt over time (Haedrich & Merrett 1990). Haedrich and Merrett (1990) argued that deep, demersal fish communities do not exist, but instead random assemblages are present. Other authors counter that argument with data illustrating strong, consistent patterns and/or community organization within the deep sea (e.g. Koslow et al. 1994; Ross & Quattrini 2007). Although we have no strong evidence for co-evolved or even interacting fish assemblages, our results illustrate non-random distributions at relatively small spatial and short temporal scales. Nevertheless, causal factors of non-random distributions likely vary geographically, and thus care should be taken when extrapolating results to large spatial scales.

4.4.2 Conservation implications

Despite dramatic declines in deep-sea fishes (Devine et al. 2006), the designation of several deep-sea fishes as at-risk in Canadian waters (COSEWIC 2007; COSEWIC 2008), the potential lengthy recovery times of these species (Baker et al. 2009), and the call for marine protected areas, very little has been done to protect deep-sea habitats within Canadian waters off Newfoundland and Labrador. The Northwest Atlantic Fisheries Organization (NAFO) temporarily closed an area off the slope of the Grand Banks (that extends into Canada's exclusive economic zone) to bottom fishing to help protect corals (NAFO 2011). This protected area runs roughly along the 800 – 1000 m contour (Rogers & Gianni 2010). Such a narrow and deep depth range has limited capacity to serve its intended conservation objectives (Rogers & Gianni 2010; Baker et al. 2012), and our results further show that it is unlikely to protect a wide range of deep-sea fishes. The non-random distribution of fishes and the distinct assemblages associated with depth and habitat types, illustrate that deep-sea conservation initiatives must protect a wide range of depths and habitat types to benefit a wide diversity of deep-sea fishes.

Outside Canada's economic exclusive zone (but off Newfoundland), NAFO is addressing deep-sea conservation. Eleven areas designated as vulnerable marine ecosystems were temporarily closed to bottom fishing in 2010 (NAFO 2010) and closures on various seamounts off Newfoundland, including the Orphan Knoll were announced in 2012 (NAFO 2012). Although the specific amounts of small-scale habitat types protected by these closures remain unknown, the closures cover a depth range shallower than 500 m to greater than 5400 m. Our analysis illustrates that a range of fish assemblages are potentially protected by these closures.

4.4.3 Species occurrences and behaviour

The species and depth ranges reported during our surveys are similar to those reported from trawl surveys in Carson Canyon off the Grand Banks during June 1980, May 1981, and September 1982 (Snelgrove & Haedrich 1985). But unlike Snelgrove and Haedrich (1985), we recorded *Synaphobranchus kaupii* and *Sebastes* spp. most often. In comparison, *Coryphaenoides rupestris* and *Macrourus berglax* were most often captured in their study. The low abundance of *S. kaupii* in their survey may be attributed to *S. kaupii*'s net avoidance behaviours (Cohen & Pawson 1977), as well as tears and problems keeping the trawl nets open (Snelgrove & Haedrich 1985). Although not the most numerous species, we also recorded many *C. rupestris*. Several surveys have shown that *C. rupestris*, a species at risk in Canada (Environment Canada 2011), is generally more abundant in canyons than the open slope (Snelgrove & Haedrich 1985). Our findings reiterate the possible importance of canyon ecosystems for *C. rupestris*.

Fish are known to react to ROVs, potentially biasing *in situ* observations (Koslow et al. 1995; Trenkel et al. 2004; Ryer et al. 2009). Fishes may respond to numerous variables including light conditions, vehicle motion and speed, noise, water displacement, substrate, temperature, current speed, and water column position (Lorance & Trenkel 2006; Stoner et al. 2008). In our study, few species were exclusively attracted to or displayed avoidance of the ROV. Instead we observed considerable within-species variation, as reported elsewhere (Lorance & Trenkel 2006; Stoner et al. 2008). Unfortunately, behavioural variation in some species may be a function of habitat characteristics (Uiblein et al. 2002; Uiblein et al. 2003; Lorance & Trenkel 2006; Stoner et al. 2008). In the Northeast Atlantic, *Synaphobranchus kaupii* exhibited a significantly higher disturbance response in the deepest waters surveyed (Uiblein et al. 2003). Therefore, our apparent assemblage patterns could be influenced by species avoiding the ROV (i.e. remaining out of our field of view) in some habitats and not by a genuine absence or lower abundances in those habitats. For example, Lorance and Trenkel (2006) found *Coryphaenoides rupestris* reacted to an ROV more often in warmer temperatures, when the ROV was close to the seafloor, and in strong currents (indirectly). If some species of corals within our study area are more abundant in warmer waters and strong currents, it may be difficult to demonstrate associations between *C. rupestris* and these corals using an ROV.

4.4.4 Notable species observations

Although we sampled only three outcrops in our survey, all of the four *Neocyttus helgae* we observed were associated with these vertical structures. Moore et al. (2008) hypothesized that seamounts act as stepping stones for *N. helgae* dispersal based on sightings of this species on seamounts off the eastern United States. The authors explained an observation of *N. helgae* in Lydonia Canyon as a localized colonization event followed by local extinction caused by various factors that prevent population persistance in canyons. Our results do not support their hypothesis. The presence of four

N. helgae in two canyons associated with relatively rare habitat features indicates the species, though relatively rare, is more widespread in the Western North Atlantic than originally thought. The apparent reported absence of *N. helgae* in this region is likely an artefact of the most common sampling gears used to date (i.e. trawls). Survey trawlers usually avoid vertical, wall structures in order to avoid gear damage.

We recorded *Anarhichas minor* five times during our surveys, a species that is currently listed as Threatened under Canada's Species at Risk Act (Environment Canada 2011). Four individuals (including 1 pair) occurred with *Keratoisis grayi* thickets and the other occurred within dense small coral habitat. Laboratory experiments performed on juvenile *A. minor* showed that when shelter was made available, individuals spent most of their time around or within the shelter (Lachance et al. 2010). In the deep sea, where shelter is relatively scarce, corals likely play a significant role in providing this shelter. These observations highlight the need for more directed research into the small-scale habitat requirements and/or preferences of deep-sea species at risk. If invertebrates such as corals provide structural habitat for this species, habitat protection must play a key role in recovery initiatives.

4.4.5 Caveats and future initiatives

We examined all fish (regardless of size) within just a single year and month, but acknowledge that corals may play different roles for fishes depending on their life stage, age, and season. For example, fish egg cases have been found attached to gorgonians and sponges off Southern California (Tissot et al. 2006), British Columbia (EN Edinger, unpublished data), and Newfoundland (Fisheries and Oceans Canada, unpublished data). Some deep-sea fish also make diurnal, annual, seasonal and/or otogenetic distributional changes. For example, in some locations groups of *C. rupestris* are thought to make daily vertical migrations off bottom to take advantage of food descending in the water column and may move to shallower waters near the end of summer and deeper waters in the winter (Atkinson 1995). A more comprehensive understanding of deep-sea habitat use, including coral areas, requires more in-depth research using techniques appropriate for studying eggs, larvae, juvenile, and adult fish on a seasonal basis and over longer temporal scales.

4.5 Conclusions

Our study found distinct fish assemblages based on both depth and habitat type. Regardless of whether corals play an obligate, functional role for fish, they remain important features within the deep sea and appear to influence fish distributions and abundances. Any conservation program aimed at protecting deep-sea ecosystems must protect a wide-range of habitats and depths to ensure that a range of species and assemblages benefit. *In situ* fish research is still in its infancy and continued directed research promises great dividends in our understanding of functional relationships in the deep sea.

4.6 Literature cited

Atkinson D.B. (1995) The biology and fishery of Roundnose Grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the North West Atlantic. In: A.G. Hopper (Ed). Deep-water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, Netherlands. 51-111 pp.

Auster P.J. (2005) Are deep-water corals important habitats for fishes? In: A. Freiwald & J.M. Roberts (Eds). Cold-water Corals and Ecosystems. Springer-Verlag, Berlin. 747-760 pp.

Bailey D.M., Collins M.A., Gordon J.D.M., Zuur A.F., Priede I.G. (2009) Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? Proceedings of the Royal Society B-Biological Sciences 276(1664): 1965-1969.

Baillon S., Hamel J.-F., Wareham V.E., Mercer A. (2012) Deep cold-water corals as nurseries for fish larvae. Frontiers in Ecology and the Environment 10(7): 351-356.

Baker K.D., Devine J.A., Haedrich R.L. (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. Environmental Biology of Fishes 85(1): 79-88.

Baker K.D., Wareham V., Snelgrove P.V.R., Haedrich R.L., Fifield D.A., Edinger E.N., Gilkinson K. (2012) Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. Marine Ecology Progress Series 445: 235-249.

Benjamin R. (2007) ClassAct Mapper. Fisheries and Oceans Canada, Dartmouth, NS.

Brodeur R.D. (2001) Habitat-specific distribution of Pacific ocean perch (*Sebastes alutus*) in Pribilof Canyon, Bering Sea. Continental Shelf Research 21: 201-224.

Buhl-Mortensen L., Vanreusel A., Gooday A.J., Levin L.A., Priede I.G., Buhl-Mortensen P., Gheerardyn H., King N.J., Raes M. (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology 31(1): 21-50.

Clarke K.R., Gorley R.N. (2006) PRIMER v6: user manual / tutorial. PRIMER-E, Plymouth.

Cohen D.M., Pawson D. (1977) Observations from the DSRV Alvin on populations of benthic fishes and selected larger invertebrates in and near DWD-106. US Department of Commmerce, NOAA, Rockville, MD.

COSEWIC (2007) COSEWIC assessment and status report on the Roughhead Grenadiers *Macrourus berglax* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa: 40 pp.

COSEWIC (2008) COSEWIC assessment and status report on the Roundnose Grenadier *Coryphaenoides rupestris* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa: 42 pp.

Costello M.J., McCrea M., Freiwald A., Lundalv T., Jonsson L., Bett B.J., van Weering T.C.E., de Haas H., Roberts J.M., Allen D. (2005) Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: A. Freiwald & J.M. Roberts (Eds). Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin. 771-805 pp.

CSSF (2010) Canadian Scientific Submersible Facility. www.ropos.com, Accessed November.

D'Onghia G., Politou C.-Y., Bozzano A., Lloris D., Rotllant G., Sion L., Mastrototaro F. (2004) Deep-water fish assemblages in the Mediterranean Sea. Scientia Marina (Barcelona) 68(Suppl. 3): 87-99.

Devine J.A., Baker K.D., Haedrich R.L. (2006) Fisheries: Deep-sea fishes qualify as endangered. Nature 439(7072): 29.

Edinger E.N., Wareham V.E., Haedrich R.L. (2007) Patterns of groundfish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. In: R.Y. George & S.D. Cairns (Eds). Conservation and Adaptive Management of Seamount and Deep-sea Coral Ecosystems. Rosenstiel

School of Marine and Atmospheric Science, University of Miami, Miami. 101-122 pp.

Environment Canada (2011) Species at Risk Public Registry. www.sararegistry.gc.ca, Accessed 13 May.

Fossa J.H., Mortensen P.B., Furevik D.M. (2002) The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471: 1-12.

Francis M.P., Hurst R., McArdle B.H., Bagley N., Anderson O.F. (2002) New Zealand demersal fish assemblages. Environmental Biology of Fishes 65: 215-234.

Haedrich R.L., Merrett N.R. (1988) Summary atlas of deep-living demersal fishes in the North Atlantic Basin. Journal of Natural History 22(5): 1325-1362.

Haedrich R.L., Merrett N.R. (1990) Little evidence for faunal zonation or communities in deep sea demersal fish faunas. Progress in Oceanography 24: 239-250.

Haedrich R.L., Rowe G.T., Polloni P.T. (1980) The megabenthic fauna in the deep sea south of New England, USA. Marine Biology 57(3): 165-179.

Hall-Spencer J., Allain V., Fossa J.H. (2002) Trawling damage to Northeast Atlantic ancient coral reefs. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1490): 507-511.

Hecker B. (1990) Variation in megafaunal assemblages on the continental margin south of New England. Deep-Sea Research Part I: Oceanographic Research Papers 37(1): 37-57.

Husebo A., Nottestad L., Fossa J.H., Furevik D.M., Jorgensen S.B. (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91-99.

Koenig C.C., Shepard A.N., Reed J.K., Coleman F.C., Brooke S.D., Brusher J., Scanlon K. (2005) Habitat and fish populations in the deep-sea *Oculina* coral ecosystem of the western Atlantic. American Fisheries Society Symposium 41: 795-805.

Koslow J.A., Boehlert G.W., Gordon J.D.M., Haedrich R.L., Lorance P., Parin N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57(3): 548-557.

Koslow J.A., Bulman C.M., Lyle J.M. (1994) The mid-slope demersal fish community off southeastern Australia. Deep-Sea Research Part I: Oceanographic Research Papers 41(1): 113-141.

Koslow J.A., Kloser R., Stanley C.A. (1995) Avoidance of a camera system by a deep-water fish, the orange roughy (*Hoplostethus atlanticus*). Deep-Sea Research Part I: Oceanographic Research Papers 42(2): 233-244.

Krieger K.J., Wing B.L. (2002) Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. Hydrobiologia 471: 83-90.

Lachance A.A., Dutil J.D., Larocque R., Daigle G. (2010) Shelter use and behaviour of juvenile spotted wolffish (*Anarhichas minor*) in an experimental context. Environmental Biology of Fishes 88(3): 207-215.

Lorance P., Souissi S., Uiblein F. (2002) Point, alpha and beta diversity of carnivorous fish along a depth gradient. Aquatic Living Resources 15: 263-271.

Lorance P., Trenkel V.M. (2006) Variability in natural behaviour, and observed reactions to an ROV, by mid-slope fish species. Journal of Experimental Marine Biology and Ecology 332(1): 106-119.

Moore J.A., Auster P.J., Calini D., Heinonen K., Barber K., Hecker B. (2008) False boarfish *Neocyttus helgae* in the Western North Atlantic. Bulletin of the Peabody Museum of Natural History 49(1): 31-41.

NAFO (2010) Northwest Atlantic Fisheries Organization Conservation and Enforcement Measures. NAFO: 95 pp.

NAFO (2011) Northwest Atlantic Fisheries Organization. www.nafo.int, Accessed 30 Sept.

NAFO (2012) Northwest Atlantic Fisheries Organization Conservation and Enforcement Measures Northwest Atlantic Fisheries Organization: 101 pp.

Roberts J.M., Wheeler A.J., Freiwald A., Cairns S. (2009) Cold-water Corals: The Biology and Geology of Deep-sea Coral Habitats. Cambridge University Press, New York: 334 pp.

Rogers A., Gianni M. (2010) The implementation of UNGA Resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas. International Programme of the State of the Ocean, London, UK: 97 pp.

Ross S.W., Quattrini A.M. (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Research Part I: Oceanographic Research Papers 54(6): 975-1007.

Ryer C.H., Stoner A.W., Iseri P.J., Spencer M.L. (2009) Effects of simulated underwater vehicle lighting on fish behavior. Marine Ecology Progress Series 391: 97-106.

Snelgrove P.V.R., Haedrich R.L. (1985) Structure of the deep demersal fish fauna off Newfoundland. Marine Ecology Progress Series 27(1-2): 99-107.

Soffker M., Sloman K.A., Hall-Spencer J. (2011) In situ observations of fish associated with coral reefs off Ireland. Deep-Sea Research Part I: Oceanographic Research Papers 58: 818-825.

Stone R. (2006) Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25(2): 229-238.

Stoner A.W., Ryer C.H., Parker S.J., Auster P.J., Wakefield W.W. (2008) Evaluating the role of fish behavior in surveys conducted with underwater vehicles. Canadian Journal of Fisheries and Aquatic Sciences 65(6): 1230-1243.

Sulak K.J., Brooks R.A., Luke K.E., Norem A.D., Randall M., Quaid A.J., Yeargin G.E., Miller J.M., Harden W.M., Caruso J.H., et al. (2007) Demersal fishes associated with *Lophelia pertusa* coral and hard-substrate biotopes on the continental slope, northern Gulf of Mexico. Bulletin of Marine Science 81(Supplement 1): 65-92.

Tissot B.N., Yoklavich M.M., Love M.S., York K., Amend M. (2006) Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. Fishery Bulletin 104(2): 167-181.

Trenkel V.M., Francis R., Lorance P., Mahevas S., Rochet M.J., Tracey D.M. (2004) Availability of deep-water fish to trawling and visual observation from a remotely operated vehicle (ROV). Marine Ecology Progress Series 284: 293-303.

Turley C.M., Roberts J.M., Guinotte J.M. (2007) Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? Coral Reefs 26(3): 445-448.

Uiblein F., Lorance P., Latrouite D. (2002) Variation in locomotion behaviour in northern cutthroat eel (*Synaphobranchus kaupi*) on the Bay of Biscay continental slope. Deep Sea Research Part I: Oceanographic Research Papers 49: 1689-1703.

Uiblein F., Lorance P., Latrouite D. (2003) Behaviour and habitat utilisation of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. Marine Ecology Progress Series 257: 223-232.

Table 4-1. ROV dives from a cruise off the southwest Grand Banks of Newfoundland in 2007, and their associated depths, time on bottom, and distance and estimated area covered.

Dive	Date	Depth range	Time on bottom (h)	Distance (km)	Estimated area (m^2)
R1065	16 – 17 July	606 – 1015 m	12.6	10.7	35,159
R1066	17 –18 July	493 – 1020 m	16.0	15.8	46,876
R1067	18 – 19 July	395 – 996 m	10.2	13.4	43,720
R1068	19 July	1990 – 2245 m	4.5	5.9	17,654
R1070	21 July	351 – 940 m	15.5	23.6	87,316
R1071	22 – 23 July	353 – 1174 m	12.8	16.9	63,353
R1072	23 – 24 July	1116 – 1900 m	18.8	19.0	52,883
Total			90.4	105.3	346,961

Table 4-2. The distance (m) and time (min) (in brackets) of each habitat and depth category surveyed with an ROV off the southwest Grand Banks of Newfoundland in 2007. Video classified as 'dead-time' was removed.

Habitat Complexity	Habitat Types	300 – 800 m	800 – 1300 m	1300 – 2300 m
High	Outcrop	150.2 (12.9)	122.2 (8.8)	224.5 (21.8)
	Dense large corals	3204.5 (145.8)	6.4 (0.5)	71.5 (1.9)
	Boulders	1471.4 (84.5)	-	-
	Sparse large corals	2889.3 (138.2)	197.6 (19.9)	16.9 (0.5)
	Dense small corals	12890.3 (612.8)	63.3 (3.6)	-
Medium	Sparse small corals	10642.9 (372.5)	385.4 (16.5)	58.8 (2.4)
	Sea pen field	2560.1 (77.5)	6511.8 (304.3)	-
	Sponge field	665.5 (16.9)	-	-
Low	Cup coral field	820.4 (23.4)	212.8 (11.3)	-
	H. insolitus field	144.1 (4.3)	157.5 (4.5)	-
	Sediment with epifauna	8406.6 (273.5)	19868.1 (822.2)	15490.6 (727.0)

Table 4-3. The number of individuals for each fish taxon observed during an *in situ* survey off the southwest Grand Banks of Newfoundland, Canada in 2007.

Taxa		Number observed
Myxinidae	*Myxine glutinosa*	2
Chimaeridae	*Hydrolagus affinis*	3
Rhinochimaeridae	*Harriotta raleighana*	19
	Harriotta haeckeli	1
Scyliorhinidae	*Apristurus profundorum*	2
Etmopteridae	*Centroscyllium fabricii*	223
Rajidae	*Rajella fyllae*	13
	Rajella bathyphila	1
	Rajidae (sp. 1)	2
	Rajidae (sp. 2)	1
	Rajidae (sp. 3)	1
	Rajidae (sp. 4)	2
	Rajidae (sp. 5)	1
	Rajidae (sp. 6)	2
	Rajidae (unknown)	5
Synaphobranchidae	*Synaphobranchus kaupii*	6586
	Simenchelys parasitica	6
Serrivomeridae	*Serrivomer beanii*	1
Notacanthidae	*Notacanthus chemnitzii*	11
Halosauridae	*Halosauropsis macrochir*	59
	Aldrovandia sp. 1	386
	Aldrovandia sp. 2	70
Argentinidae	*Argentina silus*	10
Alepocephalidae	*Alepocephalus* spp.	93
Melanostomiidae	Melanostomiidae (unknown)	7
Stomiidae	*Chauliodus sloani*	1
Ipnopidae	*Bathypterois dubius*	25
Bathysauridae	*Bathysaurus ferox*	17
Myctophidae	Myctophidae (unknown)	1663
Lophiidae	*Lophius americanus*	2
Ogcocephalidae	*Dibranchus atlanticus*	1
Macrouridae	*Coelorinchus caelorhincus*	4
	Coryphaenoides rupestris	795
	Coryphaenoides carapinus	349
	Coryphaenoides armatus	1
	Macrourus berglax	56
	Malacocephalus occidentalis	8

	Taxa	Number observed
	Nezumia bairdii	876
	Nezumia aequalis	1
	Trachyrincus murrayi	1
	Macrouridae (sp. 1)	28
	Macrouridae (sp. 2)	17
	Macrouridae (sp. 3)	77
	Macrouridae (sp. 4)	13
	Macrouridae (unknown)	871
Moridae	*Antimora rostrata*	271
	Lepidion eques	9
	Moridae (sp. 1)	29
	Moridae (unknown)	72
Lotidae	*Brosme brosme*	1
Gadidae	*Gadus morhua*	2
Phycidae	*Phycis chesteri*	141
Trachichthyidae	*Hoplostethus atlanticus*	4
Oreosomatidae	*Neocyttus helgae*	4
Scorpaenidae	*Sebastes* spp.	4767
Cottidae	*Myoxocephalus* sp. 1	1
Liparidae	Liparidae (sp. 1)	3
Zoarcidae	*Lycenchelys paxillus*	3
	Lycodes terraenovae	7
	Lycodes esmarkii	2
	Lycodes sp.	1
	Melanostigma atlanticum	38
	Zoarcidae (sp. 1)	11
	Zoarcidae (sp. 2)	1
	Zoarcidae (unknown)	12
Anarhichadidae	*Anarhichas minor*	5
	Anarhichas denticulatus	2
	Anarhichas lupus	1
Pleuronectidae	*Glyptocephalus cynoglossus*	277
	Reinhardtius hippoglossoides	51
	Hippoglossus hippoglossus	9
Pleuronectiforme (unknown)		228
Unknown	Fish unknown (sp. 1)	2
	Fish unknown (sp. 2)	10
	Fish unknown (sp. 3)	1
	Fish unknown (sp. 4)	3
	Fish unknown (sp. 5)	5
	Fish unknown (sp. 6)	29

Taxa	Number observed
Fish unknown (sp. 7)	15
Fish unknown (sp. 8)	8
Fish (unknown)	93

Table 4-4. The relative abundances (%) of unique fish taxa within each habitat type, with portions of video characterized as 'dead time' removed. 'X' identifies when a species was found only during dead time. Data collected during an *in situ* survey off the southwest Grand Banks of Newfoundland, Canada in 2007.

	Taxa	Outcrop	Dense large corals	Boulder field	Sparse large corals	Dense small corals	Sparse small corals	Sea pen field	Sponge field	Cup coral field	*H. insolitus* field	Sediment with sparse epifauna
Myxinidae	*Myxine glutinosa*			0.13								0.02
Chimaeridae	*Hydrolagus affinis*											0.05
Rhinochimaeridae	*Harriotta raleighana*					0.09		0.26				0.20
	Harriotta haeckeli											0.02
Scyliorhinidae	*Apristurus profundorum*											0.03
Etmopteridae	*Centroscyllium fabricii*		7.14		5.42	2.38	1.04	1.47	1.15			0.79
Rajidae	*Rajella fyllae*					0.33	0.13	0.09				0.02
	Rajella bathyphila											0.02
	Rajidae (sp. 1)					0.05		0.09				
	Rajidae (sp. 2)											0.02
	Rajidae (sp. 3)											0.02
	Rajidae (sp. 4)						0.09					
	Rajidae (sp. 5)					0.05						
	Rajidae (sp. 6)				0.21							0.02
Synaphobranchidae	*Synaphobranchus kaupii*	11.54	23.33	20.73	27.08	37.28	49.29	31.43	51.92	54.51	55.56	35.71
	Simenchelys parasitica											0.08
Serrivomeridae	*Serrivomer beanii*											0.02

	Taxa	Outcrop	Dense large corals	Boulder field	Sparse large corals	Dense small corals	Sparse small corals	Sea pen field	Sponge field	Cup coral field	*H. insolitus* field	Sediment with sparse epifauna
Notacanthidae	*Notacanthus chemnitzii*		0.48		0.21	0.09	0.09	0.09				0.05
Halosauridae	*Halosauropsis macrochir*						0.09					0.85
	Aldrovandia sp. 1	11.54				0.05	0.13	0.35				5.45
	Aldrovandia sp. 2							6.06				
Argentinidae	*Argentina silus*		0.71	0.13	0.21				0.77			0.03
Alepocephalidae	*Alepocephalus* spp.		0.24	0.00	0.21	0.09	X	1.56				0.99
Melanostomiidae	Melanostomiidae						X					0.05
Stomiidae	*Chauliodus sloani*											0.02
Ipnopidae	*Bathypterois dubius*							0.09				0.36
Bathysauridae	*Bathysaurus ferox*											0.27
Myctophidae	Myctophidae	26.92	10.95	X	13.96	6.71	5.97	23.03	1.15	0.80	20.00	13.34
Lophiidae	*Lophius americanus*							0.09				0.02
Ogcocephalidae	*Dibranchus atlanticus*											0.02
Macrouridae	*Coelorinchus caelorhincus*					0.05						0.03
	Coryphaenoides rupestris	7.69	9.05		10.42	4.71	3.72	13.42	3.08	0.20	6.67	4.77
	Coryphaenoides carapinus	15.38	0.71		0.21				X			5.12
	Coryphaenoides armatus											0.02
	Macrourus berglax		1.19	0.13	0.63	0.70	0.22	0.35	0.38			0.28
	Malacocephalus occidentalis						0.04	0.35				0.05
	Nezumia bairdii		6.19	1.75	7.50	9.13	5.84	7.19	5.00	1.40	6.67	4.79

	Taxa	Outcrop	Dense large corals	Boulder field	Sparse large corals	Dense small corals	Sparse small corals	Sea pen field	Sponge field	Cup coral field	*H. insolitus* field	Sediment with sparse epifauna
	Nezumia aequalis											0.02
	Trachyrincus murrayi											0.02
	Macrouridae (sp. 1)											0.44
	Macrouridae (sp. 2)											0.27
	Macrouridae (sp. 3)			0.13	0.21	0.42	1.08	0.09			2.22	0.49
	Macrouridae (sp. 4)			0.13	0.21	0.14	0.30					0.02
Moridae	*Antimora rostrata*	3.85	0.71		0.63	0.14	0.87	2.86	0.38		2.22	2.76
	Lepidion eques	X	0.71			0.05	0.09	0.09		0.20		
	Moridae (sp. 1)		0.24		0.42	0.09	0.04	1.39			2.22	0.08
Lotidae	*Brosme brosme*					0.05						
Gadidae	*Gadus morhua*			0.27								0.00
Phycidae	*Phycis chesteri*		0.48	3.77	1.04	0.75	0.48	0.00	0.38	1.20		0.54
Trachichthyidae	*Hoplostethus atlanticus*	3.85	0.48						0.38			
Oreosomatidae	*Neocyttus helgae*	15.38										
Sebastidae	*Sebastes* spp.		34.29	72.54	29.17	33.74	29.21	1.21	34.23	41.08	0.00	18.56
Cottidae	*Myoxocephalus* sp. 1		0.24									
Liparidae	Liparidae (sp. 1)					0.05	0.04					X
Zoarcidae	*Lycenchelys paxillus*					0.09						0.02
	Lycodes terraenovae							0.17				0.05
	Lycodes esmarkii											0.03
	Lycodes sp.											0.02
	Melanostigma atlanticum					0.14	0.09	1.65				0.22

	Taxa	Outcrop	Dense large corals	Boulder field	Sparse large corals	Dense small corals	Sparse small corals	Sea pen field	Sponge field	Cup coral field	*H. insolitus* field	Sediment with sparse epifauna
	Zoarcidae (sp. 1)					0.05	0.09	0.26	0.38			0.06
	Zoarcidae (sp. 2)					0.05						
Anarhichadidae	*Anarhichas minor*		0.71		0.21	0.05						
	Anarhichas denticulatus				0.21							0.02
	Anarhichas lupus			0.13								
Pleuronectidae	*Glyptocephalus cynoglossus*		0.71			2.05	0.69	5.11		0.40	2.22	2.05
	Reinhardtius hippoglossoides		0.24		0.63	0.05	0.17	0.43		0.20		0.49
	Hippoglossus hippoglossus				0.21			0.17				0.03
Unknown	Fish unknown (sp. 1)		0.24				0.04					
	Fish unknown (sp. 2)							0.17				0.09
	Fish unknown (sp. 3)	3.85										
	Fish unknown (sp. 4)										2.22	0.03
	Fish unknown (sp. 5)		0.48	0.13		0.05						
	Fish unknown (sp. 6)		0.48		0.83	0.28	0.13	0.35	0.38			0.13
	Fish unknown (sp. 7)				0.21	0.09	0.04					0.05
	Fish unknown (sp. 8)							0.17	0.38			0.06
Total number of species observed		10	23	13	23	33	29	31	14	9	9	59

Table 4-5. Behaviour and reactions of individual fish taxa observed during an *in situ* survey off the southwest Grand Banks of Newfoundland, Canada in 2007.

		Reaction to ROV			Observed behaviours				
Taxa		Attraction (%)	Avoidance (%)	No reaction (%)	Actively swimming (%)	Feeding (%)	Hiding (%)	Hovering (%)	Resting (%)
Myxinidae	*Myxine glutinosa*	-	50	50	50	-	50	-	-
Chimaeridae	*Hydrolagus affinis*	100	-	-	100	-	-	-	-
Rhinochimaeridae	*Harriotta raleighana*	84.2	-	15.8	94.7	-	-	5.3	-
	Harriotta haeckeli	100	-	-	100	-	-	-	-
Scyliorhinidae	*Apristurus profundorum*	100	-	-	100	-	-	-	-
Etmopteridae	*Centroscyllium fabricii*	91.9	0.9	7.2	99.6	-	0.4	-	-
Rajidae	*Rajella fyllae*	23.1	38.5	38.5	15.4	-	-	-	84.6
	Rajella bathyphila	-	100	-	-	-	-	-	100
	Rajidae (sp. 1)	-	-	100	50	-	50	-	-
	Rajidae (sp. 2)	-	100	-	-	-	-	-	100
	Rajidae (sp. 3)	-	100	-	0	-	-	-	100
	Rajidae (sp. 4)	-	100	-	50	-	-	-	50
	Rajidae (sp. 5)	100	-	-	100	-	-	-	0
	Rajidae (sp. 6)	-	-	100	50	-	-	-	50
Synaphobranchidae	*Synaphobranchus kaupii*	25.3	1.9	72.8	95.5	0.02	0.05	4.2	0.2
	Simenchelys parasitica	33.3	16.7	50	100	-	-	-	-
Serrivomeridae	*Serrivomer beanii*	0	0	100	100	-	-	-	-
Notacanthidae	*Notacanthus chemnitzii*	27.3	0	72.7	72.7	-	-	27.3	-
Halosauridae	*Halosauropsis macrochir*	11.9	3.4	84.7	13.6	-	-	76.3	10.2
	Aldrovandia sp. 1	7.3	7.0	85.7	14.0	-	-	80.8	5.2
	Aldrovandia sp. 2	5.7	2.9	91.4	24.3	-	-	71.4	4.3
Argentinidae	*Argentina silus*	40	30	30	90	-	-	10	-
Alepocephalidae	*Alepocephalus* spp.	67.7	5.4	26.9	76.3	-	-	23.7	-

Taxa		Reaction to ROV			Observed behaviours				
		Attraction (%)	Avoidance (%)	No reaction (%)	Actively swimming (%)	Feeding (%)	Hiding (%)	Hovering (%)	Resting (%)
Melanostomiidae	Melanostomiidae	57.1	-	42.9	57.1	-	-	42.9	-
Stomiidae	*Chauliodus sloani*	-	-	100	-	-	-	100	-
Ipnopidae	*Bathypterois dubius*	12	16	72	4	-	-	4	92
Bathysauridae	*Bathysaurus ferox*	-	-	100	5.9	-	-	-	94.1
Myctophidae	Myctophidae	86.0	3.4	10.6	91.8	-	0.1	7.9	0.2
Lophiidae	*Lophius americanus*	-	-	100	-	-	-	-	100
Ogcocephalidae	*Dibranchus atlanticus*	-	-	100	-	-	-	-	100
Macrouridae	*Coelorinchus caelorhincus*	-	-	100	25	-	-	50	25
	Coryphaenoides rupestris	11.3	2.3	86.4	24.4	-	0.6	72.8	2.1
	Coryphaenoides carapinus	13.5	4.9	81.6	20.6	-	-	71.1	8.3
	Coryphaenoides armatus	-	-	100	-	-	-	100	-
	Macrourus berglax	7.1	-	92.9	12.5	-	1.8	53.6	32.1
	Malacocephalus occidentalis	-	-	100	12.5	-	-	87.5	-
	Nezumia bairdii	6.4	1.4	92.2	15.0	-	0.1	84.1	0.8
	Nezumia aequalis	-	-	100	-	-	-	100	-
	Trachyrincus murrayi	-	-	100	-	-	-	100	-
	Macrouridae (sp. 1)	-	7.1	92.9	3.6	-	-	92.9	3.6
	Macrouridae (sp. 2)	5.9	5.9	88.2	35.3	-	-	41.2	23.5
	Macrouridae (sp. 3)	2.6	-	97.4	3.9	-	-	93.5	2.6
	Macrouridae (sp. 4)	-	-	100	30.8	-	-	61.5	7.7
Moridae	*Antimora rostrata*	31.4	2.2	66.4	73.4	-	-	25.5	1.1
	Lepidion eques	55.6	-	44.4	77.8	-	-	11.1	11.1
	Moridae (sp. 1)	55.2	3.4	41.4	82.8	-	-	17.2	-
Lotidae	*Brosme brosme*	100	-	-	100	-	-	-	-
Gadidae	*Gadus morhua*	100	-	-	100	-	-	-	-

		Reaction to ROV			Observed behaviours				
Taxa		Attraction (%)	Avoidance (%)	No reaction (%)	Actively swimming (%)	Feeding (%)	Hiding (%)	Hovering (%)	Resting (%)
Phycidae	*Phycis chesteri*	29.1	3.5	67.4	46.1	-	5.0	17.0	31.9
Trachichthyidae	*Hoplostethus atlanticus*	25	25	50	25	-	25	50	-
Oreosomatidae	*Neocyttus helgae*	25	-	75	25	-	-	75	-
Cottidae	*Myoxocephalus* sp. 1	-	-	100	100	-	-	-	-
Liparidae	Liparidae (sp. 1)	33.3	33.3	33.3	100	-	-	-	-
Zoarcidae	*Lycenchelys paxillus*	-	-	100	-	-	-	-	100
	Lycodes terraenovae	14.3	-	85.7	-	-	-	-	100
	Lycodes esmarkii	-	-	100	-	-	-	-	100
	Lycodes sp.	-	100	-	-	-	-	-	100
	Melanostigma atlanticum	21.1	2.6	76.3	63.2	-	-	36.8	-
	Zoarcidae (sp. 1)	-	-	100	27.3	-	-	36.4	36.4
	Zoarcidae (sp. 2)	-	-	100	-	-	-	-	100
Anarhichadidae	*Anarhichas minor*	-	40	60	-	-	40	-	60
	Anarhichas denticulatus	-	-	100	-	-	-	-	100
	Anarhichas lupus	-	-	100	-	-	-	-	100
Pleuronectidae	*Glyptocephalus cynoglossus*	1.8	3.6	94.6	1.4	-	2.5	-	96.0
	Reinhardtius hippoglossoides	13.7	27.5	58.8	35.3	-	2.0	-	62.7
	Hippoglossus hippoglossus	-	-	100	33.3	-	-	-	66.7
Unknown	Fish unknown (sp. 1)	-	-	100	-	-	50	-	50
	Fish unknown (sp. 2)	-	-	100	-	-	-	10	90
	Fish unknown (sp. 3)	-	-	100	-	-	-	100	-
	Fish unknown (sp. 4)	33.3	-	66.7	100	-	-	-	-
	Fish unknown (sp. 5)	20	-	80	20	-	-	-	80
	Fish unknown (sp. 6)	89.7	3.4	6.9	89.7	-	-	10.3	-
	Fish unknown (sp. 7)	100	-	-	100	-	-	-	-

	Reaction to ROV			Observed behaviours				
Taxa	Attraction (%)	Avoidance (%)	No reaction (%)	Actively swimming (%)	Feeding (%)	Hiding (%)	Hovering (%)	Resting (%)
Fish unknown (sp. 8)	50	12.5	37.5	62.5	-	-	37.5	-

Table 4-6. Results (R-statistic) of two-way Analysis of Similarities (ANOSIM) of fish assemblages observed during an *in situ* survey off the southwest Grand Banks of Newfoundland, Canada in 2007 (top right half of table). The global R-statistic equalled 0.391 (p = 0.001) and * denotes significant R statistics ($p \leq 0.05$). The lower left half of the table shows average dissimilarity results from SIMPER. Analyses were based on standardized, fourth-root transformed data.

Habitat Types	Outcrop	Dense large corals	Boulder field	Sparse large corals	Dense small corals	Sparse small corals	Sea pen field	Sponge field	Cup coral field	*H. insolitus* field	Sediment with sparse epifauna
Outcrop	-	1	1	1	0.592	0.453	0.713	1	1	0	1*
Dense large corals	58.98	-	0.510*	-0.193	0.090	0.019	0.576	-0.107	0.071	0.393	0.313
Boulder field	100	49.98	-	0.531	0.925*	0.900*	0.929	0.857	-0.143	0.821	0.763*
Sparse large corals	70.04	45.15	48.87	-	0.146	0.110	0.589*	-0.036	0.111	0.397	0.479*
Dense small corals	75.63	44.57	56.07	49.01	-	-0.068	0.551*	0.509	0.608*	0.520	0.202*
Sparse small corals	66.57	43.66	54.37	47.88	46.43	-	0.482*	0.218	0.610*	0.317	0.158
Sea pen field	62.65	55.33	63.66	55.78	69.40	54.11	-	-0.250	0.825	0.331	0.149
Sponge field	73.00	42.17	55.74	44.45	42.77	38.53	50.43	-	0	-0.250	0.091
Cup coral field	81.21	47.71	28.79	44.65	55.66	49.94	54.42	42.72	-	0	0.684*
H. insolitus field	61.64	56.47	67.80	58.13	62.23	50.91	47.85	51.81	57.52	-	0.779*
Sediment with sparse epifauna	65.62	47.67	55.34	50.29	53.66	47.46	38.71	41.70	57.52	53.06	-

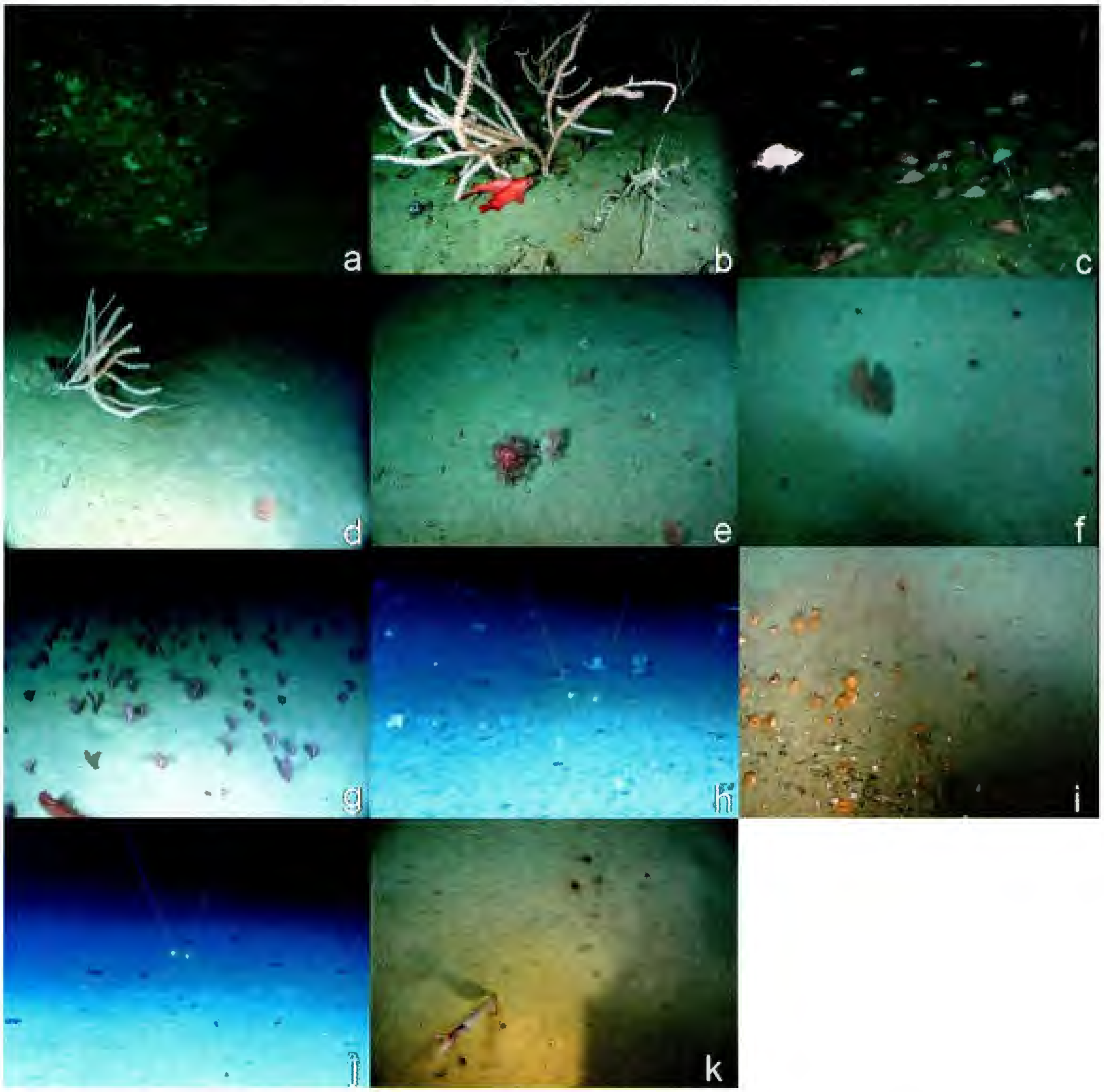
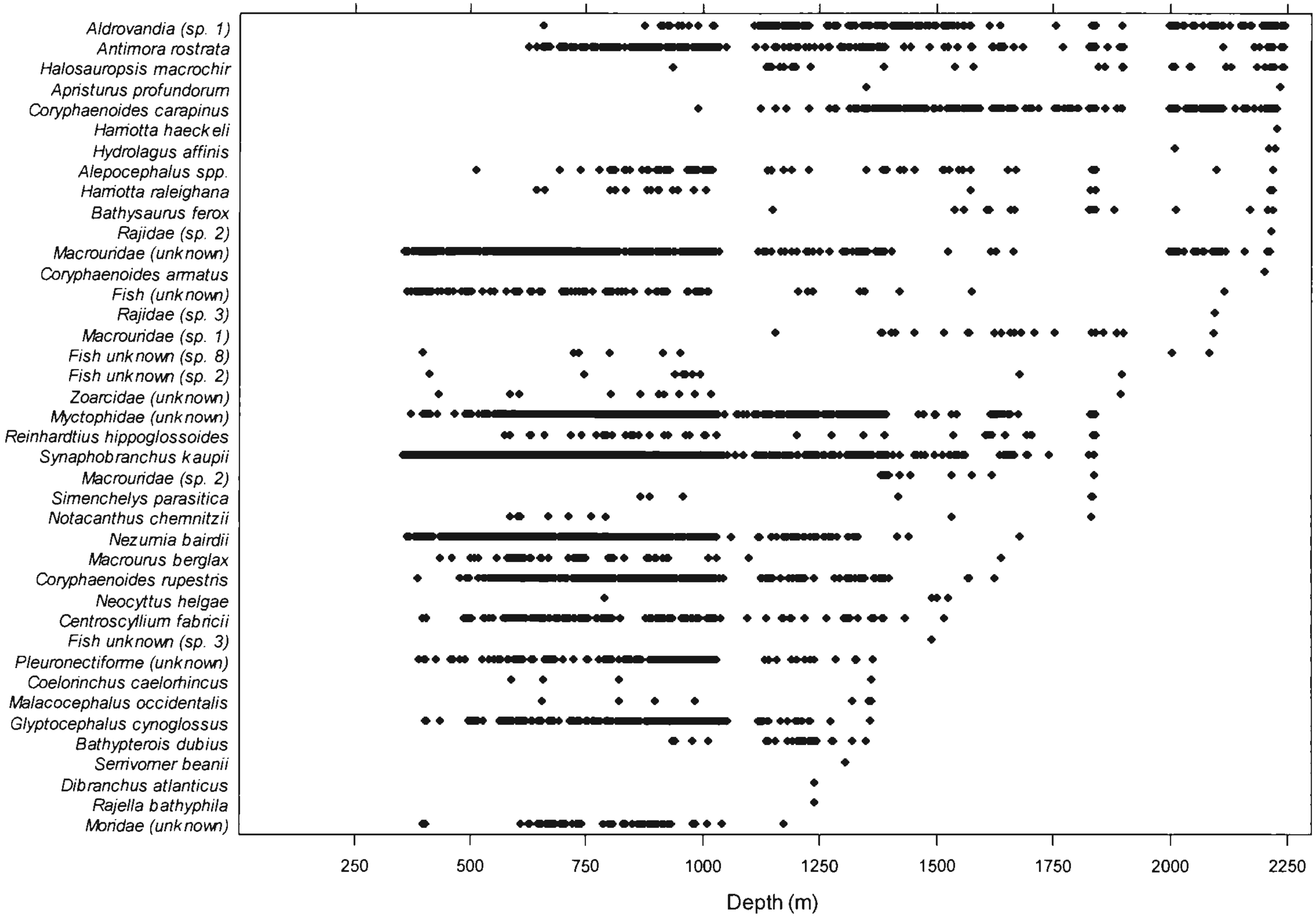


Figure 4-1. Photos depicting examples of habitats encountered (and classified) during an *in situ* survey off the southwest Grand Banks of Newfoundland in 2007: (a) outcrop, (b) dense large coral cover with *Sebastes* sp., (c) boulder field with numerous *Sebastes* spp., (d) sparse large coral cover, (e) dense small coral cover, (f) sparse small coral cover, (g) sea pen field, (h) sponge field, (i) cup coral fields, (j) *Heteropolypus* cf. *insolitus* field, and (k) fine sediments with sparse epifauna.


Aldrovandia (sp. 1)
Antimora rostrata
Halosauropsis macrochir
Apristurus profundorum
Coryphaenoides carapinus
Harriotta haeckeli
Hydrolagus affinis
Alepocephalus spp.
Harriotta raleighana
Bathysaurus ferox
Rajidae (sp. 2)
Macrouridae (unknown)
Coryphaenoides armatus
Fish (unknown)
Rajidae (sp. 3)
Macrouridae (sp. 1)
Fish unknown (sp. 8)
Fish unknown (sp. 2)
Zoarcidae (unknown)
Myctophidae (unknown)
Reinhardtius hippoglossoides
Synaphobranchus kaupii
Macrouridae (sp. 2)
Simenchelys parasitica
Notacanthus chemnitzii
Nezumia bairdii
Macrourus berglax
Coryphaenoides rupestris
Neocyttus helgae
Centroscyllium fabricii
Fish unknown (sp. 3)
Pleuronectiforme (unknown)
Coelorinchus caelorhincus
Malacocephalus occidentalis
Glyptocephalus cynoglossus
Bathypterois dubius
Serrivomer beanii
Dibranchus atlanticus
Rajella bathyphila
Moridae (unknown)
250
500
750
1000
1250
1500
1750
2000
2250
Depth (m)

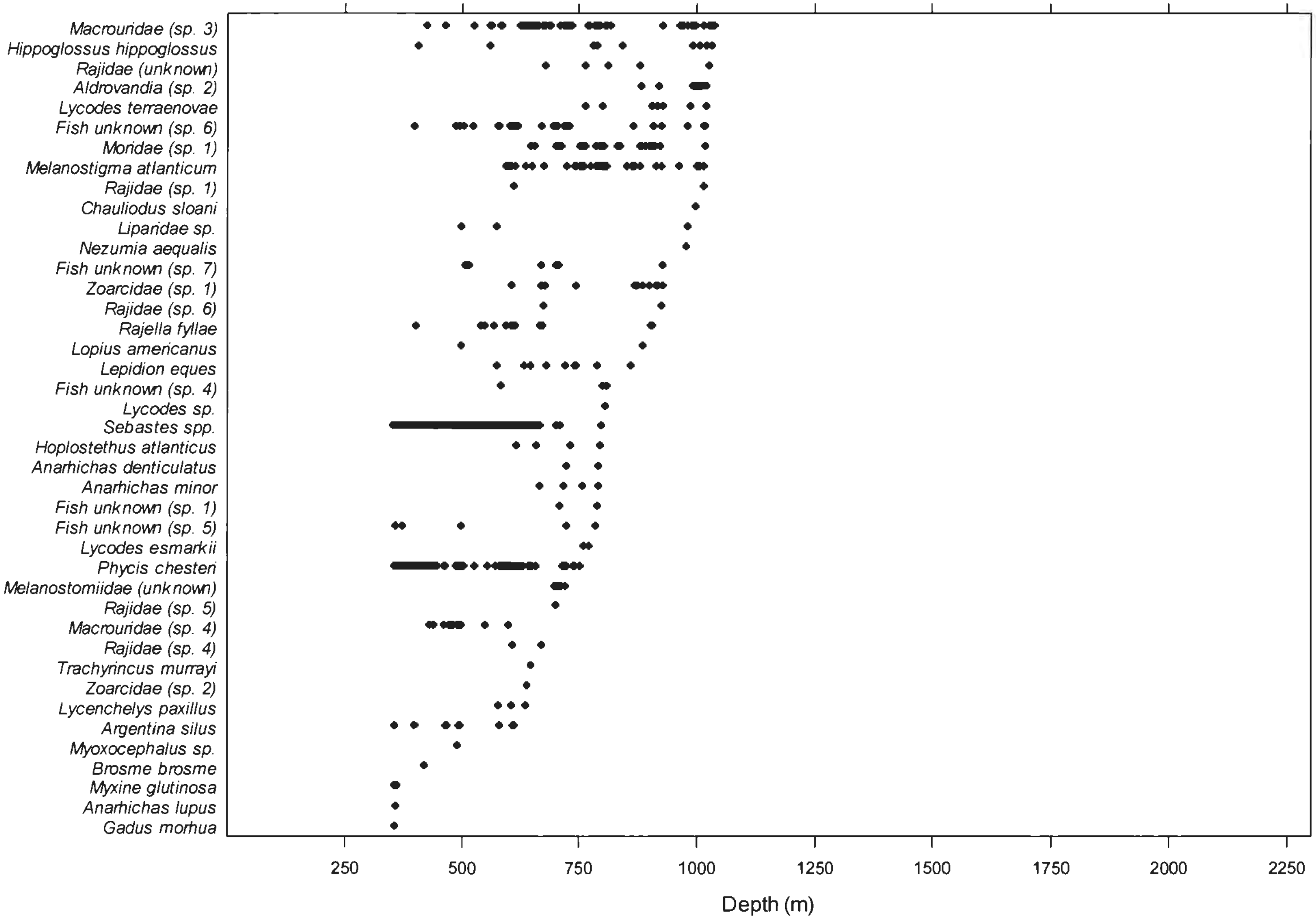

Macrouridae (sp. 3)
Hippoglossus hippoglossus
Rajidae (unknown)
Aldrovandia (sp. 2)
Lycodes terraenovae
Fish unknown (sp. 6)
Moridae (sp. 1)
Melanostigma atlanticum
Rajidae (sp. 1)
Chauliodus sloani
Liparidae sp.
Nezumia aequalis
Fish unknown (sp. 7)
Zoarcidae (sp. 1)
Rajidae (sp. 6)
Rajella fyllae
Lopius americanus
Lepidion eques
Fish unknown (sp. 4)
Lycodes sp.
Sebastes spp.
Hoplostethus atlanticus
Anarhichas denticulatus
Anarhichas minor
Fish unknown (sp. 1)
Fish unknown (sp. 5)
Lycodes esmarkii
Phycis chesteri
Melanostomiidae (unknown)
Rajidae (sp. 5)
Macrouridae (sp. 4)
Rajidae (sp. 4)
Trachyrincus murrayi
Zoarcidae (sp. 2)
Lycenchelys paxillus
Argentina silus
Myoxocephalus sp.
Brosme brosme
Myxine glutinosa
Anarhichas lupus
Gadus morhua
250
500
750
1000
1250
1500
1750
2000
2250
Depth (m)

Figure 4-2. Depth distribution of fish species observed during 2007 surveys conducted with a remotely operated vehicle (ROV) off the southwest Grand Banks of Newfoundland.

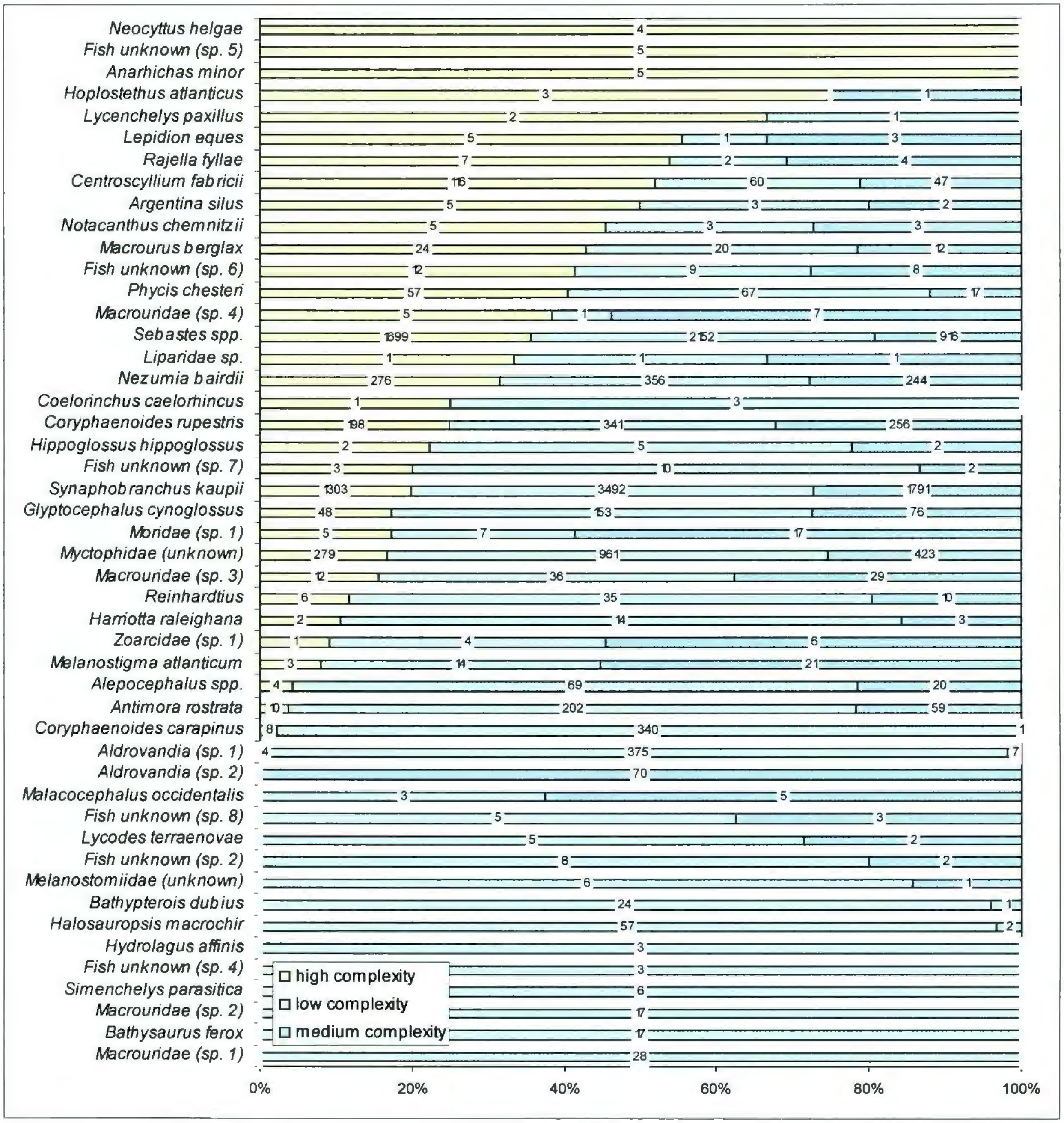


Figure 4-3. The distribution of unique fish taxa found ≥ 3 times during an *in situ* survey off the southwest Grand Banks of Newfoundland in 2007, in relation to habitat complexity (high, medium, and low). The number of individuals observed in each category is presented for each fish taxon.

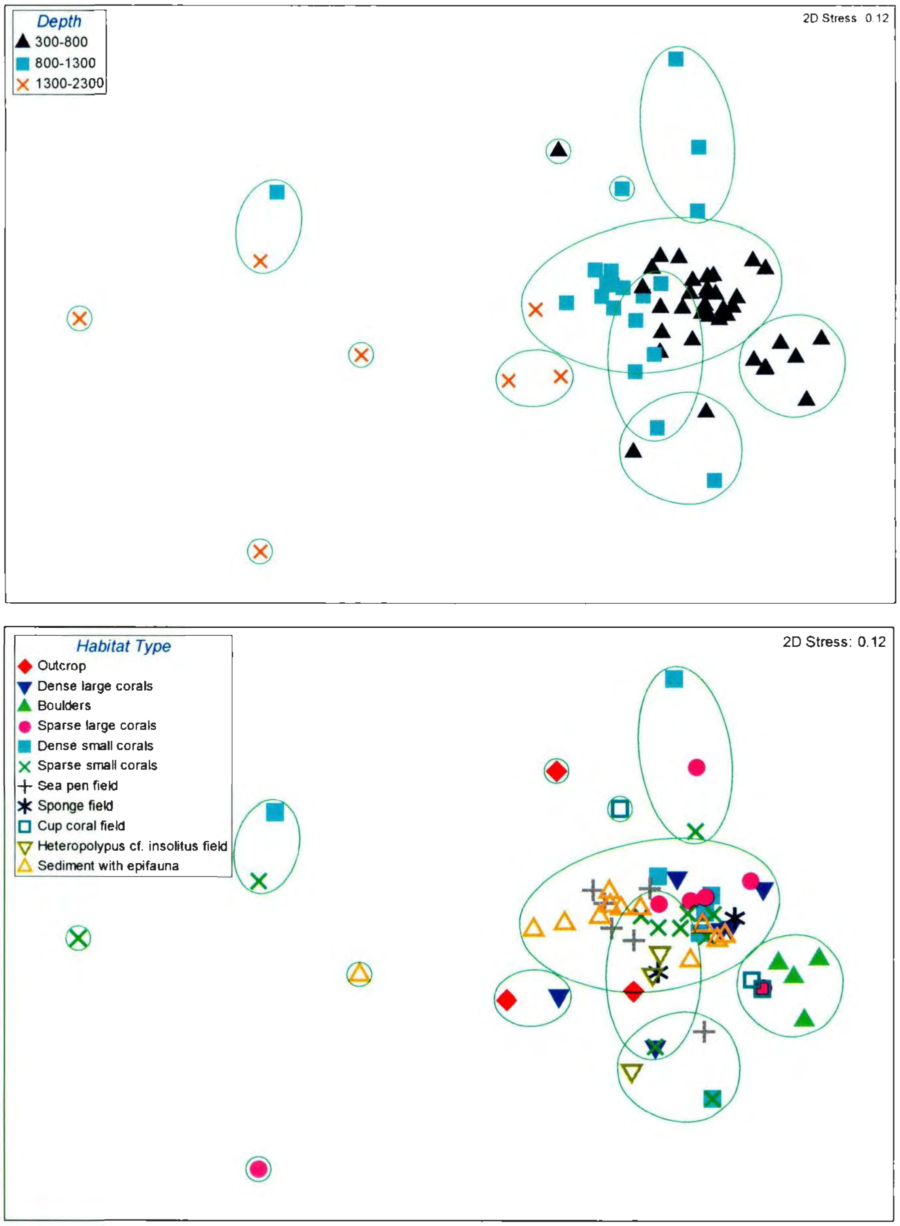


Figure 4-4. MDS plots of Bray-Curtis similarity matrix based on standardized samples and fourth-root transformed data of fish surveyed *in situ* off the southwest Grand Banks of Newfoundland in 2007. Plots are based on depth (m) (top) and habitat type (bottom) classifications. Solid lines on MDS plot correspond to clusters of 50 % similarity in dendrogram.

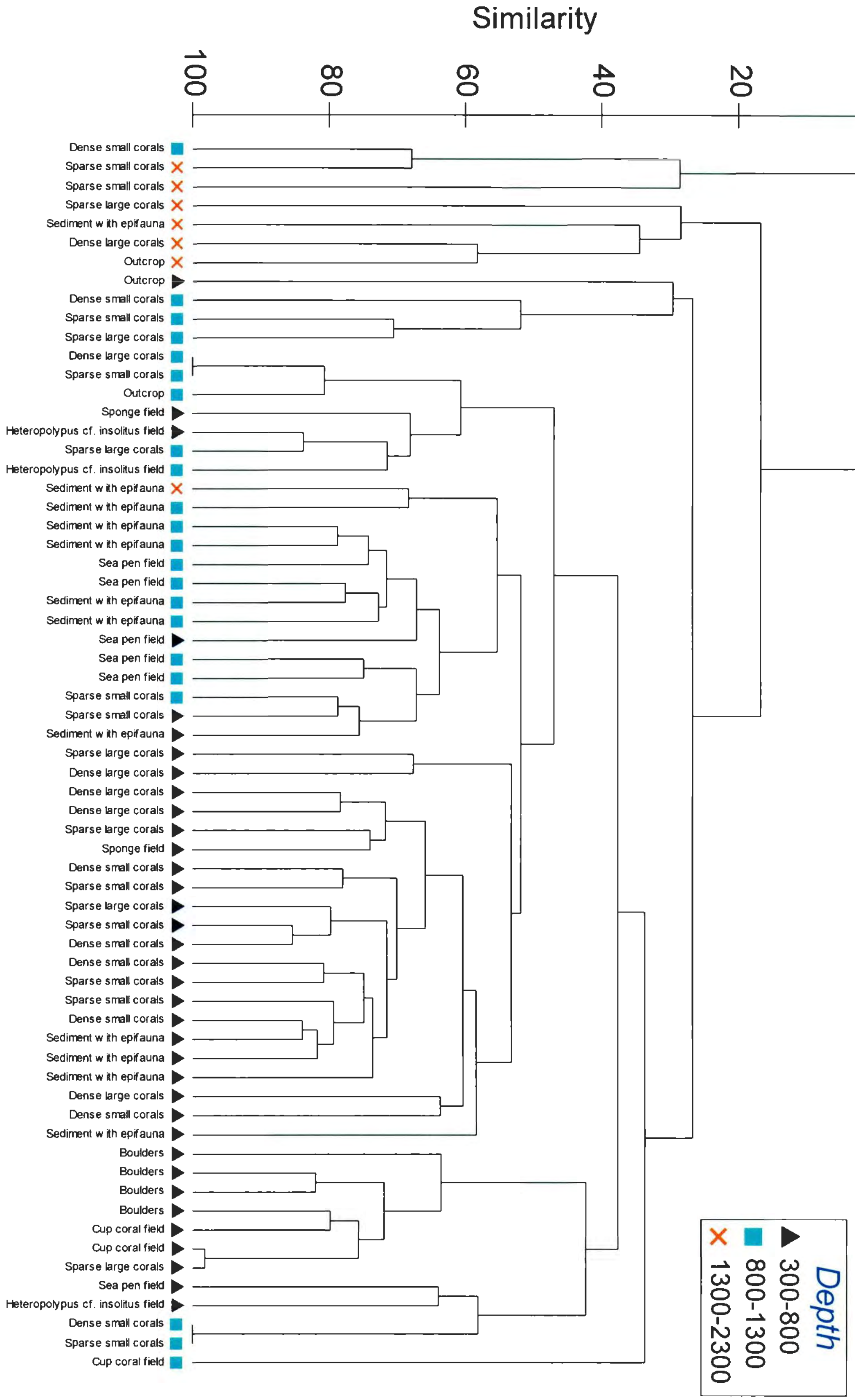

Similarity
100
80
60
40
20
0
Dense small corals
Sparse small corals
Sparse small corals
Sparse large corals
Sediment with epifauna
Dense large corals
Outcrop
Outcrop
Dense small corals
Sparse small corals
Sparse large corals
Dense large corals
Sparse small corals
Outcrop
Sponge field
Heteropolypus cf. insolitus field
Sparse large corals
Heteropolypus cf. insolitus field
Sediment with epifauna
Sediment with epifauna
Sediment with epifauna
Sediment with epifauna
Sea pen field
Sea pen field
Sediment with epifauna
Sediment with epifauna
Sea pen field
Sea pen field
Sea pen field
Sparse small corals
Sparse small corals
Sediment with epifauna
Sparse large corals
Dense large corals
Dense large corals
Dense large corals
Sparse large corals
Sponge field
Dense small corals
Sparse small corals
Sparse large corals
Sparse small corals
Dense small corals
Dense small corals
Sparse small corals
Sparse small corals
Dense small corals
Sediment with epifauna
Sediment with epifauna
Sediment with epifauna
Dense large corals
Dense small corals
Sediment with epifauna
Boulders
Boulders
Boulders
Boulders
Cup coral field
Cup coral field
Sparse large corals
Sea pen field
Heteropolypus cf. insolitus field
Dense small corals
Sparse small corals
Cup coral field
Depth
▲ 300-800
■ 800-1300
✕ 1300-2300

Figure 4-5. Dendrogram of samples created using group-average link clustering from Bray-Curtis similarities on standardized samples (fourth-root transformed) of fish surveyed *in situ* off the southwest Grand Banks of Newfoundland in 2007. Both depth (m) and habitat type classifications are presented.

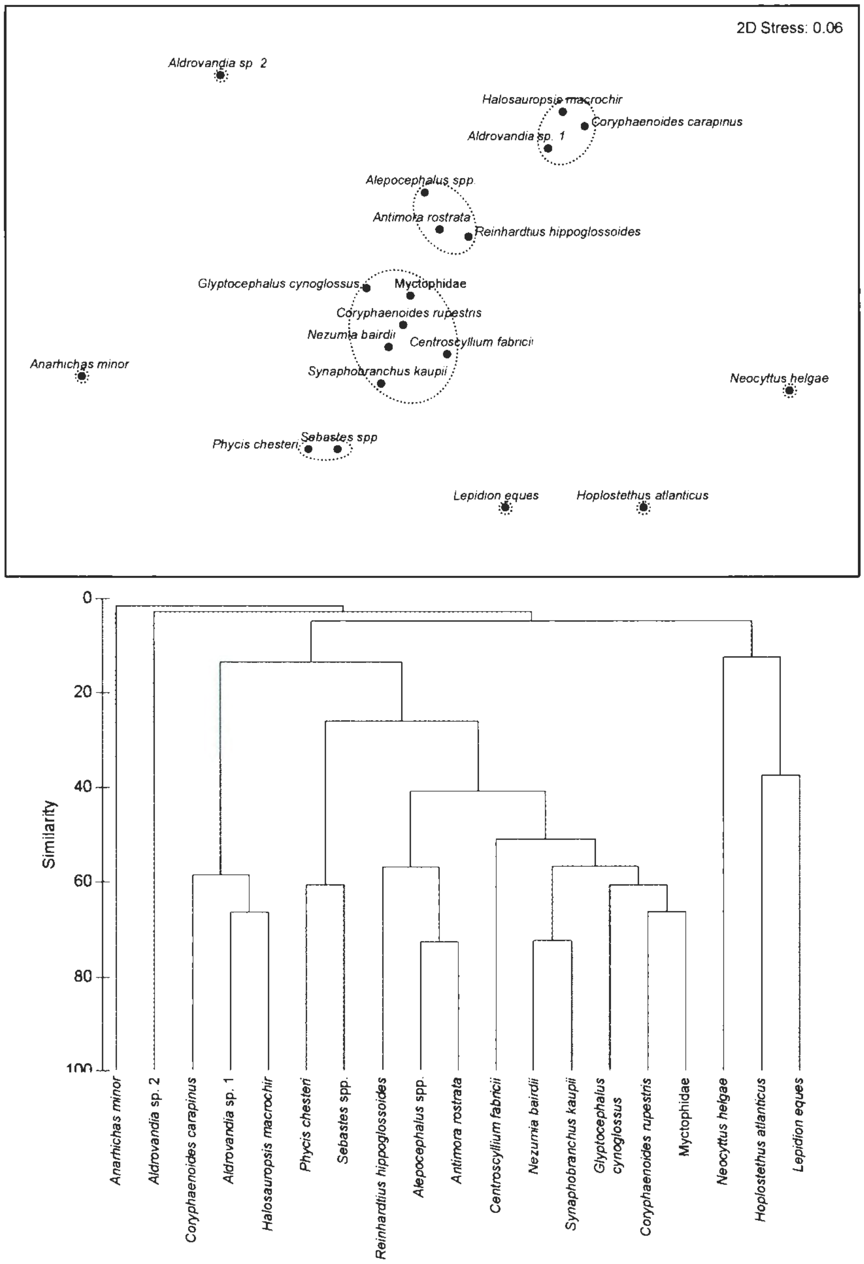


Figure 4-6. MDS plot (top) and dendrogram (bottom) of Bray-Curtis similarity matrix based on standardized samples and fish species that contribute at least 10 % to a sample (data collected using an ROV off the southwest Grand Banks of Newfoundland in 2007). Dotted lines on MDS plot correspond to clusters of 50 % similarity in dendrogram.

5 Grenadier abundance examined at varying spatial scales in deep waters off Newfoundland, Canada, with special focus on the influence of corals

Abstract

There is a growing body of research examining the effects of corals on fish communities, species abundances, and biodiversity. Yet, few studies have quantitatively examined what factors are influencing the distribution of individual fish species. In general, we know what influences the distribution of grenadiers on large spatial scales, but numerous studies have shown the distributions of organisms are often determined by various factors that change in relative importance when viewed at differing scales. Our study used video collected from three deep canyons off Newfoundland, Canada (Northwest Atlantic) to examine how the factors apparently influencing the distribution of four grenadiers (Macrouridae: *Coryphaenoides rupestris*, *Coryphaenoides carapinus*, *Nezumia bairdii*, and *Macrourus berglax*) change when assessed at varying spatial scales. We paid special attention to the influence of deep-water corals found in the study area (large gorgonians/antipatharians, small gorgonians, sea pens, soft corals, and cup corals). The factors that influenced grenadier presence and/or abundance (and the magnitude of this effect) varied as different sampling resolutions were examined. We found *C. rupestris* abundance was positively related to cup coral abundance in transects longer than 10 m, likely as a result of similar habitat preferences between both taxa. When significant relationships between depth and *C. rupestris* presence and/or abundance were found, they

were always negative. Depth was a significant predictor of *C. carapinus* abundance in transects longer than 10 m. Very few predictors of *M. berglax* abundance or presence could be found. Depth and the number of small gorgonians were consistent predictors of *N. bairdii* abundance.

5.1 Introduction

Off Atlantic Canada, some grenadiers have exhibited such dramatic population declines that two species have been assessed as species-at-risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). *Macrourus berglax* (Roughhead grenadier) declined 93 % between 1978 and 2003 (Devine et al. 2006) and was identified as 'Special Concern' in 2007 (Environment Canada 2011), while *Coryphaenoides rupestris* (Roundnose grenadier) declined 99.6 % during the same time period (Devine et al. 2006) and was assessed as 'Endangered' in 2008 (Environment Canada 2011). Consistent with many deep-sea fishes, these species are thought to be slow growing, long lived, and have relatively low fecundity, meaning that population recovery will likely be very slow, if possible at all (Baker et al. 2009). Their estimated recovery times could be even greater if their life strategies depend on other organisms vulnerable to fishing impacts such as deep-water corals. Nevertheless, assessments carried out by the Northwest Atlantic Fisheries Organization (NAFO) using a shifted baseline (Pauly 1995) and non-zero data indicate that biomass of *M. berglax* has exhibited an overall increasing trend since 1995 (NAFO 2010). This increasing trend has been attributed to, among other factors, decreased fishing mortality (Gonzalez-Costas & Murua 2008).

At large spatial scales, researchers generally understand the factors influencing grenadier distributional patterns where depth zonation plays a major role (e.g. Powell et al. 2003; Bergstad et al. 2008). For example, *C. rupestris* occurs in water depths of 180 – 2600 m, but abundance peaks at depths 400-1200 m (Cohen et al. 1990), and *M. berglax* is found in greatest concentrations between 300 and 500 m and water temperatures ranging from 1 to 4 °C (Cohen et al. 1990). In contrast, at smaller spatial scales we understand very little about the factors influencing the distribution of most species in the deep sea. *Coryphaenoides rupestris* is thought to prefer areas of weak or absent current and form dense concentrations in troughs, gorges, and terraces (Lorance et al. 2008) and sedimentary drifts (Durán Muñoz et al. 2012). During *in situ* surveys in the Northeast Atlantic, *C. rupestris* was found associated with transitional coral zones, coral debris and seabed habitats, but not reef or wreck habitats (Costello et al. 2005). Ross and Quattrini (2007) found *Nezumia bairdii* in prime reef and transition reef habitats, but not off-reef habitats off southeastern United States.

Numerous studies have shown that the factors influencing distributions and abundances of organisms can change with changing scale (e.g. He et al. 1994; Syms 1995; Hewitt et al. 1998; Eagle et al. 2001; La Mesa et al. 2011). For example, Flach (1996) showed that the factors influencing the amphipod *Corophium* distributions varied among temperature, sediment composition, biotic interactions, and family-level interactions when examined along global (thousands of km), regional (tens of km), local (km), and core (cm) scales, respectively. Hewitt et al. (1998) found more factors to be responsible for patterns in macrofauna communities as sampling resolution increased from video transects to core samples. Despite numerous findings such as these, few studies examine patterns of fish abundances at multiple spatial scales or sampling resolutions (Syms 1995; Chittaro 2004). Predictor variables detected at specific scales can help provide insight into the underlying processes generating these patterns (Syms 1995; La Mesa et al. 2011).

Our research used video collected with an ROV in three deep canyons off Newfoundland, Canada to identify factors influencing the abundance of four grenadier species: *Coryphaenoides rupestris*, *Coryphaenoides carapinus*, *Macrourus berglax*, and *Nezumia bairdii*. We examined how these factors changed at varying spatial scales (i.e. sample resolutions) with particular attention to deep-water corals found in the study area.

5.2 Methods

5.2.1 Survey design

We used the remotely operated vehicle ROPOS (Remotely Operated Platform for Ocean Science) (CSSF 2010) to examine grenadier abundance and distribution in three submarine canyons on the slopes of the Grand Banks south of Newfoundland (Halibut Channel, Haddock Channel and Desbarres Canyon) in depths from 351 to 2245 m (Table 5-1, Figure 2-1). ROPOS performed video surveys from *CCGS Hudson* in July 2007 (see Baker et al. 2012a,b for details). We planned 1-km transects along 200 m isobaths between 2200 and 600 m and along 100 m isobaths in waters equal to and shallower than 500 m. We standardized transects by keeping ROPOS as close to the bottom as possible, maintaining a constant slow speed (approx. 0.2 – 0.5 m s^{-1}) while tilting the camera down slightly on a wide-angle view in order to image the seafloor and water column directly above (Baker et al. 2012a,b). Between these pre-selected transects, we explored the area with ROPOS, captured still images and video of features of interest, and collected voucher specimens of invertebrates.

5.2.2 Video processing

We used ClassAct Mapper (Benjamin 2007) to analyze the video footage from the color video camera and collect geo-referenced data pertaining to fish, corals, sediment, and ROPOS operation mode. We identified each grenadier observed to the lowest possible taxonomic level. Video clips and frame grabs of species and/or individuals that could not be identified with certainty were sent to taxonomic experts for confirmation. To reduce double-counting of individual fish, we did not count fish that approached the field of view from behind ROPOS. ROPOS was equipped with lasers placed 10 cm apart, so whenever the orientation of a fish made it possible, we measured the total length (TL) of individuals to the nearest 5 cm using ROPOS's lasers as reference. All corals observed during video processing were also identified to the lowest possible taxonomic level.

We characterized sediment once per second using 2 descriptors: primary (most abundant) and secondary (next most abundant) substrate. Each of primary and secondary substrate were categorized based on grain size, as (1) outcrop (vertically exposed bedrock and consolidated Quaternary sediment), (2) boulder (> 25 cm), (3) cobble (5 - 25 cm), (4) gravel (0.2 – 5 cm), or (5) mud-sand (fine-grain) sediments (Thrush et al. 2001).

We recorded ROPOS operation mode at 1-s intervals (Baker et al. 2012a,b). 'Transect-mode' described any portion of the video when ROPOS followed prescribed transect methodology (described above), regardless of whether part of a pre-selected transect or not. For this study, we categorized all other ROPOS behaviour as "Other".

5.2.3 Data analysis

Corals were grouped into categories based on those used by Edinger et al. (2007a,b). *Keratoisis grayi*, *Lepidisis* sp., *Paragorgia arborea*, *Acanthogorgia armata*, *Paramuricea* spp, unidentified Isididae, and unidentified large gorgonians, as well as four antipatharians (*Bathypathes patula*, Schizopathidae n. gen et n. sp., and an unidentified antipatharian) were categorized as large corals. *Chrysogorgia agassizii*, *Radicipes gracilis*, and *Acanella arbuscula* were categorized as small gorgonians. All cup corals (*Flabellum* spp., *Desmophyllum dianthus*, *Javania cailleti*, *Vaughanella* sp., and unknown cup corals) were grouped into a single category: cup corals. *Anthomastus* spp., *Heteropolypus* cf. *insolitus*, *Duva florida*, and unidentified Neptheidae were categorized as soft corals. *Anthoptilum grandiflorum*, *Funiculina quadrangularis*, *Halipteris finmarchica*, *Kophobelemnon stelliferum*, *Pennatula* spp., *Protoptilum carpenteri*, *Distichoptilum gracile*, *Umbellula* spp., and unidentified Pennatulacea were grouped as sea pens.

Since numerous categories of sediment could be classified using our prescribed methodologies, we created a ranking/scoring system. We calculated sediment heterogeneity as 2*primary sediment + secondary sediment, where the individual value for each primary and secondary category were mud-sand = 1, gravel = 2, cobble = 3, boulders = 4, and outcrop = 5.

We summarized the abundance and lengths of *Coryphaenoides rupestris*, *Coryphaenoides carapinus*, *Macrourus berglax*, and *Nezumia bairdii* using all video data, regardless of ROV mode (i.e. both transects and other). Using only video collected during transects, we modelled the presence and abundance of *C. rupestris*, *C. carapinus*, *M. berglax*, and *N. bairdii* individually using various segment lengths. We split transects into arbitrarily-chosen lengths: 10 m, 20 m, 50 m, 100 m, 200 m, and 300 m, and counted the number of each species in each segment. We included only transect segments that were within the observed depth range of each species.

Since a large number of segments contained no grenadiers, the abundance data for each species were zero-inflated, which did not meet the assumptions for generalized linear models (GLM) of counts. Therefore, we used hurdle (zero-altered) models (Zuur et al. 2009) to model the presence/absence and abundance of each species separately, using the *Pscl* (version 1.04.1) package (Jackman et al. 2011) in R version 2.14.1 (R Dev Core Team 2012). A hurdle model is a convenient way to apply two GLMs to different facets of zero-inflated data. Firstly, a binomial GLM (the "presence/absence" sub-model) models the factors affecting the presence/absence of a given species. Secondly, a zero-truncated abundance GLM (the "abundance sub-model"), is used to model the factors affecting counts greater than zero (Zuur et al. 2009). The hurdle model implemented in the *Pscl* package automatically applies both sub-models to the correct data subset and produces the parameters estimates, their standard errors, and p-values for each of the abundance and presence/absence sub-models separately.

We included one categorical predictor, Canyon (with levels "Haddock Channel", "Halibut Channel", and "Desbarres Canyon"), six ratio scale predictors: depth, number of large corals (LCorals), number of small gorgonians (SGorg), number of soft corals (SoftCorals), number of sea pens (SeaPens), number of cup corals (CupCoral), and one interval scale predictor, overall sediment heterogeneity score (Sed) in each sub-model. Temperature was originally included in the analyses, but it exhibited strong colinearity with depth and was missing for several dives, so it was removed. Within each segment, we used the mean depth and maximum sediment heterogeneity score (Sed) as the values for that segment.

The independent variables in each of the two sub-models need not be the same, and we performed separate model selection processes for each sub-model for each species. We began with the full set of predictors listed above for each of the sub-models and simplified each sub-model in turn through backward selection to remove non-significant terms. At each step, the least significant term whose p-value was > 0.05, as judged by a likelihood ratio test between two nested models (one with and one without the term), was dropped until all remaining terms were significant (Zuur et al. 2009).

For each species, the choice of whether to use a truncated Poisson versus a truncated negative binomial distribution in the abundance sub-model depended upon whether there was excess variation (i.e. overdispersion) in the counts that could not be adequately modeled by the Poisson distribution, thereby requiring the use of the negative binomial distribution. We made this choice based on the outcome of a likelihood ratio test between abundance sub-models based on each of these distributions (Zuur et al. 2009).

5.3 Results

5.3.1 Coryphaenoides rupestris

A total of 795 *C. rupestris* were found in depths from 384 to 1623 m (Table 5-2). The average length of measured fish ($n = 450$) was 35 cm, while the largest was 70 cm (observed in Desbarres Canyon at 892 m).

Using data summarized at the finest resolution (10-m segments) (Table 5-3), we found the probability of an individual being present was positively influenced by CupCoral ($p = 0.004$) and LCorals ($p = 0.034$), but negatively influenced by Sed ($p = 0.044$) (Table 5-4). The probability of *C. rupestris* occurring in Desbarres Canyon was significantly less than in Halibut ($p < 0.0001$) and Haddock Channels ($p = 0.001$), but no significant difference between Halibut and Haddock Channels was observed ($p = 0.102$). The abundance of *C. rupestris* was also positively related to LCorals ($p = 0.034$), but negatively related to SGorg ($p = 0.003$) and depth ($p = 0.042$). The predicted abundance of *C. rupestris* in Desbarres Canyon was significantly less than in Halibut ($p = 0.001$) and Haddock Channels ($p = 0.005$), but again no significant difference between Halibut and Haddock Channels was observed. For all other segment lengths (≥ 20 m) CupCoral had a significant positive relationship with the abundance of *C. rupestris* ($p < 0.0001$), but this relationship became less dramatic as the segments increased in length (Figure 5-1).

Depth exhibited a significant negative relationship with *C. rupestris* presence in 20-m (p = 0.015), 100-m (p = 0.004), and 200-m (p = 0.043) segments.

5.3.2 Coryphaenoides carapinus

A total of 349 *C. carapinus* were found in depths from 990 to 2227 m (Table 5-2). The average length of measured individuals (n = 262) was 18 cm, but the maximum length observed was 40 cm and was recorded three times; all were recorded in Haddock Channel and were at depths of 2210 m, 2214 m, and 2094 m.

Canyon and depth predicted the probability of *C. carapinus* occurring, as well its abundance at multiple spatial scales (Table 5-4). In general, the probability of presence as well as the abundance of *C. carapinus* was greater in Haddock Channel than Desbarres Canyon, and *C. carapinus* abundance was positively related to depth. The relationship between depth and the probability of *C. carapinus* being present appeared to increase in strength as the segment lengths increased (Figure 5-1). In 50-m segments, *C. carapinus* occurrence was positively related to SGorg (p = 0.048), and in 10-m segments, occurrence was positively related to Sed (p = 0.015).

5.3.3 Macrourus berglax

Macrourus berglax was found in depths from 434 to 1638 m, and only 56 individuals were observed in the video. The average length of measured individuals (n = 32) was 41 cm. The largest individual (70 cm) was recorded in Desbarres Canyon at 899

m. Even at the largest segment size, the maximum number of *M. berglax* recorded in a segment was 1.

At the fine and coarse sampling resolutions, we found no predictors of *M. berglax* presence (Table 5-4). In 50-m segments, the probability of this species occurring was positively related to SoftCorals ($p = 0.015$), and in 100-m segments, it was positively related to LCorals ($p = 0.017$).

5.3.4 Nezumia bairdii

Nezumia bairdii was the most numerous grenadier observed in our survey (Table 5-2). It was found in depths from 362 to 1678 m and the average length of measured individuals ($n = 475$) was 25 cm. The largest individual (60 cm) was observed in Desbarres Canyon at 1024 m.

The probability of *N. bairdii* occurring was consistently related to depth, and canyon in all segment lengths up to 200 m, when only depth remained as a negative predictor of their presence ($p = 0.0002$) (Table 5-4). The relationship with depth became more dramatic as segment length increased (Figure 5-1). In every model where canyon was a significant predictor of the presence of *N. bairdii*, the probability of occurrence was significantly less in Haddock Channel compared to Halibut Channel (10-m: $p = 0.008$, 20-m: $p = 0.009$, 50-m: $p = 0.002$, 100-m: $p = 0.008$). In 10-m segments, *N. bairdii* was also more likely to be present in Desbarres Canyon than Haddock Channel ($p = 0.036$). At small spatial scales (10-m and 20-m segments), *N. bairdii* presence was positively related to SGorg (10-m: $p < 0.0001$, 20-m: $p = 0.0002$). At all scales the abundance of *N.*

bairdii (≥ 1) exhibited a positive relationship with SGorg. In segments ≥ 50 m, depth also became a significant predictor of *N. bairdii* abundance, exhibiting a negative relationship. As scale increased SGorg had a weaker influence on *N. bairdii* presence and abundance (Figure 5-1, Figure 5-2). Figure 5-2 illustrates an example of how GLM model predictions of the relationship between SGorg and abundance of *N. bairdii* change at different sample resolutions.

5.4 Discussion

5.4.1 Coryphaenoides rupestris

The depth range of *C. rupestris* documented during our surveys was within that known for this species. *Coryphaenoides rupestris* can be found in waters between 180 and 2200 m throughout much of the North Atlantic (Cohen et al. 1990), and is thought to be at greatest abundance on the upper slope, near 1000 m (Bergstad et al. 2008). They can be found in a range of water temperatures, from 1.1 to 8.5 °C (Shibanov & Vinnichenko 2008).

The effect of depth on *C. rupestris* abundance has been noted by many researchers in the past (e.g. Jorgensen 1996; Bergstad et al. 2008; Lorance et al. 2008). Magnusson and Magnusson (1995) found average catches off Iceland to be highest in depths greater than 800 m and on the Mid-Atlantic Ridge, Bergstad et al. (2008) observed largest catches near 1000 m. West of Greenland, *C. rupestris* abundance generally increased with depth to 1000 – 1200 m, but varied between years (Jorgensen 1996). Nevertheless, we found little evidence of depth influencing counts of *C. rupestris*, and instead found that as depth increased, the probability of encountering *C. rupestris* decreased. Many environmental factors change with depth and could cause such a relationship (e.g. temperature, current regime, sediment, food availability). Atkinson (1995) hypothesized that *C. rupestris* is tolerant to a wide range of temperature and other factors likely control their distributions.

Using trawl survey data collected off Newfoundland, Edinger et al. (2007b) found *C. rupestris* was more abundant in areas containing large-growing, long-lived skeletal corals (such as *Primnoa resedaeformis*, *Keratoisis grayi*, and antipatharians) at depths of 400 - 600 m. We also found a positive relationship between large corals and *C. rupestris* presence and abundance at the finest sample resolution examined. Currently no evidence exists suggesting this relationship is functional, but the idea should not be disregarded. Roundnose grenadier feed on a variety of fauna including copepods, amphipods, shrimps and cumaceans (Cohen et al. 1990). Although the stomach contents of *C. rupestris* in some parts of its range suggest that they move off bottom to forage (McLellan 1977; Bergstad et al. 2010), Podrazhanskaya (1971) found polychaetes, shrimp, sand, mud, and stones in the stomachs of *C. rupestris* and concluded that they feed heavily on bottom dwelling species in the Northwest Atlantic (Bergstad et al. 2010). Research has shown that macrofauna may be more diverse and abundant in areas with corals (Henry & Roberts 2007), and it is possible that the increased food availability in areas with large corals may contribute to the higher abundance of *C. rupestris* there.

Roundnose grenadier are thought to prefer areas of weak or absent current (Shibanov & Vinnichenko 2008) and large, dense aggregations of *C. rupestris* have been documented in areas of particularly weak currents (Lorance et al. 2008). On the Bay of Biscay continental slope, *C. rupestris* was found in a variety of habitats, but was at highest densities in relatively slow currents, over hard bottoms (Uiblein et al. 2003). Zedel and Fowler (2009) found that *Keratoisis grayi*, the most abundant large coral in our survey (Baker et al. 2012b), reduced the bottom current velocity by 13 %, when compared to areas without these corals. This phenomenon, in combination with the potential for increased food availability, could help to explain the positive relationship between *C. rupestris* abundance and large corals found at fine sample resolutions in our study.

The consistent, positive relationship between *C. rupestris* abundance and cup coral abundance over the range of segment lengths is likely a result of similar habitat preferences between the two taxa. *Flabellum* spp. were the most abundant cup corals found during our surveys (Baker et al. 2012b) and are known to prefer areas with fine sediments and slow currents (Mortensen et al. 2006; Buhl-Mortensen et al. 2007).

5.4.2 Coryphaenoides carapinus

On a large spatial scale, *C. carapinus* is known to occur throughout the North Atlantic, the southeast Atlantic, and the Indian Ocean between 384 and 5610 m (Iwamoto & Anderson 1994). The depth range recorded during our survey was well within the known depth range of this species. We found that as depth increased, the probability of *C. carapinus* occurring and its abundance also increased. This is consistent with the known ecology of this species; its maximum abundance is usually below 2000 m (near the depth limits of our survey) (Bergstad et al. 2008).

We found little evidence of strong, consistent relationships for *C. carapinus* with any of the coral groups examined.

5.4.3 Macrourus berglax

We recorded *Macrourus berglax* well within its known depth range. They can be found throughout the Arctic waters of the North Atlantic at depths 100 to 1000 m and in bottom temperatures that range from below 0 °C up to 5 °C (Cohen et al. 1990; Dolgov et al. 2008). In the Barents Sea, they were only found in areas with high salinity (34.8 – 35.09) (Dolgov et al. 2008).

We never found more than a single individual of *M. berglax* in a sample (even in the longest segments) and therefore only presence/absence models could be created for this species. The relationship between *M. berglax* presence and the abundance of soft corals and large corals were similar to those documented by Edinger et al. (2007b). Using trawl survey data collected off Newfoundland, *M. berglax* was found to be most abundant in sets that contained large gorgonians and/or antipatharians at shallow depths (200 - 400 m), but in deeper waters (400 –1000 m) *M. berglax* was most abundant in sets containing soft corals (Edinger et al. 2007b).

Although depth influences the distribution of *M. berglax* (Magnusson & Magnusson 1995; Jorgensen 1996), we found no significant relationships between depth and the presence of *M. berglax*. Previous researchers have demonstrated that the influence of depth on *M. berglax* abundance is inconsistent through time and between study areas (Gorchinsky 2007; Lorance et al. 2008). Similar to our results, Fossen et al. (2003) were only able to detect significant depth-related differences of catch rates (using trawls) in one of their six study areas.

5.4.4 Nezumia bairdii

Nezumia bairdii can be found throughout the Northwest Atlantic in waters 16 to 2295 m (Cohen et al. 1990), and therefore our observations fell well within their known depth range. We found a fairly consistent, negative relationship between depth and *N. bairdii* presence and abundance. This is consistent with the known depth distribution of this species; *N. bairdii* is most commonly found between 90 and 700 m (Cohen et al. 1990).

We found a consistent, positive relationship between small gorgonian abundance and *N. bairdii* counts. *Acanella arbuscula* was the most common small gorgonian recorded in our survey (Baker et al. 2012b). This species is known to occur in a variety of depth ranges, but colonies were more abundant in relatively shallow waters (Baker et al. 2012b), and although *A. arbuscula* was thought to prefer soft bottom habitats, we found them associated with a variety of bottom types (Baker et al. 2012b). It remains unclear what type of relationship (coincidental or functional) may exist between small gorgonians and *N. bairdii*. *Nezumia bairdii* feeds on a variety of macrofauna including euphausiids, amphipods, polychaetes, and copepods (Cohen et al. 1990), and it is unknown whether *A. arbuscula* affects the abundance of these taxa.

Nezumia bairdii was found on the flat, soft bottom of the Bay d'Espoir Fiord off Newfoundland (Haedrich & Gagnon 1991), but Ross and Quattrini (2007) found *N. bairdii* in prime and transition reef habitats, but not off reef habitats off southeastern United States. These somewhat contradictory findings with respect to habitat heterogeneity may hint at the truly generalist nature of *N. bairdii*.

5.4.5 Influence of scale

The factors that predict the presence and/or abundance of organisms can change based on the sampling resolution used in the analyses. In general, it is thought that large-scale processes can be masked by fine-scale heterogeneity at small spatial scales (Hewitt et al. 1998). We found that our predictors related to large-scale processes (depth and canyon) were significant at fine sampling resolutions, as well as at the coarser resolutions. These are similar to the findings of Hewitt et al. (1998), who reported that key predictors at larger scales were still important as resolution increased. However, in almost every case where we found depth to be a significant predictor, its relationship with presence or abundance was more pronounced at coarser resolutions. These findings suggest that studies which sample at fine resolutions can be used to detect important and fairly large-scale processes, but the relationship between the predictors, and possibly the ability to detect these relationships, may be weaker at finer resolutions.

It is also expected that as we move to coarser sampling resolutions, we lose information about fine-scale heterogeneity (He et al. 1994; Hewitt et al. 1998). At our coarsest scales of resolution (albeit this is only 300 m), we still found variables that we originally considered to represent fine-scale heterogeneity (because of their relatively patchy distributions) to be significant (e.g. cup corals, small gorgonians, large corals). Nevertheless, these variables may represent a combination of large and small scale habitat characteristics, such as current velocity, sediment types, etc.

Our results add to the ever-growing list of studies showing the importance of considering scale in ecology. Although we often found similar predictors to be significant over a range of scales, this was not always the case and the nature of the relationships often changed with scale. As a result, we clearly highlight the need for fish-habitat association studies to incorporate multiple resolutions to ensure that important variables are not overlooked due to inappropriate sampling resolutions.

5.4.6 Canyons

Submarine canyons are considered sites of high productivity and biomass, compared to other areas in the deep sea (De Leo et al. 2010). In the northern Gulf of Mexico, the greatest fish abundance was found in Mississippi Trough and DeSoto Canyon (Powell et al. 2003) and in Kaikoura Canyon off New Zealand, particularly high abundances of macrourids were found (De Leo et al. 2010). Canyons in the Northwest Atlantic were identified as potentially important for *C. rupestris* by Snelgrove and Haedrich (1985) when the species was found more often in Carson Canyon, compared to outside the canyon. They also found a similar result off New England, where canyon stations accounted for 95 % of the *C. rupestris* taken during 105 trawls made between 40 and 5000 m (Haedrich et al. 1980; Snelgrove & Haedrich 1985). Off Norway, *C.*

rupestris was found in high densities in fjords and channels (Bergstad & Isaksen 1987). *Coryphaenoides rupestris* and *N. bairdii* were among the most common species observed during our survey (Baker et al. 2012a), but our results often identified canyon as a significant predictor of grenadier presence and/or abundance. Therefore, the importance of the canyons may depend on specific characteristics of the canyon in question. The significant differences found between the canyons examined in our study suggest that when determining the abundance patterns of species, discrete areas should be examined separately, and care should be taken when making sweeping statements about the importance of broad-scale oceanographic features.

5.4.7 Caveats

In situ surveys offer a brief snapshot regarding the distribution of mobile species and are generally conducted during seasons conducive to at-sea work. As such, they do not adequately examine temporal changes in fish distributions, and associations between fishes and habitat that occur outside the survey period can go undocumented. Temporal changes can be annual, seasonal, diurnal, and/or ontogenetic. For example, in some areas groups of *C. rupestris* are thought to make daily vertical migrations off bottom to take advantage of food descending in the water column (Atkinson 1995). Nevertheless, other researchers have found no strong differences in catch rates between day and night (Bergstad 1990). *Coryphaenoides rupestris* may also move to shallower waters near the end of summer and deeper waters in winter (Atkinson 1995). Snelgrove and Headrich (1985) found *C. rupestris* exhibited a bigger-deeper relationship in Carson Canyon off

Newfoundland. Off of Greenland, the large female *M. berglax* are thought to dominate the most favourable depths, while smaller fish are found in less favourable areas (Fossen et al. 2003). These observations highlight the need for more *in situ* surveys that occur over multiple years, seasons, and timeframes to examine the temporal variability and scale of relationships.

5.5 Conclusions

Despite the growing conservation concern regarding grenadiers in the Northwest Atlantic, few studies have used *in situ* data to examine the factors influencing their abundances. We found depth influenced *C. rupestris* presence, *C. carapinus* presence and abundance, and *N. bairdii* presence and abundance. Our results also identify several unexpected, significant relationships with deep-water corals found in the study area. These highlight the need for more *in situ* research to increase our understanding of relationships and to identify causal factors. We found that the identity of significant predictors and/or the strength of the relationship between abundance and predictors changed as sample resolution changed, and therefore, our results underscore the importance of considering scale when examining patterns of fish abundances.

5.6 Literature Cited

Atkinson D.B. (1995) The biology and fishery of Roundnose Grenadier (*Coryphaenoides rupestris* Gunnerus, 1765) in the North West Atlantic. In: A.G. Hopper (Ed). Deep-water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, Netherlands. 51-111 pp.

Baker K.D., Devine J.A., Haedrich R.L. (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. Environmental Biology of Fishes 85(1): 79-88.

Baker K.D., Haedrich R.L., Snelgrove P., Wareham V., Edinger E.N., Gilkinson K. (2012a) Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. Deep Sea Research Part I: Oceanographic Research Papers 65: 171-188.

Baker K.D., Wareham V., Snelgrove P.V.R., Haedrich R.L., Fifield D.A., Edinger E.N., Gilkinson K. (2012b) Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. Marine Ecology Progress Series 445: 235-249.

Benjamin R. (2007) ClassAct Mapper. Fisheries and Oceans Canada, Dartmouth, NS.

Bergstad, O.A. (1990) Distribution, population structure, growth and reproduction of the roundnose grenadier Coryphaenodies rupestris (Pisces: Macrouridae) in the deep waters of the Skagerrak. Marine Biology 107: 25-39.

Bergstad O.A., Gjelsvik G., Schander C., Hoines A.S. (2010) Feeding ecology of *Coryphaenoides rupestris* from the Mid-Atlantic Ridge. PLoS ONE 5(5): 1-10.

Bergstad O.A., Hoines A.S., Orlov A.M., Iwamoto T., Galbraith J.K., Byrkjedal I., Uiblein F. (2008) Species composition and abundance patterns of grenadiers on the Mid-Atlantic Ridge between Iceland and the Azores. In: A.M. Orlov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. American Fisheries Society Symposium 63, Bethesda, Maryland. 65-80 pp.

Bergstad O.A., Isaksen B. (1987) Deep-water resources of the Northeast Atlantic: distribution, abundance and exploitation. Fisken og Havet 3: 1-56.

Buhl-Mortensen L., Mortensen P.B., Armsworthy S., Jackson D. (2007) Field observations of *Flabellum* spp. and laboratory study of the behavior and respiration of *Flabellum alabastrum*. Bulletin of Marine Science 81(3): 543-552.

Chittaro P.M. (2004) Fish-habitat associations across multiple spatial scales. Coral Reefs 23(2): 235-244.

Cohen D.M., Inada T., Iwamoto T., Scialabba N. (1990) Gadiform Fishes of the World (Order Gadiformes). Food and Agriculture Organization of the United Nations, Rome: 442 pp.

Costello M.J., McCrea M., Freiwald A., Lundalv T., Jonsson L., Bett B.J., van Weering T.C.E., de Haas H., Roberts J.M., Allen D. (2005) Role of cold-water *Lophelia* *pertusa* coral reefs as fish habitat in the NE Atlantic. In: A. Freiwald & J.M. Roberts (Eds). Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin. 771-805 pp.

CSSF (2010) Canadian Scientific Submersible Facility. www.ropos.com, Accessed November.

De Leo F.C., Smith C.R., Rowden A.A., Bowden D.A., Clark M.R. (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proceedings of the Royal Society B-Biological Sciences 277(1695): 2783-2792.

Devine J.A., Baker K.D., Haedrich R.L. (2006) Fisheries: Deep-sea fishes qualify as endangered. Nature 439(7072): 29.

Dolgov A.V., Drevetnyak K.V., Sokolov K.M., Grekov A.A., Shestopal I.P. (2008) Biology and fisheries of roughhead grenadier in the Barents Sea. In: A.M. Orlov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. American Fisheries Society, Symposium 63, Bethesda, Maryland. 343-363 pp.

Durán Muñoz P., Sayago-Gil M., Patrocinio T., González-Porto M., Murillo F.J., Sacau M., González E., Fernández G., Gago A. (2012) Distribution patterns of deep-sea fish and benthic invertebrates from trawlable grounds of the Hatton Bank, north-east Atlantic: effects of deep-sea bottom trawling. Journal of the Marine Biological Association of the United Kingdom: 1-16.

Eagle J.V., Jones G.P., McCormick M.I. (2001) A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). Marine Ecology Progress Series 214: 253-265.

Edinger E.N., Baker K.D., Devillers R., Wareham V. (2007a) Coldwater corals off Newfoundland and Labrador: distribution and fisheries impacts. World Wildlife Fund, Toronto, Canada: 41 pp.

Edinger E.N., Wareham V.E., Haedrich R.L. (2007b) Patterns of groundfish diversity and abundance in relation to deep-sea coral distributions in Newfoundland and Labrador waters. In: R.Y. George & S.D. Cairns (Eds). Conservation and Adaptive Management of Seamount and Deep-sea Coral Ecosystems. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami. 101-122 pp.

Environment Canada (2011). Species at Risk Public Registry. www.sararegistry.gc.ca, Accessed 13 May.

Flach E.C. (1996) Distribution of *Corophium* at different scales. Senckenbergiana maritima 27(3): 119-127.

Fossen I., Jorgensen O.A., Gundersen A.C. (2003) Roughhead grenadier (*Macrourus berglax*) in the waters off East Greenland: distribution and biology. Journal of Northwest Atlantic Fisheries Science 31: 285-298.

Gonzalez-Costas F., Murua H. (2008) An analytical assessment of the Roughhead Grenadier stock in NAFO subareas 2 and 3. In: A.M. Orlov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. American Fisheries Society, Symposium 63, Bethesda, Maryland. 319-342 pp.

Gorchinsky K.V. (2007) Distribution and length of Roughhead Grenadier by depth in NAFO Divisions 3KLMNO based on data from Russian Surveys in 1981-2006. Scientific council research document. Northwest Atlantic Fisheries Organization 07/11. Serial No. N5354: 1-13.

Haedrich R.L., Gagnon J.-M. (1991) Rock wall fauna of Newfoundland fjords. Continental Shelf Research 11: 1199-1208.

Haedrich R.L., Rowe G.T., Polloni P.T. (1980) The megabenthic fauna in the deep-sea south of New England. Marine Biology 57(3): 165-179.

He F.L., Legendre P., Bellehumeur C., LaFrankie J.V. (1994) Diversity pattern and spatial scale: a study of a tropical rain forest of Malaysia. Environmental and Ecological Statistics 1: 265-286.

Henry L.-A., Roberts, J.M. (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. Deep-Sea Research I 54: 654-672.

Hewitt J.E., Thrush S.F., Cummings V.J., Turner S.J. (1998) The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. Journal of Experimental Marine Biology and Ecology 227(2): 251-264.

Iwamoto T., Anderson E.M. (1994) Review of the grenadiers (Teleostei: Gadiformes) of southern Africa, with descriptions of four new species. Ichthyology Bulletin 61: 1-28.

Jackman S., Tahk A., Zeileis A., Maimone C., Fearon J. (2011) Package 'pscl'. Standford University California.

Jorgensen O.A. (1996) Distribution and biology of grenadiers (Macrouridae) in West Greenland waters. Journal of Northwest Atlantic Fisheries Science 18: 7-29.

La Mesa G., Molinari A., Gambaccini S., Tunesi L. (2011) Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Marine Ecology 32(1): 104-114.

Lorance P., Large P.A., Bergstad O.A., Gordon J.D.M. (2008) Grenadiers of the Northeast Atlantic - distribution, biology, fisheries, and their impacts, and developments in stock assessment and management. In: A.M. Orlov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. American Fisheries Society, Symposium 63, Bethesda, Maryland. 365-397 pp.

Magnusson J.V., Magnusson J. (1995) The distribution, relative abundance, and biology of the deep-sea fishes of the Icelandic slope and Reykjanes Ridge. In: A. Atkinson

(Ed). Deep-water Fisheries of the North Atlantic Oceanic Slope. Kluwer Academic Publishers, Netherlands. 161-199 pp.

Mortensen P.B., Buhl-Mortensen L., Gordon D.C. (2006) Distribution of deep-water corals in Atlantic Canada. Proceedings of the 10th International Coral Reef Symposium: 1832-1848.

NAFO (2010) Scientific Council Meeting - 2010: 248 pp.

Pauly D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10(10): 430.

Podrazhanskaya S.G. (1971) Feeding and migration of the roundnose greandier, *Macrourus rupestris*, in the Northwest Atlantic and Icelandic waters. International Commission for the Northwest Atlantic Fisheries, Research Document: 8.

Powell S.M., Haedrich R.L., McEachran J.D. (2003) The deep-sea demersal fish fauna of the Northern Gulf of Mexico. Journal of Northwest Atlantic Fisheries Science 31: 19-33.

RDevCoreTeam (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ross S.W., Quattrini A.M. (2007) The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Research Part I: Oceanographic Research Papers 54(6): 975-1007.

Shibanov V.N., Vinnichenko V.I. (2008) Russian investigations and the fishery of roundnose grenadier in the North Atlantic. In: A.M. Orlov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. American Fisheries Society, Symposium 63, Bethesda, Maryland. 399-412 pp.

Snelgrove P.V.R., Haedrich R.L. (1985) Structure of the deep demersal fish fauna off Newfoundland. Marine Ecology Progress Series 27(1-2): 99-107.

Syms C. (1995) Multi-scale analysis of habitat association in a guild of blennoid fishes. Marine Ecology Progress Series 125(1-3): 31-43.

Thrush S.F., Hewitt J.E., Funnell G.A., Cummings V.J., Ellis J., Schultz D., Talley D., Norkko A. (2001) Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. Marine Ecology Progress Series 223: 277-286.

Uiblein F., Lorance P., Latrouite D. (2003) Behaviour and habitat utilisation of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. Marine Ecology Progress Series 257: 223-232.

Zedel L., Fowler W.A. (2009) Comparison of boundary layer current profiles in locations with and without corals in Haddock Channel, southwest Grand Banks. In: K. Gilkinson & E.N. Edinger (Eds). The ecology of deep-sea corals of Newfoundland and Labrador waters: biogeography, life history, biogeochemistry, and relation to fish. Canadian Technical Report of Fisheries and Aquatic Sciences 97-104 pp.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York: 574 pp.

Table 5-1. Dives from an ROV cruise off Newfoundland in 2007, and their associated depths, time on bottom, and distance covered.

Dive	Canyon	Date	Depth range	Time on bottom (h)	Distance (km)	Distance in transect-mode (km)
R1065	Halibut Channel	16 – 17 July	606 – 1015 m	12.6	10.7	6.0
R1066	Haddock Channel	17 – 18 July	493 – 1020 m	16.0	15.8	10.2
R1067	Halibut Channel	18 – 19 July	395 – 996 m	10.2	13.4	7.1
R1068	Haddock Channel	19 July	1990 – 2245 m	4.5	5.9	2.5
R1070	Desbarres Canyon	21 July	351 – 940 m	15.5	23.6	15.7
R1071	Desbarres Canyon	22 – 23 July	353 – 1174 m	12.8	16.9	9.6
R1072	Desbarres Canyon	23 – 24 July	1116 – 1900 m	18.8	19.0	11.1
Total				90.4	105.3	62.2

Table 5-2. The number, maximum and average (± standard deviation) of total length (cm), and depth range of four species of grenadiers observed during an *in situ* ROV survey off Newfoundland, Canada in 2007.

Species	Number observed	Number measured	Maximum length (cm)	Average length ± standard deviation (cm)	Observed depth range (m)
Coryphaenoides rupestris	795	450	70	35 ± 10.5	384 – 1623
Coryphaenoides carapinus	349	262	40	18 ± 13.5	990 – 2227
Macrourus berglax	56	33	70	41 ± 7.5	434 – 1638
Nezumia bairdii	876	475	60	25 ± 7.6	362 – 1678

Table 5-3. Number of samples (and number of individual fish) belonging to each species at each modelled segment size. Data were collected during an *in situ* ROV survey off Newfoundland, Canada in 2007.

Species	10 m	20 m	50 m	100 m	200 m	300 m
Coryphaenoides rupestris	4344 (519)	1974 (467)	636 (394)	261 (332)	94 (237)	41 (167)
Coryphaenoides carapinus	1090 (221)	522 (206)	163 (174)	71 (154)	31 (113)	17 (63)
Macrourus berglax	3721 (33)	1709 (28)	658 (24)	191 (17)	61 (7)	30 (6)
Nezumia bairdii	4457 (569)	2059 (530)	655 (417)	267 (349)	93 (245)	47 (174)

Table 5-4. Significant predictors[1] ($p < 0.05$) of grenadier presence and abundance ($n \geq 1$) over a range of segment lengths.

Italicized predictors represent positive relationships with the variable of interest (presence or count).

	10-m		20-m		50-m		100-m		200-m		300-m	
Species	Presence	Count	Presence	Count	Presence	Count	Presence	Count	Presence	Count	Presence	Count
Coryphaenoides rupestris	Canyon Sed *LCorals* *CupCoral*	Depth Canyon *LCorals* SGorg	Depth Canyon SGorg	*CupCoral*	Canyon	*CupCoral*	Depth	*CupCoral*	Depth Canyon *LCorals* *SeaPen*	*CupCoral* *Sed*	-	Depth *CupCoral*
Coryphaenoides carapinus	Canyon *Sed*	Canyon	*Depth*	Canyon	*Depth* Canyon *SGorg*	*Depth*	*Depth* Canyon	*Depth*	*Depth*	*Depth*	-	-
Macrourus berglax	-	-	-	-	*SoftCorals*	-	*LCorals*	-	-	-	-	-
Nezumia bairdii	Depth Canyon *SGorg*	*SGorg*	Depth Canyon *SGorg*	*SGorg*	Depth Canyon	Depth *SGorg* *SoftCoral*	Depth Canyon	Depth Canyon *SGorg* *SoftCorals* SeaPen LCorals	Depth	Depth *SGorg*	Depth	Depth Canyon *SGorg*

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[1] LCorals represents the number of *Keratoisis grayi*, *Lepidisis* sp., *Paragorgia arborea*, *Acanthogorgia armata*, *Paramuricea* spp, unidentified Isididae, unidentified large gorgonians, and antipatharians in each transect. The number of *Chrysogorgia agassizii*, *Radicipes gracilis*, and *Acanella arbuscula* observed defines SGorg. CupCoral is defined by the number of cupcorals in each transect. SoftCorals is the total number of *Anthomastus* spp., *Heteropolypus* cf. *insolitus*, *Duva florida*, and unidentified Neptheidae observed in each transect. SeaPen is the number of sea pens observed in each transect. Sed (sediment heterogeneity) was calculated as 2*primary sediment + secondary sediment, where the individual value for each primary and secondary category were mud-sand = 1, gravel = 2, cobble = 3, boulders = 4, and outcrop = 5. Depth is average depth (m) for each transect. Canyon is a categorical variable comprising of Haddock Channel, Halibut Channel, and Desbarres Canyon.

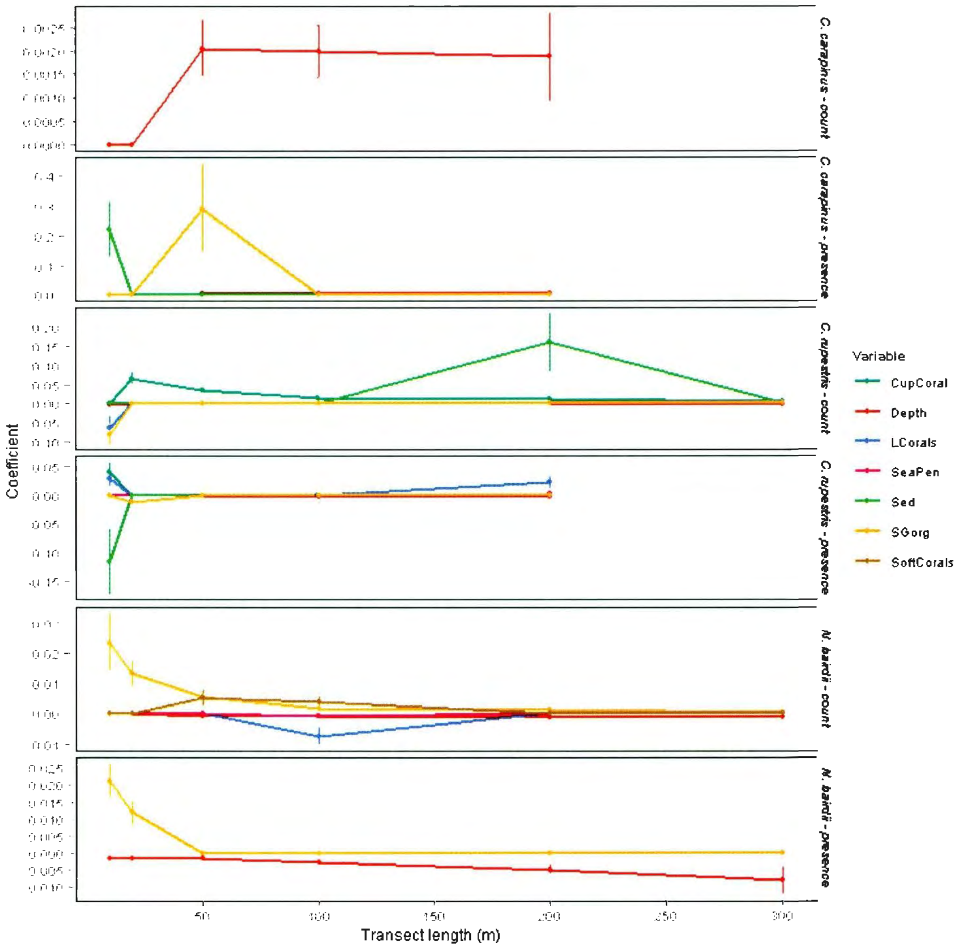

Figure 5-1. The effect of scale on coefficient values from models predicting grenadier presence and abundance, from video data collected off the Grand Banks, Newfoundland in 2007[1].

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[1] LCorals represents the number of *Keratoisis grayi*, *Lepidisis* sp., *Paragorgia arborea*, *Acanthogorgia armata*, *Paramuricea* spp, unidentified Isididae, and unidentified large gorgonians, as well as antipatharians. The number of *Chrysogorgia agassizii*, *Radicipes gracilis*, and *Acanella arbuscula* observed defines SGorg. CupCoral is defined by the number of cupcorals in each transect. SoftCorals is the total number of *Anthomastus* spp., *Heteropolypus* cf. *insolitus*, *Duva florida*, and unidentified Neptheidae observed in each transect. SeaPen is the number of sea pens observed in each transect. Sed (sediment heterogeneity) was calculated as 2*primary sediment + secondary sediment, where the individual value for each primary and secondary category were mud-sand = 1, gravel = 2, cobble = 3, boulders = 4, and outcrop = 5. Depth is average depth (m) for each transect.

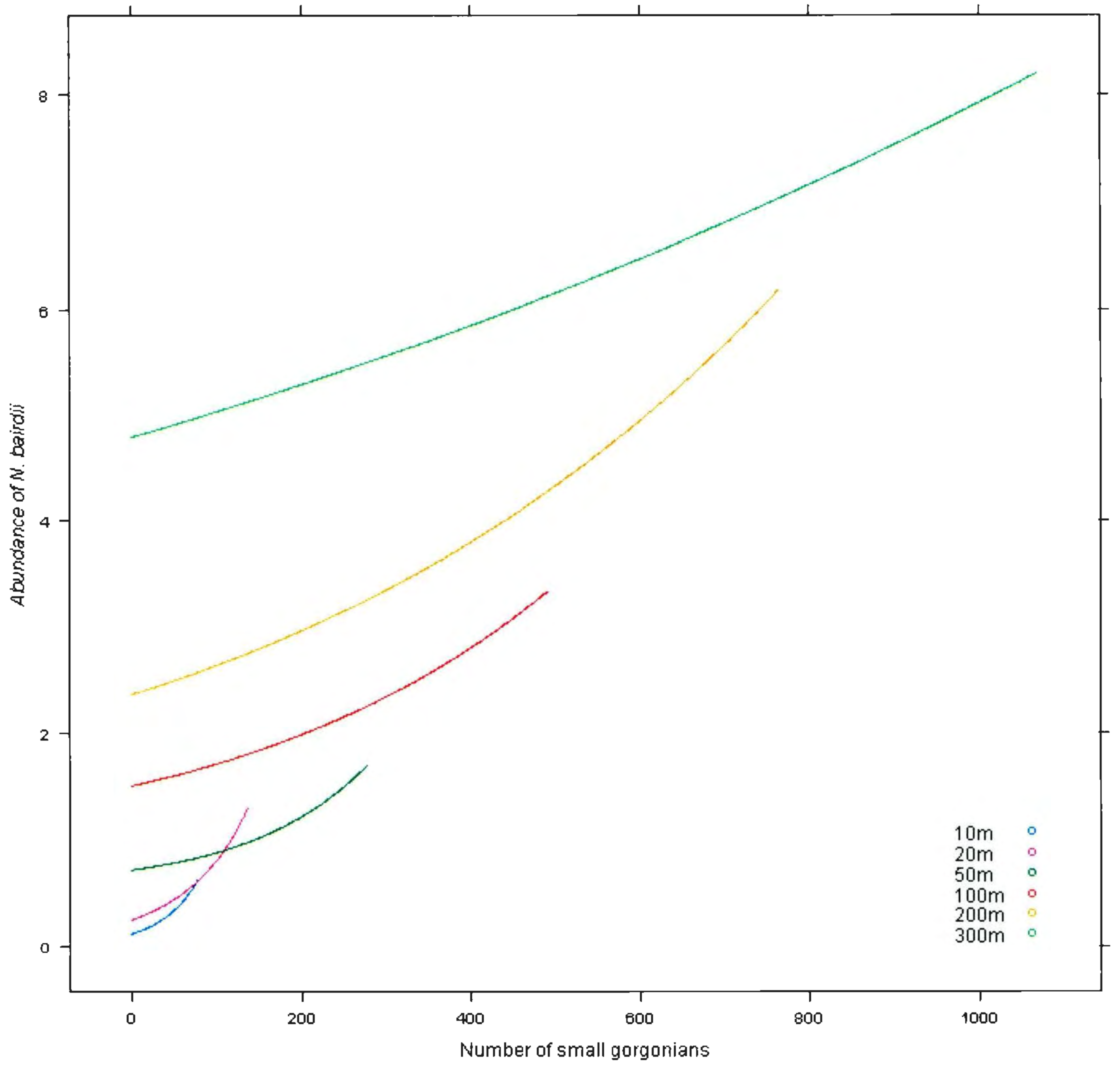

Figure 5-2. Counts of *Nezumia bairdii* predicted by the number of small gorgonians using Generalized Linear Models for each segment length. The models used a truncated Poisson error distribution with log link. For all models, the median depth (792 m) and number of sea pens (2), soft corals (0), and large corals (0) were held constant, while the number of small gorgonians varied.

6 Predicted recovery times of deep-sea fishes in Canada's Atlantic[1]

Abstract

Because of their slow growth rates, late maturity, and long potential lifespans, deep-sea fishes are vulnerable to and theoretically slow to recover from overexploitation and bycatch. As industrial fishing moved into the deep sea, population declines were predicted and five species were shown to meet The World Conservation Union (IUCN) criteria for endangered species in Atlantic Canadian waters and two other deep-living species were assessed as threatened by the Committee on the Status of Endangered Wildlife in Canada. Definitive assignment to an IUCN category for most species is hampered by a lack of basic biological information, especially species specific generation times. Lack of biological information also limits efforts to determine possible recovery times, especially with respect to calculating intrinsic rates of population growth (r). For two Atlantic grenadiers (where r could be estimated using life-history parameters and standard life table techniques), the time to recovery with no fishing mortality could range from over a decade to over a century. This broad range results from the general

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[1] This chapter was published as part of a longer article that included an additional analysis regarding population trends of deep-sea fishes in Canada's Atlantic: Baker KD, Devine JA, Haedrich RL (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. Environmental Biology of Fishes 85: 79-88.

As a result, Baker et al. (2009) is cited within this chapter in reference to the analyses regarding population declines.

uncertainty of life-history characteristics of these deep-sea species. Given the documented declines, the lack of basic data on life-history parameters, and the conservative assumption that recovery rates are likely to be prolonged, we argue that it is imperative to conduct additional studies pertaining to life history characteristics of deep-sea fishes and implement conservation measures in the deep sea immediately.

6.1 Introduction

Conservation in the deep sea is in its infancy relative to terrestrial and shallow-water ecosystems. The expanding footprint of fisheries and associated improvements in fishing technology have increased concern over the vulnerability of deep-sea species to overexploitation and loss as bycatch (Koslow et al. 2000; Roberts 2002). In the North Atlantic, the mean fishing depth has increased steadily since 1990 at a rate of 32.1 m per decade (Morato et al. 2006) and currently, 40 % of trawling grounds in the world lie deeper than the continental shelves (Roberts 2002).

Despite limited knowledge regarding the biology of many deep-sea fishes, there are examples of species that are known to be of concern. The Atlantic wolffish (*Anarhichas lupus*), a slow-growing, late-maturing, territorial fish whose populations in the western North Atlantic had declined over 80 %, was declared a Canadian species-at-risk in 1999 (O'Dea & Haedrich 2002). Two other wolffish (*A. minor* and *A. denticulatus*) and cusk (*Brosme brosme)* were subsequently assessed as Threatened and the grenadier *Macrourus berglax* was assessed as Special Concern (Environment Canada 2007). Devine et al. (2006) showed that abundances of five species of deep-sea fishes

(*Antimora rostrata, Bathyraja spinicauda, Coryphaenoides rupestris, Macrourus berglax* and *Notacanthus chemnitzi*) from the same geographic area had declined to such an extent that they met The World Conservation Union (IUCN) criteria for endangered. Using IUCN criteria, a species is considered endangered if it has declined > 70 % over 10 years or 3 generations (whichever is longer) and the causes of the reduction have ceased, are understood, and are reversible (IUCN 2001). The species listed above could be assessed because there were adequate time-series survey data and the generation time of most were known or could be estimated.

There is a need to focus on population rebuilding and future recovery (Safina et al. 2005). The same characteristics that make deep-sea species vulnerable to depletion should also make any recovery slow. Life-history traits typical of deep-sea fishes, such as large body size, slow growth, and late maturity are significantly correlated to slower maximum population growth rates (Denney et al. 2002). Recovery times have been estimated for sharks (Simpfendorfer 2000) and other fishes (Safina et al. 2005) using basic life-history characteristics and population information.

The purposes of this paper are two-fold. Based on the analysis of deep-sea species declines presented in Baker et al. (2009), we estimate recovery times (where possible) for declining species using estimated potential rates of increase (as inferred from published data on their biology). Then, we investigate the sensitivity of recovery time to minimal fishing mortality.

6.2 Methods

6.2.1 Intrinsic rate of population growth (r)

The intrinsic rate of increase (r) quantifies how much a population can increase in a given time period. Information pertaining to life-history characteristics for all species that exhibited declines in Baker et al. (2009) was collected from various sources, including peer-reviewed articles (e.g. Gordon & Mauchline 1996; Nash & Geffen 2005) and discussions with researchers from various institutions (e.g. Woods Hole Oceanographic Institution, Flødevigen Marine Research Station) to determine if r could be estimated. If this information was not available, life-history traits were estimated using life-history data for closely-related species wherever possible. All life-history characteristics were in reference to females.

The estimate of r was calculated for species with adequate age-specific life history information using standard life table techniques (e.g. Simpfendorfer 2000; Krohne 2001). Specifically, they were estimated using the Euler equation, where x is age in years, l_x is survival to age x, and m_x is the expected female offspring for one female at age x:

$$\Sigma e^{-rx} l_x m_x = 1.0$$

Survival from age 0 to 1 is unknown for most deep-sea species. However, Anderson (1984) found that less than 1 % of redfish larvae survived from April through July on Flemish Cap, Newfoundland. These early and rapid declines are common in fish populations (Cushing 1974) and therefore 1 % survival from age 0 to 1 was used for the majority of trials to determine r. This approximation most likely underestimates mortality in the first year. Mortality past age 1 was calculated using two common techniques:

$$\ln(Z) = 1.44 - 0.982 * \ln(w) \text{ (Hoenig 1983)}$$

and

$$M = 1.6 * K \text{ (Jensen 1996)}$$

where Z is total mortality (natural mortality + fishing mortality), w is maximum age (years), M is natural mortality, and K is the von Bertalanffy growth parameter.

6.2.1.1 Macrourus berglax

Age specific length and maturity relationships were outlined by Murua (2003). These were considered the best available data for this species and were thus used for this analysis. Whenever possible, data and relationships specific to the bottom survey (1991-2001) were used (rather than commercial data, which presumably target specific size classes) to minimize sampling bias.

The coefficients of the von Bertalanffy growth curves (in particular K) varied among survey years. The two extreme values (0.062, 0.024) and the mean (0.038) of K were used to estimate mortality.

Murua (2003) recorded the maximum age of *M. berglax* to be near 28 years and age at first maturity as 11 years. The proportion of mature females at a given age was found by the following equation from Murua (2003):

$$\text{Mature proportion} = e^{[-18.785+(1.205x)]}\,(1+e^{[-18.785+(1.205x)]})^{-1}.$$

Total fecundity at a given age was also calculated using a relationship highlighted by Murua (2003):

Total fecundity = $1401.5\ e^{0.132x}$

Although the sex ratio of *M. berglax* is known to change with age (Murua 2003), it was assumed to be 1:1 at age 0. The reproductive periodicity (*RP*) of *M. berglax* is unknown, but energy budgets show that some grenadiers may not reproduce on an annual basis and could even be semelparous (Drazen 2002; Drazen 2008). As a result, *r* was estimated for *M. berglax* assuming that mature individuals spawned every year, individuals spawned every other year ($RP = 2$), and individuals only spawned once at their maximum reproductive potential (19 years of age).

6.2.1.2 Coryphaenoides rupestris

The maximum recorded age for *C. rupestris* is approximately 60 years and the age of first maturity, 50 % maturity, and 100 % maturity are thought to be near 6, 10, and 16 years, respectively (Bergstad 1990). The relationship between age and L was found using von Bertalanffy growth-curve terms $K = 0.100$, $L_\infty = 18.1$ cm, and $x_0 = -0.9$, where L_∞ is asymptotic pre-anal length (cm), and x_0 is the theoretical age when length is zero (Bergstad 1990). Growth coefficients equal to 0.100, 0.086, and 0.114 were used to estimate mortality (Bergstad 1990).

Fecundity at a given length was calculated using the following equation from Allain (2001):

Log (fecundity) = $3.4 * \text{Log}(L) - 0.09$

The proportion of mature females at a given age was approximated using the relationship shown by Bergstad (1990).

The sex ratio of *C. rupestris* was assumed to be 1:1 at age 0. *RP* is also debated for *C. rupestris* so various scenarios were used, similar to those used for *M. berglax*. The age of maximum reproductive potential for *C. rupestris* is 16 years.

6.2.2 Recovery times

Estimated population declines and their 95 % confidence limits from Devine et al. (2006) were used with the intrinsic rates of increase in a Schaefer model (Schaefer 1954) to estimate recovery time for each species (similar to Safina et al. 2005). The magnitude of the population decline identified by Devine et al. (2006) was considered to indicate a similar change in biomass (Moss 2002). The first trial assumed that all fishing mortality and disturbances were removed from the system. But a total absence of fishing mortality and disturbances are highly unlikely, so recovery time was also estimated assuming an arbitrary fishing loss of only 5 % total biomass annually. This is equivalent to annual harvest rates of Atlantic cod (*Gadus morhua*) off Newfoundland during the 16th and 18th centuries and was meant to represent fishing mortality related to bycatch or a low level of disturbance (Rose 2004). In comparison, annual harvest rates for Atlantic cod exceeded 45 % in the early 1990s during heavy exploitation (Rose 2004).

6.3 Results

After an extensive investigation, it was determined that length/age data were available for only a very few of the fishes that had declined. In most cases, the species had never been aged and therefore age at maturity, maximum age, and fecundity as a function of age could not be determined or even estimated (Table 6-1). Even fewer species had associated age-related, life-history parameters needed to create life history tables, and thereby estimate r. Thus, *M. berglax* and *C. rupestris* were the only species that could be studied in detail.

Natural mortality estimates for *M. berglax* varied greatly depending on K and ranged from 0.0432 to 0.0992 (Table 6-2). Z was estimated as 0.1600 using the model from Hoenig (1983). Values of M, l_1, and RP were varied to determine a range of possible values for r, which ranged from 0.0820 to 0.4397. Recovery time for *M. berglax* was estimated to be between 18 and 125 years (Table 6-3). When a catch of 5 % was included in the model to account for bycatch in deep-sea fisheries, the estimated time to recovery ranged from 19 to 248 years (Table 6-4).

C. rupestris natural mortality estimates ranged from 0.1376 to 0.1824 (Table 6-2), but Z was estimated to be only 0.0757. The estimates of r for this species also varied greatly depending on the range of parameters used in the life table (Table 6-5). The recovery times when fishing loss was not included in the model ranged from 14 to 80 years. When catch was set at 5 %, the estimated time to recovery ranged from 16 to 136 years (Table 6-4).

6.4 Discussion

Trawling is known to drastically change the benthic habitat, resulting in a more homogenous environment (Watling & Norse 1998; Koslow et al. 2001). Although little is known about the association and importance of corals for deep-sea fishes in the Northwest Atlantic, deep-water corals are thought to play an important role in ecosystem structure (Husebo et al. 2002). These corals are easily damaged by trawling and have very slow growth rates and thus recovery times. If their presence is important for the survival of the fishes that have exhibited declines, recovery times for fishes could be on the order of centuries, if they are even possible.

There is insufficient data for the deep-sea species that declined in Canada's Atlantic Ocean to generate precise life tables and recovery-time estimates. This data gap highlights the drastic lag of science in relation to present-day disturbances and the need for more extensive research in the deep sea (Haedrich et al. 2001). Deep-sea fishes (including those that are not economically important) should be aged and studied in detail to determine the possible indirect influences of human activities.

The values of r and recovery time for *C. rupestris* and *M. berglax* were wide-ranging and can only be considered 'soft' estimates. Nonetheless, given that the deep-sea fishery had already begun off Canada by 1978 (Haedrich et al. 2001), the target for recovery used in this analysis is most likely an underestimate. Moreover, the 'known' life-history parameters for these deep-sea fishes have likely changed as a result of recent disturbances and therefore do not represent those of a pristine population.

When minimal fishing mortality was included in the model, the estimated times to recovery increased. There are few areas on the slope where disturbance and fishing mortality are absent, even in the deep sea; thus the estimates that include fishing mortality are probably more realistic. Although *C. rupestris* and *M. berglax* are no longer targeted fisheries in Atlantic Canada, other deep-sea fisheries still occur and bycatch remains a problem.

Future management decisions should be based on strong science and the precautionary principle. The burden of proof should be reversed to prevent fisheries from being developed without first understanding the basic biology of the target species and those that will be caught as bycatch. In the meantime, large no-take marine protected areas should be created to not only protect the target species, but also habitat. These prudent measures would help ensure that ignorance is not used an excuse for causing long-lasting effects in the deep-sea ecosystem. The results clearly show that any conservation measure established for the deep-sea ecosystem could be slow to demonstrate significant results, so action should be taken quickly and lack of instant results should not be justification for discontinuing conservation initiatives.

6.5 Conclusions

Many of the basic life-history characteristics needed to manage fish populations are not yet known for deep-sea fishes, but based on what is known, reversal could take more than a century, if reversible at all. Research is urgently needed to ensure appropriate management strategies are developed for deep-sea fishes.

6.6 Literature cited

Able K.W., Irion W. (1985) Distribution and reproductive seasonality of snailfishes and lumpfishes in the St. Lawrence River estuary and the Gulf of St. Lawrence. Canadian Journal of Zoology-Revue Canadienne De Zoologie 63(7): 1622-1628.

Alekseyev F.Y., Alekseyeva Y.I., Zakharov A.N. (1992) Vitellogenesis, nature of spawning, fecundity, and gonad maturity stages of the roundnose grenadier, *Coryphaenoides rupestris*, in the North Atlantic. Journal of Ichthyology 32: 32-45.

Allain V. (2001) Reproductive strategies of three deep-water benthopelagic fishes from the northeast Atlantic Ocean. Fisheries Research 51(2-3): 165-176.

Anderson J.T. (1984) Early life history of redfish (*Sebastes* spp.) on Flemish Cap. Canadian Journal of Fisheries and Aquatic Sciences 41(7): 1106-1116.

Andriashev A.P. (1986) Zoarcidae. In: P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen & E. Tortonese (Eds). Fishes of the Northeastern Atlantic and the Mediterranean. UNESCO, Paris. 1130-1150 pp.

Baker K.D., Devine J.A., Haedrich R.L. (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. Environmental Biology of Fishes 85(1): 79-88.

Bergstad O.A. (1990) Distribution, population-structure, growth and reproduction of the roundnose grenadier *Coryphaenoides rupestris* (Pisces, Macrouridae) in the deep waters of the Skagerrak. Marine Biology 107(1): 25-39.

Coggan R.A., Gordon J.D.M., Merrett N.R. (1998) Abundance, distribution, reproduction and diet of notacanthid fishes from the north-east Atlantic. Journal of Fish Biology 52(5): 1038-1057.

COSEWIC (2001) COSEWIC assessment and status report on the northern wolffish *Anarhichas denticulatus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

COSEWIC (2001) COSEWIC Status Report on the Spotted Wolffish (*Anarhichas minor*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

COSEWIC (2003) COSEWIC assessment and status report on the cusk *Brosme brosme* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Crabtree R.E., Sulak K.J., Musick J.A. (1985) Biology and distribution of species of *Polyacanthonotus* (Pisces: Notacanthiformes) in the western North Atlantic. Bulletin of Marine Science 36(2): 235-248.

Cushing D.H. (1974) The possible density-dependence of larval mortality and adult mortality in fishes. In: J. Blaxter (Ed). The Early Life History of Fish. Springer-Verlag, Berlin. 103-111 pp.

Denney N.H., Jennings S., Reynolds J.D. (2002) Life-history correlates of maximum population growth rates in marine fishes. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1506): 2229-2237.

Devine J.A., Baker K.D., Haedrich R.L. (2006) Fisheries: Deep-sea fishes qualify as endangered. Nature 439(7072): 29.

Drazen J.C. (2002) Energy budgets and feeding rates of *Coryphaenoides acrolepis* and *C. armatus*. Marine Biology 140(4): 677-686.

Drazen J.C. (2008) Energetics of grenadier fishes. In: A.M. Orloov & T. Iwamoto (Eds). Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries 203-223 pp.

Environment Canada (2007) Species at Risk Public Registry. www.sararegistry.gc.ca, Accessed 13 May.

Frisk M.G., Miller T.J., Fogarty M.J. (2002) The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. ICES Journal of Marine Science 59(3): 576-586.

Gordon J.D.M. (2004) Biology of deep sea fishes. Deep-sea Fisheries Symposium. Woods Hole Oceanographic Institute, Woods Hole, MA.

Gordon J.D.M., Mauchline J. (1996) The distribution and diet of the dominant, slope-dwelling eel, *Synaphobranchus kaupi*, of the Rockall Trough. Journal of the Marine Biological Association of the United Kingdom 76(2): 493-503.

Gusev E.V., Shevelev M.S. (1997) New data on the individual fecundity of the wolffishes of the genus *Anarhichas* in the Barents Sea. Journal of Ichthyology 37: 381-388.

Haedrich R.L., Merrett N.R., O'Dea N.R. (2001) Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. Fisheries Research 51(2-3): 113-122.

Hoenig J.M. (1983) Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 81(4): 898-903.

Husebo A., Nottestad L., Fossa J.H., Furevik D.M., Jorgensen S.B. (2002) Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471: 91-99.

IUCN (2001) IUCN Red List Categories and Criteria, Version 3.1. IUCN, Cambridge.

Jensen A.L. (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53: 820–822.

Kelly C.J., Connolly P.L., Bracken J.J. (1997) Age estimation, growth, maturity and distribution of the roundnose grenadier from the Rockall trough. Journal of Fish Biology 50(1): 1-17.

Klein-MacPhee G. (2002) Silver hakes. Family Merluccidae. In: B.B. Collette & G. Klein-MacPhee (Eds). Bigelow and Schroeder's Fishes of the Gulf of Maine. Smithsonian Institution Press, Washington.

Koslow J.A., Boehlert G.W., Gordon J.D.M., Haedrich R.L., Lorance P., Parin N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. ICES Journal of Marine Science 57(3): 548-557.

Koslow J.A., Gowlett-Holmes K., Lowry J.K., O'Hara T., Poore G.C.B., Williams A. (2001) Seamount benthic macrofauna off southern Tasmania: Community structure and impacts of trawling. Marine Ecology Progress Series 213: 111-125.

Krohne D. (2001) Instructor's Edition: General Ecology. Brooks/Cole, California.

Magnusson J.V. (2001) Distribution and some other biological parameters of two morid species *Lepidion eques* (Gunther, 1887) and *Antimora rostrata* (Gunther, 1878) in Icelandic waters. Fisheries Research 51(2-3): 267-281.

Morato T., Watson R., Pitcher T.J., Pauly D. (2006) Fishing down the deep. Fish and Fisheries 7(1): 24-34.

Moss A.L. (2002) Change in abundance and extent of occurrence of demersal marine fishes: quantitative assessments based on research survey data. Environmental Science. Memorial University of Newfoundland, St. John's, NL.

Murua H. (2003) Population structure, growth and reproduction of roughhead grenadier on the Flemish Cap and Flemish Pass. Journal of Fish Biology 63(2): 356-373.

Murua H., Motos L. (2000) Reproductive biology of roughhead grenadier (*Macrourus berglax* Lacepede, 1801) (Pisces, Macrouridae), in Northwest Atlantic waters. Sarsia 85(5-6): 393-402.

Nash R.D.M. (1986) Aspects of the general biology of Vahl eelpout, *Lycodes vahlii gracilis* M. Sars, 1867 (Pisces, Zoarcidae) in Oslofjorden, Norway. Sarsia 71(3-4): 289-296.

Nash R.D.M., Geffen A.J. (2005) Aspects of the general biology of Sars' eelpout, *Lycenchelys sarsi* (Collett, 1871) (Pisces, Zoarcidae), in Oslofjorden, Norway. Marine Biology Research 1(1): 33-38.

O'Dea N.R., Haedrich R.L. (2002) A review of the status of the Atlantic Wolffish, *Anarhichas lupus*, in Canada. Canadian Field-Naturalist 116(3): 423-432.

Oldham W.S. (1972) Biology of Scotian Shelf cusk, *Brosme brosme*. International Convention for the Northwest Atlantic Fisheries Research Bulletin 9: 85-98.

Roberts C.M. (2002) Deep impact: the rising toll of fishing in the deep sea. Trends in Ecology & Evolution 17(5): 242-245.

Rose G.A. (2004) Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Canadian Journal of Fisheries and Aquatic Sciences 61(9): 1553-1557.

Safina C., Rosenberg A.A., Myers R.A., Quinn T.J., Collie J.S. (2005) US ocean fish recovery: Staying the course. Science 309(5735): 707-708.

Schaefer M. (1954) Some aspects of the dynamics of populations important to the management of commercial marine fishes. Bulletin of the Inter-Tropical Tuna Commission 1: 27-56.

Simpfendorfer C.A. (2000) Predicting population recovery rates for endangered western Atlantic sawfishes using demographic analysis. Environmental Biology of Fishes 58(4): 371-377.

Watling L., Norse E.A. (1998) Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. Conservation Biology 12(6): 1180-1197.

Table 6-1. Life-history characteristics of species that have declined significantly. α is the estimated age (years) at 50 % maturity and *w* is the estimated maximum age (years).

Species	α (years)	*w* (years)	Fecundity	References
Careproctus ranula	-	-	10-20	Able and Irion (1985)
Lycenchelys sp.	3-5	6+	20-40	Nash and Geffen (2005)
Lycodes esmarki	-	-	1200	Andriashev (1986)
Lycodes reticulatus	-	-	-	
Lycodes vahli	-	-	18-93	Andriashev (1986); Nash (1986)
Merluccius albidus	-	-	340,000	Klein-MacPhee (2002)
Polyacanthonotus rissoanus	-	-	2,000 – 60,000	Crabtree et al. (1985); Coggan et al. (1998)
Synaphobranchus kaupi	-	8 (?)	111,507 - 119,467	Gordon and Mauchline (1996); Gordon (2004)
Antimora rostrata	~13	23	-	Magnusson (2001)
Bathyraja spinicauda	12	50	47	Frisk et al. (2002)
Coryphaenoides rupestris	10	60	8,700 - 56,000	Alekseyev et al. (1992); Kelly et al. (1997)
Macrourus berglax	13-16	28	8,500 - 79,220	Murua and Motos (2000); Murua (2003)
Notacanthus chemnitzi	-	-	9,000 - 30,000	Gordon (2004)
Anarhichas denticulatus	5	14	27,000	Gusev and Shevelev (1997); COSEWIC (2001)
Anarhichas lupus	8-10	20	-	O'Dea and Haedrich (2002)
Anarhichas minor	7-10	21	19,000	Gusev and Shevelev (1997); COSEWIC (2001)
Brosme brosme	7		1,000,000	Oldham (1972); COSEWIC (2003)

Table 6-2. Estimates of mortality for *M. berglax* and *C. rupestris* based on published models. *K* is the Von Bertalanffy growth curve coefficient and *w* is the maximum age (years).

Species	Model	Parameters	Estimate of mortality
M. berglax	Hoenig (1983)	$w = 28$	0.1600
	Jensen (1996)	$K = 0.027$	0.0432
	Jensen (1996)	$K = 0.062$	0.0992
	Jensen (1996)	$K = 0.038$	0.0608
C. rupestris	Hoenig (1983)	$w = 60$	0.0757
	Jensen (1996)	$K = 0.100$	0.1600
	Jensen (1996)	$K = 0.086$	0.1376
	Jensen (1996)	$K = 0.114$	0.1824

Table 6-3. Estimates of intrinsic rates of increase and recovery time, based on possible life-history characteristics of *M. berglax* and estimated declines (mean and 95 % confidence intervals) from Devine et al. (2006). M is estimated mortality past age 1, l_1 is estimated survival to age 1, RP is reproductive periodicity, and r is the calculated intrinsic rate of increase. These results assume there are no fishing impacts.

				Recovery time (years) for population decline estimates		
M	l_1	RP	r	Lower CI 80.4 %	Mean 88.1 %	Upper CI 94.1 %
0.1600	0.01	1	0.2020	42	45	49
0.1600	0.01	2	0.1655	52	56	61
0.1600	0.01	Once (x=19)	0.0820	107	115	125
0.1600	0.1	1	0.3296	25	27	29
0.0432	0.01	1	0.3126	26	28	31
0.0432	0.01	2	0.2762	30	32	36
0.0432	0.1	1	0.4397	18	19	22
0.0608	0.01	1	0.2960	28	30	33
0.0608	0.01	2	0.2595	32	35	38
0.0608	0.1	1	0.4231	19	20	22
0.0992	0.01	1	0.2596	32	35	38
0.0992	0.01	2	0.2231	38	41	45
0.0992	0.1	1	0.3869	21	22	25

Table 6-4. Recovery time (years) for *M. berglax* and *C. rupestris* based on several potential values of *r* and estimated population declines. These results assume a fisheries catch equal to 5 % of the total population.

Species	*r*	Decline	Proportion of original population reached	Recovery time (years)
M. berglax	0.2020	88.1 %	75.2 %	53
	0.0820	94.1 %	39.0 %	248
	0.2762	88.1 %	81.9 %	39
	0.4397	80.4 %	88.6 %	19
C. rupestris	0.5681	88.4 %	91.2 %	16
	0.2787	96.4 %	82.1 %	50
	0.2420	96.4 %	79.3 %	49
	0.1570	99.4 %	68.2 %	136

Table 6-5. Estimates of intrinsic rates of increase and recovery time, based on possible life-history characteristics of *C. rupestris* and the estimated declines (mean and 95 % confidence intervals) from Devine et al. (2006). M is estimated mortality past age 1, l_1 is estimated survival to age 1, RP is reproductive periodicity, and r is the calculated intrinsic rate of increase. These results assume no fishing impacts.

				Recovery time (years) for population decline estimates		
M	l_1	RP	r	Lower CI 88.4 %	Mean 96.4 %	Upper CI 99.4 %
0.0757	0.01	1	0.3559	25	29	35
0.0757	0.01	2	0.2989	30	35	42
0.0757	0.01	Once (x=16)	0.1570	59	68	80
0.0757	0.1	1	0.5681	14	17	21
0.160	0.01	1	0.2787	32	37	45
0.160	0.01	2	0.2214	41	47	57
0.160	0.1	1	0.4922	17	20	25
0.1376	0.01	1	0.2992	30	35	42
0.1376	0.01	2	0.2420	38	43	52
0.1376	0.1	1	0.5124	16	19	24
0.1824	0.01	1	0.2582	35	40	48
0.1824	0.01	2	0.2008	46	53	62
0.1824	0.1	1	0.4720	18	21	26

7 General Conclusions

Though current fishing activity penetrates well into the deep sea off Newfoundland and Labrador, we still know very little about the distribution, biology, ecology, and small-scale habitat preferences of the taxa living there. The 2007 research cruise (used for the majority of analyses presented in this dissertation) represents one of the first extensive *in situ* surveys in deep waters off Newfoundland. Video from seven dives completed over eight days, spanning depths of 351 to 2245 m offer a small glimpse of species living on the canyons' seafloor, how they are distributed, and the factors influencing their distributions.

By surveying 105 km of bottom, I documented over 160,000 coral colonies, comprising 28 species that collectively spanned the entire depth range of the dives and every bottom type examined. However, corals were not randomly distributed throughout the sampling area. Bottom type and depth both helped define unique assemblages. For example, *Keratoisis grayi*, *Anthomastus* spp., and *Acanthogorgia armata* co-occurred at relatively shallow depths within boulders and cobble.

Environmental factors clearly influence the current distribution and abundance of corals, but so do anthropogenic activities, specifically trawling. Building on other research around the world, I documented a negative influence of trawling on deep-sea corals. *Keratoisis grayi* was significantly less abundant, smaller in size and more likely to be dead as trawling increased, but somewhat surprisingly, they were more likely to occur where trawling was evident. This linkage may result from trawlers targeting preferred locations for *K. grayi*, perhaps because of differences in the distribution of fishes between areas with and without these large corals.

I used video data to determine whether depth and habitat define unique assemblages of fishes. Although no distinct fish assemblage associated with large corals such as *K. grayi*, I did find distinct assemblages based on both depth and habitats. For example, boulder fields supported high relative abundances of *Sebastes* spp., an absence of *Coryphaenoides rupestris* and *Glyptocephalus cynoglossus*, and relatively low abundances of myctophids and *Nezumia bairdii,* when compared to other habitat categories.

When I examined the distribution of individual fish species, more clearly defined relationships with corals and depth became evident. Nevertheless, the factors influencing the fishes varied as I examined different sampling resolutions. In general, depth and the number of small gorgonians were predictors of *Nezumia bairdii* abundance, whereas *Coryphaenoides rupestris* abundance related positively to abundance of cup corals. Depth was often a significant predictor of *Coryphaenoides carapinus* abundance.

Although we know very little about the general biology of many deep-sea fishes, great declines have been documented in several species, including species that are not (and never were) targeted by a fishery. Based on what we know, we can expect long recovery times for these fishes even after the removal of fishing pressure.

The results of this dissertation also highlight the need for continued, dedicated research in Newfoundland and Labrador's deep sea and throughout the chapters I propose several main directions for future research:

- More *in situ* surveys should be conducted that record additional variables of interest, such as current velocity and direction, multibeam bathymetry, temperature, and sedimentation rates.
- Additional *in situ* surveys of fishes should be conducted that examine patterns at various spatial and temporal scales providing for the adequate analysis of relationships of various life stages in reference to observed patterns.
- Deep-sea fishes (including those that are not economically important) should be aged and studied in detail to determine indirected influences of human activities.

7.1 Progress toward sustainable deep-sea management

Documented and suspected population declines, increasing evidence of seafloor destruction, limited knowledge regarding deep-sea species, and overall vulnerability of deep-sea taxa, led to the call for a global moratorium on bottom trawling in the high seas in 2006. Over 1,400 scientists joined the campaign by signing a statement calling for the protection of deep-sea coral and sponge ecosystems (DSCC 2012). An international high-seas bottom trawling moratorium was never adopted – among the countries opposed to the scientifically-backed moratorium was Canada (a country with no high-seas bottom trawling vessels) (DSCC 2012).

Instead, in 2006 the United Nations General Assembly (UNGA) adopted Resolution 61/105, calling for the long-term sustainability of deep-sea fish stocks, and adopted guidelines for its implementation in 2008. The resolution called for timely actions to ensure sustainable deep-sea fisheries and protection of vulnerable deep-sea ecosystems (UNGA 2007; Rogers & Gianni 2010). Highlights of the guidelines included a list of criteria to consider when conducting assessments to determine whether deep-sea fishing activities will likely produce significant adverse impacts, characteristics that should be used as criteria for identifying vulnerable marine ecosystems (VMEs) (e.g. uniqueness or rarity, functional significance, structural complexity), and factors to consider when determining the scale and significance of an impact (Rogers & Gianni 2010). In 2009, experts determined that the resolution implementation was inadequate and additional provisions were added emphasizing that Resolution 61/105 should be adopted before allowing bottom fishing on the high seas and calling upon states to take action immediately (individually or through Regional Fisheries Management Organizations (RFMO) (UNGA 2009; Rogers & Gianni 2010).

In May 2011, I participated in a workshop examining the overall impact and outstanding issues of the UNGA resolutions with 21 other scientists from around the world. We drew three main conclusions: "(1) The UNGA resolutions had not been fully implemented, (2) deep-sea fisheries were not being managed for long-term sustainability; and (3) VMEs were not being given sufficient protection from significant adverse impacts" (Weaver et al. 2011).

While several RFMOs are making considerable strides toward deep-sea conservation (e.g. Convention on the Conservation of Antarctic Marine Living Resources - CCAMLR), actions by others, such as the Northwest Atlantic Fisheries Organization (NAFO) fall short of meeting targets. Reviews of the implementation of Resolutions 61/105 and 64/72 in 2010 and 2011 by the Deep Sea Conservation Coalition and colleagues highlighted the fact that NAFO had no Contracting Parties conduct impact assessments, had repeatedly ignored recommendations by the Scientific Committee (e.g. 2009 redfish quotas), attempted to manage very few deep-sea species (both targeted and non-target), and set unrealistically high thresholds to identify VMEs (Rogers & Gianni 2010; Gianni et al. 2011).

NAFO has made progress toward protecting benthic marine ecosystems by closing portions of six seamounts and 12 coral and sponge areas. However, all closures are temporary (set to expire in 2014). Based on the findings presented in Chapter 6, these protected areas or any other conservation efforts in the deep sea cannot be expected to produce change quickly. Any recovery should be expected to require decades at the very least, and not just simply several years. As such, closed areas should be permanent, not temporary. The NAFO closures occur in areas where little fishing occurred in the past (> 99 % of the past fishing area remains open), open areas lack specific measures to prevent significant adverse impacts, and no measures to protect deep-sea fish have been adopted (Rogers & Gianni 2010; Gianni et al. 2011).

Off Newfoundland and Labrador within Canada's exclusive economic zone (EEZ), where presumably conservation measures should be more easily created and enforced, true effective and sustainable deep-sea management remains more a vague idea than an implementation target. In 2007, Fisheries and Oceans Canada, along with NAFO, created a coral protection zone in NAFO zone 3O, along the Southwest Grand Banks. Despite urging from scientists to move the zone into shallower water, the zone was created near the 800 – 1000 m isobath, thereby providing no protection for the larger number of corals and most fragile species known to occur in nearby (shallower) waters. Based on the findings presented in the previous chapters and outlined above, it is clear that in order to protect a wide range of species, deep-sea conservation efforts (particularly protected areas or closed areas) must also span a wide range of depths and habitat types.

Despite numerous deep-sea dwelling species assessed by COSEWIC as Species at Risk, only three wolffish species have been designated under Canada's Species at Risk Act (SARA). In fact, of the 40 Atlantic fish species and populations currently considered at risk by COSEWIC, 34 are not designated as such under SARA (Environment Canada 2013). This means that although these species meet the criteria for species at risk, they receive no extra federal protection (e.g. critical habitat protection).

Recent (2012) changes to Canada's Fisheries Act removed the protection of fish habitat. The Fisheries Act once prohibited activities that harm the habitat of fish in Canadian waters, but the Act currently protects only fished species from 'serious' harm (House Of Commons Of Canada 2012). This change occurred despite strong evidence that habitat loss causes fish population declines, despite strong opposition from fisheries scientists, and despite Canada's international responsibilities, such as the Convention on Biological Diversity (Favaro et al. 2012). How these changes will translate into changes for deep-sea management remains to be seen. Regardless, it is clear that further studies (such as those presented in Chapters 4 and 5) are needed to evaluate the broader distribution patterns and habitat requirements important for the survival of deep-sea fishes.

The general lack of substantial progress towards effective sustainable deep-sea management begs the question of whether such an idea is even feasible. In 2010, I participated in a workshop aimed at determining whether ecosystem-based deep-sea fishing could be truly sustainable. In general, our answer was "yes", but the monitoring, assessments, surveillance, enforcement, reduction of catch (both targeted and non-targeted) to sustainable levels, and time to allow adequate recovery from past mistakes necessary for sustainable deep-sea fisheries drew into question the economic viability of such a task (Watling et al. 2011). Another team of authors tackled that same question in a 2012 publication, but also considered economics (Norse et al. 2012). They concluded "instead of mining fish from the least-suitable places on Earth, an ecologically and economically preferable strategy would be rebuilding and sustainably fishing resilient populations in the most suitable places, namely shallower and more productive marine ecosystems that are closer to markets" (Norse et al. 2012).

7.2 Literature cited

DSCC (2012) Deep Sea Conservation Coalition. http://www.savethehighseas.org/whatsbeendone/, Accessed 23 July.

Environment Canada (2013) Species at Risk Public Registry. www.sararegistry.gc.ca, Accessed 12 March.

Favaro B., Reynolds J.D., Cote I. (2012) Canada's weakening aquatic protection. Science 337: 154.

Gianni M., Currie D.J., Fuller S., Speer L., Ardron J., Weeber B., Gibson M., Roberts G., Sack K., Owen S., et al. (2011) Unfinished business: a review of the implementation of the provisions of UNGA resolutions 61/105 and 64/72 related to the management of bottom fisheries in areas beyond national jurisdiction. Deep Sea Conservation Coalition.

House Of Commons Of Canada (2012) Bill C-38.

Norse E.A., Brooke S., Cheung W.W.L., Clark M.R., Ekeland L., Froese R., Gjerde K.M., Haedrich R.L., Heppell S.S., Morato T., et al. (2012) Sustainability of deep-sea fisheries. Marine Policy 36(2): 307-320.

Rogers A., Gianni M. (2010) The implementation of UNGA Resolutions 61/105 and 64/72 in the management of deep-sea fisheries on the high seas. International Programme of the State of the Ocean, London, UK: 97 pp.

UNGA (2007) Resolution 61/105 Sustainable fisheries, including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 realted to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, and related instruments.

UNGA (2009) Resolution 64/72 Sustainable fisheries, including through the 1995 Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea of 10 December 1982 realted to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, and related instruments.

Watling L., Haedrich R.L., Devine J.A., Drazen J.C., Dunn A., Gianni M., Baker K.D., Cailliet G.M., Figueiredo I., Kyne P.M., et al. (2011) Can ecosystem-based deep-sea fishing be sustained? Univeristy of Maine, Walpole, ME: 84 pp.

Weaver P.P.E., Benn A., Arana P., Ardron J., Bailey D.M., Baker K.D., Billett D.S.M., Clark M., Davies A.J., Durán Muñoz P., et al. (2011) The impact of deep-sea fisheries and implementation of the UNGA Resolutions 61/105 and 64/72. Report of an international scientific workshop. National Oceanography Centre, Southampton, UK: 45 pp.

Appendix A : Detailed SIMPER results (from Chapter 4)

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

Depth Class Analysis:

Groups 300 – 800 m & 1300 – 2300 m

Species	300-800 Average Abundance	1300-2300 Average Abundance	% Contribution	Cumulative %
Sebastes spp..	1.93	0	9.75	9.75
Synaphobranchus kaupii	2.36	0.81	9.25	19
Coryphaenoides carapinus	0	1.81	7.47	26.47
Nezumia bairdii	1.46	0.15	6.99	33.47
Halosauropsis macrochir	0	1.2	6.97	40.44
Myctophidae (unknown)	1.28	0.82	6.29	46.73
Coryphaenoides rupestris	1.17	0.18	5.96	52.69

Groups 300 – 800 m & 800 – 1300 m

Species	300-800 Average Abundance	800-1300 Average Abundance	% Contribution	Cumulative %
Sebastes spp..	1.93	0	12.48	12.48
Coryphaenoides rupestris	1.17	1.59	8.45	20.93
Myctophidae (unknown)	1.28	1.53	7.66	28.59
Nezumia bairdii	1.46	1.1	6.17	34.76
Synaphobranchus kaupii	2.36	2.07	5.76	40.52
Glyptocephalus cynoglossus	0.61	0.81	4.67	45.19
Centroscyllium fabricii	0.61	0.64	4.56	49.76

Antimora rostrata	0.41	0.6	4.09	53.85

Groups 1300 – 2300 m & 800 – 1300 m

Species	1300-2300 Average Abundance	800-1300 Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	0.81	2.07	14.71	14.71
Halosauropsis macrochir	1.2	0.09	13.57	28.28
Coryphaenoides rupestris	0.18	1.59	8.82	37.1
Aldrovandia (sp 1)	1.33	0.42	7.94	45.04
Coryphaenoides carapinus	1.81	0.05	7.8	52.84

Habitat Types Analysis:

Groups Boulders & Dense large corals

Species	Boulders Average Abundance	Dense large corals Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	0	1.13	15.16	15.16
Myctophidae (unknown)	0	1.6	11.26	26.42
Nezumia bairdii	0.87	1.1	7.41	33.83
Phycis chesteri	0.75	0.44	7.31	41.14
Macrourus berglax	0.24	0.47	6.31	47.45
Centroscyllium fabricii	0	0.81	5.9	53.35

Groups Boulders & Dense small corals

Species	Boulders Average Abundance	Dense small corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	0	1	10.61	10.61
Coryphaenoides rupestris	0	1.34	9.89	20.5

Glyptocephalus cynoglossus	0	0.68	7.09	27.59
Centroscyllium fabricii	0	0.64	6.55	34.15
Nezumia bairdii	0.87	1.11	6.24	40.39
Sebastes spp.	2.91	1.31	5.28	45.67
Phycis chesteri	0.75	0.59	5.05	50.72

Groups Dense large corals & Dense small corals

Species	Dense large corals Average Abundance	Dense small corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.6	1	12.79	12.79
Synaphobranchus kaupii	2.16	1.94	9.52	22.3
Coryphaenoides rupestris	1.13	1.34	5.5	27.8
Glyptocephalus cynoglossus	0.47	0.68	4.88	32.68
Centroscyllium fabricii	0.81	0.64	4.83	37.51
Phycis chesteri	0.44	0.59	4.52	42.02
Macrourus berglax	0.47	0.49	4.32	46.35
Anarhichas minor	0.4	0.09	4.02	50.36

Groups Boulders & Outcrop

Species	Boulders Average Abundance	Outcrop Average Abundance	% Contribution	Cumulative %
Sebastes spp.	2.91	0	17.34	17.34
Coryphaenoides rupestris	0	1.39	13.26	30.6
Hoplostethus atlanticus	0	0.75	13.26	43.86
Myctophidae (unknown)	0	2.3	13.26	57.12

Groups Dense large corals & Outcrop

Species	Dense large corals Average Abundance	Outcrop Average Abundance	% Contribution	Cumulative %
Neocyttus helgae	0	1.45	13.37	13.37

Sebastes spp.	1.5	0	11.49	24.86
Synaphobranchus kaupii	2.16	1.31	11.25	36.11
Hoplostethus atlanticus	0.16	0.75	10.14	46.25
Nezumia bairdii	1.1	0	8.05	54.3

Groups Dense small corals & Outcrop

Species	Dense small corals Average Abundance	Outcrop Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.94	1.31	16.27	16.27
Myctophidae (unknown)	1	2.3	15.29	31.55
Coryphaenoides rupestris	1.34	1.39	10.5	42.06
Hoplostethus atlanticus	0	0.75	6.64	48.69
Neocyttus helgae	0	1.45	6.64	55.33

Groups Boulders & Sparse large corals

Species	Boulders Average Abundance	Sparse large corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	0	1.13	12.43	12.43
Coryphaenoides rupestris	0	1.56	10.43	22.86
Nezumia bairdii	0.87	1.53	9.72	32.57
Phycis chesteri	0.75	0.48	6.86	39.43
Centroscyllium fabricii	0	0.94	5.87	45.3
Sebastes spp.	2.91	1.32	5.6	50.9

Groups Dense large corals & Sparse large corals

Species	Dense large corals Average Abundance	Sparse large corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.6	1.13	11.25	11.25

Centroscyllium fabricii	0.81	0.94	9.73	20.98
Coryphaenoides rupestris	1.13	1.56	9.64	30.62
Synaphobranchus kaupii	2.16	1.53	8.03	38.65
Anarhichas minor	0.4	0.2	5.17	43.82
Phycis chesteri	0.44	0.48	5.1	48.92
Nezumia bairdii	1.1	1.53	4.87	53.79

Groups Dense small corals & Sparse large corals

Species	Dense small corals Average Abundance	Sparse large corals Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.34	1.56	11.85	11.85
Centroscyllium fabricii	0.64	0.94	11.11	22.96
Nezumia bairdii	1.11	1.53	8.48	31.44
Synaphobranchus kaupii	1.94	1.53	7.68	39.12
Myctophidae (unknown)	1	1.13	7.12	46.24
Glyptocephalus cynoglossus	0.68	0	5.07	51.32

Groups Outcrop & Sparse large corals

Species	Outcrop Average Abundance	Sparse large corals Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.31	1.53	13.72	13.72
Nezumia bairdii	0	1.53	11.33	25.05
Myctophidae (unknown)	2.3	1.13	11.11	36.16
Neocyttus helgae	1.45	0	10.63	46.79
Sebastes spp.	0	1.32	8.32	55.11

Groups Boulders & Sea pen field

Species	Boulders Average	Sea pen field Average	% Contribution	Cumulative %

	Abundance	Abundance		
Sebastes spp.	2.91	0.22	20.5	20.5
Glyptocephalus cynoglossus	0	1.63	12.75	33.26
Nezumia bairdii	0.87	1.72	6.57	39.83
Synaphobranchus kaupii	2.14	2.39	6.15	45.98
Myctophidae (unknown)	0	1.82	5.92	51.9

Groups Dense large corals & Sea pen field

Species	Dense large corals Average Abundance	Sea pen field Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.13	1.5	10.15	10.15
Glyptocephalus cynoglossus	0.47	1.63	9.33	19.48
Sebastes spp.	1.5	0.22	8.63	28.12
Myctophidae (unknown)	1.6	1.82	6.41	34.53
Nezumia bairdii	1.1	1.72	5.4	39.92
Synaphobranchus kaupii	2.16	2.39	5.17	45.1
Alepocephalus spp.	0.3	1.08	5.09	50.19

Groups Dense small corals & Sea pen field

Species	Dense small corals Average Abundance	Sea pen field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1	1.82	10.76	10.76
Coryphaenoides rupestris	1.34	1.5	8.54	19.3
Glyptocephalus cynoglossus	0.68	1.63	7.52	26.81
Synaphobranchus kaupii	1.94	2.39	7.52	34.33
Nezumia bairdii	1.11	1.72	7.3	41.63
Alepocephalus spp.	0.09	1.08	6.29	47.92
Antimora rostrata	0.29	0.81	5.03	52.95

Groups Outcrop & Sea pen field

Species	Outcrop Average Abundance	Sea pen field Average Abundance	% Contribution	Cumulative %
Nezumia bairdii	0	1.72	11.97	11.97
Glyptocephalus cynoglossus	0	1.63	11.4	23.37
Synaphobranchus kaupii	1.31	2.39	8.07	31.44
Alepocephalus spp.	0	1.08	6.99	38.43
Myctophidae (unknown)	2.3	1.82	6.3	44.73
Hoplostethus atlanticus	0.75	0	5.91	50.64

Groups Sparse large corals & Sea pen field

Species	Sparse large corals Average Abundance	Sea pen field Average Abundance	% Contribution	Cumulative %
Glyptocephalus cynoglossus	0	1.63	11.29	11.29
Myctophidae (unknown)	1.13	1.82	8.73	20.02
Coryphaenoides rupestris	1.56	1.5	7.56	27.58
Centroscyllium fabricii	0.94	0.53	6.55	34.12
Synaphobranchus kaupii	1.53	2.39	6.54	40.66
Sebastes spp.	1.32	0.22	6.47	47.13
Alepocephalus spp.	0.11	1.08	6.18	53.31

Groups Boulders & Sparse small corals

Species	Boulders Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	0	1.19	13.06	13.06
Coryphaenoides rupestris	0	1.07	10.28	23.34
Centroscyllium fabricii	0	0.68	7.05	30.39
Antimora rostrata	0	0.54	6.98	37.36
Glyptocephalus cynoglossus	0	0.52	6.69	44.05

Sebastes spp.	2.91	0.97	6.12	50.17

Groups Dense large corals & Sparse small corals

Species	Dense large corals Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.6	1.19	10.49	10.49
Centroscyllium fabricii	0.81	0.68	7.96	18.45
Antimora rostrata	0.47	0.54	7.36	25.81
Synaphobranchus kaupii	2.16	2.07	6.6	32.42
Glyptocephalus cynoglossus	0.47	0.52	5.33	37.75
Macrourus berglax	0.47	0.32	4.9	42.64
Coryphaenoides rupestris	1.13	1.07	4.57	47.21
Phycis chesteri	0.44	0.25	4.08	51.3

Groups Dense small corals & Sparse small corals

Species	Dense small corals Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.94	2.07	14.79	14.79
Coryphaenoides rupestris	1.34	1.07	10.59	25.38
Myctophidae (unknown)	1	1.19	8.84	34.22
Aldrovandia (sp 1)	0.4	0.31	8	42.22
Centroscyllium fabricii	0.64	0.68	5.78	48
Nezumia bairdii	1.11	1.05	4.91	52.91

Groups Outcrop & Sparse small corals

Species	Outcrop Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.31	2.07	11.5	11.5

Myctophidae (unknown)	2.3	1.19	10.85	22.35
Neocyttus helgae	1.45	0	9.38	31.73
Coryphaenoides rupestris	1.39	1.07	7.97	39.7
Nezumia bairdii	0	1.05	6.79	46.48
Hoplostethus atlanticus	0.75	0	6.06	52.54

Groups Sparse large corals & Sparse small corals

Species	Sparse large corals Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.56	1.07	10.39	10.39
Synaphobranchus kaupii	1.53	2.07	8.49	18.89
Myctophidae (unknown)	1.13	1.19	8.03	26.92
Centroscyllium fabricii	0.94	0.68	8	34.92
Coryphaenoides carapinus	0.45	0	6.1	41.02
Halosauropsis macrochir	0	0.51	5.47	46.48
Nezumia bairdii	1.53	1.05	5.31	51.79

Groups Sea pen field & Sparse small corals

Species	Sea pen field Average Abundance	Sparse small corals Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.82	1.19	9.11	9.11
Coryphaenoides rupestris	1.5	1.07	8.77	17.88
Glyptocephalus cynoglossus	1.63	0.52	8.14	26.02
Alepocephalus spp.	1.08	0	7.27	33.29
Antimora rostrata	0.81	0.54	6.79	40.08
Nezumia bairdii	1.72	1.05	5.52	45.59
Centroscyllium fabricii	0.53	0.68	4.9	50.49

Groups Boulders & Sponge field

Species	Boulders Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	2.91	1.32	16.28	16.28
Coryphaenoides rupestris	0	1.36	12.63	28.91
Myctophidae (unknown)	0	1.04	9.48	38.38
Phycis chesteri	0.75	0.43	6.31	44.69
Synaphobranchus kaupii	2.14	2.76	6.2	50.89

Groups Dense large corals & Sponge field

Species	Dense large corals Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.5	1.32	13.85	13.85
Synaphobranchus kaupii	2.16	2.76	7.15	21
Myctophidae (unknown)	1.6	1.04	6.7	27.7
Macrourus berglax	0.47	0.43	6.42	34.12
Centroscyllium fabricii	0.81	0.57	6.33	40.45
Phycis chesteri	0.44	0.43	6.08	46.53
Glyptocephalus cynoglossus	0.47	0	5.91	52.44

Groups Dense small corals & Sponge field

Species	Dense small corals Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.31	1.32	10.61	10.61
Glyptocephalus cynoglossus	0.68	0	8.12	18.73
Centroscyllium fabricii	0.64	0.57	5.67	24.39
Rajella fyllae	0.39	0	4.62	29.01
Macrourus berglax	0.49	0.43	4.38	33.39
Macrouridae (sp 3)	0.35	0	4.3	37.69

Zoarcidae (sp 1)	0.1	0.53	4.3	42
Phycis chesteri	0.59	0.43	4.28	46.27
Myctophidae (unknown)	1	1.04	4.22	50.5

Groups Outcrop & Sponge field

Species	Outcrop Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.31	2.76	18.4	18.4
Neocyttus helgae	1.45	0	14.72	33.12
Hoplostethus atlanticus	0.75	0.43	12.28	45.41
Nezumia bairdii	0	1.5	9.86	55.26

Groups Sparse large corals & Sponge field

Species	Sparse large corals Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.32	1.32	12.52	12.52
Myctophidae (unknown)	1.13	1.04	8.98	21.5
Centroscyllium fabricii	0.94	0.57	6.22	27.72
Coryphaenoides rupestris	1.56	1.36	6.2	33.92
Synaphobranchus kaupii	1.53	2.76	5.48	39.4
Phycis chesteri	0.48	0.43	5.28	44.68
Zoarcidae (sp 1)	0	0.53	5.14	49.82
Antimora rostrata	0.15	0.53	4.98	54.8

Groups Sea pen field & Sponge field

Species	Sea pen field Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Glyptocephalus cynoglossus	1.63	0	13.03	13.03
Sebastes spp.	0.22	1.32	10.12	23.15
Coryphaenoides rupestris	1.5	1.36	9.86	33.01

Myctophidae (unknown)	1.82	1.04	9.08	42.1
Antimora rostrata	0.81	0.53	5.12	47.22
Zoarcidae (sp 1)	0.36	0.53	4.93	52.15

Groups Sparse small corals & Sponge field

Species	Sparse small corals Average Abundance	Sponge field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	0.97	1.32	12.96	12.96
Glyptocephalus cynoglossus	0.52	0	8.1	21.06
Centroscyllium fabricii	0.68	0.57	6.37	27.43
Myctophidae (unknown)	1.19	1.04	6.22	33.66
Antimora rostrata	0.54	0.53	5.93	39.59
Zoarcidae (sp 1)	0.23	0.53	5.28	44.87
Macrouridae (sp 3)	0.38	0	4.94	49.81
Phycis chesteri	0.25	0.43	4.48	54.3

Groups Boulders & Sediment with epifauna

Species	Boulders Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	0	1.79	12.98	12.98
Coryphaenoides rupestris	0	1.39	9.67	22.65
Sebastes spp.	2.91	0.79	7.6	30.25
Glyptocephalus cynoglossus	0	1.04	6.85	37.1
Centroscyllium fabricii	0	0.87	6.11	43.21
Phycis chesteri	0.75	0.22	5.41	48.62
Antimora rostrata	0	1.1	4.73	53.35

Groups Dense large corals & Sediment with epifauna

Species	Dense large corals Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Glyptocephalus cynoglossus	0.47	1.04	6.18	6.18
Centroscyllium fabricii	0.81	0.87	5.97	12.15
Coryphaenoides rupestris	1.13	1.39	5.58	17.73
Myctophidae (unknown)	1.6	1.79	5.45	23.18
Antimora rostrata	0.47	1.1	5.18	28.36
Macrourus berglax	0.47	0.59	4.77	33.13
Sebastes spp.	1.5	0.79	4.52	37.66
Nezumia bairdii	1.1	1.4	4.29	41.95
Macrouridae (sp 3)	0	0.46	3.61	45.56
Phycis chesteri	0.44	0.22	3.6	49.16
Synaphobranchus kaupii	2.16	2.18	3.49	52.65

Groups Dense small corals & Sediment with epifauna

Species	Dense small corals Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1	1.79	7.74	7.74
Nezumia bairdii	1.11	1.4	6.11	13.86
Coryphaenoides rupestris	1.34	1.39	6.07	19.93
Synaphobranchus kaupii	1.94	2.18	5.7	25.63
Antimora rostrata	0.29	1.1	5.36	30.99
Glyptocephalus cynoglossus	0.68	1.04	5.08	36.07
Centroscyllium fabricii	0.64	0.87	5.02	41.09
Aldrovandia (sp 1)	0.4	0.73	3.78	44.87
Alepocephalus spp.	0.09	0.68	3.75	48.62
Macrourus berglax	0.49	0.59	3.38	52

Groups Outcrop & Sediment with epifauna

Species	Outcrop Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Nezumia bairdii	0	1.4	7.74	7.74
Synaphobranchus kaupii	1.31	2.18	7.47	15.21
Neocyttus helgae	1.45	0	7.17	22.38
Glyptocephalus cynoglossus	0	1.04	5.7	28.08
Hoplostethus atlanticus	0.75	0	5.64	33.72
Antimora rostrata	0.54	1.1	4.86	38.58
Sebastes spp.	0	0.79	4.79	43.37
Centroscyllium fabricii	0	0.87	4.73	48.1
Myctophidae (unknown)	2.3	1.79	3.76	51.86

Groups Sparse large corals & Sediment with epifauna

Species	Sparse large corals Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.13	1.79	7.12	7.12
Glyptocephalus cynoglossus	0	1.04	6.88	14
Antimora rostrata	0.15	1.1	6.07	20.07
Coryphaenoides rupestris	1.56	1.39	5.85	25.92
Synaphobranchus kaupii	1.53	2.18	4.99	30.91
Centroscyllium fabricii	0.94	0.87	4.8	35.72
Macrourus berglax	0.15	0.59	3.92	39.64
Alepocephalus spp.	0.11	0.68	3.67	43.31
Macrouridae (sp 3)	0.11	0.46	3.3	46.6
Reinhardtius hippoglossoides	0.26	0.42	3.25	49.85
Aldrovandia (sp 1)	0	0.73	2.96	52.81

Groups Sea pen field & Sediment with epifauna

Species	Sea pen field Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Centroscyllium fabricii	0.53	0.87	5.02	5.02
Sebastes spp.	0.22	0.79	4.91	9.93
Myctophidae (unknown)	1.82	1.79	4.7	14.62
Antimora rostrata	0.81	1.1	4.69	19.31
Coryphaenoides rupestris	1.5	1.39	4.55	23.86
Macrourus berglax	0.37	0.59	4.46	28.31
Macrouridae (sp 3)	0.12	0.46	3.94	32.25
Melanostigma atlanticum	0.53	0.36	3.87	36.12
Aldrovandia (sp 1)	0.29	0.73	3.52	39.64
Moridae (sp 1)	0.52	0.13	3.43	43.07
Reinhardtius hippoglossoides	0.49	0.42	3.38	46.44
Glyptocephalus cynoglossus	1.63	1.04	3.23	49.68
Harriotta raleighana	0.36	0.4	2.72	52.39

Groups Sparse small corals & Sediment with epifauna

Species	Sparse small corals Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.19	1.79	6.14	6.14
Antimora rostrata	0.54	1.1	6.13	12.26
Coryphaenoides rupestris	1.07	1.39	5.51	17.77
Glyptocephalus cynoglossus	0.52	1.04	5.29	23.06
Centroscyllium fabricii	0.68	0.87	4.39	27.44
Nezumia bairdii	1.05	1.4	4.27	31.72
Alepocephalus spp.	0	0.68	4.15	35.86
Aldrovandia (sp 1)	0.31	0.73	3.88	39.74
Macrourus berglax	0.32	0.59	3.62	43.36
Macrouridae (sp 3)	0.38	0.46	3.47	46.83

Reinhardtius hippoglossoides	0.25	0.42	3.21	50.05

Groups Sponge field & Sediment with epifauna

Species	Sponge field Average Abundance	Sediment with epifauna Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.32	0.79	11.76	11.76
Glyptocephalus cynoglossus	0	1.04	7.81	19.58
Myctophidae (unknown)	1.04	1.79	5.93	25.51
Centroscyllium fabricii	0.57	0.87	5.41	30.92
Zoarcidae (sp 1)	0.53	0.13	4.98	35.89
Macrouridae (sp 3)	0	0.46	4.7	40.59
Antimora rostrata	0.53	1.1	4.53	45.13
Fish unknown (sp 6)	0.43	0.25	4.32	49.45
Macrourus berglax	0.43	0.59	4.24	53.68

Groups Boulders & *Heteropolypus* cf. *insolitus* field

Species	Boulders Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	2.91	0	26.47	26.47
Coryphaenoides rupestris	0	1.24	10.22	36.69
Nezumia bairdii	0.87	1.2	8.75	45.44
Myctophidae (unknown)	0	1.43	8.6	54.04

Groups Dense large corals & *Heteropolypus* cf. *insolitus* field

Species	Dense large corals Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.5	0	16.42	16.42
Coryphaenoides rupestris	1.13	1.24	9.87	26.29

Nezumia bairdii	1.1	1.2	8.92	35.21
Myctophidae (unknown)	1.6	1.43	7.3	42.51
Glyptocephalus cynoglossus	0.47	0.57	6.22	48.73
Macrouridae (sp 3)	0	0.57	6.06	54.79

Groups Dense small corals & *Heteropolypus* cf. *insolitus* field

Species	Dense small corals Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1	1.43	10.67	10.67
Sebastes spp.	1.31	0	9.61	20.28
Coryphaenoides rupestris	1.34	1.24	9.27	29.55
Nezumia bairdii	1.11	1.2	9.01	38.55
Synaphobranchus kaupii	1.94	2.72	6.56	45.11
Centroscyllium fabricii	0.64	0	4.49	49.6
Moridae (sp 1)	0.1	0.47	4.43	54.03

Groups Outcrop & *Heteropolypus* cf. *insolitus* field

Species	Outcrop Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Synaphobranchus kaupii	1.31	2.72	18.23	18.23
Hoplostethus atlanticus	0.75	0	13.95	32.18
Neocyttus helgae	1.45	0	13.95	46.13
Nezumia bairdii	0	1.2	10.97	57.11

Groups Sparse large corals & *Heteropolypus* cf. *insolitus* field

Species	Sparse large corals Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.32	0	14.41	14.41

Coryphaenoides rupestris	1.56	1.24	9.81	24.21
Myctophidae (unknown)	1.13	1.43	9.65	33.86
Centroscyllium fabricii	0.94	0	7.05	40.91
Synaphobranchus kaupii	1.53	2.72	6.66	47.57
Nezumia bairdii	1.53	1.2	6.52	54.09

Groups Sea pen field & *Heteropolypus* cf. *insolitus* field

Species	Sea pen field Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Glyptocephalus cynoglossus	1.63	0.57	10.66	10.66
Antimora rostrata	0.81	0.57	8.67	19.33
Coryphaenoides rupestris	1.5	1.24	7.27	26.6
Alepocephalus spp.	1.08	0	6.61	33.22
Myctophidae (unknown)	1.82	1.43	6.12	39.34
Nezumia bairdii	1.72	1.2	6.08	45.41
Moridae (sp 1)	0.52	0.47	5.55	50.97

Groups Sparse small corals & *Heteropolypus* cf. *insolitus* field

Species	Sparse small corals Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	0.97	0	12.02	12.02
Coryphaenoides rupestris	1.07	1.24	10.55	22.57
Myctophidae (unknown)	1.19	1.43	10.23	32.8
Nezumia bairdii	1.05	1.2	8.81	41.61
Centroscyllium fabricii	0.68	0	7	48.61
Macrouridae (sp 3)	0.38	0.57	5.62	54.24

Groups Sponge field & *Heteropolypus* cf. *insolitus* field

Species	Sponge field Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.36	1.24	11.07	11.07
Sebastes spp.	1.32	0	10.81	21.88
Nezumia bairdii	1.5	1.2	9.36	31.24
Myctophidae (unknown)	1.04	1.43	9.28	40.52
Glyptocephalus cynoglossus	0	0.57	8.25	48.77
Macrouridae (sp 3)	0	0.57	8.25	57.01

Groups Sediment with epifauna & *Heteropolypus* cf. *insolitus* field

Species	Sediment with epifauna Average Abundance	*Heteropolypus* cf. *insolitus* field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	0.79	0	9.69	9.69
Glyptocephalus cynoglossus	1.04	0.57	7.11	16.81
Antimora rostrata	1.1	0.57	7.04	23.84
Coryphaenoides rupestris	1.39	1.24	6.64	30.48
Myctophidae (unknown)	1.79	1.43	6.33	36.82
Centroscyllium fabricii	0.87	0	6.22	43.03
Macrouridae (sp 3)	0.46	0.57	5.42	48.45
Nezumia bairdii	1.4	1.2	5.16	53.62

Groups Boulders & Cup coral field

Species	Boulders Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Nezumia bairdii	0.87	1	17.54	17.54
Phycis chesteri	0.75	0.35	15.84	33.38
Synaphobranchus kaupii	2.14	2.5	13.84	47.22
Sebastes spp.	2.91	1.62	11.27	58.49

Groups Dense large corals & Cup coral field

Species	Dense large corals Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.13	0.67	17.32	17.32
Myctophidae (unknown)	1.6	0.32	12.65	29.97
Glyptocephalus cynoglossus	0.47	0.8	9.05	39.02
Synaphobranchus kaupii	2.16	2.5	7.29	46.31
Phycis chesteri	0.44	0.35	6.2	52.51

Groups Dense small corals & Cup coral field

Species	Dense small corals Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.34	0.67	13.03	13.03
Glyptocephalus cynoglossus	0.68	0.8	12.88	25.9
Reinhardtius hippoglossoides	0.1	0.67	6.9	32.8
Lepidion eques	0.1	0.67	6.88	39.68
Synaphobranchus kaupii	1.94	2.5	6.57	46.25
Myctophidae (unknown)	1	0.32	5.93	52.18

Groups Outcrop & Cup coral field

Species	Outcrop Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	2.3	0.32	15.26	15.26
Synaphobranchus kaupii	1.31	2.5	14.23	29.49
Sebastes spp.	0	1.62	11.99	41.48
Coryphaenoides rupestris	1.39	0.67	11.25	52.73

Groups Sparse large corals & Cup coral field

Species	Sparse large corals Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.13	0.32	11.87	11.87
Coryphaenoides rupestris	1.56	0.67	11.34	23.21
Centroscyllium fabricii	0.94	0	9.41	32.62
Nezumia bairdii	1.53	1	8.2	40.82
Reinhardtius hippoglossoides	0.26	0.67	7.93	48.75
Synaphobranchus kaupii	1.53	2.5	7.03	55.78

Groups Sea pen field & Cup coral field

Species	Sea pen field Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.82	0.32	11.29	11.29
Glyptocephalus cynoglossus	1.63	0.8	9.74	21.03
Sebastes spp.	0.22	1.62	9.71	30.74
Nezumia bairdii	1.72	1	7.98	38.72
Lepidion eques	0.12	0.67	7.6	46.32
Alepocephalus spp.	1.08	0	5.91	52.24

Groups Sparse small corals & Cup coral field

Species	Sparse small corals Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Coryphaenoides rupestris	1.07	0.67	12.69	12.69
Glyptocephalus cynoglossus	0.52	0.8	12.14	24.84
Myctophidae (unknown)	1.19	0.32	10.99	35.82
Lepidion eques	0.11	0.67	7.9	43.73
Centroscyllium fabricii	0.68	0	7.34	51.07

Groups Sponge field & Cup coral field

Species	Sponge field Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	1.32	1.62	17.88	17.88
Coryphaenoides rupestris	1.36	0.67	16.76	34.64
Antimora rostrata	0.53	0	7.33	41.97
Zoarcidae (sp 1)	0.53	0	7.33	49.3
Myctophidae (unknown)	1.04	0.32	7.04	56.34

Groups Sediment with epifauna & Cup coral field

Species	Sediment with epifauna Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Myctophidae (unknown)	1.79	0.32	10.94	10.94
Coryphaenoides rupestris	1.39	0.67	7.41	18.35
Glyptocephalus cynoglossus	1.04	0.8	6.71	25.06
Centroscyllium fabricii	0.87	0	6.39	31.45
Antimora rostrata	1.1	0	6.07	37.52
Nezumia bairdii	1.4	1	5.67	43.19
Macrourus berglax	0.59	0	4.59	47.78
Macrouridae (sp 3)	0.46	0	4	51.78

Groups *Heteropolypus* cf. *insolitus* field & Cup coral field

Species	*Heteropolypus* cf. *insolitus* field Average Abundance	Cup coral field Average Abundance	% Contribution	Cumulative %
Sebastes spp.	0	1.62	21.02	21.02
Myctophidae (unknown)	1.43	0.32	12.16	33.18
Glyptocephalus cynoglossus	0.57	0.8	11.45	44.63
Nezumia bairdii	1.2	1	11.25	55.88